8-1979

An Investigation of the Environmental Relationships of Selected Forest Habitat Types in Northern Utah

Penelope Morgan Lawton
Utah State University

Recommended Citation

Lawton, Penelope Morgan, "An Investigation of the Environmental Relationships of Selected Forest Habitat Types in Northern Utah" (1979). *All Graduate Theses and Dissertations*. 3283.
https://digitalcommons.usu.edu/etd/3283

AN INVESTIGATION OF THE ENVIRONMENTAL RELATIONSHIPS OF SELECTED FOREST HABITAT TYPES IN NORTHERN UTAH

by

Penelope Morgan Lawton

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Forest Ecology

UTAH STATE UNIVERSITY
Logan, Utah

1979

ACKNOWLEDGEMENTS

The Utah State Agricultural Experiment Station provided financial support for this study through Project 704. Additional funding was provided to me by the Utah State University Graduate Fellowship program during the 1978-1979 school year.

I would like to acknowledge my Graduate Committee, Dr. Jan Henderson, Dr. James MacMahon, and Dr. George Hart, for their assistance in this study and critical review of the thesis. I would like to thank Dr. David Turner of the Department of Applied Statistics and Computer Science, Utah State University for his assistance with the data analysis.

The WISCON computer program was provided by Dr. James MacMahon. I wish also to thank Bob Bayn and Ron Mauk for use of their plotting and association table programs. The stepwise regression, analysis of variance, and SPSS programs used in this study were made available to me through the Department of Applied Statistics and Computer Science, Utah State University.

I thank Jim Riley for help with computer programs. Special thanks are extended to my husband, Rick, and my parents for their help and support throughout the thesis program.

Penelope M. Lawton

TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS i

LIST OF TABLES iv

LIST OF FIGURES vi

ABSTRACT viii

INTRODUCTION 1

LITERATURE REVIEW 5

  Environmental relationships of vegetation classification systems 5
  The habitat type classification system 7

STUDY AREA DESCRIPTION 10

  Climate 10
  Soils and bedrock 14

METHODS 18

  Vegetation field methods 19
  Physical environmental variables 21

    Maximum and minimum air temperature 21
    Soil temperature 21
    Soil moisture 22
    Plant moisture stress 22
    Soil descriptions 23
    Incident solar radiation 24
    Phenology 24

  Analysis of data 24

    Analysis of variance 25
    Ordination 25
    Direct gradient analyses 27
    Regression analysis 28

RESULTS 31

  Plant moisture stress 31
  Variability and difference of habitat type environments 35

TABLE OF CONTENTS (Continued)

Page

Ordination 39
Direct gradient analyses 47

Single factor environmental gradients 47
Multiple factor environmental gradients 56

Comparison of analyses 60

DISCUSSION 62

Representation of vegetation gradients by ordination axes 62
Environmental gradients corresponding to vegetation gradients 63

Single factor gradients 63
Multiple factor gradients 65

Regression model for the first ordination axis 65
Regression models for the second ordination axis 66
Correlation with vegetation gradients 67

An hypothesis 69

Plant moisture stress 69

Temperature and moisture effects 70
Direct measurement of plant moisture 71

Habitat type relationships 72

SUMMARY AND CONCLUSIONS 78

LITERATURE CITED 81

APPENDICES 85

LIST OF TABLES

Table Page

1. Mean monthly temperatures (°C) measured at central climate measuring station in USU College Forest 12

2. Mean monthly temperatures (°C) measured at Utah State University, Logan, Utah 13

3. Monthly precipitation (cm) measured at Utah State University, Logan, Utah 15

4. Monthly precipitation (cm) measured at central climate measuring station in USU College Forest 16

5. Number of stands observed during each segment of this study by habitat type 20

6. Environmental variables used in correlation matrix calculations and step-wise regression analysis for prediction of ordination axis stand coordinates. All measurements are from 1978 as discussed in text 29

7. Plant moisture stress measurements by species and stand number, summer 1978 32

8. Results of Bartlett's test of homogeneity of variances and relative variability of types for each environmental variable measured 36

9. F-ratio and probability of a greater F-ratio than computed occurring as calculated in analysis of variance. If significance ($p \leq .05$) is found, results of Tukey's honestly significant multiple comparison procedure to locate significantly different means are shown 40

10. Pearson correlation coefficients between axes of ordinations I and II 46

11. Correlation of measured environmental variables with Ordination I axis stand coordinates 49

LIST OF TABLES (Continued)

Table Page

12. Regression models predicting Ordination I axis coordinates of sampled based on measurements of environmental variables 57

13. Stand physiography, seasonal data (1978) and estimated total yearly incident solar radiation 87

14. Maximum and minimum air temperatures (°C) by month, 1978 88

15. Soil temperature (°C) at 20 cm by date of observation, 1978 90

16. Soil temperature (°C) at 50 cm by date of observation, 1978 91

17. Soil moisture (percent of dry weight) at 20 cm by date of observation, 1978 92

18. Soils and bedrock data 94

19. Estimate of available soil water capacity based on texture class, estimated volume occupied by rock fragments, and depth of horizons. Value is calculated for each horizon, summed to 100 cm or bedrock if soil was shallower than 100 cm 96

20. Calculated stand coordinates on axes of Ordination I and II by habitat type 98

21. Predicted stand coordinates for axes of Ordination I by habitat type. Regression models A, B, C are for axis 1 (27 stands), axis 2 (26 stands), and axis 2 (21 stands) respectively 99

22. Association table showing relative percent canopy cover of overstory and undergrowth vascular plant species occurring on all plots 101

LIST OF FIGURES

Figure Page

1. Map of study area showing location of stands and weather stations 11

2. Ordination I. Stand position along each axis indicates relative similarity of each stand to stands objectively chosen as endpoints for each axis. The endstands of the first axis are the least similar to each other of all possible pairs of stands. Second axis endstands are dissimilar both to first axis endstands and to each other. Average similarity between stands is calculated using the Bray and Curtis (1957) similarity index with importance of both overstory and undergrowth vascular plant species expressed as relative percent canopy cover. Less important species, as defined in text, were not included in the calculations 44

3. Ordination II. Stand position along each axis indicates relative similarity of each stand to stands objectively chosen as endpoints for each axis. The endstands of the first axis are the least similar to each other of all possible pairs of stands. Second axis endstands are dissimilar both to first axis endstands and to each other. Average similarity between stands is calculated using the Bray and Curtis (1957) similarity index with importance of both overstory and undergrowth vascular plant species expressed as relative percent canopy cover. Less important species, as defined in text, were not included in the calculations 45

4. Stand position in relation to elevation and topographic-moisture gradients. Stand position on horizontal axis defined as discussed in text, scaled from 0 (mesic) to 10 (xeric) 48

5. Stand position in relation to gradients of estimated percent volume of coarse rock fragments in the surface 20 cm of soil and soil temperature based on measurements at 20 cm 51

LIST OF FIGURES (Continued)

Figure Page

6. Stand position in relation to gradients of estimated percent volume of coarse rock fragments in the surface 20 cm of soil and soil temperature based on measurements at 50 cm 52

7. Stand position in relation to gradients of length of growing season as measured by the number of days between date of snowmelt and date of first frost in the fall and soil temperature based on measurements at 20 cm 53

8. Stand position in relation to gradients of length of growing season as measured by the number of days between date of snowmelt and date of first frost in the fall and soil temperature based on measurements at 50 cm 54

9. Ordination produced by stand coordinates predicted by regression models A (axis 1) and B (axis 2), based on linear combination of environmental measurements 58

10. Ordination produced by stand coordinates predicted by regression models A (axis 1) and C (axis 2), based on linear combination of environmental measurements 59

11. Hypothesized relationships of habitat types to gradients of soil moisture and atmospheric stress. Soil moisture stress is here considered to be influenced by factors affecting the capacity of the soil to provide moisture to plant roots. Atmospheric stress is considered to be primarily influenced by temperature, incident solar radiation, and length of growint season . . . 73

12. Frequency of similarity values by classes from matrix of pair-wise comparisons between stands calculated for Ordination I. Range of values is from 0.00 to 76.19. Upper ten percent are considered significant (above 47.50) 100

ABSTRACT

An Investigation of Environmental Relationships of Selected Forest Habitat Types in Northern Utah

by

Penelope M. Lawton, Master of Science

Utah State University, 1979

Major professor: Jan A. Henderson
Department: Forestry and Outdoor Recreation

It was the purpose of this study to examine an assumption basic to the forest habitat type classification system. Included in each habitat type is all land capable of supporting a single climax plant community type. In practice, land is grouped based on species composition, relative abundance, and successional trends of the vegetation supported by the land. Land units of the same habitat type are assumed to represent similar environments. No previous critical evaluation of this assumption has been done.

Land in the study area had been previously classified under the habitat type system. Relationships between vegetation and environment were studied in the _Abies lasiocarpa/Pedicularis racemosa_, _Abies lasiocarpa/Osmorhiza chilensis_, _Abies lasiocarpa/Berberis repens_, _Pseudotsuga menziesii/Physocarpus malvaceus_, _Pseudotsuga menziesii/Berberis repens_, and _Pseudotsuga menziesii/Cercocarpus ledifolius_ habitat types. Environmental variables potentially important in determining the vegetation characteristics defining the habitat types were measured over two summers (1977 and 1978) in stands representative of these types. These measurements showed these habitat types to occupy significantly different environments for most environmental variables studied. Environments were more variable between than within the habitat types.

Two-dimensional direct gradient analyses for single and multiple environmental variables were compared to ordination results to find which of the environmental variables measured might determine the vegetation gradients indicated by the ordination. Gradients of elevation, maximum and minimum air temperature, and estimated annual incident solar radiation did not correlate well with ordination axes. Best correlation, 0.78 and 0.74 respectively, resulted for summer soil temperature measured at 50 cm for one ordination axis and, for the second ordination axis, a linear combination of soil moisture percentage at 20 cm, estimated percent volume of coarse rock fragments in the soil, and available soil water storage capacity estimated from soil texture class and percent rock.

These temperature and moisture variables are felt to be important through their influence on plant moisture stress. Direct measurement of predawn plant moisture stress on conifer saplings did not differentiate between habitat types. Results were highly variable. This was attributed to morphological and microhabitat influences such as disease, rooting pattern and shading which may obscure larger scale environmental differences between stands.

It is hypothesized that vegetation in these habitat types responds to environmental gradients that determine the availability of soil moisture to plant roots to meet transpirational demand and atmospheric influences on that demand. Hypotheses of the relationships of the habitat types to these environmental gradients were developed.

It is tentatively concluded that the habitat type classification system is effective in stratifying the physical environment in terms of environmental factors which are physiologically meaningful to the vegetation characteristics defining the habitat type classes.

(102 pages)

INTRODUCTION

The habitat type concept was developed by Daubenmire and Daubenmire (1968) to provide an ecologically based land classification system for management purposes. Included in each habitat type is all land capable of supporting a single climax plant community type (Henderson et al. 1976). Classification is based on plant species composition, relative abundance, and successional trends of the vegetation supported by the land. Characteristics of climate, soil, disturbance, and time relationships are also taken into account in the definition of habitat type classes (Daubenmire and Daubenmire 1968). It is assumed that land units of the same habitat type represent similar environments, different from land units of other habitat types in some aspect of the environment important to management.

Daubenmire (1952; Daubenmire and Daubenmire 1968) based his original classification of eastern Washington and northern Idaho on descriptions of mature stands as examples of "climax plant associations." He felt one could best understand the environmental relationships of vegetation through classification of these communities which are assumed to be in equilibrium with the physical environment. Vegetation differences on different sites are attributed to environmental rather than disturbance effects. Land supporting disturbed vegetation is related to land classes defined for mature stands through successional trends of the vegetation supported by the land.

The definition of habitat type classes emphasizes plant species composition and abundance. The classes are arbitrary divisions of a continuum of individual species distributions along a gradient. If the vegetation responds to environmental gradients, different combinations of species will indicate different portions of those environmental gradients.

The response of vegetation to management or natural disturbance is dependent on the physical environment. If the habitat type classification does group land into units of similar environment as assumed, similar vegetation response can be expected from units of land within the same habitat type. The more reliable the prediction of a particular portion of the environment gradient and the less variable that portion is, the better the prediction of the vegetation response. This depends on the reliability with which combinations of plant species defining the habitat type classes indicate particular portions of an environmental gradient. Habitat types should be different environmentally and the environmental differences between classes should have cause and effect relationships to the vegetation differences defining the habitat type classes. The divisions of the environmental gradient should not be broad and overlapping. If these conditions are not met, the knowledge that a given piece of land belongs to a particular habitat type is not particularly useful in predicting vegetation response to management because the range of environmental conditions over which that habitat type can occur is large.

The habitat type classification has proven useful in a variety of management applications (Pfister 1976, Arno and Pfister 1977). However, no critical evaluation of the effectiveness of the habitat type classification system in stratifying the physical environment has been done.

It is the purpose of this study to provide a first step in such an evaluation by investigating the relationship between selected habitat types in northern Utah and environmental gradients. Land in the study area has been classified into habitat types by Pfister (1972) for the subalpine forests and Henderson et al. (1976) who extended Pfister's work to forest communities of lower elevations. Environmental variables examined are chosen to be potentially important in determining the vegetation parameters characterizing and differentiating habitat types. The specific objectives are:

1. To measure environmental parameters in stands representative of selected forest habitat types in northern Utah as described by Pfister (1972) and Henderson et al. (1976).

2. To determine if these habitat types are significantly different environmentally and if environmental variation is greater between than within habitat types.

3. To define major vegetation gradients and develop hypotheses about what environmental gradients correspond to these vegetation gradients.

4. To characterize the physical environment occupied by different habitat types through comparison of the relationships of the types along environmental gradients.

The environmental measurements are assumed to be representative of environmental conditions of other years. This implies that the environmental factors shown to be important in differentiating stands representative of the habitat types based on the short-term measurements obtained in this study have been important in the past in determining the distribution of plant species by which the habitat type classes are defined.

LITERATURE REVIEW

Environmental relationships of vegetation classification systems

There have been few investigations of the environmental relationships of vegetation classification systems in vegetation similar to that occurring in the study area. Del Moral and Watson (1978) analyzed the gradient structure of forest vegetation in the mountains of central Washington through ordination and direct measurement of environmental parameters. Elevation, soil surface pH, soil surface organic fraction, and an index of moisture and insolation based on aspect, slope, and radiation were the environmental factors considered. Two-dimensional ordinations based on tree and undergrowth species were calculated separately for low and high elevation sites in three regions; eastern, central, and western. Ordination axes were correlated to temperature and moisture variables based on known environmental relationships of species included in the calculations. Position of stands along measured elevation and moisture-insolation index gradients were also calculated. Results were presented as mosaic diagrams for each region in which stand position produced by the direct environmental measurements were modified according to ordination results. Community types to which the stands belonged were then identified. The pattern of community types in the two-dimensional mosaic diagrams relates the types to gradients of elevation and the calculated moisture-insolation index.

In a study similar to the present one, Zobel et al.(1976) investigated environmental relationships in the H. J. Andrews Experimental Ecological Reserve in Oregon. Vegetation of this area was classified by Dyrness et al. (1974). Eighteen stands representative of 16 community types they described were selected for study. Dyrness et al. (1974) had hypothesized that the two major axes of variation in vegetation corresponded to gradients of temperature and moisture. Interzonal differences were felt to be primarily temperature controlled while moisture differentiated communities within zones. Zobel et al. (1976) measured soil temperature, plant moisture stress, and soil moisture within the selected stands over a 3 year period. Temperature Growth Index (Cleary and Waring 1967) and plant moisture stress were determined to be the environmental variables corresponding best to the vegetation similarity axes. Where stands deviated from expected trends based on temperature and moisture measurements, nitrogen was thought to be limiting.

Peet (1978) studied the relationships of forest vegetation of the southern Rocky Mountains to gradients of elevation and moisture. These environmental variables were found to describe the vegetation distribution satisfactorily. He considered predominantly overstory species distributions and broad community types defined by overstory species without consideration of associated undergrowth species.

Despain (1973) conducted a similar study in the Bighorn Mountains of Wyoming. He also considered broad community types based on overstory vegetation. Little precipitation occurs there. Geologic substrate and climatic variables controlling soil-water relationships were found to be important in determining vegetation distribution.

These studies consider the environmental relationships of land classification systems based on vegetation the land currently supports. No studies have been done which investigate land classification systems based on characteristics of the vegetation the land can potentially support in relation to environmental gradients. It is assumed that habitat classification of land by similarity of climax plant associations segregates land into units of similar environment. This assumption has not been experimentally tested.

The habitat type classification system

The habitat type classification system was developed by Daubenmire (1952, Daubenmire and Daubenmire 1968) as a comprehensive ecological classification of land. The concept bears strong similarity to Finnish (Cajander 1926) and Soviet (Sukachev and Dylis 1964) work. Land units, called habitat types, are delineated based on characterization of "climax plant associations" (Daubenmire and Daubenmire 1968). Characteristics of climate, soil, disturbance, and time relationships are also taken into account (Daubenmire and Daubenmire 1968).

Land supporting vegetation of other than near-climax successional status may be classified under the habitat type classification system. Daubenmire (1952, Daubenmire and Daubenmire 1968) based his classification on old growth forest stands as examples of the "climax plant associations." He felt one could best understand the environmental relationships of vegetation through study of such communities which are assumed to be in equilibrium with their physical environment. This assumes that vegetation differences between sites are primarily a reflection of environmental differences rather than disturbance, chance occurrence of species, or other factors. Land supporting disturbed vegetation is related through successional trends to land units supporting "climax plant associations." In practice, the climax overstory species is indicated by examination of size and age class distributions of individuals of each overstory species present on a given site. Undergrowth vegetation in mature stands is assumed to approximate climax composition and dominance. Classification of land supporting early successional vegetation where indicator species used in the classification may not be present relies on inference of environmental similarity to land units already classified. The environmental characteristics generally considered are elevation, slope steepness and configuration, and topographic position.

More recent classifications have stressed environmental stratification over a complete description of the climax plant associations (Pfister 1972, Henderson et al. 1976, Pfister et al. 1977). Classes are defined based on similarity of plant species composition and abundance. Methods of analysis in these and similar studies (Henderson and West 1977, Kerr and Henderson 1979) have included use of association tables of coverage values by species, similarity matrices, cluster analysis, and ordination. Physiography and bedrock characteristics are considered in the final delineation of classes. However, description of environments occupied by different habitat types has been predominantly qualitative and inferred from vegetation characteristics.

While slope, aspect, elevation, and soil and bedrock type are often strongly correlated with temperature, moisture, and nutrient availability, they do not have direct physiological significance to plant growth and development. For instance, environments which are very similar physiologically to a plant may be produced by quite different combinations of slope, aspect, and elevation. The usefulness of the habitat type classification relies on vegetation species composition and abundance to indicate classes of similar environments. If evaluation of the effectiveness of the habitat type class system in stratifying the environment is to be meaningful, it must be in terms of environmental factors which have direct physiological cause and effect importance to the vegetation characterizing and differentiating the habitat types. Actual measurement and comparison of environmental factors such as temperature, moisture, and nutrient availability on different habitat types has not been done.

STUDY AREA DESCRIPTION

The study sites were located in the Bear River Mountains north and east of Logan, Utah in Cache and Rich Counties. These sites were located in stands representative of the six most common forest habitat types in this area. A map of the study area and stand locations is shown in Figure 1.

Elevation of the study sites ranged from approximately 1580 to 2635 m. Selected forest stands at middle to high elevations occurred on a variety of slopes and aspects. Lower elevation sites most often occupied steep slopes of northerly aspect.

Climate

Weather stations in the area are located in the USU College Forest at an elevation of 2591 m (8500 ft) and at Utah State University at the mouth of Logan Canyon at 1457 m (4780 ft). The higher elevation station is in the vicinity of the highest Abla/Pera[1] study sites. The USU station is below the lowest stands representing the Psme/Phma habitat type. Locations of these weather stations are also indicated in Figure 1.

