INTERRELATIONS OF AUTECOLOGICAL CHARACTERISTICS OF FOREST HERBS

A thesis submitted to the Graduate School of the University of Wisconsin in partial fulfillmemt of the requirements for the degree of Doctor of Philosophy.

by
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Date August 1, 19 52

To Professors: Curtis

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This thesis having been approved in respect to form and mechanical execution is referred to you for judgment upon its substantial merit.

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Approved as satisfying in substance the doctoral thesis requirement of the University of Wisconsin.

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Date Aug 15, 1952

ACKNOWLEDGEMENTS

It is with a deep sense of gratitude that I express my appreciation of the assistance rendered by various persons during the course of this investigation.

The University Computing Service was kind enough to permit use of their IBM facilities. Especial thanks are due Mr. Fred Gruenberger for his assistance in the computations.

Dr. John T. Curtis, who conceived the problem, time after time helped the writer out of difficulties in procedure or interpretation with his invaluable advice and criticism.

Assistance in the determination of life history characteristics, and in various other ways, has been given by Mrs. Margaret Bergseng, Dr. Robert T. Brown, Mr. Edward E. Terrell, and Mr. James Zimmerman.

Lastly, my wife, Joan, has been of considerable assistance by aiding in field determinations, computations, and preparation of the manuscript.

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I. INTRODUCTION

A. General Statement

A comprehensive study of the major plant communities of Wisconsin was begun in 1948. Three phases of this broad program have been completed previous to the present undertaking. Dr. Robert P. McIntosh (1950) studied the upland forest communities in southern Wisconsin by means of an adaptation of the mass-collection technique. He found that the various forest communities are not distinguishable entities, rather, they merge into one another without sharp boundaries. Consequently, he devised a continuum index whereby forest stands may be related to each other by reference to their tree composition.

In 1951 Mr. Douglas Lindsay used weed distribution as a method of distinguishing the tension zone, a boundary which separates the floristic province of southern Wisconsin from that of the northern portion of the state.

Dr. Robert T. Brown (1951) studied the upland forests of northern Wisconsin in a somewhat similar manner to that of McIntosh and was able to construct a similar continuum.

These two forest continua were established on the basis of phytosociological studies of the tree composition of many stands. Both investigators have demonstrated that various species of forest herbs exhibit definite trends when their commonness is plotted against the continuum index. The northern and southern forest continua of Wisconsin,

therefore, may be utilized as foundations for autecological investigations of the lesser vegetation growing in these forests.

The present study has been undertaken for the purpose of providing a view of the distribution of various autecological characteristics of the lesser vegetation of the two forest continua. The first requisite for such a study is a knowledge of the variations in occurrence of the species to be studied. This information has been compiled from the field data gathered in conjunction with previous investigations. In general, it may be said that the results substantiate the findings of McIntosh and Brown who studied the distribution of only a few species of the herbs. A more intensive study of this subject is at present being conducted by Miss Margaret Gilbert.

The plan of the present investigation consists of the determination of various life history characteristics of a large number of woodland herbs. These findings, when weighted according to the commonness of the species possessing them, yield curves which disclose trends in the occurrence of these various characteristics along the two forest continua.

The life history characteristics previously mentioned are to some extent dependent upon the assumption that morphology is correlated with physiology. Thus the structure of a plant may indicate various physiological demands which it makes upon its environment. Additional studies, based upon

the physiology of a number of species, are presented in a later part of this paper.

Inasmuch as most previous studies have contrasted plants of open sunny habitats (heliophytes) with species of dense shade (sciophytes) little is known in this regard of the autecology of plants of intermediate sites. The present study, on the other hand, attempts to fill this void, in part, in that it is concerned with a broad range of sciophytes, from the pioneer to the climax forest communities.

Whether a particular characteristic has actual "survival value" for the plants normally found in a certain portion of the continuum is impossible to say at this time. The present study constitutes a survey of the variations in occurrence of the lesser vegetation and of many autecological characteristics of that vegetation. It is hoped that the results of this study will form a springboard for future investigators who may wish to study intensively the survival value of any of these characteristics.

B. Literature Review

No attempt is here made to review all of the literature pertaining to differences between sun and shade plants. The following discussion and the extensive summaries of various aspects of these differences which may be found in Clements (1905), Warming (1909), Combes (1910), Hanson (1917), Burgerstein (1920, 1925), Maximov (1929), and Rabinowitch (1945) serve to demonstrate that there are many such differences.

Maximov (1929) credits Stahl as having made the first real study of structural differences between sun and shade leaves (1883). In general, sun leaves have more palisade tissue, less spongy tissue, thicker cuticle, thicker epidermal cell walls, fewer and/or smaller intercellular spaces, and more stomata per unit leaf area.

Later studies have added such other differences as the following: sun leaves are smaller and thicker and are held obliquely or parallel to the sun's rays. The epidermis of sun leaves is thick and lacks chlorophyll. The lateral walls of epidermal cells are not as sinuous in sun leaves as in shade leaves. Stomata are found usually on the lower surface of sun leaves and are often sunken below the general surface of the leaf, while the stomata of shade species are found on both the upper and lower leaf surfaces and are either level with or raised above the general surface (Warming 1909).

Stomatal frequency of 150 species of woodland herbs was studied by Salisbury (1928). He found that the number of stomata per unit area of leaf surface increases from the midrib to the edges, from the base to the tip of the leaf, and from the base to the top of the plant. In general, stomatal size increases with an increase in moisture, but the total pore area decreases. The numerical ratio of stomata to all epidermal cells per unit area is constant for sun and shade leaves. Therefore stomatal frequency variations are due largely to variations in the size of all epi-

dermal cells. Variations in stomatal frequency can be correlated with various types of forest.

The sun leaves of many tree species are smaller and have narrower and deeper lobes and larger teeth than do the shade leaves on the same individual trees (Hanson 1917). The tendency of sun leaves to be concave, often hinging along the midrib, while the shade leaves on the same plants are flat, was noted by Bergen (1909).

Studies by Woodhead (1904) demonstrated, for various herb species, certain structural differences among individuals growing in different plant communities. Pioneer species in mesic habitats tend to assume leaf and stem characteristics of shade plants, such as thinner, broader leaves, less stem mechanical tissue, thinner cuticle, thinner spidermal cell walls and more chloroplasts. Mesic species found in more xeric sites, on the other hand, exhibited similar differences, but the trend was in the opposite direction.

According to Eberhardt (1900) a decrease in humidity results in the formation of more sclerenchyma and woody tissue, and with these, a thicker stem.

The development of conducting tissue has also been studied by Zalenski (1902), who measured the length of vascular tissue per unit area of leaf. In general, the conducting elements were found to be much more highly developed in species of dry, open sites than in those of woodlands and other moist environments. Similar comparisons, but between

the sun and shade leaves of the same plant, were made by Schuster (1908), with similar results.