The climate is continental in character with long cold winters and short dry summers with some seasonal thunderstorms. The mean annual temperature at the high elevation station is 0.0°C, with monthly means ranging from -9.8°C in January to 14.7°C in July (Table 1). The mean annual temperature at USU is 8.7°C, ranging

---

[1] Habitat type names abbreviated as in Table 5.

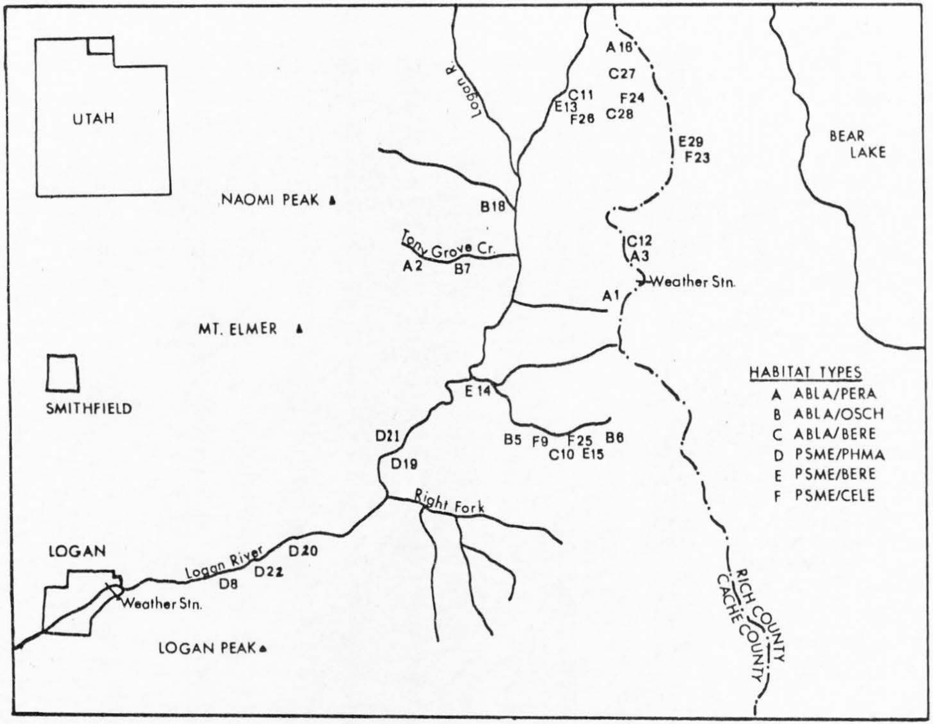


Figure 1. Map of study area showing location of stands and weather stations.

Table 1. Mean monthly temperatures (°C) measured at central climate measuring station in USU College Forest (adapted from Lomas 1977).

Month	Mean monthly temperature (°C)						
	1970	1971	1972	1973	1974	1975	1976
January	--	--	-11.3	-7.7	-11.6	-10.3	-8.2
February	--	--	-10.1	-5.0	-8.8	-9.2	-5.8
March	--	--	-5.4	-4.2	-3.8	-7.3	-7.5
April	--	-3.4	-3.7	-1.5	2.3	-6.1	-0.9
May	--	1.8	2.7	6.2	5.1	0.2	4.3
June	8.9	9.0	8.6	10.7	12.5	6.0	7.1
July	15.2	15.2	13.8	13.4	15.7	14.4	15.2
August	16.5	15.6	13.6	13.6	12.2	11.9	11.2
September	7.9	5.7	8.1	--	9.7	9.7	8.3
October	1.7	1.2	1.8	--	4.6	1.0	2.9
November	-3.9	-5.6	-5.6	-5.8	-4.6	--	--
December	--	-11.8	-9.2	--	-9.8	-7.5	--

Table 2. Mean monthly temperatures (°C) measured at Utah State University, Logan, Utah (from Office of the State Climatologist, Logan, Utah).

	Mean monthly temperature (°C)						
Month	1971	1972	1973	1974	1975	1976	1977
January	-2.3	-3.0	-7.3	-4.4	-5.1	-4.8	-5.8
February	-0.9	0.1	-4.2	-4.4	-2.1	-4.3	-1.8
March	1.6	6.6	1.8	4.7	2.2	-2.2	1.2
April	7.4	7.4	6.3	7.3	4.2	7.3	10.1
May	13.1	13.9	13.7	13.4	10.2	14.7	10.9
June	17.6	19.2	17.4	20.4	15.7	16.8	21.2
July	22.3	22.1	21.9	23.2	24.0	23.3	22.4
August	23.3	22.3	22.3	21.8	20.2	19.9	21.3
September	14.0	15.2	14.4	17.7	16.6	17.2	16.4
October	7.4	10.6	10.7	10.9	9.6	9.4	11.1
November	1.6	1.8	3.4	3.7	1.6	4.5	3.4
December	-4.7	-7.0	-1.1	-3.3	-0.8	-1.6	0.9

from -4.7°C in January to 22.7°C in July (Table 2). There is a sharp gradient in precipitation with elevation. The average annual precipitation recorded at USU from 1971 to 1977 was 48.86 cm (Table 3). At the higher elevation station average annual precipitation was 105.84 for the six years of record (Table 4). Most precipitation falls as snow between November and April. Depth of snowpack may reach 9 feet at high elevations and snow remains until June or early July (Lomas 1977). In lower elevation stands, snowpack did not remain beyond mid-April in the spring of 1978 (personal observation).

Field study took place during the summers of 1977 and 1978, with a few observations occurring during the intervening winter. Total precipitation for June, July, and August, 1977 recorded at the USU weather station was 300 percent of normal (Climatological Data 1977). The following summer was unusually dry with 56 percent of normal precipitation measured at the USU station for the same 3 months (Climatological Data 1978). Comparable precipitation data were not available for higher elevations. Snow accumulation during the intervening winter was slightly above average in the mountains with approximately 120 percent of normal water content (Whaley et al. 1978).

Soils and bedrock

A deep canyon has been cut by the Logan River to expose predominantly limestone and dolomite bedrock at lower elevations. Areas at high elevations are mostly underlain by the Wasatch formation, a red conglomerate consisting of quartzite, sandstone, and shale. This is sedimentary in origin and has been uplifted and block faulted since its formation in the early Tertiary Period (Lomas 1977).

Table 3. Monthly precipitation (cm) measured at Utah State University, Logan, Utah (from Office of the State Climatologist, Logan, Utah).

Month	1971	1972	1973	1974	1975	1976	1977
January	4.93	2.11	3.76	3.99	3.22	2.49	2.74
February	2.77	.89	2.87	4.34	2.77	7.82	1.37
March	6.25	2.26	5.18	3.07	7.52	6.88	5.38
April	7.72	9.70	3.68	6.81	6.30	8.05	.69
May	3.68	.43	3.45	2.77	4.85	2.21	8.53
June	5.33	4.75	3.68	2.01	2.67	5.03	.53
July	.46	.10	3.56	.66	2.56	2.90	2.62
August	3.05	.86	2.72	.61	.66	4.90	12.80
September	3.10	3.96	12.52	.31	.51	1.55	3.73
October	11.15	6.40	3.35	7.44	10.40	2.01	3.43
November	3.30	3.89	4.44	2.18	4.19	.10	3.96
December	5.08	2.59	5.31	2.67	3.33	.20	5.51
TOTAL	56.82	37.95	54.53	34.39	49.00	44.15	51.31

Table 4. Monthly precipitation (cm) measured at central climate measuring station in USU College Forest (adapted from Lomas 1977).

Month	1970	1971	1972	1973	1974	1975	1976
January	22.61	20.19	26.54	6.83	13.77	13.92	10.08
February	2.92	2.16	13.46	7.67	9.22	14.15	12.06
March	9.27	15.85	11.30	14.83	15.11	13.39	14.15
April	10.54	7.70	15.24	9.14	7.75	10.95	8.79
May	8.26	4.83	.89	4.19	5.89	10.06	3.66
June	4.95	2.92	7.24	4.09	2.16	6.48	3.71
July	1.83	1.22	0.00	3.68	3.48	1.55	3.30
August	.64	2.97	1.65	3.35	.84	1.32	1.80
September	4.19	4.55	6.22	7.03	.38	1.47	2.84
October	13.28	11.20	8.30	3.86	8.86	9.80	--
November	23.67	8.51	7.57	18.03	5.41	13.69	--
December	18.39	19.28	20.80	17.98	11.00	7.59	--
TOTAL	120.55	101.38	119.21	100.68	83.87	104.37	

The Abla/Pera and Abla/Osch habitat types generally occur on the Wasatch Conglomerate. Several stands of these types occupy quartzite and sandstone glacial till near Tony Grove Creek. Stands of other types occur on deep fine-textured soils derived from limestone, dolomite, and sandstone members of the Jefferson, Garden City, Laketown, and Bloomington formations (Williams 1946).

The soils of the various habitat types are typically Cryoboralfs (Abla/Pera), Cryoborolls (Abla/Bere and Psme/Cele), Haploxerolls (Psme/Phma) and Xerolls and Borolls (Abla/Osch and Psme/Bere).

METHODS

This study examines the environment of selected forest habitat types in northern Utah. The objective was to develop hypotheses of the relationship of the habitat type classification to environmental variables which could have cause and effect relationships with the vegetation characteristics differentiating the habitat type classes. This will lead to evaluation of the effectiveness of the classification in stratifying the physical environment.

Six forest habitat types were selected for study. These include Abies lasiocarpa/Pedicularis racemosa (Abla/Pera), Abies lasiocarpa/Osmorhiza chilensis (Abla/Osch), Abies lasiocarpa/Berberis repens (Abla/Bere), Pseudotsuga menziesii/Physocarpus malvaceus (Psme/Phma), Pseudotsuga menziesii/Cercocarpus ledifolius (Psme/Cele), and Pseudotsuga menziesii/Berberis repens (Psme/Bere). These types cover extensive areas within the study area, and are important regionally (Steele et al. 1975, Henderson et al. 1976, Pfister et al. 1977).

Physical environmental variables were measured in stands chosen to be typical of each habitat type as described by Henderson et al. (1976). The forest stands selected for study sites exhibited uneven overstory diameter and age class distributions. An attempt was made to encompass some of the range in elevation and plant species composition characteristic of each habitat type as described by Henderson et al. (1976). Additional criteria for stand selection were accessibility and avoidance of excessively disturbed sites.

However, these factors were not allowed to force selection of stands not meeting the above requirements.

The study extended from July 1977 to October 1978. The first summer constituted a pilot study to obtain preliminary data and test field methods. Fifteen stands were studied including one on the Abies lasiocarpa/Vaccinium membranaceum (Abla/Vame) habitat type in addition to the six habitat types named above. Only one stand represented some types. The following summer 13 additional stands were selected. This increased the number of sampled stands to 27 distributed among the six habitat types named above. The Abla/Vame habitat type was not studied in favor of establishing more stands in the other types. This type is of minor importance in this area and only two suitable representative stands were found. The number of stands of each type observed each year is shown in Table 5.

Vegetation field methods

Vegetation composition and percent cover by species for each stand were determined on a temporary 1000 m^2 circular plot. Plot center was permanently marked and referenced. All species of vascular plants occurring on the plot were identified and percent canopy cover for each species was ocularly estimated. Each tree species was tallied by diameter at breast height in two-decimeter classes. Percent canopy cover of each tree species was estimated as a total for all individuals present and by breast-height diameter class (less than 1 dm, 1-3 dm, and greater than 3 dm).

Table 5. Number of stands observed during each segment of this study by habitat type.

	Summer 1977	Winter 1977-78	Summer 1978
Abla/Pera[1]	3	2	4
Abla/Osch	3	3	4
Abla/Bere	3	3	5
Abla/Vame	1	0	0
Psme/Phma	1	1	5
Psme/Bere	3	3	4
Psme/Cele	1	1	5
TOTAL	15	13	27

---

[1] Abbreviations of habitat names:

Abla/Pera - *Abies lasiocarpa/Pedicularis racemosa*
Abla/Osch - *Abies lasiocarpa/Osmorhiza chilensis*
Abla/Bere - *Abies lasiocarpa/Berberis repens*
Psme/Phma - *Pseudotsuga menziesii/Physocarpus malvaceus*
Psme/Bere - *Pseudotsuga menziesii/Berberis repens*
Psme/Cele - *Pseudotsuga menziesii/Cercocarpus ledifolius*.

Physical environmental variables

Percent slope and aspect were determined by clinometer and handheld azimuth compass. Plots were located on 7 1/2 minute USGS topographic quandrangles and approximate elevations determined. Other environmental variables were evaluated in the following manner:

Maximum and minimum air temperature. One maximum-minimum thermometer with shelter cap was located permanently near the plot center of each stand. These were nailed to the north side of a tree trunk at approximately breast height (1.5 m). The thermometers were located to be shaded from direct sun and sun flecks. Temperatures were read for each plot every few days. Every week during the field season temperature data were collected from all stands in one day to provide common time periods for between plot comparisons. A single winter minimum air temperature was determined for each stand for the entire period between 1 October 1977 and 1 June 1978. Thermometers were calibrated twice during the first summer using a mercury in glass thermometer and at the beginning and middle of the second summer using a copper-constantan thermocouple thermometer. Temperatures were read to the nearest 0.5° C.

Soil temperature. During the first summer soil temperature was determined with a conventional probe thermometer at 20 cm below the soil litter interface. Each measurement was an average of five to seven measurements within the stand taken to represent the dominant character of the stand. For the second summer the probe measurements were combined with thermocouple measurements. A Wescor, Inc. model

TH50 thermometer with internal reference of 0°C and 25°C was used. Copper-constantan thermocouples were buried at 0 cm, 20 cm, and 50 cm below the soil litter interface at two locations within the stand. The 20 cm probe thermometer was used to select sites of average temperature and exposure within the stand for location of the thermocouples and to take additional measurements when the thermocouple temperatures were read. Temperatures were read to the nearest 0.5°C with the probe thermometer and to the nearest 0.1°C with the thermocouple thermometer.

The Wescor thermometer was used to calibrate both the 20 cm soil thermometer and the maximum-minimum air thermometers. The Wescor thermometer is accurate within ± 0.4°C for soil temperatures ranging from -9.5 to 1.6°C (Andersen 1979). Soil temperatures were measured weekly. Due to problems of accessibility of all plots within a short time period these measurements were not taken at the same time of day in each plot. An attempt was made to correct for diurnal soil temperature pattern but data discussed are uncorrected. Most measurements were taken in the 3 hour period before 1:00 pm MDT.

Soil moisture. The dry weight percentage moisture content of the soil was determined to the nearest 0.1 percent using a calcium carbide soil moisture pressure bomb (Speedy moisture tester, Soiltest, Inc.). This instrument was calibrated gravimetrically and was accurate to ± 3.31 percent. Weekly soil moisture measurements were taken at one point in each stand near the soil temperature sampling site.

Plant moisture stress. This was determined by pressure bomb (Waring and Cleary 1967) to the nearest 0.1 atm on twigs from 1-meter tall seedlings of the conifer species important in each stand. Measurements were taken at predawn minimums as determined by diurnal measurements on the same species. Data were collected for at least one tree of each species on each plot with three to five measurements per tree. Plant moisture stress for all plots was determined periodically throughout the first summer of this study.

It was found impossible to obtain reliable measurements within a short time period in 15 stands spread over a large area. Variation in data results was large. In the interest of examining other possible environmental variables and increasing the number of stands sampled, plant moisture stress was not measured the following summer.

Soil descriptions. Soil pits were dug on all plots to a depth of 100 cm or bedrock if soil was shallower than 100 cm. Descriptions were done by Rick Lawton, soil scientist, Soil Conservation Service. Variables described include, for each horizon, upper and lower boundaries, ocularly estimated percent coarse rock fragments by volume in gravel (0.2-7.5 cm), cobble (7.5-25 cm), and stone (greater than 25 cm) size classes, texture class, approximate percent clay, structure, pH, effervescence, and moist soil color. This information was combined with soil temperature data to classify the soil in each stand to the great group (Soil Survey Staff 1975). Type of bedrock from which the soil was derived was also determined. Available water storage capacity of the soil was estimated based on texture class and percent rock fragments by volume using formulas from Erickson and Searle (1974). Values for each horizon were summed to yield a total to 100 cm or bedrock if the soil was shallower than 100 cm. Available soil water storage capacity was expressed both as an absolute number of cm available in the soil profile and as a percentage of the soil depth.

Incident solar radiation. An estimate of the yearly total incident solar radiation was obtained using the slope and aspect determined for each plot and tables from Buffo et al. (1972). Table values were linearly interpolated for slope and aspect. Values are for 40° north latitude.

Phenology. Observations of phenology of both overstory and undergrowth species were recorded for the summer of 1978. Estimates of date of budbreak of conifers by species and date of snowmelt defined as the last day snow covered more than 10 percent of the plot were recorded. From these observations and the maximum-minimum air temperature readings two estimates of length of growing season were obtained for each stand. These were the approximate number of days between budbreak of conifers and the first frost and between snowmelt and first frost.

Analysis of data

Stands and locations within stands for measurement of environmental variables were subjectively chosen due to limitations of time and equipment. Resulting bias in the sample is recognized. Nonparametric statistical methods were rejected as being overly conservative due to the small sample size. The parametric tests employed are robust to assumptions violated (Sokal and Rohlf 1969), except random sampling which is also an assumption of nonparametric statistical methods. Had sampling been random, the parametric tests used below would have been used for data analysis.

Analysis of variance. A single classification analysis of variance was done for each environmental variable using the STATPAC/ONE WAY program.[2] Stratification of the data was by habitat type. Where observations were missing, the values were coded and not included in the data analysis. F-ratio and probability of occurrence of an F-ratio greater than the computed value were calculated. These results were used to test whether variance is significantly ($p \leq .05$) greater between or within habitat types for each environmental variable analyzed. The calculated F-ratio was also used to test for significant ($p \leq .05$) difference in the means for different habitat types. If significance was found, Tukey's honestly significant multiple comparison procedure (Sokal and Rohlf 1969) was performed to locate those differences.

Statistics of mean, variance, standard deviation, standard error, range, and maximum and minimum values were calculated for each environmental variable over all habitat types using a program from the Statistical Package for the Social Sciences (Nie et al. 1975). Standard deviation by habitat type was used to determine which habitat types were most variable for environmental parameters measured.

Ordination. This was accomplished using WISCON a FORTRAN IV program written by Walter Valentine. The computations used Beal's (1960) modification of the Bray-Curtis (1957) method. The data are

---

[2] USU Information Processing Laboratory, 1977.

input as a matrix of elements P_{ij}, representing the relative percent canopy cover of I species in J stands. Relative percent canopy cover for each species was computed separately for overstory and undergrowth vegetation. Both were used in the ordination. Data in the matrix were doubly standardized as discussed by Cottam et al. (1973). This is accomplished by first making each P_{ij} a percentage of the maximum value encountered in any stand for each of the I species. Then, for each of the J stands the P_{ij}'s are expressed as a percentage of the total $\sum_{j=1}^{J} P_{ij}$. The formula for calculating the percent similarity between stands j and K using unstandardized data is

$$PS(j,k) = \frac{200 \cdot \sum_{i=1}^{I} \min(P_{ij}, P_{ik})}{\sum_{i=1}^{I} (P_{ij} + P_{ik})}$$

(Bray and Curtis 1957, after Czekanowski). When data are standardized as above, the percent similarity formula reduces to

$$PS\ (j,k) = \sum_{i=1}^{I} \min\ (P_{ij}, P_{ik}).$$

The Bray-Curtis similarity measure was chosen for several reasons. It has been used widely in ordination of plant communities (Cottam et al. 1973) and the assumptions on which it is based are simple. Recent comparative studies of different ordination techniques have shown the Bray-Curtis method to do well on a variety of criteria, even when the assumptions are not met (Gauch and Whittaker 1972, Cottam et al. 1973, Phillips 1977). Bray-Curtis ordination of doubly standardized data is preferred over the same ordination based on unstandardized data (Cottam et al. 1973).