McDougall and Penfound (1928), in studying cross-sections of sun and shade stems from the same individual plants, found that the sun stems are thicker, with shorter internodes. They have more sclerenchyma, much more xylem, and less pith, all on a percentage basis. In addition, the tracheal walls are thicker in the sun stems.

Shirley (1929) has shown that at low light intensities various plants contain more oven-dry matter in their aerial parts than in the roots. With an increase in illumination the proportion of dry matter in the tops increases. However, at 20 per cent of full sunlight, maximum height of the plants is attained, a decrease being noted with either augmentation or diminution of the amount of light. The total leaf area per plant behaves in a similar manner.

The shallow depths reached by the roots of forest plants, in contrast to the great depths of the species more characteristic of open sites, has been mentioned by Weaver (1919). In a sugar maple woods in southern Wisconsin it was found that the root systems of the herbs were predominantly to be found in the A_1 soil horizon (Scully 1942).

According to Maximov (1929) sun plants require a better developed root system since they transpire at a greater rate than do shade plants. It has been found that if a plant is moved from shade to bright sunlight more roots are developed

and more conducting elements are formed in the axial organs. He has summed many of these differences between sun and shade plants in the following manner:

> "All influences which result in a greatly increased loss of water by the plant, or a restricted supply of water to the developing leaves, lead to essentially similar changes of leaf structure. These structural changes, which may be termed 'xeromorphic', tend to facilitate the water supply and simultaneously to increase the gaseous exchanges. By virtue of this, xeromorphic plants are distinguished not by a lower but by a higher rate of such processes as transpiration and assimilation."

In order to test the hypothesis that previously described structural differences parallel physiological differences, Géneau (1892) conducted a series of intensive experiments. Expressing his results on the basis of unit area of leaf surface, he found considerable differences, up to 400 per cent, for transpiration, respiration and photosynthetic rates. In all cases the sun leaves gave the higher values. He also found that the leaves of sun plants have more oven-dry matter than the leaves of shade plants of the same species, both when expressed as percentage of fresh weight and on a unit-leaf-surface-area basis.

The concentration of chlorophyll in sun and shade plants of the same species and its effect on the production of oven-dry matter was studied by Lubimenko (1908). In general, he found that shade leaves contain more chlorophyll per unit of leaf area and larger chloroplasts. However, sun plants contain more dry matter. He concluded that more light is needed for maximum dry weight production than for maximum

chlorophyll formation. Maximum dry weight production in chlorophyll-poor plants occurs at or near full sunlight, but in plants rich in chlorophyll it takes place at much lower light intensities. In general stems show less development in sun than in shade, while roots show more. He believed that light also exerts an effect on assimilation, probably by influencing formation and destruction of enzymes.

Boysen Jensen (1919) studied Sinapsis alba, a heliophyte grown in full daylight, and Oxalis acetosella, a sciophyte grown in deep shade. He found that Sinapsis photosynthesizes and respires at approximately eight times the rate of Oxalis. Expressing the total increase in dry weight over a period of four weeks as average daily dry matter increase as a percentage of initial dry weight, he found a value of 15 per cent for Sinapsis and 2.1 per cent for Oxalis. Photosynthetic and respiration rates are equal in Sinapsis at a light intensity five times as great as that for Oxalis.

Rabinowitch (1951) has pointed out that the leaves of shade species are often of a darker green color, because of the presence of more chlorophyll per unit area or unit volume. Shade leaves are more efficient light absorbers. The light saturation rate in shade plants is usually much lower than that in sun plants.

Intensive investigations by Hesselman led to the following statements. In spring most plants exhibit a high rate of photosynthetic activity and this rate continues into the

summer in the case of shade species. In the case of shade plants, however, the measurable photosynthetic rate (excess above compensation point) decreases appreciably, frequently to zero, as the forest canopy closes above them. Along with this reduction in photosynthetic rate a decrease in respiration occurs. Forest herbs which appear as vernals in slightly reduced light and persist through the summer in dense shade have a much better development of photosynthetic tissues than species which grow and persist in moderately reduced light.

As long ago as 1909 Warming pointed out that an alcoholic solution of chlorophyll from shade leaves is decolorized by bright light much more rapidly than one from sun leaves. Rabinowitch (1945) quotes various authors as having demonstrated that shade leaves have more chlorophyll and a higher ratio of chlorophyll b : a than do sun leaves. He also states that chlorophyll b improves the utilization of the 450-480 mu light range, which is common under trees. Strain (1949) notes that plants with a high concentration of chlorophyll b (b:a=$\frac{1}{2}$) often lose the b faster than the a , reaching a ratio of b : a = 1/4 or 1/5, when exposed to bright light.

The susceptibility of the chlorophyll of climax species of forest herbs to destruction by exposure to bright sunlight has been described by Kerner (1895) as follows:

> "In the depth of beech-groves the Woodruff (Asperula odorata) raises its leaves arranged in whorls on the stem; over it the thickly-leaved branches of the

> beeches bend together, forming a roof through whose interstices only here and there a weak sunbeam finds its way into the depths. In the dim light the leaf-stars of the Woodruff appear of a deep, dark-green tint. Now the axe of the woodcutter resounds through the forest--the beeches are felled, the shading roof of foliage is demolished, and the floor of the wood is exposed to the glaring sunbeams. Within two weeks the Woodruff can no longer be recognized; it has become sickly and pale; the leaf-stars have lost their dark green, and the chlorophyll has been destroyed by the glaring light. The same thing occurs with ferns as with the Woodruff....All these plants are not organized to adapt themselves, in the case of an alteration of the illumination of their habitat, to the new conditions and to protect themselves from the undimmed rays falling on them. They are only fitted for the shady floor of the wood, and an over-abundance of light is their death."

Blackman and Wilson (1951) believe that shade plants may best be characterized as those species which exhibit a pronounced rise in leaf-area ratio from an initial low value in bright sunlight as the amount of illumination is decreased. Sun plants, on the other hand, have a high leaf-area ratio in full sunlight and little change in this value is noted at lower light intensities. Leaf-area ratio is defined by these authors as the relation of total leaf area to total plant weight.

That the osmotic pressure of sun leaves tends to be higher than that of shade leaves on the same trees was shown by Monselise (1951). In studying various kinds of citrus trees he found differences of 15 per cent.

In the investigations of Dietrich (1926), heliophytes were found to transpire much more rapidly than sciophytes on a unit leaf area basis, regardless of whether sun or shade individuals were used and of whether the experiments were

conducted in sun or shade.

Huber (1924) worked with sun and shade branches of oak and measured the stem cross-section area of the active xylem per unit area of leaf surface. These values he compared with the transpiration rates. The transpiration rate of shade leaves was 60 per cent that of the sun leaves, but the active xylem per unit leaf area of shade branches was only 50 per cent that of the sun branches. Since more water passes through the xylem cross-section per unit time in the shade branches there is a greater resistance to water passage. Therefore, when more water is being lost through transpiration the sun branches can overcome their increased resistance but the shade branches are unable to do this and consequently wilting occurs.

According to the investigations of Maximov (1938), sun plants do not exhibit wilting until 25 to 30 per cent of their turgid water content has been lost because the cell wall is very distended in the turgid condition and still remains elastic after a great decrease in volume of the cell. Shade plants, on the other hand, exhibit definite signs of wilting after losing only 2 to 3 per cent of their water content because the cell walls are not distended, even though under tension, and therefore collapse with slight decrease in cell volume.

The reproductive capacity of more than 300 species of British plants representing different habitats was studied by Salisbury (1942). He found that weight of seed or fruit

increases with an increase in the amount of shade occurring in the normal habitat of the various species. With advance in succession of plant communities the seed weight rises, and this in turn indicates an increase in the amount of reserve food supplied the embryo. An exception to this relationship is found in the case of parasites and saprophytes which depend to some extent upon nutrition derived from their hosts. Species which exhibit a mycorrhizal relationship constitute a similar exception. Schimper (1903) pointed out the occurrence of the majority of higher saprophytes in densely shaded habitats.

Salisbury found, further, that the number of seeds produced per plant decreases with an increasing amount of shade. Species which reproduce vegetatively and which have few or no seeds are mainly found in dense shade.

In his classical monograph on the dissemination of seeds and fruits by ants, Sernander (1906) showed that the seeds of many plants bear external appendages, of various structural origins, which he termed elaiosomes. These bodies usually contain oils or other substances which are apparently attractive to ants (Haberlandt 1914). The disseminules are carried by ants for storage in their nests. Later, after the eliaosome has been consumed, the seeds, otherwise unharmed, are cast out in the vicinity of the nest. Frequently the eliasome is eaten while the seed is being transported to the nest and the seed is then discarded (Gates 1941). It is interesting to note the results of various viability tests

conducted with such seeds after the elaiosomes had been removed. In general, viability was unchanged, but in a few species many more seeds germinated than did those in the control series.

Sernander studied the occurrence of these myrmecochores, species with ant-distributed seeds or fruits, in various plant communities of Europe. For example, he found that of all the species of herbs normally occurring in the forests of southern Bavaria, myrmecochores constitute 19 per cent of the herbs characteristic of woodlands and only 7 per cent of the herbs more characteristic of open sites. Of the species found in a birch-aspen stand 16.7 per cent were myrmecochores; in a slightly grazed birch-aspen stand with young spruces, 27 per cent; and in a spruce stand, 50 per cent. In a beech woods which had been cut and which contained young birch, aspen, and beech seedlings, only 2.6 per cent of the species were myrmecochores; in a later stage with the saplings 1 - 3 meters tall, 4 per cent; and in an even later stage with a closed canopy of beech, 22.6 per cent. Consulting various floras and lists of species characteristic of the different kinds of European forest, he found that pine woods contain four such species; spruce woods, 9; birch-aspen woods, 15; beech woods, 44; and mixed oak woods, 78 such species.

The association of vernal species of herbs with climax deciduous forests has been pointed out by Warming (1909).

Many of these species require afterripening of the seeds because the embryo is not well developed at the time of seed dispersal, a result of the short vegetative period of the parent plants. He also noted the commonness of tubers, bulbs, and other specialized types of overwintering organs in these terminal forest stages. In contrast to the beech woods, the oak forests contain many more shrubs and grasses. Most of the oak forest herbs blossom in the spring after the closure of the forest canopy.

Salisbury (1925) recognized four major types of forest herb, with respect to phenology. The pre-vernal type puts forth leaves early in spring, or even during the previous autumn. These species manufacture most of their food before the leafing of the trees above them and wither as the forest shade increases. Since these plants avoid the dense shade of summer they are able to grow in the extremely shady habitat of the climax forest.

The summergreen type includes those species which form leaves after the tree canopy has commenced to close. These forms are more characteristic of forests which admit more light. Also included in this type are those species with leaves which appear early and remain intact throughout the growing season. They are consequently found in dark woodlands.

The wintergreen type includes those species in which the photosynthetic organs are formed in autumn. These remain active for only a relatively short interval, but may be replaced so that the plants bear leaves throughout the year.

Many of these plants are found in forest sites with even, year-round illumination.

Species of the evergreen type bear the same set of leaves throughout the year. They are not commonly found in stands with dense shade in summer.

With regard to phenology, Salisbury (1921) has noted that leaf development in the spring starts in the bottom stratum and proceeds at a later date to the higher levels. The average date of leaf appearance among the forest herbs is February 19th, while for the shrub layer the average date is March 21st, and for the trees, May 13th. Most of the woodland species blossom in June, but many of the common species flower during May. On the other hand, the species of non-forested habitats bloom during July. Schimper (1903) has noted the greater production of flowers in sun species as contrasted with shade plants.

The importance of cryptophytes in the vernal flora and of hemicryptophytes in the aestival flora has been noted by Cain (1945) as well as by many others. The literature pertaining to Raunkaier's life forms will be reviewed more fully in a later section of this paper.

II. LIFE HISTORY CHARACTERISTICS

A. Methods

In order to determine the importance of herb species in the various phases of forest vegetation some method for the delimitation of the forest complex was needed. For this purpose the upland forest continuum of Curtis and McIntosh (1951) in southern Wisconsin and the similar continuum for the upland forests of the northern part of the state (Brown and Curtis 1952) were utilized. These continua embrace the gradient from the pioneer forest stages, with their high light intensities, immature soils, and variable moisture conditions, to the climax forests with their extreme shade, mature soils and constant, abundant moisture conditions.

1. Average Frequency Curves

Since, as is explained later in this paper, various life history characteristics were to be weighted according to the importance of the species possessing them, it was necessary to determine the continuum distribution of these species. These values were also used in the selection of the species to be studied.

The stands used in the study of the northern continuum are the 116 utilized by Brown (1951). For the southern continuum studies the data obtained in 96 stands were available. These were largely the same stands as were used by Curtis and McIntosh (1951), but included six additional stands with continuum index values between 300 and 600. Due to an irregularity in the data of some of the stands in southern

Wisconsin, certain values for a few species have been based upon different numbers of stands. The range of this variation is shown in table 1.