The purpose of the ordination was to represent major trends in vegetation. All overstory species were included in the calculations; however, not all undergrowth species encountered were included. Two methods were employed to remove the less important species. Both were done after the original vegetation data had been converted to relative percent canopy cover. The first method, used to produce Ordination I, removed species that occurred in fewer than four stands or with a maximum cover of less than three percent in any stand. The second method, which produced Ordination II, summed relative percent cover from greatest to smallest for each stand until a cumulative percent cover of 85 percent was obtained. Remaining species were lumped and entered as a single "species." This lumped class varied from 12 to 15 percent of the total undergrowth cover, but should have little effect on the similarity relationships between stands.

Direct gradient analyses. Stands were arranged in two dimensions defined by elevation and aspect gradients. The aspects were arranged along the horizontal axis to represent a topographic-moisture gradient similar to that used by Whittaker and Niering (1965) and Peet (1978).

A correlation matrix of all environmental variables and ordination axes was calculated using the Pearson correlation coefficient.

Direct gradient analyses (sensu Whittaker 1967) were performed using those environmental variables which showed high correlation with the ordination axes. Soil temperature observations for different dates were subjectively combined into a single gradient for each depth (20 and 50 cm) emphasizing the relative position of the stands. This gradient was scaled from 0 to 10. Two-dimensional arrangements of stands were compared to that produced by ordination.

Pearson's correlation coefficient was calculated to compare stand position along environmental and ordination axes. Results were used to determine if axes based on single environmental variables corresponded to vegetation gradients and separated habitat types as represented by selected stands satisfactorily.

Regression analysis. Stepwise regression analysis was performed to develop axes based on linear combinations of several environmental variables that best predicted relative stand positions on ordination axes. This was accomplished with NEWSTEP, a FORTRAN IV program written by Dr. David Turner. Measured environmental variables were the independent variables and coordinates of stands along ordination axes the dependent variables.

A list of variables included in this analysis is shown in Table 6. Choice of variables to add to or delete from the model was dependent on the partial correlation and the calculated F-ratio to enter (if not already in the model) or delete (if already in). These values change each time a variable is added to or deleted from the model. Variables were added until addition of another variable did not increase the R^2 value by more than 10 percent. Three regression models were developed, one for axis 1 and two for axis 2 of the ordination.

Table 6. Environmental variables used in correlation matrix calculations and step-wise regression analysis for prediction of ordination axis stand coordinates. All measurements are from 1978 as discussed in text.

Environmental variables	Number of stands observed
Physiography	
Elevation (feet)	27
Slope (percent)	27
Aspect (cosine)	27
Length of growing season	
Number of days from date of budbreak to first frost	27
Number of days from date of snowmelt to first frost	27
Incident solar radiation	
Estimated annual total ($cal \cdot cm^{-2} \cdot yr^{-1}$)	27
Air temperature	
Winter minimum	13
June maximum	13
June minimum	7
July maximum	27
July minimum	27
August maximum	27
August minimum	27
September maximum	23
September minimum	22
Soil temperature at 20 cm	
30 May	6
20 June	11
27 June	20
5 July	9
11 July	27
20 July	27
25 July	11
2 August	27
9 August	13
17 August	27
22 August	27
1 October	25

Table 6. Continued.

Environmental variables	Number of stands observed
Soil temperature at 50 cm	
25 July	11
2 August	27
9 August	14
17 August	27
22 August	27
1 October	23
Soil moisture at 20 cm	
11 July	24
19 July	20
26 July	8
2 August	22
9 August	3
16 August	21
22 August	27
1 October	23
Other soil variables	
Soil depth	26
Estimated percent volume of coarse rock fragments in surface 20 cm	26
Approximate percent clay in surface 20 cm	26
Available soil water storage capacity	
as cm available in soil profile	26
as percentage of soil depth	26

RESULTS

Plant moisture stress

Plant moisture stress (PMS) is a measure of the pressure potential of the xylem sap (Boyer 1967). The word stress here refers to the physical stress on the water column and does not imply a measure of the physiological effect this has on the plant. PMS is affected by both atmospheric and soil conditions. The minimum value is controlled by the soil moisture conditions around a plant's root system. Thus, predawn minimum PMS values have been used as a physiologically meaningful measure of soil moisture availability to plants.

Zobel et al. (1976) found PMS useful in differentiating plant community types. Measurements in this study did not distinguish consistently between stands on different habitat types. Indicated relationships of habitat types were not the same from one measurement period to the next (Table 7). Variation in measurements on a single tree and between individuals of the same species was often as large as that between stands (Table 7). PMS was quite different for some stands on the same habitat types. Variation in data results is not discussed by Zobel et al. (1975) and the values they present are quite similar for different community types. Additional measurements may show that the community types are not significantly different in terms of measured PMS.

Plant moisture stress was measured on different species in different stands. When individuals of different species were measured in the same stand, PMS values were not the same. The differences

Table 7. Plant moisture stress measurements by species and stand number, summer 1977.

Date	Habitat type	Plot number	Tree species[1]	Plant moisture stress (atmospheres)	
				Average	All measurements
3 Aug	Abla/Pera	1	Abla	8.7	7.4, 8.0, 8.8, 9.1, 10.4
			Pien	5.1	3.1, 3.4, 3.6, 6.4, 6.6, 7.4
4 Aug	Abla/Pera	2	Abla[2]	5.6	4.8, 5.1, 7.0
			Abla	13.7	12.8, 14.1, 14.3
			Pien	7.1	6.0, 7.6, 7.8
1 Aug	Abla/Pera	3	Abla	5.0	4.5, 4.9, 5.7
			Pien	5.8	5.6, 5.7, 6.0
2 Aug	Abla/Bere	11	Abla	10.0	8.9, 10.4, 10.7
1 Aug	Abla/Bere	12	Abla	7.4	7.2, 7.6
			Abla	8.0	8.0, 8.0
5 Aug	Psme/Phma	8	Psme	22.8	22.6, 23.0
			Psme	23.4	22.9, 23.2, 24.0
2 Aug	Psme/Bere	13	Psme	15.4	14.6, 14.8, 15.3, 15.7, 16.6
5 Aug	Psme/Bere	14	Psme	14.7	14.6, 14.6, 14.9
			Psme	15.6	14.9, 15.7, 16.1
9 Aug	Abla/Osch	5	Abla	14.6	14.4, 14.5, 14.8
10 Aug	Abla/Osch	6	Abla	12.5	12.4, 12.5, 12.6

Table 7. Continued.

Date	Habitat type	Plot number	Tree species[1]	Plant moisture stress (atmospheres)	
				Average	All measurements
10 Aug	Abla/Bere	10	Abla	11.2	11.0, 11.1, 11.6
10 Aug	Psme/Bere	15	Psme	12.3	17.0, 17.1, 17.1
9 Aug	Psme/Cele	9	Psme	14.2	13.8, 14.0, 14.8
			Psme	17.1	17.0, 17.1, 17.1
			Psme	17.2	15.8, 16.1, 16.4, 17.2, 17.8 19.8
23 Aug	Abla/Pera	2	Abla	5.7	5.3, 5.4, 6.4
			Abla	5.8	5.6, 5.8, 5.9
			Abla	10.6	10.4, 10.6, 10.7
			Pien	4.9	4.7, 4.9, 5.0
			Pien	6.0	4.8, 6.0, 6.1, 7.0
24 Aug	Abla/Osch	5	Abla	5.4	4.1, 5.1, 5.2, 5.4, 7.4
			Abla	8.0	7.0, 7.3, 9.2, 11.0
22 Aug	Abla/Osch	6	Abla	4.9	4.1, 4.4, 4.9, 5.2, 6.0
23 Aug	Abla/Osch	7	Abla	4.7	4.1, 4.5, 4.6, 4.9, 5.1, 5.3
			Abla	6.0	5.4, 5.9, 6.4, 6.4
22 Aug	Abla/Bere	10	Abla	4.9	3.8, 4.1, 4.6, 5.4, 6.8

Table 7. Continued.

Date	Habitat type	Plot number	Tree species[1]	Plant moisture stress (atmospheres)	
				Average	All measurements
22 Aug	Psme/Bere	15	Psme	6.3	4.1, 6.6, 7.0, 7.4
24 Aug	Psme/Cele	9	Psme	7.7	7.0, 7.2, 8.0, 8.6
			Psme	9.5	7.9, 9.8, 9.8, 10.6

---

[1] Tree species: Abla = *Abies lasiocarpa*, Pien = *Picea engelmannii*, Psme = *Pseudotsuga menziesii*.

[2] Measurements are for different individuals when the species is indicated more than once for the same plot number.

were not consistent between Picea engelmannii and Abies lasiocarpa. PMS measured on Pseudotsuga menziesii was consistently higher than that measured on Abies lasiocarpa. Zobel et al. (1976) did not find consistent differences between species and they felt that the use of different species contributed no systematic error to the data.

Zobel et al. (1976) explained exceptions to expected PMS values as occurring in stands growing on different geologic substrate than the majority of stands sampled. In this study stands occur on a variety of substrates. This may be an additional source of data error.

Variability and difference of habitat type environments

Measurements of environmental variables in sampled stands are listed in Appendix A. Results of the analysis of variance and other statistical analyses are presented in the following tables.

Study sites were chosen to be representative of each habitat type. Environmental measurements in these stands should describe the variation along the vegetation gradients well. However, exact choice of sample site will affect environmental measurements. Thus, measured difference between stands may not reflect the average difference between those stands for the environmental variables measured.

Variance of most environmental factors was not significantly different between habitat types (Table 8). Soil temperature was more variable in the Abla/Osch, Abla/Bere and Psme/Phma habitat types with temperature measurements at 20 cm and 50 cm showing similar trends. Maximum

Table 8. Results of Bartlett's test of homogeneity of variances and relative variability of types for each environmental variable measured.

Environmental variable	F-ratio	Probability	Significance[1]	Most variable types[2]	Least variable types
Physiography					
Elevation	.969	.436	NS	5	1, 6
Percent slope	1.493	.190	NS	4, 5	1
Aspect (cosine)	.263	.933	NS	5	4
Length of growing season					
Number of days from date of budbreak to first frost	2.321	.042	**	4, 6	1, 3
Number of days from date of snowmelt to first frost	2.128	.061	*	4, 5	1
Incident solar radiation	3.345	.006	**	3	1
Air temperature					
Winter minimum	1.445	.237	NS	3, 5	1
June maximum	.418	.741	NS	1	5
June minimum	.308	.585	NS	3	5
July maximum	4.581	.0004	**	1	2, 4
July minimum	1.848	.102	NS	4, 5	6
August maximum	2.205	.053	*	6	3
August minimum	.939	.455	NS	4	2
September maximum	4.708	.0004	**	4	2, 5
September minimum	1.356	.242	NS	4, 6	2

Table 8. Continued.

Environmental variable	F-ratio	Probability	Significance[1]	Most variable types[2]	Least variable types
Soil temperature at 20 cm					
20 June	.445	.644	NS	2	3
27 June	.988	.426	NS	6	4
5 July	1.372	.271	NS	1	2, 4
11 July	.671	.646	NS	1	4
20 July	1.114	.351	NS	5	2, 4
25 July	.497	.686	NS	2	1
2 August	1.897	.093	*	5	3, 4
9 August	.864	.491	NS	6	1, 3
17 August	1.925	.089	*	5	3
22 August	1.179	.318	NS	1	-
1 October	2.455	.033	**	6	2, 4
Soil temperature at 50 cm					
2 August	1.250	.286	NS	5	3
9 August	1.420	.228	NS	6	3, 4
17 August	2.694	.020	**	5	2, 3
22 August	1.180	.318	NS	6	1, 2
1 October	2.333	.042	**	6	2
Soil moisture at 20 cm					
11 July	3.032	.011	**	1	3, 5
19 July	3.018	.012	**	1	3
26 July	4.781	.041	**	1	4
2 August	2.462	.033	**	4	5
16 August	.174	.952	NS	6, 4	1, 3, 5
22 August	1.721	.128	NS	6	1
1 October	.939	.456	NS	5, 6	1, 2

Table 8. Continued.

Environmental variable	F-ratio	Probability	Significance[1]	Most variable types[2]	Least variable types
Other soil variables					
Soil depth	2.827	.097	*	6	1, 2
Estimated percent volume of coarse rock fragments in surface 20 cm	.852	.513	NS	5	2
Approximate percent clay in surface 20 cm	2.540	.028	**	3, 5	2
Available soil water storage capacity					
as cm available in soil profile	.748	.588	NS	3	1, 6
as percentage of soil depth	1.300	.265	NS	3, 4	5, 6

---

[1] Significance: NS = not significant ($p \leq .10$), * = significant ($p \leq .10$), ** = significant ($p \leq .05$).

[2] Habitat type codes: 1 = Abla/Pera, 2 = Abla/Osch, 3 = Abla/Bere, 4 = Psme/Phma, 5 = Psme/Bere, 6 = Psme/Cele.

air temperatures were generally most variable in the Abla/Pera type and least so in the Abla/Osch and Psme/Bere habitat types. Psme/Phma had the most variable minimum air temperature, and Abla/Osch the least. Types with variable maximum air temperatures generally had less variable minimum air temperatures relative to other types. No types were consistently more or less variable for soil moisture than others.

The F-ratios and probability of greater F-ratio values occurring as calculated in the analysis of variance are shown in Table 9. These were used to test the hypothesis that environmental factors are significantly ($p \leq .05$) different in different habitat types. If a significant difference in the means was indicated, Tukey's statistical procedure was used as shown in Table 9. Habitat types are ranked by means of environmental measurements. Those covered by a common line are homogeneous; those not covered by a common line are significantly different.

The same calculated F-ratios and probabilities (Table 9) indicated the ratio of environmental variance between to within types for each factor examined. Variability for most environmental factors was significantly ($p \leq .05$) greater between types than within them. Exceptions were all but one measurement of soil moisture, soil depth, percent clay, and maximum and minimum air temperature for winter, June, July, and September.

Ordination

The ordination results are shown in Figures 2 and 3. Both are based on relative percent canopy cover of overstory and undergrowth

Table 9 . F-ratio and probability of a greater F-ratio than computed occurring as calculated in analysis of variance. If significance ($p \leq .05$) is found, results of Tukey's honestly significant multiple comparison procedure to locate significantly different means are shown.

Environmental variable	F-ratio	Probability	Significance[1]	Tukey's HSD[2]
Physiography				
Elevation	10.949	.0000	**	1 6 3 5 2 4[3]
Percent slope	6.528	.0008	**	1 2 3 6 5 4
Aspect (cosine)	6.388	.0011	**	6 3 1 5 2 4
Length of growing season				
Number of days from date of budbreak to first frost	22.264	.0000	**	1 3 5 6 2 4
Number of days from date of snowmelt to first frost	46.676	.0000	**	1 3 5 2 6 4
Incident solar radiation	3.527	.0180	**	4 3 5 2 1 6
Air temperature				
Winter minimum	1.219	.3715	NS	
June maximum	.735	.5636	NS	
June minimum	4.029	.1383	NS	
July maximum	.970	.4583	NS	
July minimum	2.360	.0755	*	
August maximum	3.604	.0165	**	1 3 2 5 6 4
August minimum	2.716	.0481	**	3 6 1 5 2 4

Table 9. Continued.

Environmental variable	F-ratio	Probability	Significance[1]	Tukey's HSD[2]
September maximum	.678	.6459	NS	
September minimum	2.733	.0571	*	
Soil temperature at 20 cm				
30 May	.951	.5494	NS	
20 June	1.843	.2515	NS	
27 June	14.519	.0000	**	1 3 2 5 6 4[3]
5 July	4.748	.0833	*	
11 July	3.424	.0203	**	1 3 2 5 4 6
20 July	6.853	.0006	**	1 3 5 2 4 6
25 July	11.986	.0060	**	1 3 2 5 6
2 August	13.063	.0000	**	1 3 2 5 4 6
9 August	12.361	.0027	**	1 3 5 2 6 4
17 August	26.558	.0000	**	1 3 2 5 6 4
22 August	25.059	.0000	**	1 3 2 5 4 6
1 October	2.455	.0707	*	

Table 9. Continued.

Environmental variable	F-ratio	Probability	Significance[1]	Tukey's HSD[2]
Soil temperature at 50 cm				
25 July	20.405	.0015	**	1 3 2 5 6 [3]
2 August	16.592	.0000	**	1 3 2 5 4 6
9 August	14.750	.0007	**	3 1 5 2 4 6
17 August	30.790	.0000	**	1 3 2 5 4 6
22 August	19.115	.0000	**	1 3 2 5 4 6
1 October	7.676	.0006	**	1 3 5 2 4 6
Soil moisture at 20 cm				
11 July	3.022	.0375	**	1 2 3 5 4 6
19 July	.574	.7190	NS	
26 July	.671	.4728	NS	
2 August	1.901	.1502	NS	
9 August	--	--	--	
16 August	.214	.9265	NS	
22 August	.565	.7255	NS	
1 October	.601	.7002	NS	

Table 9. Continued.

Environmental variable	F-ratio	Probability	Significance[1]	Tukey's HSD[2]
Other soil variables				
Soil depth	2.250	.1843	NS	
Estimated percent volume coarse rock fragments in surface 20 cm	6.696	.0008	**	2 3 1 4 6 5[3]
Approximate percent clay in surface 20 cm	.819	.5507	NS	
Available soil water storage capacity				
-as cm available in soil profile	4.193	.0091	**	$\overline{3\ 2\ 1\ 4\ 5\ 6}$
-as percentage of soil depth	3.790	.0161	**	3 2 1 6 5 4

---

[1] Significance: NS = not significance ($p \leq .10$), * = significant ($p \leq .10$), ** = significant ($p \leq .05$).

[2] Results of Tukey's HSD: Habitat types are ranked by means of environmental measurements. Those covered by a common line are homogeneous, those not covered by a common line are significantly different.

[3] Habitat type codes: 1 = Abla/Pera, 2 = Abla/Osch, 3 = Abla/Bere, 4 = Psme/Phma, 5 = Psme/Bere, 6 = Psme/Cele.

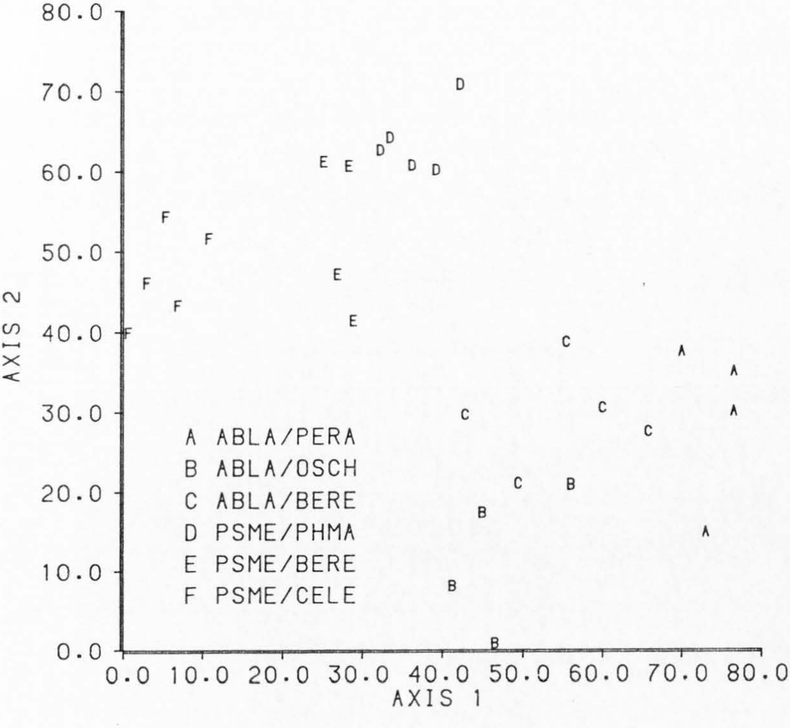


Figure 2. Ordination I. Stand position along each axis indicates relative similarity of each stand to stands objectively chosen as endpoints for each axis. The endstands of the first axis are the least similar to each other of all possible pairs of stands. Second axis endstands are dissimilar both to first axis endstands and to each other. Average similarity between stands is calculated using the Bray and Curtis (1957) similarity index with importance of both overstory and undergrowth vascular plant species expressed as relative percent canopy cover. Less important species, as defined in text, were not included in the calculations.