The procedure for determining the importance of each species along the continuum was as follows. The available data included frequency of each species occurring in a particular stand, based upon twenty quadrats, 1m. x 1m., and a presence list for each stand. A species which appears on the presence list, but which did not occur in any of the quadrats, was assigned a frequency value of one per cent. This practice was based upon the assumption that a fivefold increase in either size or number of quadrats would result in the occurrence of many of these species in a quadrat.

The frequencies of a particular species in all of the stands in one continuum interval, a subject to be explained in the following section, were added and the sum was divided by the total number of stands included within that interval, thus yielding an average frequency value for that species in the continuum interval. In this manner nine average frequency values were determined for each species which occurred in any stand.

2. Size of Continuum Interval

The use of the continuum intervals as described above was a purely arbitrary selection. This selection was based upon the ease of dividing the continuum into nine equal-sized intervals of such size that they included the whole range of the continuum. Nine values were considered to constitute a

Continuum Interval	Northern Wisconsin	Southern Wisconsin
300- 600	9	6
600- 900	8	6 - 8
900-1200	12	11 - 13
1200-1500	17	10 - 11
1500-1800	14	17 - 21
1800-2100	8	13 - 14
2100-2400	13	14
2400-2700	25	8 - 10
2700-3000	10	0
Total	116	85 - 96

Table 1. Numbers of stands for which herb quadrat frequency data were available, arranged according to intervals along the two continua.

sufficient number of points for the plotting of the resulting curves. However, there was no assurance that the frequency curves for the various species would not be radically different if a different continuum interval size had been selected.

In order to clarify this question, average frequency curves for twenty species were calculated on the basis of nine different interval selections. The characteristics of these different methods of subdividing the continuum are presented in table 2. One disadvantage of four of these methods is that portions of the continuum are omitted.

There are several points which should be considered in the selection of the interval to be used. The number of intervals should not be so large that the resulting number of stands per interval is very small. The consequence would be a large number of points for the plotting of curves, but the validity of any one point, being based upon only a few stands, would be open to serious doubt. The validity of this statement is shown in figure 1 by the curve based upon 27 one-hundred unit intervals. The curve does not show the minimum, optimum, and maximum ranges for development of the species as they occur within the limits of the continuum, but the individual values are subject to much variation.

On the other hand, the intervals should not be excessively large. In the case of nine-hundred unit intervals, there are only three points for the plotting of a curve, certainly an insufficient number, even though the number of

Interval Size	First Interval	Number of Intervals	Continuum Ranges Excluded
100	300- 400	27	
200	300- 500	13	2900-3000
200	400- 600	13	300- 400
300	300- 600	9	
300	400- 700	8	300- 400 2800-3000
300	500- 800	8	300- 500 2900-3000
450	300- 750	5	
540	300- 840	4	
900	300-1200	3	

Table 2. Continuum intervals and methods of staggering these for study of effect of various arrangements on the resulting average frequency curves.

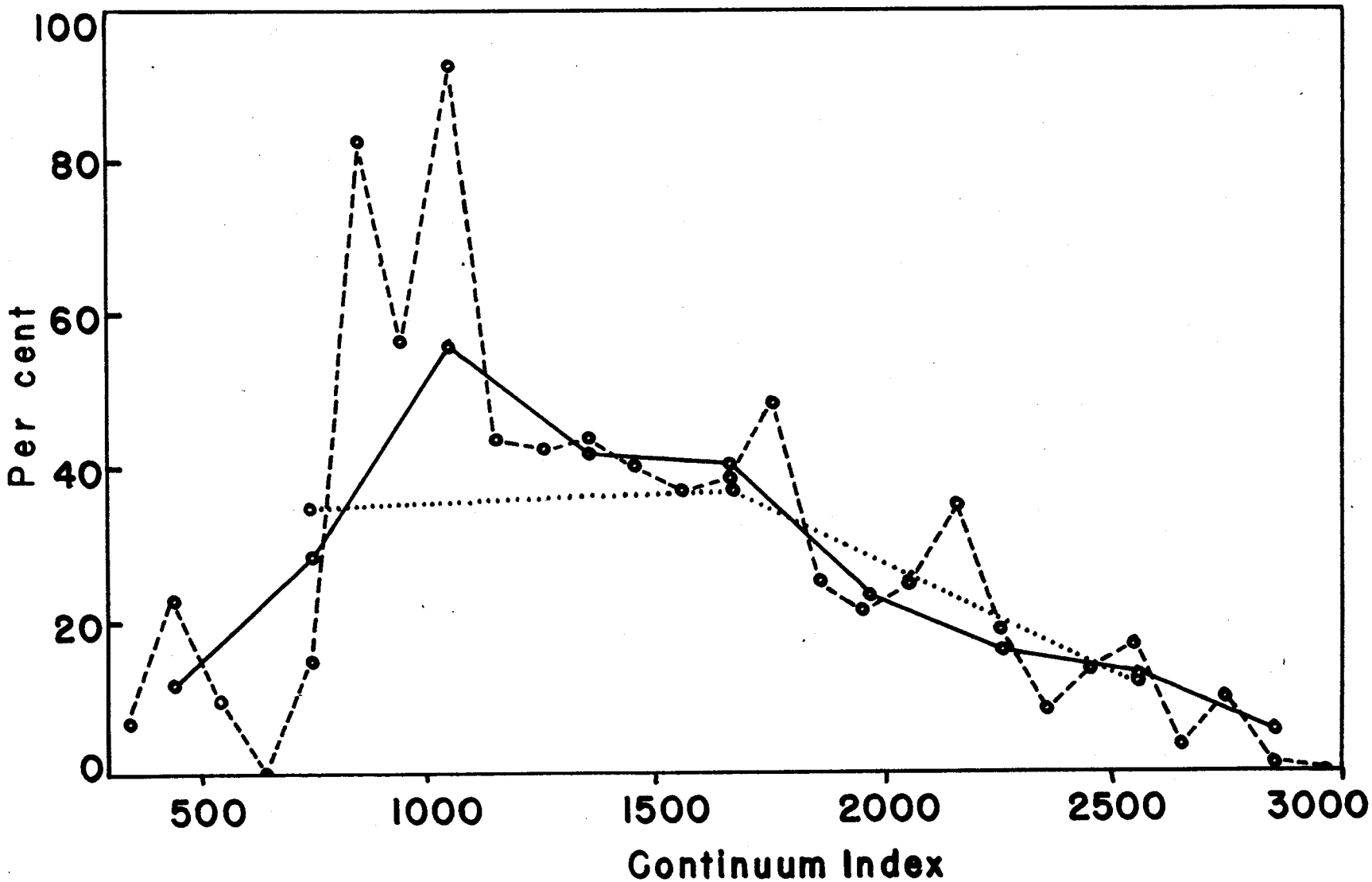
Figure 1

Effect of continuum interval size upon average frequency curves for *Aster macrophyllus* along the northern continuum

------ 27 100-unit intervals

———— 9 300-unit intervals

••••••• 3 900-unit intervals


100
80
60
40
20
0
Per cent
500
1000
1500
2000
2500
3000
Continuum Index

stands upon which each value is based is extremely large. Each of these intervals covers a wide range of environmental conditions, within one of which a species may rise from minimum to optimum development. The narrow limits of occurence of some species would thus be obscured.

The ideal interval size, then, is one which includes a sufficient number of stands to render the average values fairly reliable. At the same time the environmental range included within any interval should not be so broad that important changes in the importance of a species within that interval are obscured. The number of intervals must be sufficiently large that the plotting of curves is facilitated. If these requirements are met the resulting curve should demonstrate a clear trend, provided one exists, without the necessity of applying moving averages. The interval size which most nearly approaches this optimum is the 300-unit continuum interval.

There still remains the problem of the effect of location of the intervals upon the resulting curves. It is reasonable to suppose that the average frequency of a species in the 300-600 range would be different from that in the 400-700 and 500-800 ranges. In figure 2 are shown two such curves for Aster macrophyllus. The differences between these curves are seen to be of minor importance. Similar differences were found with the other 19 species studied in like manner. Inasmuch as the first of these three arrangements encompasses the whole range of the continuum, while the other

Figure 2

Presence and average frequency curves for

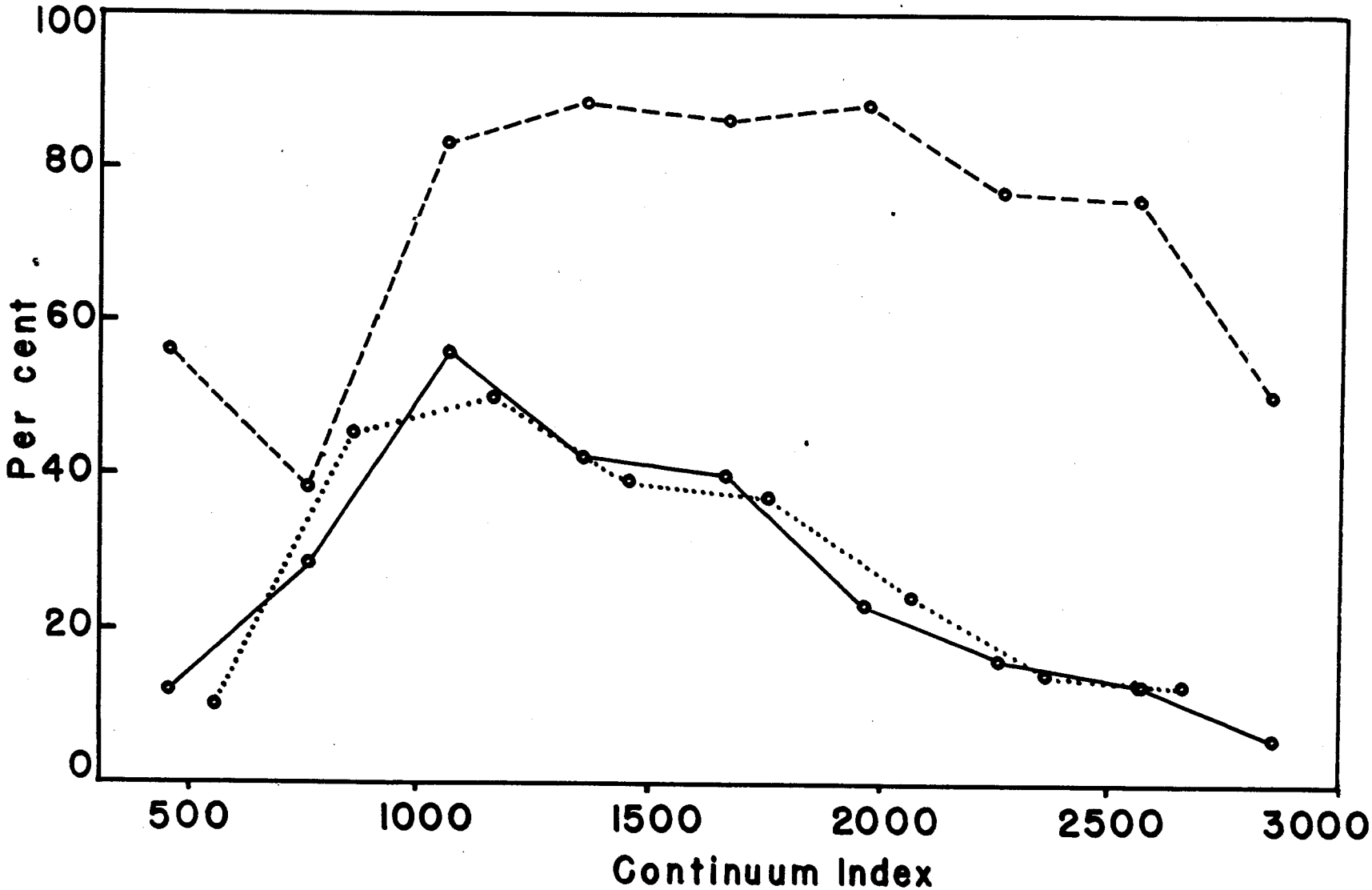
Aster macrophyllus

along the northern continuum

\- - - - - - - Presence

_____ Frequency, 300-600, etc.

. . . . . Frequency, 400-700, etc.


100
80
60
40
20
0
Per cent
500
1000
1500
2000
2500
3000
Continuum Index

two methods omit certain portions, the 300-600 spacing of three-hundred-unit intervals was adopted.

Admittedly, density would be the ideal measure to use as the basis of this study. However, since the determination of herb density is a very time-consuming procedure, and involves subjective judgment as to the distinguishing of single plants, this characteristic was not included in the available data. Two measures of herb distribution were, however, available, namely presence and frequency. The relative value of using presence as a measure of herb importance in the various continuum intervals was therefore investigated.

In figure 2 is plotted the presence curve for Aster macrophyllus for comparison with the average frequency curve, both based upon the 300-600 interval system. Three characteristic features of such comparisons are readily apparent. Presence values are normally considerably higher than the corresponding average frequency figures. This fact leads to a lessening of the value of presence for the present purposes because presence values may reach a value of 100 per cent.

For example, Geranium maculatum in southern Wisconsin occurs in 92 of the 96 stands included in this study. The presence curve for this species is a straight line at 100 per cent throughout the continuum, but dropping to 50 per cent in the first interval and to 92 per cent in the last interval. The environmental range within which this species reaches optimum development is only vaguely indicated by

such a curve. The average frequency curve for this species exhibits a pronounced peak in the fourth interval, as is shown in figure 3.