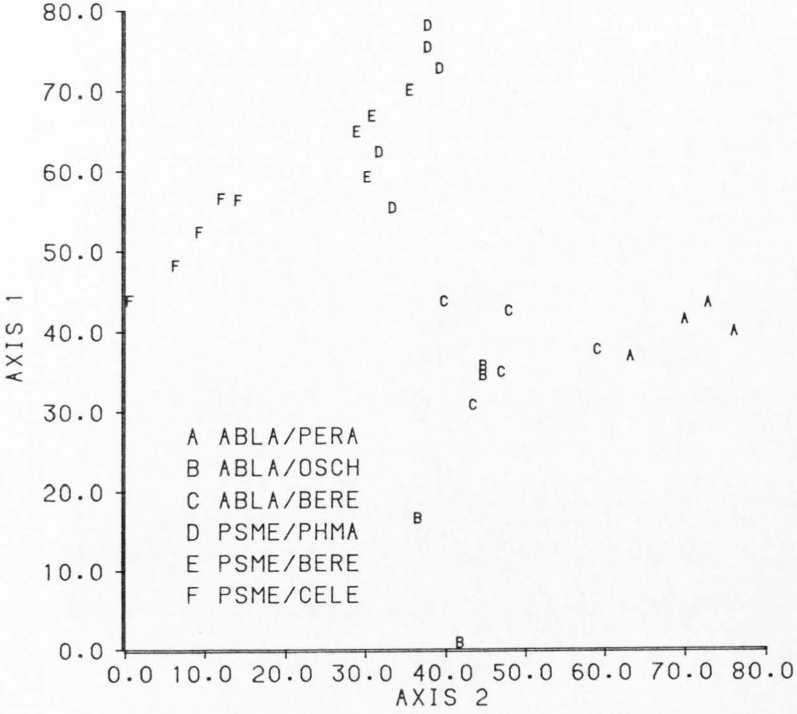


Figure 3. Ordination II. Stand position along each axis indicates relative similarity of each stand to stands objectively chosen as endpoints for each axis. The endstands of the first axis are the least similar to each other of all possible pairs of stands. Second axis endstands are dissimilar both to first axis endstands and to each other. Average similarity between stands is calculated using the Bray and Curtis (1957) similarity index with importance of both overstory and undergrowth vascular plant species expressed as relative percent canopy cover. Less important species, as defined in text, were not included in the calculations.

species with different methods employed for removing unimportant undergrowth species as discussed previously. Patterns of types are very similar in the two resulting ordinations and axes are highly correlated (Table 10). Corresponding axes were chosen in different order by the computer algorithm.

Table 10. Pearson correlation coefficients between axes of ordinations I and II.

		Ordination I	
		Axis 1	Axis 2
Ordination II	Axis 1	-.3790	.9257
	Axis 2	.9793	-.3913

Ordination I was felt to differentiate the types better than Ordination II. It also satisfied intuitive feelings of those building the original classification more satisfactorily (Henderson and Mauk 1979). For these reasons, and the high correlation of corresponding axes, Ordination I is the only ordination subjected to further analysis.

Direct gradient analyses

Single factor environmental gradients. Axes were developed to represent elevation and topographic-moisture gradients. The latter was based primarily on aspect subjectively arranged from mesic to xeric as NE, N, NW, E, W, SE, S, to SW as done by Whittaker and Niering (1965). Stand position on this axis was modified to represent slope, configuration, and topographic position effects on moisture for the individual stands. This gradient analysis is shown in Figure 4.

The habitat type pattern is not dominated by the effect of increasing aridity at lower elevations which should cause a shift in type position to more mesic conditions at lower elevations (Whittaker 1975). The Psme/Cele habitat type, in particular, does not follow this relationship. Comparison of these stands to others randomly selected from the stands used to build the classification (data provided by R. L. Mauk) showed the stands selected for this study were representative of the habitat type relationships to these environmental gradients.

Habitat types were not differentiated well, nor did this analysis represent well the relationships indicated by the ordination. Each type occupies a wide portion of the gradients and the types overlap.

Correlation between environmental variables and ordination axes were calculated using Pearson's correlation coefficient. The results are shown in Table 11. Environmental variables that were significantly highly correlated with the ordination axes were used to perform direct gradient analyses. The two-dimensional arrangement of stands along selected gradients are shown in Figures 5, 6, 7, and 8.

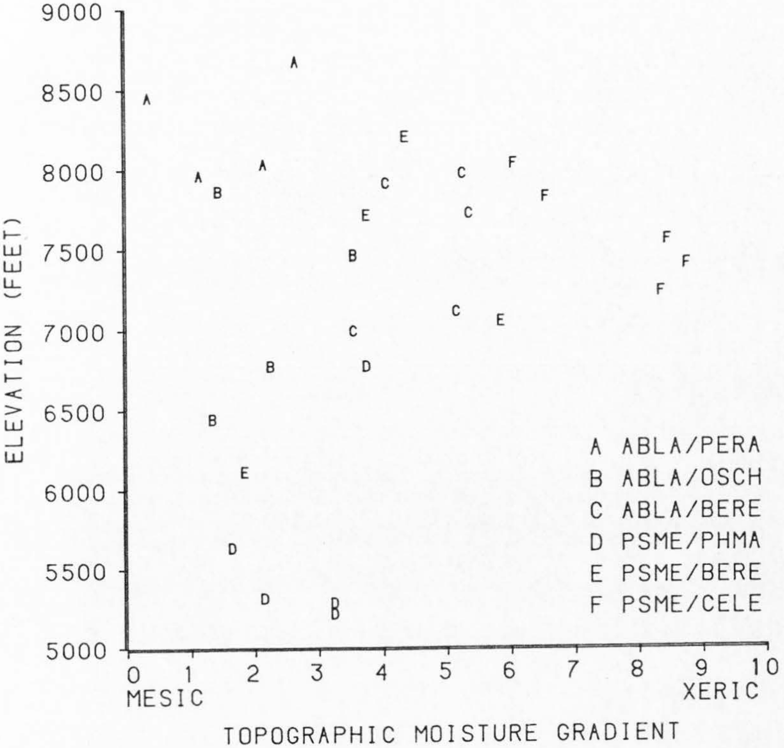


Figure 4. Stand position in relation to elevation and topographic-moisture gradients. Stand position on horizontal axis defined as discussed in text, scaled from 0 (mesic) to 10 (xeric).

Table 11. Correlation of measured environmental variables with Ordination I axis stand coordinates.

Environmental variable	Axis 1	Axis 2
Physiography		
Elevation	.2514[1] (.103)[2]	-.3650 (.031)
Percent slope	-.4636 (.007)	.5550 (.001)
Aspect (cosine)	.4884 (.006)	-.1076 (.296)
Length of growing season		
Number of days from budbreak to first frost	-.1415 (.241)	.4184 (.015)
Number of days from snowmelt to first frost	-.6188 (.001)	.6200 (.001)
Incident solar radiation	-.1134 (.287)	-.2807 (.078)
Air temperature		
Winter minimum	-.1638 (.296)	.2826 (.175)
June maximum	-.0483 (.438)	.1347 (.330
June minimum	.8085 (.014)	-.1993 (.334)
July maximum	-.1958 (.164)	.1850 (.178)
July minimum	-.1804 (.184)	.1763 (.189)
August maximum	-.5275 (.002)	.3284 (.047)
August minimum	.0831 (.340)	.2429 (.111)
September maximum	.1170 (.297)	-.2527 (.122)
September minimum	-.3132 (.078)	.1027 (.325)
Soil temperature at 20 cm		
30 May	-.5526 (.128)	.6117 (.098)
20 June	-.7911 (.002)	.3615 (.137)
27 June	-.7322 (.001)	.6931 (.001)
5 July	-.8414 (.002)	.4309 (.123)
11 July	-.5728 (.001)	.4400 (.011)
20 July	-.6340 (.001)	.3898 (.022)
25 July	-.8932 (.001)	.3417 (.152)
2 August	-.7344 (.001)	.5869 (.001)
9 August	-.7800 (.001)	.4538 (.060)
17 August	-.7382 (.001)	.5926 (.001)
22 August	-.7533 (.001)	.6302 (.001)
1 October	-.5496 (.002)	.2442 (.120)

Table 11. Continued.

Environmental variable	Axis 1	Axis 2
Soil temperature at 50 cm		
25 July	-.9337[1] (.001)[2]	.3027 (.183)
2 August	-.7833 (.001)	.5625 (.001)
9 August	.7665 (.001)	.5007 (.034)
17 August	-.7725 (.001)	.6041 (.001)
22 August	-.7544 (.001)	.5856 (.001)
1 October	-.7167 (.001)	.3832 (.036)
Soil moisture at 20 cm		
11 July	.5806 (.001)	-.2573 (.112)
19 July	.3156 (.088)	-.1245 (.301)
26 July	.5955 (.060)	-.0806 (.425)
2 August	.3068 (.082)	.2840 (.100)
9 August	1.0000 (.001)	-.3041 (.402)
16 August	.2159 (.174)	.2771 (.112)
22 August	-.1851 (.178)	.1041 (.303)
1 October	-.2447 (.130)	.1943 (.187)
Other soil variables		
Soil depth	.6119 (.001)	-.0864 (.337)
Estimated percent volume of coarse rock fragments in surface 20 cm	-.5554 (.002)	.7121 (.001)
Approximate percent clay in surface 20 cm	.0575 (.390)	.0698 (.367)
Available soil water storage capacity		
as cm available in soil profile	.5374 (.002)	-.3753 (.029)
as percentage of soil depth	.3892 (.025)	-.4538 (.010)

---

[1] Pearson correlation coefficient = r.

[2] Significance calculated using student's t-distribution.

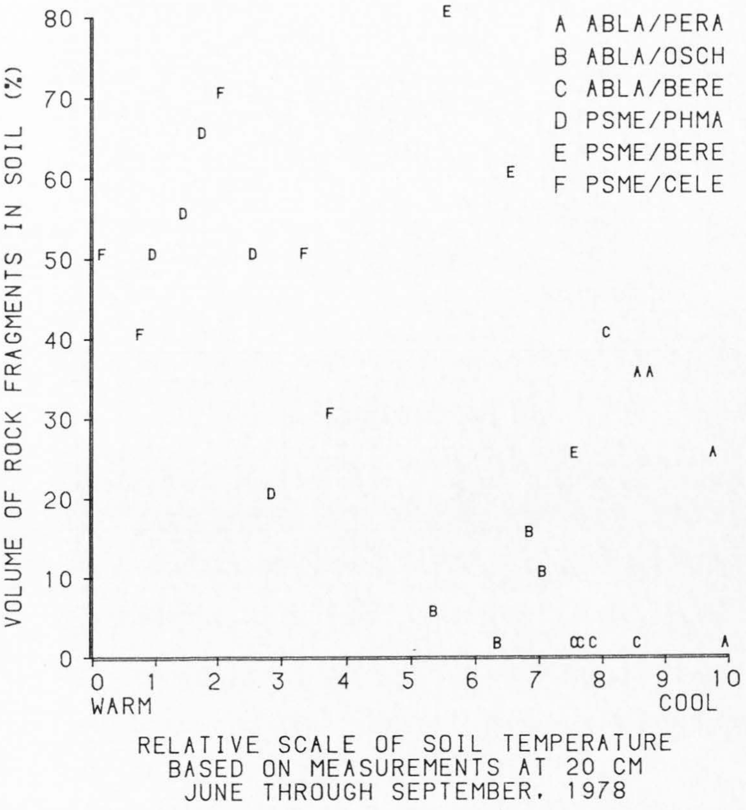


Figure 5. Stand position in relation to gradients of estimated percent volume of coarse rock fragments in surface 20 cm of soil and soil temperature based on measurements at 20 cm.

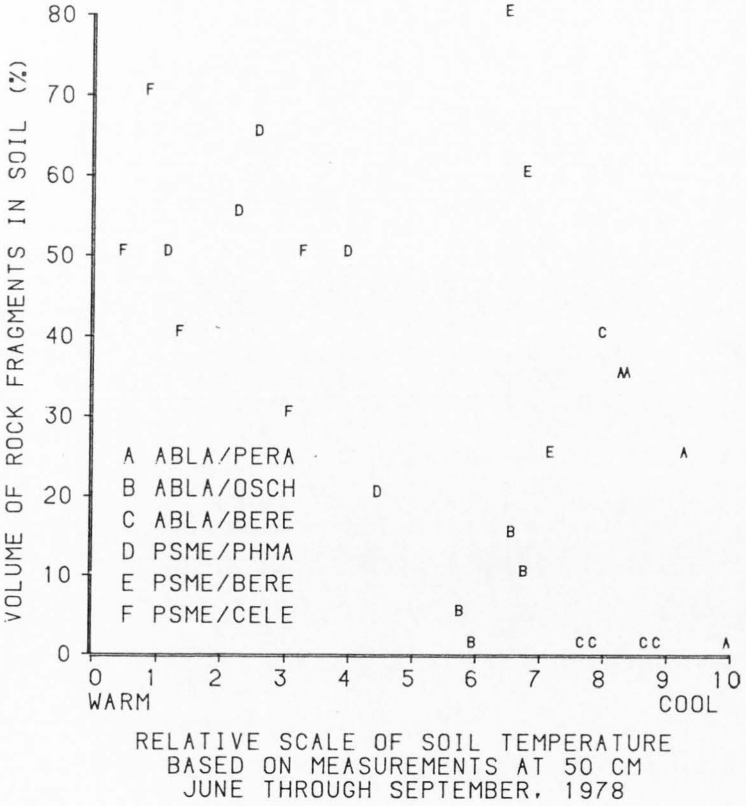


Figure 6. Stand position in relation to gradients of estimated percent volume of coarse rock fragments in the surface 20 cm of soil and soil temperature based on measurements at 50 cm.

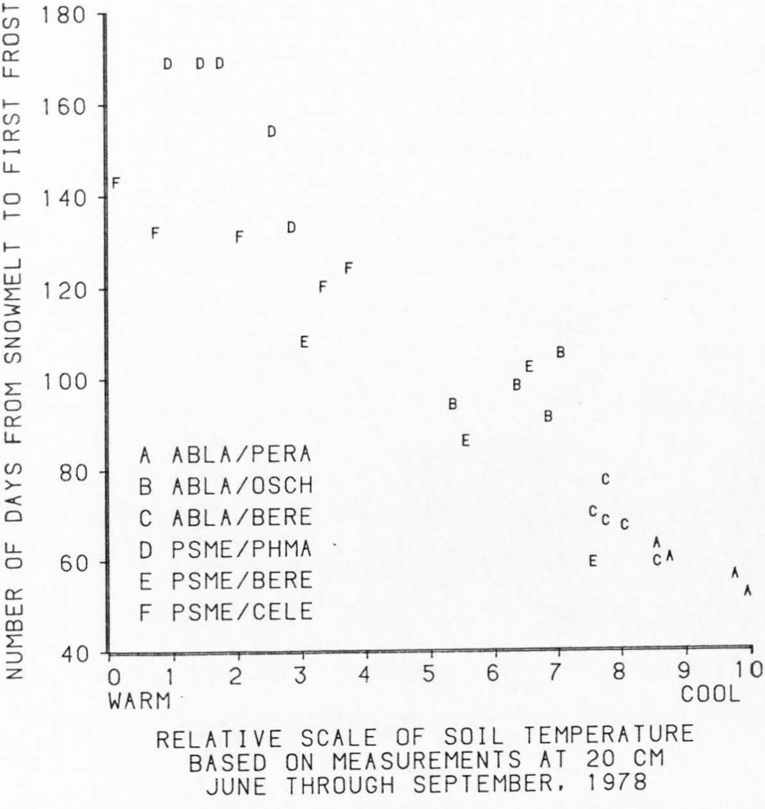


Figure 7. Stand position in relation to gradients of length of growing season as measured by the number of days between date of snowmelt and date of first frost in the fall and soil temperature based on measurements at 20 cm.

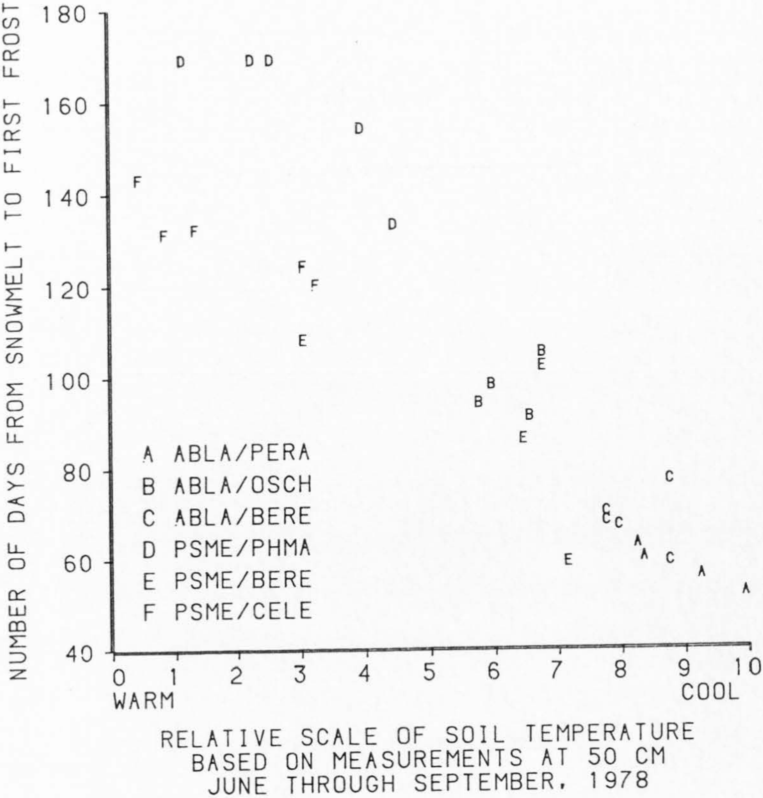


Figure 8. Stand position in relation to gradients of length of growing season as measured by the number of days between date of snowmelt and date of first frost in the fall and soil temperature based on measurements at 50 cm.

All soil temperature measurements showed a high correlation with axis 1 of the ordination. These measurements were combined into a single gradient for each depth sampled. The calculated partial correlation of these soil temperature gradients with axis 1 is 0.7628 for the 20 cm measurements and 0.7831 for the 50 cm measurements. The relative position of stands is similar for both soil temperature axes. The correlation between the soil temperature measurements at 20 and 50 cm is 0.9818. Thus, the stand arrangements are similar in the two dimensional gradient analyses when the gradients shown here on the vertical axes are the same.

In Figures 5 and 6 the environmental factors are ones which affect moisture availability and temperature. The habitat types do not separate well, particularly for those habitat types characterized by an *Abies lasiocarpa* overstory. The *Psme/Cele* and *Psme/Phma* habitat types represent the same environment based on these measurements.

In Figures 7 and 8 the horizontal axis represents a soil temperature gradient. The length of growing season as measured by the number of days between snowmelt and first frost may be correlated with both temperature and moisture availability to plants. Thus the vertical axis may represent a complex temperature and moisture availability index. The soil temperature gradient in both cases shows a high correlation with the seasonal axis. This correlation is -0.9289 for soil temperature at 20 cm and -0.8385 for soil temperature at 50 cm. The correlation is not surprising since soil temperature is dependent on the seasonal moisture and temperature regime.

Multiple factor environmental gradients. The direct gradient analyses show that no two-dimensional combination of environmental measurements was able to separate the habitat types and represent the vegetation relationships indicated by the ordination satisfactorily. Vegetation gradients may respond to several environmental factors simultaneously. Stepwise regression analysis was performed to select combinations of environmental factors which correspond to the vegetation gradients indicated by the ordination axes.