The tendency of presence curves to exhibit a prolonged peak is shown in figure 2. Comparison of this curve with the average frequency curve also shows a common tendency of the presence peak to begin at the same or a higher continuum index value than the average frequency peak, although in a few cases it peaks at a lower continuum index value. The width of the presence peak renders difficult the determination of the interval in which the species is most common.

For these reasons, then, the index of importance used throughout this study is the average frequency curve based upon nine 300-unit intervals extending from 300-600, 600-900, et cetera. It should be pointed out, however, that the presence curve was calculated along with the average frequency curve for each species. For the most part these presence curves tend to parallel the frequency curves. They have been of value in the interpretation of those frequency curves which exhibit a plateau at the peak value.

3. Species Selection

Inasmuch as the present study is concerned with the lesser vegetation of the forest, phanerophytes were excluded from consideration. As a result, various woody plants, mainly chamaephytes, were included. The use of the term "herb" throughout this paper is therefore not warranted if used in the narrow sense. "Lesser vegetation" might be preferable,

Figure 3

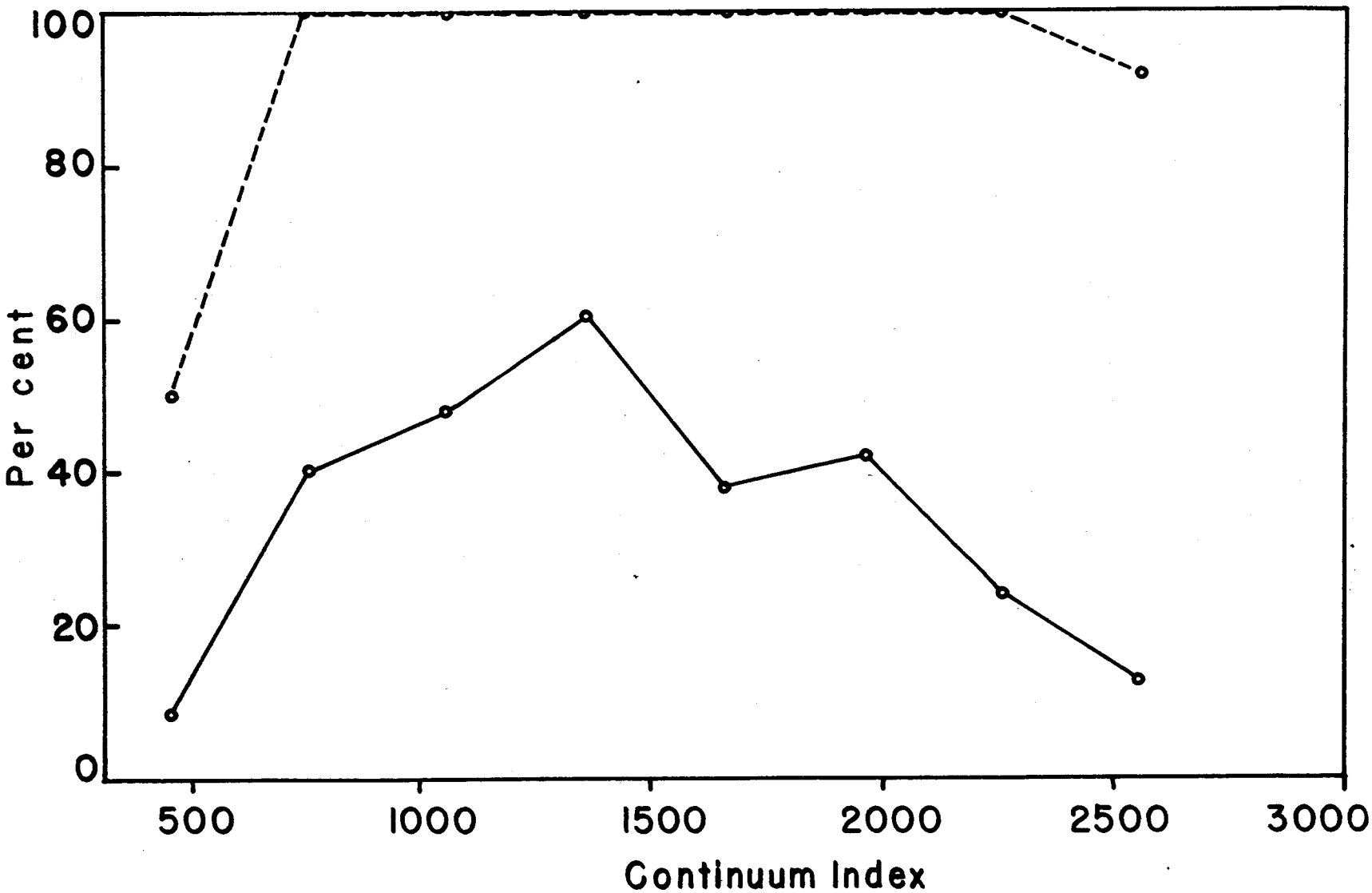
Presence and average frequency curves for

Geranium maculatum

along the southern continuum

------- Presence

_____ Average frequency


100
80
60
40
20
0
Per cent
500
1000
1500
2000
2500
3000
Continuum Index

but for the sake of brevity "herb" will be used.

The average frequency curve, as described above, was determined for each species appearing in any of the stands utilized in this study. All species which reached an average frequency greater than 1.5 per cent in any continuum interval were included in the list of species to be studied. In other words, the species included are common enough to occur in three of every 200 quadrats laid in stands with a limited environmental range. This arbitrary, but objective, criterion served to eliminate a large number of species which, if included, would have doubled the extent of the field determinations without altering the results appreciably. Within a particular continuum interval, for example, one species with an average frequency of 50 per cent would carry the same weight as fifty other species each with an average frequency of one per cent. Clearly, the additional precision obtained by including all species would not have justified the greatly increased expenditure of time and expense involved.

The northern and southern continuum species lists resulting from application of the two criteria outlined above each contain 114 species, of which 65 species are mutual.

4. Determination of Life History Characteristics

The available literature has been searched for information on the life history characteristics of the species included in this study. Since many of these references consist of short notes, they are not included in the literature review, unless otherwise of importance. They are all, however,

included in the bibliography. Mention is made of the more important ones in the following explanations and definitions of the characteristics studied.

In general, except where impracticable, all determinations were made in the field after consulting the literature and herbarium specimens. In some cases various authors were found to disagree. In most of such instances the species and characteristic in question were rechecked in the field.

Figure 4 is a copy of the data form used in the field studies. One page was devoted to each species and the series of sheets was carried in a heavy three-ring loose leaf notebook which could be kept closed by a large rubber strap cut from an inner tube. In addition, a cord threaded through the rings and forming a loop outside the notebook facilitated carrying by serving as a shoulder strap. The characteristics listed in the first column of figure 4 were determined for twelve individuals in as many different forest stands for each species of herb. These determinations were recorded in the twelve columns next to the list of characteristics. An attempt was made to study each species in those stands in which it was common.