The regression analysis used environmental variables as the independent variables and the Ordination I axis coordinates as the dependent variables. Three predictive models were developed including one for axis 1 (Model A) and two for axis 2 (Models B and C) of the ordination. The difference between models B and C is in the environmental variables included and the number of observations of these variables in the stands. Observation of one stand was missing for the variables included in Model B, and six observations were missing for the variables in Model C, thus these models were based on only 26 and 21 stands respectively. The regression models and their r^2 values are presented in Table 11. Use of more than 3 variables in any model did not increase the correlation between the predicted ordination axis coordinates and the original axis coordinates significantly. Inclusion of additional variables in the regression models did not raise r^2 above 0.80 for any model.

Ordination of stands based on coordinates predicted from these models are shown in Figures 9 and 10. Coordinates of original ordination axes and predicted values are listed in Appendix B.

Table 12. Regression models predicting Ordination I axis coordinates of sampled stands based on measurements of environmental variables.

Model A

Predicted axis 1 coordinate = 106.1 + .509 (Number of days from date of budbreak to first frost)
- 2.906 (Soil temperature at 50 cm, 2 August 1978)
- 8.670 (Soil temperature at 50 cm, 17 August 1978)

$r^2 = .759$

Model B

Predicted axis 2 coordinate = -23.19 + .668 (Estimated percent volume of coarse rock fragments in soil surface)
+ 2.704 (Available soil water storage capacity in cm of water)
+ .161 (Number of days from date of snow melt to first frost)

$r^2 = .656$

Model C

Predicted axis 2 coordinate = -39.04 + .834 (Estimated percent volume of coarse rock fragments in soil surface)
+ 2.723 (Available soil water storage capacity in cm of water)
+ 1.590 (Soil moisture at 20 cm, 2 August, 1978)

$r^2 = .735$

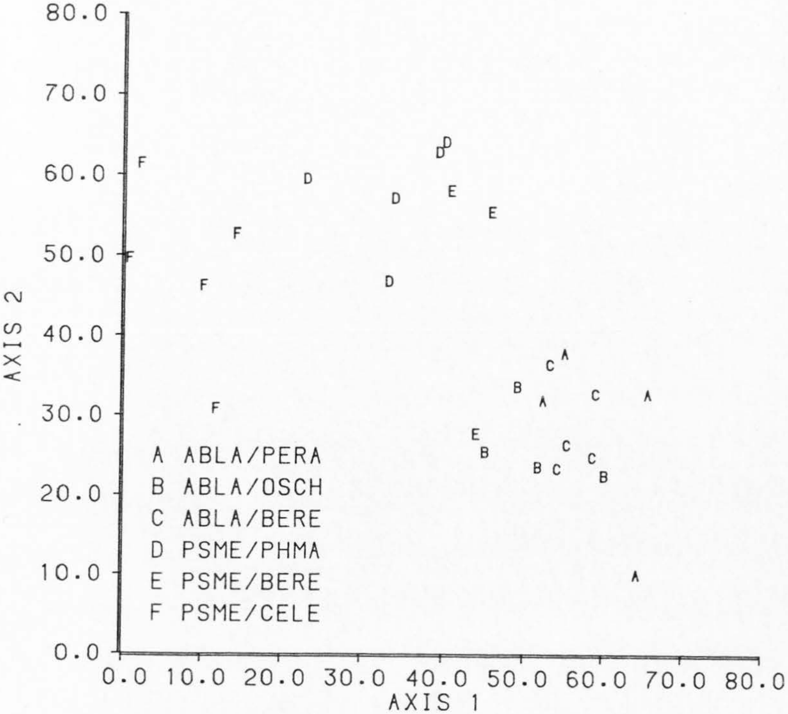


Figure 9. Ordination produced by stand coordinates predicted by regression models A (axis 1) and B (axis 2), based on linear combination of environmental measurements.

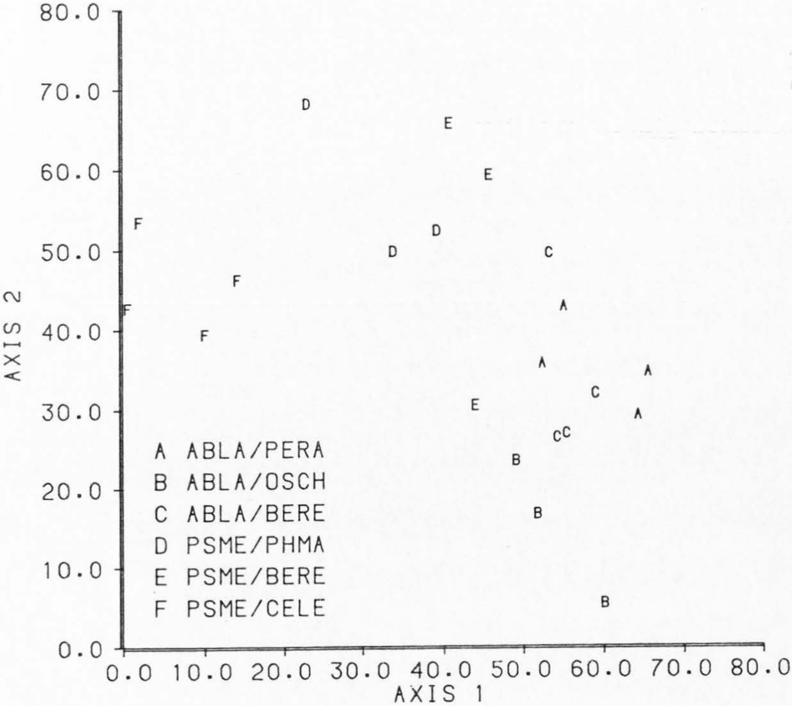


Figure 10. Ordination produced by stand coordinates predicted by regression models A (axis 1) and C (axis 2), based on linear combination of environmental measurements.

Comparison of analyses

The direct gradient analyses shown in Figures 5, 6, 7, and 8 do a fair job of separating the habitat types. However, the relationships of the habitat types do not correspond well with those indicated by the ordination (Figure 2).

The soil temperature axes indicate that Psme/Bere is more similar to the Abla habitat types and Abla/Osch in particular than is shown in the ordination. The temperature gradients do not differentiate between Psme/Cele and Psme/Phma. The snowmelt to frost seasonal measurement better represents similarity relationships shown in the ordination than does the percent rock fragment measurement. The percent rock fragment measurement does not differentiate between Psme/Cele and Psme/Phma and indicates that Psme/Bere occupies a wide range of environments from moist to dry as indicated by this measurement. These types are more distinct and narrowly defined by the second ordination axis than by either of these directly measured moisture gradients.

The ordinations (Figures 9 and 10) based on regression models are very similar. Both indicate Psme/Phma to be more similar to Psme/Cele than is shown by the original ordination (Figure 2). The Abla habitat types cluster in both predicted ordinations although separation is better for that based on models A and C (Figure 10) than that based on models A and B (Figure 9).

Although the habitat types are shown to be different by the ordination calculations, the correlation between the predicted ordination axes and the Ordination I axes is not high. Vegetation differences of the habitat types may be due to the response of vegetation to factors other than environmental or they may be an artifact of stand selection. Vegetation characterizing and differentiating the habitat types may respond to different environmental variables than those examined. For instance, Psme/Phma is similar environmentally to the Abla habitat types because they both occupy steep northerly aspects. This is not indicated by the environmental variables used in either the single or the multiple factor direct gradient analyses.

DISCUSSION

Representation of vegetation gradients by ordination axes

Ordination arranges photosociological data, in this case from forest stands representative of selected habitat types in northern Utah, along several continuous axes in an attempt to represent complex vegetation patterns in a simpler, more interpretable form. Positions of stands along ordination axes indicate similarity relationships of stands in terms of plant species composition and relative abundance. Ideally, axes represent vegetation gradients which correspond to environmental gradients.

The Bray-Curtis ordination performed in this study produced two vegetation axes (Figure 2). A third axis, determined by the computer algorithm, did not further differentiate stands as relative position of stands was the same for the first and third axes. Similar stands should be positioned close together and less similar stands should be further apart if the ordination represents the major trends of variation in vegetation well. This is the case for the ordination calculated. Stands within the same habitat type were significantly more similar (see Appendix B) to one another than to stands of other habitat types in most cases. Where relative position of stands in the ordination field indicated stands were similar to more than one habitat type, examination of vegetation of the stand verified their intermediate character. The relationships of the habitat types indicated by the relative position of sampled stands supports the intuitive feelings of the builders of the habitat type classification (Henderson and Mauk 1979). For these reasons the ordination is felt to adequately represent the major vegetation gradients of the sampled stands in two dimensions.

Environmental gradients corresponding to vegetation gradients

The ordination indicates Abla/Pera and Psme/Bere are the endpoints of the vegetation gradient defined by the first axis, while Psme/Phma and Abla/Osch occupy the extremes of the second axis. The builders of the classification feel these ordination axes are related to temperature and moisture availability respectively (Henderson, Mauk and Youngblood 1979). Stands chosen as endpoints for the ordination axes are the same as would have been subjectively chosen to represent general temperature and moisture gradients based on field observations and qualitative descriptions of environments characteristic of these habitat types by Henderson et al. (1976).

Single factor gradients. Direct gradient analyses produced two-dimensional arrangements of stands in relation to measured environmental gradients. Elevation and topographic-moisture gradients did not separate habitat types nor represent ordination relationships well. Other variables analyzed were those that were significantly correlated with ordination axes. These were soil temperature gradients based on measurements at 20 and 50 cm, estimated percent volume of coarse rock fragments in the surface 20 cm of soil, and the number of days from date of snowmelt to date of the first frost in the fall.

These environmental variables are temperature and moisture related. Soil temperature is one aspect of the temperature regime. The 20 cm soil temperature is influenced by diurnal air temperature fluctuation while soil temperature at 50 cm reflects past seasonal air temperature patterns due to the time lag of temperature penetration into the soil (Bannister 1976). Percent rock in the soil is a measure of soil space unavailable for moisture storage or root penetration, thus this environmental variable is an important influence on the availability of soil moisture to plants. The length of growing season as measured by the number of days between snowmelt and first frost in the fall is indicative of both temperature and moisture regimes.

The soil temperature gradients based on measurements at 20 and 50 cm are highly correlated. Relative positions of stands on these two axes are very similar to one another and to that along the first axis of the ordination. For the vertical axis, correlation between stand positions along the ordination axes and along axes defined by environmental variables is better for the axis based on percent rock than for the seasonal axis. However, habitat types are more distinct and relationships between types correspond more closely to ordination results for the snowmelt to first frost and soil temperature gradient analysis than for the percent rock and soil temperature gradient analysis. Stand relationships in these direct gradient analyses with single environmental gradients defining axes did not explain vegetation gradients indicated by the ordination well. Stands of different habitat types did not form distinct clusters, nor did relationships of stands correspond well to those indicated by ordination.

The results of the calculation of correlation between environmental variables and the ordination suggest the vegetation gradients indicated by the ordination respond to temperature (axis 1) and moisture (axis 2) or a combination of temperature and moisture variables (axis 2). The results of the direct gradient analyses support this conclusion. Both analyses suggest these vegetation gradients correspond to environmental gradients defined by more than one measured environmental parameter such as percent rock or length of growing season.

Multiple factor gradients. Regression analysis was performed to develop linear combinations of measured environmental variables which might better predict ordination axes. Variables used in the models were selected objectively and were not purposely chosen to represent temperature or moisture gradients. Three regression models were developed, one predicting stand coordinates of the first ordination axis (Model A) and two for prediction of coordinates of the second axis (Models B and C).

Regression model for the first ordination axis: This axis is again indicated to be a soil temperature axis. Model A variables are soil temperature measured at 50 cm on two different dates in August, 1978 and length of growing season as indicated by the number of days from the date of conifer bud break to the date of the first frost in the fall.

This measurement of length of growing season may be considered primarily an indication of temperature. Moisture is probably not limiting in any of these habitat types when conifer budbreak occurs. Zobel et al. (1976) similarly define length of growing season for calculation of Temperature Growth Index as being from date of budbreak of conifer saplings to the date of the second frost in the fall.

Regression models for the second ordination axis: The models developed for prediction of stand coordinates of this axis include variables related to moisture availability to plants. Both include estimated percent volume of coarse rock fragments in the soil surface and available water storage capacity expressed as centimeters in the soil profile to 100 cm or bedrock if soil is shallower than 100 cm. In addition to these variables Model B includes number of days from date of snowmelt to first frost as a measure of length of growing season and Model C includes August soil moisture percentage at 20 cm.

The date of first frost was quite uniform over the entire study area. Thus, variability in the length of growing season from date of snowmelt to date of first frost is due mostly to differences in date of snowmelt. This is affected both by the winter accumulation of snow and the temperature regime at each site. In this area most precipitation occurs during the winter, hence amount of snow and timing and nature of runoff are very important to the availability of moisture for plant growth.

The August soil moisture percentage is an indication of seasonally available water. Plant moisture stress reaches a maximum in August (Table 7). Soil moisture supply at this time is potentially important in determining plant species distribution and abundance through its effect on plant moisture stress. If soils are rocky, soil moisture storage capacity is limited and the amount of moisture held by the fine portion of the soil is critical.

Correlation with vegetation gradients: Environmental gradients defined by linear combinations of environmental variables did not improve correlation with ordination axes significantly over gradients based on single environmental parameters. Correlation with the first ordination axis was not much improved by multiple factor models over single factor models. Correlation with the second ordination axis improved significantly. The relationships of the habitat types indicated by multiple factor environmental gradients corresponded more closely to ordination results than that produced by single factor gradients. The difference was primarily due to changes along the moisture gradient corresponding to the second ordination axis. Relationships of stands indicated by temperature measurements already correlated well with the first ordination axis.

Correlation is only moderate. This is not unexpected since the stands included in the ordination analysis occupy a wide range of environments. Both single and multiple factor environmental gradients represent average relative importance of these factors along the entire vegetation gradient. The relative importance of the environmental factors should not be expected to be the same in all parts of the environmental gradient. Vegetation characteristics may still respond to temperature and moisture environmental variables along the entire gradient. However, the relative importance of expressions of these will change so that different measured environmental parameters may characterize the habitat types in different portions of the vegetation gradient.

This is indicated by the clustering of the *Abies lasiocarpa* habitat types in both predicted ordinations. Neither the temperature variables included in regression model A nor the moisture variables of model B separate these three habitat types. When measured soil moisture percentage in August is used (Model C) the *Abla/Osch* habitat type is separated from the *Abla/Pera* and *Abla/Bere* habitat types.

These three habitat types occur at high elevations where available water storage capacity in the soil is not as strongly limiting as in the *Pseudotsuga menziesii* habitat types. This is due both to heavy winter snow accumulation and the occurrence of more precipitation at higher elevations (Tables 3 and 4). Soil moisture at 20 cm is useful in differentiating the *Abla/Osch* type from *Abla/Bere* and *Abla/Pera* habitat types. Other variables which differentiate the three sites are air and soil temperature, percent slope, and soil pH and organic matter content. The growing season was longer and soil temperatures, maximum air temperatures in July, August, and September and minimum temperature in August were all higher for *Abla/Osch* sites. The *Abla/Bere* type generally occurs on steeper slopes than the *Abla/Pera* type. The soils are also less acid and higher in organic matter as indicated by the dark color in the *Abla/Bere* habitat type.

Other reasons correlation of the environmental gradients with the ordination axes is not high may be related to selection of sampling locations including both the choice of a particular stand and the location of the environmental measurements taken within the stand. Different locations of these sites may influence the correlation, particularly if the measurements are not representative of stands or types. Another important influence on the correlation is stochasticity. The composition and relative abundance of species in plant communities is not wholly determined by environmental effects. There is an element of chance both in the order in which species colonize a place and the kind and frequency of disturbance that may occur there. These may have long lasting effects on the characteristics of the plant community. Such stochastic effects may increase the variability of the relationship between vegetation and environment.

An hypothesis

In this study vegetation gradients have been shown to be correlated with temperature and moisture gradients. It is hypothesized that vegetation is responding to these environmental gradients through their effect on plant moisture stress.

Plant moisture stress. Moisture stress is significant to plant growth and development. Water deficits have been shown to cause reduction in growth (Bannister 1976). Cell expansion, photosynthesis, respiration, and many other metabolic processes are affected by water stress (Bannister 1976).

Plant moisture stress is a function of moisture supply and demand. Soil moisture conditions such as water storage capacity and hydraulic conductivity affect the availability of moisture for uptake by plant roots. Atmospheric conditions such as radiation, air temperature, moisture content of the air, and wind speed affect evaporation and transpiration rates from plant leaves. Moisture stress may occur when soil moisture availability is low, when atmospheric stress is high, or when a combination of these factors causes moisture demand to exceed moisture supply.

Temperature and moisture effects: Temperature variables which corresponded to vegetation gradients were soil temperature measured at 20 and 50 cm and length of growing season as indicated by the number of days between budbreak and the first frost in the fall.

Soil temperatures measured at 20 and 50 cm on 17 and 22 August are highly significant for difference between habitat types (Table 9). These soil temperature measurements also correlated highly with the first ordination axis and the measurement for 17 August was included in the multiple factor environmental gradient regression model. Maximum predawn plant moisture stress was measured at approximately this time (Table 7). This lends support to the hypothesis that soil temperature is an important direct influence on plant moisture stress or a useful indicator of some other factor that influences plant moisture stress.

The correlation of soil temperature and plant moisture stress may be the result of several important effects. Soil temperatures are an important influence on the radiation environment of leaves which is an important factor in transpiration rate (Bannister 1976). Soil temperature directly affects any metabolic process occurring in the roots including active uptake of water by roots. Correlation of soil temperature may also be a reflection of the importance of air temperature. Soil temperatures reflect air temperature patterns which may not adequately be represented physiologically by maximum and minimum air temperature measurements.

The moisture variables indicated to be important by this study are percent volume of coarse rock fragments in the soil, available water storage capacity, soil moisture percentage at 20 cm measured in August, and length of growing season defined as the number of days from date of snowmelt to the first frost in the fall. These are all important in determining moisture availability in the soil for uptake by plant roots as previously discussed.

Direct measurement of plant moisture stress: Plant moisture stress measured by pressure bomb on conifer saplings did not differentiate types well. Variability in data results (Table 7) and accessibility of stands limited usefulness of this measurement. Although this method directly measures the water stress experienced by these trees, many other variables than atmospheric and soil moisture stress are integrated by this measurement. Disease, rooting pattern, competition, shading and other microhabitat characteristics will affect the plant moisture stress experienced by an individual plant. These effects may obscure larger scale environmental differences between stands. Direct measurement of the environmental variables most important in determining PMS is probably more useful than inference about these variables through plant moisture stress measurement for investigating environmental differences between stands.

Habitat type relationships. The hypothesized relationship of the habitat types included in this study is shown in Figure 11. The horizontal axis represents a gradient of atmospheric influences and the vertical axis soil moisture effects on plant moisture stress. In general these axes correspond to temperature and moisture environmental variables respectively.

The arrangement of the habitat types in Figure 11 is purely subjective, based on measurement of environmental factors, ordination results, and field observation of environmental characteristics not included in the analysis. These include inferences about the radiation environment of each type including timing of radiation input relative to air temperature patterns. This is affected by elevation, slope, and aspect. Winter snow accumulation is also considered as it affects potential availability of water for summer plant growth and is an important influence on soil temperature. The growing season for many plants may be limited by availability of moisture in the soil in late summer. The influences of winter snow accumulation, water storage capacity of the soil, and timing of plant growth relative to moisture availability were also taken into account in development of hypothesized relationships of the habitat types.

The Abla/Pera habitat type is cold and moist. It occurs at high elevations on deep, acid soils of the Wasatch formation. Snowfall

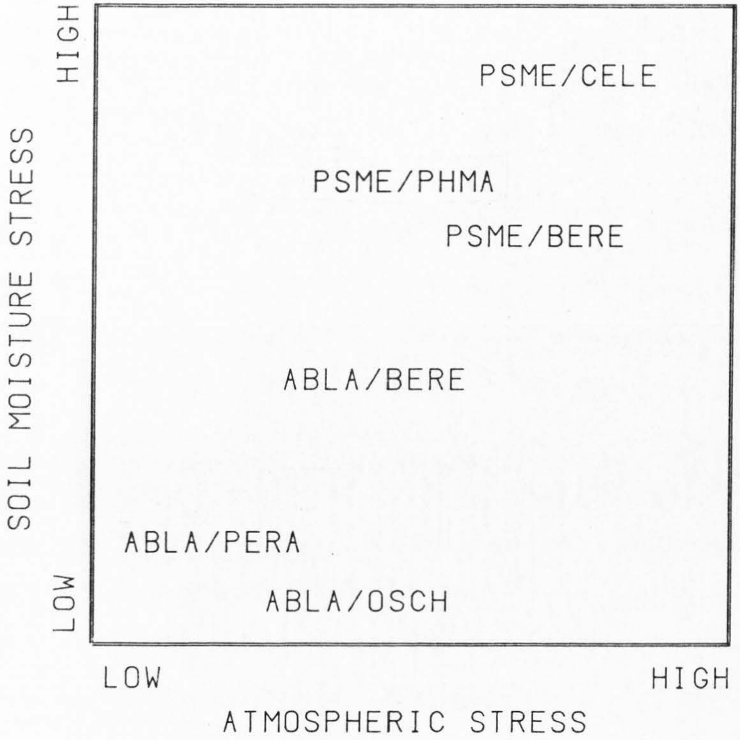


Figure 11. Hypothesized relationships of habitat types to gradients of soil moisture and atmospheric stress. Soil moisture stress is here considered to be influenced by factors affecting the capacity of the soil to provide moisture to the plant roots. Atmospheric stress is considered to be primarily influenced by temperature, incident solar radiation, and length of growing season.

is heavy and snowpack remains until late June or early July. The soils remain moist throughout the short growing season. This combination of factors indicates low atmospheric and soil moisture stresses.

Stands on the Abla/Osch habitat type also occupy environments of low soil moisture and atmospheric stresses. These occur at middle to high elevations on deep fine textured soils. Although the stand in the Tony Grove area is indicated to have shallow soil, the rock portion of the soil consists of mostly large boulders. Tree roots may extend quite far down between these rocks. The fine portion of the soil retains water late in the summer as indicated by the soil moisture measurements. Soils were quite moist at a depth of 1 meter when soil pits were dug in late August of 1978. The type is warmer than Abla/Pera. Based on these observations, it is hypothesized that the Abla/Osch habitat type experiences lower soil moisture stress and higher atmospheric stress than the Abla/Pera habitat type.

The Abla/Bere and Psme/Bere habitat types are intermediate in character for both gradients. Both have cold air and soil temperatures and rocky soils. The Psme/Bere type occupies steeper rockier sites on drier aspects than the Abla/Bere type.

The Psme/Phma habitat type is indicated to have high atmospheric stress because it occurs at low elevations, is typified by warm air and soil temperatures, and has a long growing season. This type receives less incident solar radiation than either Psme/Cele or Psme/Bere due to its occurrence on very steep north facing slopes.

Not much snow accumulates on these types and soils are often rocky and shallow indicating high soil moisture stress.

The Psme/Cele habitat type represents both high soil moisture stress and high atmospheric stress. These sites occur on south facing slopes and ridges at middle to high elevations. Summer air and soil temperatures are high relative to the other habitat types. There is little snow accumulation on these sites in the winter and slopes are bare early in the spring. Thus, little moisture is potentially available for soil storage. Soils probably dry early in the summer due to low soil moisture recharge by snowmelt and the high evaporation and transpiration potentials associated with exposure to wind and high incident solar radiation. Conifer budbreak did not occur until 2 months after snowmelt in these stands. This may indicate the growing season is short on this habitat type for most plants if summer drought is limiting.

The stand relationships hypothesized in Figure 11 are based on environmental measurements but are conjectural in nature. This hypothesis needs further testing to determine if it is a useful generalization of the habitat type relations in the Logan Canyon area, Utah. If valid, the hypothesized relationships are probably applicable to adjacent areas supporting similar vegetation. Danger in extrapolation of this generalization to other areas before supporting data are obtained should be recognized.

The purpose of this study was to investigate how effective the habitat type classification system is in stratifying the physical environment. Stands were selected to be representative of habitat types described in the classifications of the study area developed by Pfister (1972) and Henderson et al. (1976). It would be surprising if selection of stands by this criteria, where the habitat type classes, are defined based on the presence of a combination of several species did not yield stands that differed environmentally. If the habitat type classification system is to be useful for management purposes, the types must not only be different environmentally but the environmental factors differentiating the types should be important in determining the vegetation parameters characterizing the types. The environmental differences should also be meaningful to management applications.

It is hypothesized that the temperature and moisture environmental variables shown to correlate to the vegetation gradients indicated by the ordination axes are important in determining plant species distribution through their effect on plant moisture stress. Further study of the environmental relationships of habitat types is needed to test this hypothesis and determine if the habitat type classification is effective in stratifying the physical environment. Better measurement of the environmental variables examined in this study and investigation of other variables are needed. The environmental variables examined here are potentially important in determining plant moisture stress influences but methods of evaluation are crude and imprecise, particularly for the moisture gradient. Soil and air temperatures should be measured continuously rather than as point-in-time or maximum and minimum values. A measure of effective precipitation, that portion of the precipitation that is not lost to evaporation, runoff, and drainage and is actually available for utilization by plants is needed. A more physiologically meaningful measurement of length of growing season than either included here is also needed. Such a measurement must emphasize the limitation of plant growth by low soil temperature in early spring and moisture availability or low air temperature in late summer. Emphasis on those variables which are important to soil moisture and atmospheric influences on plant moisture stress may clarify the relationships between habitat types and improve correlation of environmental and ordination axes. Choice of environmental variables to consider and methods for their evaluation may be simplified.

SUMMARY AND CONCLUSIONS

The conclusions of this study are based on the premise that the environmental relationships between stands indicated by the measurements obtained are representative of these relationships in other years. This implies that the variables shown to be important in characterizing and differentiating stands representative of the habitat types are important to the growth and establishment of the plant species on which the habitat type classification is based. Plant communities develop over long periods of time so that vegetation occurring on the land is influenced by both past and present environmental factors. The habitat type concept considers time and successional relationships of the vegetation. If conclusions about the environmental relationships of habitat types, which are based on short term environmental measurements such as those obtained in this study, are to be valid, present environmental relationships of the vegetation occurring on the habitat types must be similar to those of the past and future.

Based on the acceptance of this premise, my data show:

1. The habitat types studied are significantly different and the environment is more variable between the types than within them for most environmental factors measured.

2. There are two principal vegetation gradients in these habitat types.

3. The directly measured environmental variables that correspond best to the vegetation gradients indicated by the ordination axes are

summer soil temperature measured at 50 cm for one axis and a linear combination of variables affecting soil moisture supply for the other axis. These variables are soil moisture percentage measured at 20 cm, estimated percent volume of coarse rock fragments in the soil, and estimated available water storage capacity in the surface meter of soil calculated from percent rock fragment and soil textural class data.

4. It is felt these temperature and moisture variables are physiologically significant to plant growth and development through their effect on plant moisture stress. These variables determine the availability of soil moisture to plant roots to meet transpirational demand and atmospheric influences on that demand. An hypothesis of the relationships of the habitat types to these environmental gradients is presented in the form of a two-dimensional gradient analysis.

5. Direct measurement of predawn minimum plant moisture stress on conifer saplings did not differentiate habitat types satisfactorily. It is felt that this measurement integrates many microhabitat environmental factors which obscure the larger scale environmental differences between stands.

6. It is tentatively concluded that the forest habitat types examined in this study do represent different environments. This land classification system is effective in stratifying the physical environment in terms of environmental parameters which are both physiologically meaningful to vegetation characteristics defining the habitat type classes and have important implications to management applications.

The habitat type classification system has proven useful in a variety of management applications (Pfister 1976, Arno and Pfister 1977). This study shows that the habitat types are not highly variable and broadly overlapping in terms of environment. Since the response of vegetation is dependent on the physical environment, this lends support to the conclusion that knowledge of the habitat type class of a particular piece of land is useful in predicting the response of vegetation to management manipulation or natural disturbance.

LITERATURE CITED

Andersen, D. 1979. Personal communication.

Arno, S. F. and R. D. Pfister. 1977. Habitat types: An improved system for classifying Montana's forests. Western Wildlands. Montana For. and Conserv. Exp. Stn. Univ. of Montana, Missoula. 6 pp.

Bannister, P. 1976. Introduction to physiological plant ecology. Wiley, New York. 273 pp.

Beals, E. W. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. 72:156-181.

Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. Q. Rev. Biol. 27:251-265.

Boyer, J. S. 1967. Leaf water potentials measured with a pressure chamber. Plant Physiol. 42:133-137.

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

Buffo, J., L. J. Fritschen, and J. L. Murphy. 1972. Direct solar radiation on various slopes from 0 to 60 degrees north latitude. USDA For. Serv. Res. Pap. PNW-142. 74 pp.

Cajander, A. K. 1926. The theory of forest types. Acta. For. Fenn. 29:1-108.

Cleary, B. D. and R. H. Waring. 1969. Temperature: Collection of data and its analysis for the interpretation of plant growth and distribution. Can. J. Bot. 47:167-173.

Climatological Data--Utah. 1977. Vol. 79, U.S. Dept. Commerce, Nat. Oceanic and Atmospheric Adm., Environmental Data Service.

Climatological Data--Utah. 1978. Vol. 80, U.S. Dept. Commerce, Nat. Oceanic and Atmospheric Adm., Environmental Data Service.

Cottam, G., F. G. Goff, and R. H. Whittaker. 1973. Wisconsin comparative ordination, pp. 195-221. In: Whittaker, R. H. (ed.) Ordination and classification of communities. Handbook of Vegetation Science 5. Junk, The Hague.

Cooper, S. V. 1975. Forest habitat types of northwestern Wyoming and contiguous portions of Montana and Idaho. Ph.D. Diss. Wash. State Univ., Pullman. 190 pp.

Daubenmire, R. F. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monogr. 22:301-330.

Daubenmire, R. F. and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agr. Exp. Stn., Tech. Bull. 60, 104 pp.

Del Moral, R. and A. F. Watson. 1978. Gradient structure of forest vegetation in the central Washington Cascades. Vegetatio 38:29-48.

Despain, D. G. 1973. Vegetation of the Bighorn Mountains, Wyoming, in relation to substrate and climate. Ecol. Monogr. 43:329-355.

Dyrness, C. T., J. F. Franklin, and W. H. Moir. 1974. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. US IBP Coniferous Forest Biome Bull. 4. University of Washington, Seattle. 123 pp.

Erickson, A. J. and G. P. Searle. 1974. Settlement-potential ratings of soils for low buildings--Utah. USDA Soil Conservation Service.

Gauch, H. G., Jr., and R. H. Whittaker. 1972. Comparison of ordination techniques. Ecology 53:868-875.

Henderson, J. A. 1978. ECOSYM-Potential vegetation classification. 12 pp. Appendix Report #7. In: Henderson, J. A. and L. S. Davis. ECOSYM: A classification and information system for wildland resource management. Department of Forestry and Outdoor Recreation. Utah State Univ., Logan.

Henderson, J. A. and R. L. Mauk. 1979. Personal communication.

Henderson, J. A., R. L. Mauk, D. L. Anderson, R. Ketchie, P. Lawton, S. Simon, R. H. Sperger, R. W. Young, and A. Youngblood. 1976. Preliminary forest habitat types of northwestern Utah and adjacent Idaho. Department of Forestry and Outdoor Recreation, Utah State Univ., Logan, 99 pp.

Henderson, J. A., R. L. Mauk, and A. Youngblood. 1979. Personal communication.

Henderson, J. A. and N. E. West. 1977. ECOSYM-Vegetation classification. 89 pp. Appendix Report #6. In: Henderson, J. A. and L. S. Davis. ECOSYM: A classification and information system for wildland resources management. Department of Forestry and Outdoor Recreation, Utah State Univ., Logan.

Hoffman, G. R. and R. R. Alexander. 1976. Forest vegetation of the Bighorn Mountains, Wyoming: a habitat type classification. USDA For. Serv. Res. Pap. RM-170. 38 pp.

Kerr, C. W. and J. A. Henderson. 1979. Upland-potential vegetation classification and map for a test area, Manti LaSal National Forest. 98 pp. Report #15. In: Henderson, J. A. and L. S. Davis. ECOSYM: A classification and information system for wildland resource management. Department of Forestry and Outdoor Recreation. Utah State Univ., Logan.

Lomas, D. A. 1977. Soil water depletion following clearcutting small plots in a spruce-fir forest in northern Utah. M.S. Thesis. Utah State Univ., Logan. 91 pp.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sciences, 2nd ed. McGraw-Hill, New York. 675 pp.

Peet, R. K. 1978. Latitudinal variation in southern Rocky Mountain forests. J. Biogeog. 5:275-289.

Pfister, R. D. 1972. Vegetation and soils in the subalpine forests of Utah. Ph.D. Diss. Washington State Univ., Pullman. 98 pp.

Pfister, R. D. 1976. Land capability assessment by habitat types, pp. 312-325. In: America's renewable resource potential-1975: the turning point. Proc. Soc. Am. For., Washington, D.C. 503 pp.

Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rep. INT-34. Ogden, Utah.

Phillips, D. L. 1978. Polynomial ordination: Field and computer simulation of a new method. Vegetatio 37:129-140.

Soil Survey Staff. 1975. Soil taxonomy. USDA, Soil Conservation Service. Agriculture Handbook No. 436.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. Freeman, San Francisco. 776 pp.

Steele, R., D. Ondov, S. V. Cooper, and R. D. Pfister. 1977. Preliminary forest habitat types of eastern Idaho and western Wyoming. USDA For. Serv., Intermtn. For. and Range Exp. Stn. Interim Report, 147 pp., mimeo.

Steele, R., R. D. Pfister, R. A. Ryker, and J. A. Kittams. 1975. Forest habitat types of central Idaho. USDA For. Serv. Intermtn. For. and Range Exp. Stn. Ogden, Utah.

Sukachev, V. and N. Dylis. 1964. Fundamentals of forest biogeocoenology. (Transl. by J. M. MacLennon, 1968). Oliver and Boyd, Edinburgh. 672 pp.

Waring, R. H. and B. D. Cleary. 1967. Plant moisture stress: Evaluation by pressure bomb. Science 155:1248-1254.

Whaley, B. L., K. C. Jones, and L. K. Lytton. 1978. Water supply outlook for Utah. USDA, Soil Conservation Service.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biol. Reviews 42:207-264.

Whittaker, R. H. 1975. Communities and ecosystems, 2nd ed. MacMillan, New York. 387 pp.

Whittaker, R. H. and W. A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona. (II) A gradient analysis of the south slope. Ecology 46:429-452.

Williams, J. S. 1946. Geologic map of the Logan quadrangle, Utah. Bull. Geol. Soc. Am., Vol. 59, plate 1.

Wirsing, J. M. and R. R. Alexander. 1975. Forest habitat types on the Medicine Bow National Forest, southeastern Wyoming: Preliminary Report. USDA For. Serv. Gen. Tech. Rep. RM-12. 11 pp.

Zobel, D. B., A. McKee, G. M. Hawk, and C. T. Dyrness. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecol. Monogr. 46:135-156.

APPENDICES

Appendix A

Environmental data

Table 13. Stand physiography, seasonal data (1978), and estimated total yearly incident solar radiation.

Habitat type	Plot number	Elevation (meters)	Percent slope	Aspect (azimuth)	Date of budbreak	Date of snowmelt	Date of first frost	Number of days from budbreak to first frost	Number of days from snowmelt to first frost	Estimated total incident solar radiation ($cal \cdot cm^{-2} \cdot yr^{-1}$)
Abla/Pera	1	2634	8	76	6/25	7/01	8/25	60	55	197322
	2	2418	17	3	6/25	6/28	8/25	62	59	174455
	3	2439	10	304	6/16	6/26	8/19	65	62	192217
	16	2567	8	30	6/24	6/30	8/20	57	51	190488
Abla/Osch	5	2265	18	304	6/08	5/20	8/30	84	93	184537
	6	2387	10	360	6/12	5/28	8/25	75	90	185463
	7	2055	37	334	5/28	5/20	9/01	96	104	147361
	18	1954	18	21	6/08	5/20	8/25	79	97	174458
Abla/Bere	10	2421	14	275	6/18	6/10	8/25	68	76	197506
	11	2122	54	332	6/06	6/07	8/12	67	66	123684
	12	2402	26	274	6/16	6/23	8/19	63	58	194245
	27	2344	7	258	6/10	6/10	8/18	69	69	200094
	28	2158	33	279	6/10	6/12	8/18	69	67	187599
Psme/Phma	8	1610	44	359	5/15	4/01	9/15	124	168	129989
	19	1707	81	12	5/15	4/01	9/15	123	168	88763
	20	1579	77	328	5/15	4/01	9/15	123	168	105069
	21	2055	82	304	5/15	4/05	8/15	92	132	129008
	22	1601	38	319	5/15	4/01	9/01	108	153	154150
Psme/Bere	13	2140	45	264	6/07	5/15	8/12	66	58	195263
	14	1854	71	38	6/02	5/05	8/20	79	107	116019
	15	2491	23	344	6/22	6/01	8/25	64	85	166303
	29	2341	38	305	6/18	5/15	8/24	67	101	164822
Psme/Cele	9	2293	44	173	6/05	4/10	8/30	86	142	239061
	23	2375	34	282	6/18	4/15	8/24	67	131	184781
	24	2247	29	230	6/10	4/10	8/12	63	123	219679
	25	2439	27	260	6/15	4/15	8/12	58	119	202822
	26	2195	51	220	6/05	4/10	8/18	74	130	230326

Table 14. Maximum and minimum air temperatures (°C) by month, 1978.

Habitat type	Plot number	Winter[1] minimum	June maximum	June minimum	July maximum	July minimum	August maximum	August minimum	Sept. maximum	Sept. minimum
Abla/Pera	1	ND[2]	ND	ND	24.5	6.5	24.5	2.0	23.0	-6.0
	2	-18.5	25.5	ND	36.5	5.0	26.5	0.5	27.0	-6.0
	3	-20.5	22.5	ND	38.0	4.0	25.0	0.0	22.5	-7.0
	16	ND	ND	ND	28.0	3.0	24.0	0.0	21.5	-6.5
Abla/Osch	5	-15.0	24.5	ND	28.5	5.5	28.0	2.0	26.0	-3.5
	6	-15.0	23.0	ND	28.0	3.5	28.0	1.0	25.5	-5.5
	7	-16.5	23.5	-1.5	29.0	6.0	28.0	2.0	26.0	-5.0
	18	ND	ND	ND	29.5	5.5	31.0	1.0	27.5	-3.5
Abla/Bere	10	-15.0	23.0	3.0	28.5	3.5	28.0	1.5	28.0	-5.5
	11	-22.5	25.5	-3.5	31.0	2.5	27.5	-2.0	25.5	-10.0
	12	-23.5	26.0	0.5	29.5	2.0	28.5	0.0	25.5	-8.5
	27	ND	ND	ND	31.0	2.5	28.5	0.0	26.0	-6.0
	28	ND	ND	ND	30.0	5.0	29.0	-0.5	25.5	-6.0
Psme/Phma	8	- 3.5	27.0	-1.0	31.0	6.5	31.0	3.5	ND	ND
	19	ND	ND	ND	32.0	6.0	28.5	2.5	ND	ND
	20	ND	ND	ND	31.5	8.5	31.5	3.0	11.5	ND
	21	ND	ND	ND	31.5	2.0	32.0	-1.0	29.0	-5.0
	22	ND	ND	ND	32.5	5.5	28.5	3.5	29.0	-1.0
Psme/Bere	13	-18.5	24.5	-4.0	29.5	3.0	33.0	-1.0	27.0	-9.0
	14	-25.0	22.0	-6.5	30.5	0.5	30.0	1.0	ND	ND
	15	-16.5	23.0	ND	27.5	5.0	27.5	1.0	25.5	-6.0
	29	ND	ND	ND	28.5	4.5	27.0	1.5	25.5	-5.5

Table 14. Continued.