The life history characteristics studied are listed according to the code presented in figure 5. However, since some of the categories are subject to various interpretations, the distinctions used in this study require definition.

In many cases the plants do not fall into clear subdivisions. Rather, intermediates occur between the various

Figure 4

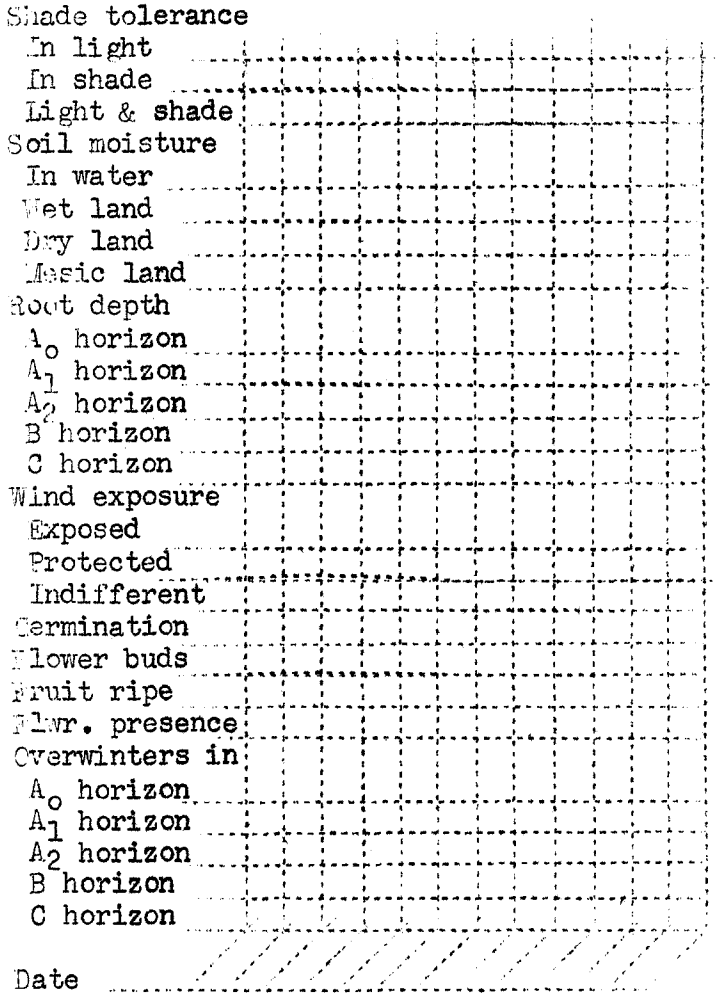
Data form for recording

of field observations

Data Form No. 26 Plant Ecology Research Univ. of Wisconsin

LIFE HISTORY CHARACTERISTICS Species: _____

Key Characters: _____



Photosynthesis
- Vernal
- Ver. & Autumnal
- Growing season
- Evergreen
- Winter rosette

Leaf size

Mature canopy
- Height
- Depth
- Diameter
- Density

Root system
- Tap root
- Fibrous
- Fascicled
- Tuberous

Overwinters as
- Corm
- Bulb
- Rhizome
- Aerial buds
- Seeds
- Root tuber
- Root bud

Pollination
- Wind
- Insect
- Both
- Cleistogamous
- Water

Effect of fire
- No effect
- Killed
- Weakened
- Stump sprouts
- More flowers

Grazing effect
- No effect
- Benefited
- Eaten
- Trampled out

Veg. repro.
- Absent
- Roots
- Rhizome
- Runners
- Layers
- Freed parts
- Stump sprouts

Seed dispersal
- Plumed
- Fleshy
- Nuts
- Hypochil
- Stick-tight
- Explosive
- Winged
- Small & light
- Tumbleweed
- No spec'l way

Dissimilar related species: _____

Observations: _____

categories as set up. In some cases, redefinition of the groupings has eliminated these difficulties. In other cases, however, alternative groupings were either not possible, or presented the same difficulties with regard to other species. In such cases, wherever possible, the species in question were assigned to the category which seems to be more important ecologically. For example, in classifying the various species according to type of canopy, Aster macrophyllus was included in the basal rosette group instead of the cauline group because the cauline canopy is found only on flowering specimens and these are much less common than the vegetative stems. In the cases where the importance or commonness of the alternatives was not known, additional categories were erected.

Life forms are used as defined by Raunkaier (1934) and as also described by Ennis (1928) and McDonald (1937). As stated previously, phanerophytes were excluded. The definition of chamaephytes as normally used, namely plants with aerial overwintering buds less than 25 cm. above ground level, was not followed strictly. Rather, the original concept of Raunkaier (who, incidentally said 20-30 cm.) that chamaephytes are plants with their aerial buds protected by snow during the winter, was selected. Nowhere in the literature has mention been found of what constitutes the surface of the ground; whether it should be considered the surface of the A_0 or A_1 horizon. Hemicryptophytes are defined as species

with overwintering buds below the ground level. Throughout the present study, therefore, the surface of the A_1 has been selected as the "surface of the ground". In accordance with the usage of Raunkaier, the one winter annual included in this study, Galium aparine, was classified as a therophyte. These are plants which pass the unfavorable season as seeds. The assumption is that for this species of Galium the dense shade of summer in a maple woods is the unfavorable season.

Characteristic number three, "depth of roots," was found to require only two subdivisions although the field studies were undertaken with a category for each soil horizon listed on the field form. The first subdivision, "A_1 horizon," includes those species whose roots were consistently found in that soil layer. The second group, "indifferent," means that the roots of an individual specimen were found in more than one horizon, so that the location of the roots could not be predicted before digging. This feature was found to be common for the individual plants of the species assigned to this category.

"Overwintering organ" (number four) includes groupings which are for the most part self-explanatory. In general the definitions of Coulter, Barnes and Cowles (1931) were followed. A comprehensive discussion is also given by Holm (1929). As in the case of life form determinations, the overwintering buds used for classification, when there are commonly two types, are those which will open to form new vegetative stems. "Crown buds" as used herein are

equivalent to one group of the "crown formers" of Hitchcock (1899, 1900), namely species which form the buds at the base of the previous year's stem. "Root buds" are adventitious buds formed on roots (Holm 1925).

"Overwintering organ depth" (number five) includes the subdivision "indifferent". This category is defined differently from that in number three, "depth of roots". In the present instance, no species were found with the overwintering buds of the individual specimen located in more than one horizon. However, in certain species, the buds of some individuals were found in a horizon different from that of other plants of the same species. If this variation was prominent among the twelve individuals sampled, the species was included in the "indifferent" group.