Habitat type	Plot number	Winter[1] minimum	June maximum	June minimum	July maximum	July minimum	August maximum	August minimum	Sept. maximum	Sept. minimum
Psme/Cele	9	-17.0	25.0	ND	32.0	6.0	31.0	1.5	25.0	-2.0
	23	ND	ND	ND	35.5	5.0	34.5	0.5	26.5	-7.0
	24	ND	ND	ND	28.5	5.0	29.0	0.0	16.0	-2.5
	25	ND	ND	ND	27.0	5.5	25.5	0.0	22.0	-6.0
	26	ND	ND	ND	31.5	5.5	29.0	-1.0	ND	ND

---

[1] Winter minimum from 1 October 1977 to 1 June 1978.

[2] ND = No data; stand not observed.

Table 15. Soil temperature (°C) at 20 cm by date of observation, 1978.

Habitat type	Plot #	Date											
		30 May	20 June	27 June	5 July	11 July	20 July	25 July	2 Aug.	9 Aug.	17 Aug.	22 Aug.	1 Oct.
Abla/Pera	1	ND[1]	ND	4.0	5.4	7.5	9.1	7.8	7.8	8.6	6.2	6.8	5.1
	2	ND	ND	4.8	ND	11.9	11.3	ND	8.3	ND	7.5	7.1	6.1
	3	ND	3.0	7.1	7.9	10.1	8.9	ND	9.7	9.1	6.8	7.8	5.5
	16	ND	ND	5.9	ND	8.0	8.0	6.6	6.9	ND	6.3	6.5	4.1
Abla/Osch	5	ND	9.3	10.4	8.0	11.3	11.4	10.7	10.8	ND	9.3	9.1	7.2
	6	ND	6.2	8.3	7.8	8.6	10.5	8.5	8.6	ND	8.4	7.5	6.3
	7	4.0	ND	7.2	ND	9.2	9.6	ND	9.4	9.6	8.3	8.2	6.7
	18	ND	ND	ND	ND	11.1	10.6	ND	10.5	11.2	9.1	8.5	6.1
Abla/Bere	10	ND	4.9	6.5	7.4	8.7	8.7	7.7	8.3	ND	7.6	6.8	6.0
	11	1.7	6.6	8.5	ND	10.1	9.5	8.5	8.5	9.2	7.4	7.7	3.6
	12	ND	5.2	8.5	8.9	11.9	8.3	ND	9.4	9.1	7.1	7.9	5.2
	27	ND	ND	ND	ND	9.2	10.0	9.3	8.9	ND	7.8	8.3	5.4
	28	ND	ND	ND	ND	10.0	11.9	7.7	8.3	8.5	7.7	8.2	4.8
Psme/Phma	8	7.2	10.3	12.3	ND	11.7	11.9	ND	12.6	ND	11.2	11.3	6.5
	19	ND	ND	12.7	ND	13.1	13.0	ND	13.1	ND	11.4	11.4	6.5
	20	ND	ND	12.5	ND	11.9	12.6	ND	14.0	ND	12.4	12.3	6.4
	21	ND	ND	12.8	ND	12.7	13.6	ND	13.0	13.2	10.9	10.7	5.4
	22	ND	ND	11.4	ND	11.3	12.4	ND	12.1	ND	11.0	11.2	6.6
Psme/Bere	13	3.0	7.7	9.3	ND	10.2	9.3	ND	9.9	10.5	8.0	8.2	5.3
	14	6.0	9.5	ND	ND	12.5	12.7	ND	14.3	ND	11.3	9.7	ND
	15	ND	6.1	8.2	8.5	11.5	10.8	9.6	9.7	ND	8.7	8.4	7.1
	29	8.0	ND	ND	ND	9.6	8.0	ND	9.4	9.6	8.4	8.5	6.3
Psme/Cele	9	ND	10.3	13.5	10.7	14.6	14.7	ND	15.0	ND	11.3	13.2	11.6
	23	ND	ND	12.5	ND	13.6	13.6	ND	14.8	15.5	11.3	12.6	6.5
	24	ND	ND	9.2	ND	10.8	11.4	12.0	12.0	12.6	9.9	10.8	6.6
	25	ND	ND	ND	10.3	11.7	15.4	12.5	11.7	ND	10.6	9.7	6.8
	26	ND	ND	ND	ND	11.0	12.0	ND	13.5	13.4	11.9	12.5	ND

[1] ND = No data observation.

Table 16. Soil temperature (°C) at 50 cm by date of observation, 1978.

Habitat type	Plot #	Dates					
		25 July	2 Aug.	9 Aug.	17 Aug.	22 Aug.	1 Oct.
Abla/Pera	1	5.5	6.4	7.7	6.1	6.2	5.1
	2	ND[1]	7.7	ND	7.3	6.7	5.6
	3	ND	8.2	8.6	7.0	6.9	ND
	16	5.6	6.0	ND	6.2	5.8	3.8
Abla/Osch	5	9.0	9.4	ND	8.4	8.3	7.1
	6	6.8	7.2	ND	8.3	6.8	6.2
	7	ND	8.6	8.5	8.1	7.6	6.4
	18	ND	9.3	9.4	8.6	8.0	6.6
Abla/Bere	10	6.1	6.6	ND	7.3	6.0	5.7
	11	7.2	7.7	7.8	7.5	7.0	4.4
	12	ND	6.8	7.4	6.9	6.8	ND
	27	7.0	7.6	ND	7.4	6.8	5.3
	28	6.8	7.4	7.6	7.6	7.4	5.3
Psme/Phma	8	ND	11.5	ND	11.1	10.7	7.4
	19	ND	11.9	11.4	11.0	10.0	7.6
	20	ND	13.3	ND	12.4	11.9	7.2
	21	ND	11.8	11.7	9.9	9.6	6.5
	22	ND	10.2	ND	11.3	9.6	7.3
Psme/Bere	13	ND	9.5	9.4	7.9	6.6	5.7
	14	ND	12.6	ND	11.0	9.4	ND
	15	8.0	8.5	ND	8.5	7.9	6.9
	29	ND	7.9	8.4	8.3	7.8	6.0
Psme/Cele	9	ND	14.0	ND	11.0	12.5	11.3
	23	ND	13.5	15.0	11.7	11.5	7.0
	24	10.7	11.4	11.6	10.8	9.7	7.5
	25	11.8	11.1	ND	10.8	9.4	8.5
	26	ND	13.4	13.4	11.9	12.2	ND

---

[1] ND = No data observation.

Table 17. Soil moisture (percent of dry weight) at 20 cm by date of observation, 1978.

Habitat type	Plot #	Date							
		11 July	19 July	26 July	2 Aug.	9 Aug.	16 Aug.	22 Aug.	1 Oct.
Abla/Pera	1	24.0	16.7	13.6	13.9	ND	30.3	12.7	13.6
	2	18.4	13.9	ND	14.5	ND	14.6	15.4	21.6
	3	20.1	13.6	ND	15.6	ND	20.1	15.2	14.2
	16	36.5	31.6	30.2	27.1	ND	32.8	16.2	24.3
Abla/Osch	5	14.9	14.1	ND	12.3	ND	ND	30.3	24.9
	6	21.1	17.0	13.8	13.1	ND	ND	15.1	16.6
	7	17.0	14.6	ND	8.6	ND	15.7	17.6	21.8
	18	17.5	14.9	ND	ND	13.4	15.7	16.7	11.0
Abla/Bere	10	18.2	17.8	ND	ND	ND	ND	16.9	19.8
	11	ND	17.8	17.6	20.6	ND	19.7	22.4	32.7
	12	16.1	16.3	ND	15.1	ND	32.7	14.0	12.6
	27	17.3	ND	15.2	17.1	ND	14.7	18.0	28.8
	28	17.3	ND	17.5	18.5	ND	13.6	19.1	24.1
Psme/Phma	8	17.2	ND	ND	ND	ND	20.7	17.8	19.2
	19	15.8	ND	ND	14.5	ND	16.8	16.3	ND
	20	ND	ND	ND	27.1	ND	36.3	22.9	ND
	21	11.9	11.0	ND	ND	12.0	14.5	15.6	10.9
	22	17.2	16.3	ND	15.5	ND	37.1	20.7	26.1
Psme/Bere	13	16.0	14.0	ND	14.8	ND	14.4	14.9	14.0
	14	18.2	ND	ND	14.1	ND	30.4	27.0	ND
	15	ND	14.9	18.6	14.9	ND	ND	21.2	47.4
	29	17.0	17.0	ND	16.2	ND	17.5	17.0	20.9

Table 17. Continued.

Habitat type	Plot #	Date							
		11 July	19 July	26 July	2 Aug.	9 Aug.	16 Aug.	22 Aug.	1 Oct.
Psme/Cele	9	10.2	13.6	ND	15.0	ND	ND	20.9	ND
	23	15.7	14.4	ND	14.6	ND	36.4	29.3	27.7
	24	12.4	ND	6.8	ND	7.1	13.4	10.3	18.6
	25	20.0	19.7	ND	12.4	ND	ND	15.4	40.6
	26	17.0	15.1	ND	10.8	ND	12.8	15.6	14.8

[1] ND = No data observation.

Table 18. Soils and bedrock data.

Habitat type	Plot #	Horizon number	Horizon boundaries (cm) Upper	Horizon boundaries (cm) Lower	Texture[1] code	Percent[2] gravel	Percent cobble	Percent stone	pH	Effervescence code[3]	Approximate percent clay	Soil color[4]	Soil great group[5]	Bedrock Type
Abla/Pera	1	1	0	11	1	15	0	0	ND[6]	1	14	10 YR3/3	Cryoboralf	Conglomerate, quartzite, and sandstone
		2	11	85	1	30	5	0	ND	1	13	10 YR4/3		
		3	85	100	6	40	5	0	ND	1	5	7.5 YR5/4		
	2	1	0	25	1	25	10	0	5.6	1	22	10 YR3/4	Cryoboralf	Conglomerate, quartzite, and sandstone
		2	25	59	2	30	20	0	5.8	1	15	7.5 YR4/6		
		3	59	100	1	30	20	10	5.8	1	21	10 YR5/6		
	3	1	0	32	1	35	0	0	5.8	1	22	7.5 YR3/4	Cryoboralf	Sandstone and quartzite
		2	32	61	1	40	10	0	5.6	1	25	7.5 YR4/6		
		3	61	100	4	50	10	0	5.8	1	40	2.5 YR4/6		
	16	1	0	30	1	0	0	0	6.0	1	18	10 YR3/3	Cryoboralf	Quartzite
		2	30	78	2	5	10	65	5.8	1	15	7.5 YR5/4		
		3	78	100	0	5	10	65	5.6	1	ND	ND		
Abla/Osch	5	1	0	34	1	5	0	0	6.4	1	20	10 YR2/1	Paleboroll	Limestone
		2	34	71	4	25	0	0	6.4	1	38	10 YR3/2		
		3	71	100	4	40	0	0	6.4	1	35	5 YR3/4		
	6	1	0	27	1	15	0	0	6.2	1	22	7.5 YR3/3	Cryoboroll	Sandstone and quartzite
		2	27	48	1	40	0	0	6.2	1	27	7.5 YR4/4		
		3	48	100	5	60	10	0	6.4	1	50	5 YR4/6		
	7	1	0	21	1	10	0	0	6.4	1	20	10 YR2/1	Argixeroll	Limestone, quartzite, and sandstone
		2	21	45	1	45	0	0	6.4	1	22	10 YR4/4		
		3	45	100	4	45	10	0	6.2	1	40	7.5 YR4/4		
	18	1	0	31	1	0	0	0	6.4	1	20	7.5 YR3/2	Haploxeroll	Sandstone
		2	31	62	1	25	0	0	6.2	1	22	10 YR3/4		
		3	62	100	1	30	0	0	6.0	1	22	10 YR4/4		
Abla/Bere	10	1	0	22	1	0	0	0	6.4	1	20	7.5 YR3/2	Cryoboroll	Limestone
		2	22	41	4	0	0	0	6.2	1	27	10 YR3/4		
		3	41	100	4	30	0	0	6.6	1	35	10 YR3/4		
	11	1	0	24	1	10	20	10	6.6	1	17	7.5 YR6/2	Cryoboroll	Limestone
		2	24	54	1	30	25	20	6.6	1	20	10 YR3/4		
		3	54	100	1	70	0	10	6.6	1	15	10 YR4/3		
	12	1	0	35	1	0	0	0	6.2	1	22	10 YR3/4	Cryoboroll	Shale and quartzite
		2	35	63	4	0	0	0	6.2	1	30	7.5 YR4/6		
		3	63	100	5	10	0	0	6.0	1	45	5 YR4/6		
	27	1	0	24	4	0	0	0	6.6	1	40	10 YR3/3	Cryoboroll	Limestone
		2	24	53	4	0	0	0	6.6	1	40	10 YR4/3		
		3	53	100	4	0	20	40	6.6	1	40	10 YR4/3		
	28	1	0	32	1	0	0	0	6.2	1	27	10 YR4/3	Cryoboralf	Limestone
		2	32	61	4	0	0	0	6.4	1	45	10 YR4/4		
		3	61	100	5	10	0	0	6.2	1	50	10 YR5/4		

Table 18. Continued.

Habitat type	Plot #	Horizon number	Horizon boundaries (cm)		Texture[1] code	Percent[2] gravel	Percent cobble	Percent stone	pH	Effervescence code[3]	Approximate percent clay	Soil color[4]	Soil great group[5]	Bedrock type
			Upper	Lower										
Psme/Phma	8	1	0	28	2	30	35	0	6.8	2	25	10 YR4/3	Haploxeroll	Limestone
		2	28	100	1	30	30	20	7.0	4	25	10 YR6/3		
	19	1	0	25	1	30	25	0	6.6	1	17	10 YR3/2	Haploxeroll	Limestone
		2	25	60	1	35	30	0	6.8	2	20	10 YR4/3		
		3	60	100	1	50	15	10	7.0	4	24	10 YR4/3		
	20	1	0	30	1	30	20	0	6.6	1	20	10 YR3/2	Haploxeroll	Limestone
		2	30	65	1	40	30	5	6.8	2	22	10 YR5/3		
		3	65	100	1	45	20	10	7.2	4	25	10 YR5/3		
	21	1	0	28	3	0	20	0	6.4	1	27	10 YR3/2	Haploxeroll	Limestone
		2	28	62	3	20	0	0	6.6	1	27	10 YR3/3		
		3	62	100	3	0	55	0	6.6	1	29	10 YR3/3		
	22	1	0	30	1	40	0	10	6.8	1	15	10 YR3/2	Haploxeroll	Limestone
		2	30	75	1	55	25	0	6.8	2	15	10 YR4/3		
		3	75	100	1	60	20	0	7.0	2	17	10 YR4/3		
Psme/Bere	13	1	0	26	1	25	0	0	6.6	2	20	7.5 YR3/2	Haploxeroll	Limestone
		2	26	54	1	50	0	10	6.8	2	22	10 YR3/4		
		3	54	92	0	60	10	0	6.8	2	ND	ND		
	14	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	Limestone
	15	1	0	28	1	30	20	30	6.6	1	17	10 YR2/1	Argixeroll	Limestone
		2	28	100	1	30	20	30	7.0	2	35	10 YR3/3		
	29	1	0	28	4	15	25	20	6.6	4	35	10 YR3/3	Cryoboroll	Limestone
		2	28	64	4	25	20	30	6.2	4	40	10 YR4/3		
		3	64	100	4	35	20	30	6.8	4	40	10 YR4/4		
Psme/Cele	9	1	0	25	1	40	10	0	6.4	1	18	10 YR3/3	Cryoboroll	Limestone
		2	25	85	1	60	10	10	6.8	2	21	10 YR4/5		
	23	1	0	28	3	35	0	5	6.6	1	25	10 YR3/3	Cryoboroll	Limestone
		2	28	57	1	55	0	0	6.8	1	23	10 YR3/3		
		3	57	100	0	75	10	0	7.6	3	ND	ND		
	24	1	0	20	1	20	0	10	6.4	1	17	10 YR3/4	Cryoboroll	Limestone
		2	20	50	1	10	0	60	6.4	1	20	10 YR3/6		
	25	1	0	31	1	25	10	15	6.4	1	18	10 YR3/3	Cryoboroll	Limestone
		2	31	85	1	45	10	20	6.8	2	21	10 YR4/5		
	26	1	0	29	1	50	10	10	6.6	2	18	10 YR3/4	Cryoboroll	Limestone
		2	29	83	1	50	10	20	6.8	2	23	10 YR4/4		

---

[1] Soil texture class: 0=no texture determined, 1=loam, 2=silt loam, 3=silty clay loam, 4=clay loam, 5=clay, 6=sandy loam.

[2] Percent rock is ocularly estimated volume of coarse rock fragments in the soil in these size classes: gravel (.2-7.5 cm), cobble (7.5-25 cm), and stone (greater than 25 cm).

[3] Effervescence code: 1=none, 2=slight, 3=strong, 4=very strong.

[4] Soil color is in Munsell Color Chart standard notation.

[5] Soil Survey Staff 1975.

[6] No data observation.

Table 19. Estimate of available soil water capacity based on texture class, estimated volume occupied by rock fragments, and depth of horizons. Value is calculated for each horizon, summed to 100 cm or bedrock if soil was shallower than 100 cm using formulas from Erickson and Searle (1974).

Habitat type	Plot #	Soil depth	Available water storage in soil profile (cm of water)	Available water storage expressed as a percentage of soil depth (cm of water/ cm of soil)
Abla/Pera	1	100	11	.11
	2	100	8	.08
	3	100	10	.10
	16	100	9	.09
Abla/Osch	5	100	14	.14
	6	70	8	.11
	7	70	8	.11
	18	89	12	.13
Abla/Bere	10	79	6	.07
	11	100	8	.08
	12	100	8	.08
	27	84	13	.15
	28	100	8	.08
Psme/Phma	8	85	7	.08
	19	100	9	.09
	20	50	5	.10
	21	75	6	.08
	22	83	6	.07
Psme/Bere	13	85	13	.15
	14	100	8	.08
	15	100	17	.17
	29	100	14	.14
Psme/Cele	9	74	13	.18
	23	92	9	.10
	24	ND[1]	ND	ND
	25	60	5	.08
	26	100	8	.08

---

[1] ND = no data observation.

Appendix B

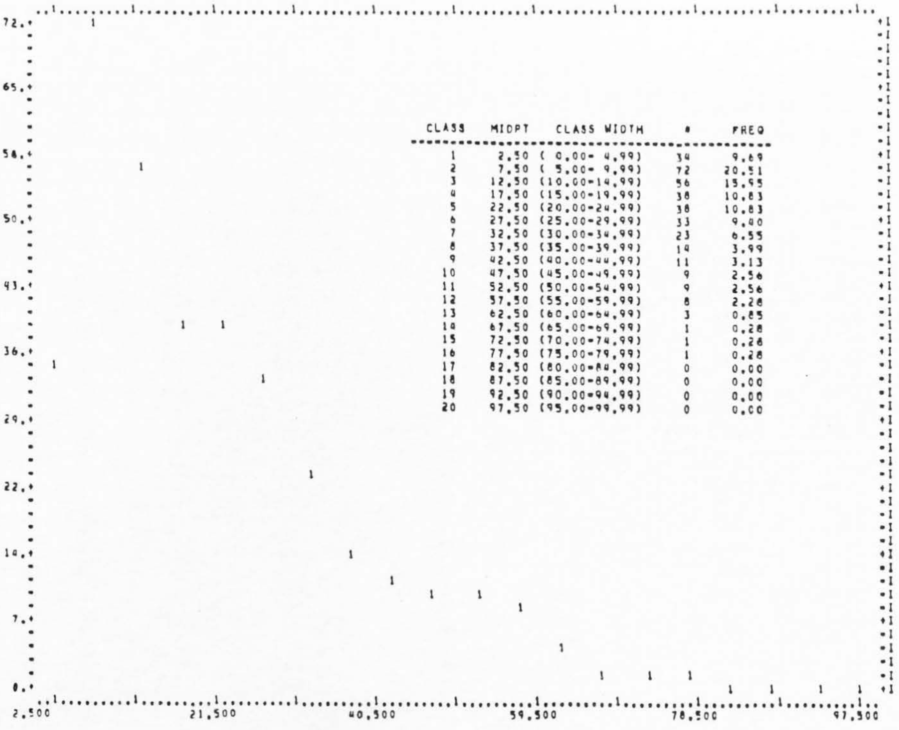
Calculated ordination axis coordinates and significance of similarity values

Table 20. Calculated stand coordinates on axes of Ordination I and II by habitat type.

Habitat type	Plot #	Ordination I		Ordination II	
		Axis 1	Axis 2	Axis 1	Axis 2
Abla/Pera	1	76.19	34.43	39.26	75.64
	2	72.70	14.25	36.20	62.78
	3	69.57	36.92	40.78	69.51
	16	76.19	29.43	42.85	72.39
Abla/Osch	5	44.55	16.75	35.05	44.21
	6	55.58	20.25	33.89	44.21
	7	46.15	0.00	0.00	41.37
	18	40.88	7.49	15.98	36.08
Abla/Bere	10	59.53	29.89	41.92	47.42
	11	42.43	29.02	43.14	39.30
	12	65.33	26.90	37.03	58.60
	27	54.91	38.11	34.27	46.47
	28	48.98	20.40	30.18	42.95
Psme/Phma	8	32.98	63.59	77.41	37.25
	19	35.67	60.13	54.76	32.96
	20	41.67	70.17	74.69	37.25
	21	31.77	62.02	61.75	31.29
	22	38.71	59.55	72.06	38.74
Psme/Bere	13	26.48	46.54	66.24	30.42
	14	28.45	40.80	58.63	29.86
	15	27.84	60.04	69.42	35.03
	29	24.70	60.59	64.29	28.54
Psme/Cele	9	4.93	53.73	55.91	11.71
	23	10.43	50.97	55.72	13.79
	24	0.00	39.29	43.29	0.00
	25	6.51	42.71	51.77	8.98
	26	2.58	45.49	47.61	6.01

Table 21. Predicted stand coordinates for axes of Ordination I by habitat type. Regression models A, B, and C are for axis 1 (27 stands), axis 2 (26 stands), and axis 2 (21 stands) respectively.

Habitat type	Plot #	Model A Axis 1	Model B Axis 2	Model C Axis 2
Abla/Pera	1	65.16	32.12	33.87
	2	52.00	31.33	35.00
	3	54.68	37.23	42.19
	16	63.93	9.38	28.55
Abla/Osch	5	48.72	33.02	22.80
	6	51.40	22.99	16.08
	7	59.75	21.91	4.75
	18	44.73	24.92	-
Abla/Bere	10	58.25	24.23	-
	11	22.81	35.80	48.87
	12	58.59	32.14	31.25
	27	54.99	25.81	26.26
	28	53.83	22.78	25.77
Psme/Phma	8	39.57	63.55	-
	19	38.76	62.28	51.68
	20	22.56	58.94	67.55
	21	32.81	46.62	-
	22	33.47	56.52	49.10
Psme/Bere	13	43.60	27.20	29.85
	14	14.33	-	-
	15	40.29	57.46	65.01
	29	45.29	54.80	58.56
Psme/Cele	9	13.83	52.04	45.58
	23	-0.46	49.00	42.05
	24	11.41	30.21	-
	25	9.74	45.62	38.73
	26	1.66	60.75	52.87



```
CLASS   MIDPT   CLASS WIDTH        #       FREQ
-----------------------------------------------
  1      2,50 ( 0,00- 4,99)       34       9,69
  2      7,50 ( 5,00- 9,99)       72      20,51
  3     12,50 (10,00-14,99)       56      15,95
  4     17,50 (15,00-19,99)       38      10,83
  5     22,50 (20,00-24,99)       38      10,83
  6     27,50 (25,00-29,99)       33       9,40
  7     32,50 (30,00-34,99)       23       6,55
  8     37,50 (35,00-39,99)       14       3,99
  9     42,50 (40,00-44,99)       11       3,13
 10     47,50 (45,00-49,99)        9       2,56
 11     52,50 (50,00-54,99)        9       2,56
 12     57,50 (55,00-59,99)        8       2,28
 13     62,50 (60,00-64,99)        3       0,85
 14     67,50 (65,00-69,99)        1       0,28
 15     72,50 (70,00-74,99)        1       0,28
 16     77,50 (75,00-79,99)        1       0,28
 17     82,50 (80,00-84,99)        0       0,00
 18     87,50 (85,00-89,99)        0       0,00
 19     92,50 (90,00-94,99)        0       0,00
 20     97,50 (95,00-99,99)        0       0,00
```

Figure 12. Frequency of similarity values by classes from matrix of pair-wise comparisons between stands calculated for Ordination I. Range of values is from 0.00 to 76.19. Upper ten percent are considered significant (above 47.50).

Table 22. Association table showing relative percent canopy cover of overstory and undergrowth vascular plant species occurring on all plots.

STAND NUMBERS.....

SPECIES[1]...	CONS[2]	1	2	3	16	5	6	7	18	8	19	20	21	22	9	23	24	25	26	10	11	12	27	28	13	14	15	29
101 ABILA1	C= 48	14	05	19	05	19	07	09	18	.	.	.	.	.	.	.	.	.	.	23	19	21	27	09	.	.	.	.
102 ABILA2	C= 52	04	06	01	14	19	47	15	26	.	.	.	.	.	.	.	.	.	.	41	37	21	36	16	.4	.	.	.
103 ABILA3	C= 44	05	08	.	07	26	18	64	23	.	.	.	.	.	.	.	.	.	.	36	09	05	27	44	.	.	.	.
104 ACEGRA	C= 19	.	.	.	.	.	.	.	.3	.	09	04	17	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.
105 JUNSC1	C= 15	.	.	.	.	.	.	.	.	.	09	05	08	05	.	.	.	.	.	.	.	.	.	.	.	.	.	.
106 JUNSC2	C= 22	.	.	.	.	.	.	.	.	.	03	.	03	05	11	.	.	.	01	.	.	.	.	.	.4	.	.	.
107 PICEN1	C= 19	04	09	.4	05	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.3	.	.	.	.	.	.
108 PICEN2	C= 19	08	26	01	41	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.3	.	.	.	.	.	.
109 PICEN3	C= 19	59	45	04	27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	26	.	.	.	.	.	.
110 PINCO1	C= 4	.	.	.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
111 PINCO2	C= 11	.	.	.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	09	.	04	.	.	.	.
112 PINCO3	C= 11	.	.	74	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17	.	16	.	.	.	.
113 PINFL1	C= 11	.	.	.	.	.	.	.	.	.	.	.	.	.	04	.	.	.	.	.	.	.	.	.	.4	.4	.	.
114 PINFL2	C= 7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15	.	50	.	.	.	.	.	.	.	.	.
115 PINFL3	C= 19	.	.	.	.	.	.	.	.	.	.	.	.	.	11	.	02	.	.	.	.	.	.	.	13	09	01	.
116 POPTR1	C= 26	.	.	.	.	03	06	.3	07	.	.	.	.	.	.	.	.	.	.	.	.4	.3	.	.	.4	.	.	.
117 POPTR2	C= 15	.	.	.	.	04	07	02	09	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
118 POPTR3	C= 7	.	.	.	.	.	.3	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
119 PSEME1	C= 44	.	.	.	.	.3	.	.	.	.	14	13	13	02	04	25	08	.	.	.	.	.	.	.	20	01	.3	23
120 PSEME2	C= 78	.	.	.	.	08	08	.	14	78	57	68	33	41	11	25	15	38	25	.3	30	.	04	03	26	57	36	46
121 PSEME3	C= 63	.	.	.	.	19	06	.	.	22	09	.	25	35	58	50	.	62	25	.	04	.	05	07	39	32	60	31
201 ACEGLA	C= 7	.	.	.	.	.	.	.	.	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	01	.	.
202 ACTRUB	C= 7	.	.	.	.	.	.4	06	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
203 AMEALN	C= 52	.	.	01	.	.	.	.	08	03	03	.3	05	.9	.	01	09	.	.	.	02	.	.	.	01	04	01	.8
204 ARTARB	C= 7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	02	.	04	.	.	.	.	.	.	.	.	.
205 ARTTRI	C= 22	.	.	.	.	.	.	.	.	.	.	.	.	.	.2	03	.7	08	07	.	.	.	.	.	.3	.	.	.
206 BERREP	C= 59	.	.	.	.	.7	.	.	01	.2	10	.	.	.	37	03	02	04	07	.	28	.	14	19	02	09	22	13
207 CERLED	C= 19	.	.	.	.	.	.	.	.	.	.	.	.	.	29	29	45	37	34	.	.	.	.	.	.	.	.	.
208 CHRVIS	C= 19	.	.	.	.	.	.	.	.	.	.	.	.	.	.2	01	05	09	02	.	.	.	.	.	.	.	.	.
209 CORSTO	C= 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	09	.	.
210 LONUTA	C= 22	03	01	01	01	.	.	.	.	.	.	.	.	.	.	.	.	.	.	05	.	15	.	.	.	.	.	.
211 PACMYM	C= 70	.9	03	01	01	.	.	.	01	02	01	.8	.	.	.2	.	.	.	.7	09	07	05	04	26	74	09	16	66
212 PHYMAL	C= 19	.	.	.	.	.	.	.	.	04	19	81	31	63	.	.	.	.	.	.	.	.	.	.	.	.	.	.
213 PRUVIR	C= 37	.	.	.	.	.	.	.	.	02	32	02	23	03	.	.	.	.	07	.	.	.	.	.	04	04	01	.8
214 RIBCER	C= 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.5	.	.	.	.	.	.	.	.	.	.
215 RIBMON	C= 4	.	03	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
216 RIBVIS	C= 11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	05	.	05	.	.	.	.	.	.8
217 ROSSPP	C= 52	.	.	.	.	.	.	.	01	03	10	04	08	.9	.	.	.	.	.	01	02	05	04	01	.3	13	.	03
218 SAMRAC	C= 7	.	.	.	.	02	.	.	.	.	.	.	.	.	.	.	.	.5	.	.	.	.	.	.	.	.	.	.
219 SHECAN	C= 4	.	.	01	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
220 SYMORE	C= 74	.	01	01	.	04	06	.	04	02	.	.	.	.	06	29	05	06	09	09	15	05	27	09	06	01	31	.8
301 AGRSPI	C= 19	.	.	.	.	.	.	.	.	.	.	.	.	.	05	03	05	04	11	.	.	.	.	.	.	.	.	.
302 AGRTRA	C= 33	.	.	.	.	.7	.	.	.	.	13	.	05	.	04	12	02	06	.	.	.	.	.	.	01	.	06	.
303 BROMAR	C= 37	.9	.	.	.	.	04	16	14	.	.	.	.	.3	.	05	.	12	.	.	.	05	.	.	.3	01	.	.
304 BROTEC	C= 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	04	.	.	.	.	.	.	.	.	.	.
305 CARGEY	C= 7	.	.	.	.	.	.	.	.	.6	.	02	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
306 CARROS	C= 48	06	07	01	10	.7	03	.	.	.	01	.3	.	.	.	.	.	.	.	05	.	05	04	01	02	.	.	.
307 ELYCIN	C= 4	.	.	.	.	.	.	.	.	.	.	.	.5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
308 LEUKIN	C= 26	.	.	.	.	.	.	.	.	.	.	.	.	.	07	06	04	06	05	.	.	.	.	.	.	.	03	.8
309 ORYZOP	C= 4	.	.	.	.	.	.	.	.	.	.	.	.	.	02	.	.	.	.	.	.	.	.	.	.	.	.	.
310 POACUR	C= 22	.	.	.	.	.	01	.	.	.	.	.	03	.	.	.	.	.	.	01	.	.	.	01	.3	04	.	.
311 POANER	C= 56	.9	.	01	01	.	.4	.	.	.6	03	02	.	.3	.	01	.	.	.	01	02	.	04	.	.3	.	03	.6
312 ELYGLA	C= 7	.	.	.	.	.	.	.	01	.	01	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
401 ACHMIL	C= 30	.9	01	.	01	.	.4	.	.	.	01	.	.5	.	.	.	.	.5	.	01	.	.	.	.	.	.	.	.
402 AGAURT	C= 15	.	.	.	.	04	.	.	01	.	.	.	.5	.	.	.	.	.	.	01	.	.	.	.	.	.	.	.
403 ARCMIN	C= 11	.	.	.	.	.	.	.	.	02	.	.3	.	.3	.	.	.	.	.	.	.	.	.	.	.	.	.	.
404 ARNCOR	C= 59	13	.	45	18	.	01	.	.	.8	.	03	05	03	.	.	.	.	.	05	07	05	27	23	.	01	01	05
405 ARNLAT	C= 7	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	02	.	.	.	.	.	.	.
406 AQUCOE	C= 26	.	03	01	01	.7	.4	.	.	.	.	.	.	.	.	.	.	.	.	01	02	.	.	.	.	.	.	.
407 ASTENG	C= 30	16	01	01	10	.	01	.	.	.	.	.3	05	.	.	.	.	.	.	.	.	.	.	.	.	.	01	.
408 BALSAG	C= 30	.	.	.	.	.	.	.	.	.	.	.	.	.	03	05	05	02	09	.	.	.	.	.	.3	.	01	.8
409 CASCHR	C= 7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.3	.	01	.
410 CASLIN	C= 7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	02	.	.	.	.	05	.	.	.	.	.	.
411 CHEALB	C= 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.2	.	.	.	.	.	.	.	.	.	.	.	.	.
412 CIRCAN	C= 11	.	.	.	.	.	.	.	.	.	.	.	.	.	02	.	.7	.	.	.	.	.	.	.	.3	.	.	.
413 CLEPSE	C= 22	.	.	.	.	.	.	.	.	.	03	.	06	.9	.	.	.	.	.	.	15	.	.	01	.	34	.	.
414 CREACU	C= 15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.4	02	02	02	.	.	.	.	.	.	.	.	.
415 DESCAL	C= 15	.	.	.	.	02	.4	.	01	.	.	.	.	.	.	.	.	.	.	01	.	.	.	.	.	.	.	.
416 DISTRA	C= 33	.	.	.	.	.	.	06	01	02	01	.3	.5	.9	.	.	.	.	.	.	02	.	.	.	.	01	.	.
417 EPIANG	C= 4	.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
418 ERIPER	C= 7	.9	.	.	.	.	.	.	.	.	.	.	.	.	.2	.	.	.	.	.	.	.	.	.	.	.	.	.
419 ERISPE	C= 19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	05	.	02	.	.	.	.	.	01	.	01	05
420 ERIHER	C= 11	.	.	.	.	.	.	.	.	.	.	.	.	.	.8	01	.7	.	.	.	.	.	.	.	.	.	.	.
421 ERYCAP	C= 7	.	.	.	.	.	.	.	.	.	.	.	.	.	.2	.5	.	.	.	.	.	.	.	.	.	.	.	.
422 ERYGRA	C= 4	.	.	.	04	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
423 FRAVES	C= 30	.	03	.	.	.	.	05	04	.	01	.3	02	.	.	.	.	.	.	.	02	.	.	.	.	01	.	.
424 GALAPA	C= 7	.	.	.	.	.	.	.	.	.2	.	.3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
425 GALBOR	C= 26	.	01	.	.	.	.	05	01	.2	.	.	.	03	.	.	.	.	.	.	02	.	.	.	.	04	.	.
426 GERFRE	C= 26	.9	.	01	.	.	.4	05	01	.	.	.	.	.	.	.	.	.	.	01	.	.	.	01	.	.	.	.
427 GERRIC	C= 7	.	01	.	04	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
428 GILAGG	C= 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.2	.	.	.	.	.	.	.	.	.	.	.	.	.
429 HACFLU	C= 19	.	01	.	.	.	.	06	04	.	.	.3	.	.	.	.	.	.	.	.	.	.	.	.	.3	.	.	.
430 HIEALB	C= 15	06	01	05	04	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
431 LATLAN	C= 4	.	.	.	.	.	.	.	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
432 LATLEU	C= 11	.	.	.	.	67	69	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
433 LIGFIL	C= 11	06	.	05	04	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
434 LUPSPP	C= 15	.9	01	.	01	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	05	.	.	.	.
435 MITSTA	C= 41	.	01	.	.	02	.	06	06	.2	01	.3	02	.3	.	.	.	.	.	.	.	.	.	.	.3	01	.	.
436 MONPER	C= 11	.	.	.	.	.	.	.	.	02	.	.8	.	.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.
437 OSMCHI	C= 59	09	07	05	04	13	08	.	18	.8	.	.6	.	02	.	.	.	.	.	01	02	05	04	.	.	01	01	.
438 OSMOCC	C= 7	.	.	.	.	.	.	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.3	.	.	.
439 PEDRAC	C= 19	16	44	28	27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15	.	.	.	.	.	.
440 PENWHI	C= 4	.	01	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
441 POLFOL	C= 7	.	.	.	.	.	.4	.	01	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
442 POTGLA	C= 19	.9	01	.	.	.7	01	.	.	.	.	.	.	.	.	.	.	.	.	01	.	.	.	.	.	.	.	.
443 PYRSEC	C= 22	.9	03	01	04	.	.	.	.	.	.	.	.	.	.	.	.	.	.	09	.	.	04	.	.	.	.	.
444 RUDOCC	C= 11	.	01	.	.	.	.4	.	08	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
445 SEDDEB	C= 11	.	.	.	.	.	.	.	.	.	.	.	.5	.	.	.	.	.	.	.	02	.	.	.	.	01	.	.
446 SILMEN	C= 30	.	01	.	.	.	.	.	.	.8	.	.3	.	.	.	.	.	.	.	26	02	05	04	.	.3	.	.	.
447 SMIRAC	C= 26	.	.	.	.	.	.	06	01	.	.	.3	.5	.9	.	.	.	.	.	.	02	.	.	.	01	.	.	.
448 SMISTE	C= 4	.	.	.	.	.	.	.	.	.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
449 STEJAM	C= 63	03	03	01	04	.	01	.	01	08	06	.	.	.3	.	.	.	02	.7	19	02	05	.	.	.3	.	10	.8
450 SWERAD	C= 11	.	01	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	02	.	.	05	.	.	.	.
451 THAFEN	C= 59	.	03	.	.	02	.4	06	01	.	03	.	.	.	.8	.	.	02	.	01	.	05	04	05	02	01	01	.8
452 URTGRA	C= 4	.	.	.	.	.	.	.	.	.6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
453 VALOCC	C= 7	.	.	.	.	.	.4	.	01	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
454 VIOACU	C= 4	.	.	.	.	.	.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
455 VIOPUR	C= 7	.	.	.	.	.	.	06	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	01	.	.
456 ZIGPAN	C= 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.5	.	.	.	.	.	.	.	.	.	.

[1] Species codes: Abbreviations are first three letters of generic and specific names. Overstory species were divided into breast-height diameter classes 1=less than 1 dm, 2=1-2.5 dm, 3=greater than 2.5 dm. For ordination calculations, the relative percent canopy cover of these classes were summed to yield a single value.

[2] Constancy of occurrence of plant species on plots (number of plots where a particular species was found).

This table was produced using ASSTAB, a FORTRAN IV program written by Ronald A. Mauk.