Only one subdivision, "detached parts", of characteristic number six requires definition. This is an example of the erection of an additional grouping to include exceptional cases. Only two species are here included, Cystopteris bulbifera, because of its bulblets, and Dicentra cucullaria, because of its peculiar vegetative reproduction mechanism. Horizontal roots contract and thus pull apart the enlarged petiole bases clustered at the base of the parent plant (Rimbach 1900).

The eighth characteristic, namely "canopy type", was subdivided arbitrarily according to the following definitions. "Canopy lacking" includes obligate parasites and

saprophytes, of which, however, only two species, Epifagus virginiana and Conopholis americana, are included in the lists of species. An "umbrella-like canopy" is almost without depth. It is illustrated by such species as Podophyllum peltatum and Botrychium virginianum. A "prostrate canopy" is the type possessed by reclining species, such as Mitchella repens and Galium aparine. Species exhibiting a basal canopy include Clintonia borealis and, primarily, other acaulescent plants. A cauline canopy is that type which includes leaves arranged in depth along the upright stem, as in Aralia racemosa and Caulophyllum thalictroides.

The leaf size classes in characteristics number 10 and 11 follow the definitions of Raunkaier (1934). Leptophylls are species with leaves of an area less than 25 square millimeters. Successive boundary areas are obtained by multiplying this first value successively by 9. A problem arises regarding the leaflet of compound leaves. Should each leaflet be considered a leaf, as Raunkaier decided, or should the whole compound leaf be measured as a unit? In her studies, Esten (1932) agreed with the decision of Raunkaier, while Withrow (1932), on the other hand, preferred to consider the whole compound leaf as one leaf. In the present study both systems were used so that a comparison of the results might be attempted.

Only a few of the categories in number 16, "seed or fruit dispersal mechanism", require definition. The subdivision "small and light" includes those species which

have disseminules capable of being carried by the wind because of extremely small size, as is the case with Goodyera pubescens and the various species of Pyrola. The term "elaiosome" was proposed by Sernander (1906) and is discussed in the literature review.

Characteristic number 18, "season of flower bud formation", is concerned with the presence of recognizable embryonic flowers inside the buds during the winter. The only comprehensive studies of this characteristic which have been found in the literature are those of Foerste (1883, 1891). Such embryonic flowers are so well developed that Foerste was able to identify Clintonia borealis, a species previously unknown to him, by means of the flower parts found in the buds of winter specimens.

The use of Turrill's extended scheme (characteristic number 19) was prompted by MacDonald's inclusion of this classification in her extensive study (1937). The numbers assigned to the subdivisions in the present study are different from the ones used by her. One disadvantage of this method, as its inventor pointed out (1929), is the possibility of including one species in more than one subdivision. In the present study an attempt was made to include each species only in that category which it fits best.

Since Turrill's extended scheme allows for the possibility of classifying one species into more than one category, this difficulty has been partially overcome by separating that portion of the scheme which deals with the presence

or absence of spines, thorns, et cetera. This feature was erected as a distinct characteristic (number 21). Any such projections which might serve to deter grazing animals were included in the first subdivision, for example, the soft, but poisonous, hairs of Laportea canadensis.

The twentieth system of classification herein adopted concerns taxonomic stability. The species were assigned to the various categories after an examination of the remarks and treatment of each species in Fernald (1950). Species containing two or more varieties were considered to be unstable. The description of but one variety or the mention of several forms were considered to constitute an adequate basis for classifying a species as intermediate. Those species for which no varieties, and at most one form, were mentioned, were included in the stable group.

5. Use of IBM Machines

Through the courtesy of members of the University Computing Service the use of their International Business Machine facilities was made possible. Expansion of the scope of the investigation was thereby made possible. Without such facilities the necessary computations might have limited appreciably the number of characteristics studied.

The coded characteristics were punched on International Business Machine cards. The nine average-frequency values for each species were rounded to whole numbers and these values were punched in nine consecutive two-column fields.

All data for a particular species appeared on one card. The cards were also punched for identification of the species they represent. For each species, the page number and the number of that species as treated on the page in Gray's Manual of Botany, 8th edition, was punched on the card. This system permitted the arrangement of cards in accordance with accepted taxonomic sequence and offered the further advantage that additional species could be added and dovetailed into place.

Working with the deck of cards for one continuum at a time, the cards were sorted with respect to one life history characteristic. Thus the cards for all cryptophytes were separated from the cards for the other life forms. By means of the tabulating machine, the average frequency values of these cards were totalled separately in the nine fields. The resulting series of figures constitutes a measure of the commonness of individual plants possessing the characteristic in question in the nine continuum intervals. In addition to summing the frequency values, the tabulator also counted the number of species contributing to the total in each field.

B. Results

1. Average Frequency Curves

The nine average frequency values as determined for each species studied are presented in table 3 for the northern continuum and in table 4 for the southern. Since no stands in the latter have as yet been found with a continuum index value in the 2700-3000 range, there are only eight average frequency values for the southern species.

Inspection of these series of values indicates the usefulness of the continua for plotting the occurrence of the lesser vegetation. In general, the values fall away in both directions from a peak of importance. It should be pointed out that these data offer no assurance that those species which exhibit a monotopic, i.e. distinctly pioneer or climax, distribution are at their optimum development within the limits of these continua. For example Fragaria virginiana occurs commonly in oak openings and prairies, while Laportea canadensis extends into bottomland forests in great profusion.

Furthermore, although it is not one of the characteristics included in this study, the vitality of various species has been noted during the field investigations. While these observations are incidental, it may not be amiss to include them here. Various pioneer species serve admirably to illustrate the effect of insufficient light. Such plants as Apocynum androsaemifolium and Amorpha canescens are found in many forest stands, but usually are of small stature and rarely

Table 3

Average frequency values based upon

nine 300-unit intervals along

the northern continuum

Species	Continuum Intervals								
	300 -600	600 -900	900 -1200	1200 -1500	1500 -1800	1800 -2100	2100 -2400	2400 -2700	2700 -3000
Actaea pachypoda					2		1	1	1
Adiantum pedatum						3	4	3	10
Allium tricoccum									2
Anemone cylindrica		2							
Anemone quinquefolia	20	5	18	29	22	7	3	5	19
Apocynum androsaemifolium	6	2	4	3	2	1			
Aquilegia canadensis			4	3	2				
Aralia nudicaulis	5	11	16	27	34	1	16	14	19
Aralia racemosa					1			2	2
Arctostaphylos uva-ursi	4								
Arenaria lateriflora		1		4					
Arisaema atrorubens					1	1	6	5	9
Asarum canadense								2	
Aster macrophyllus	12	28	56	42	40	23	16	13	6
Aster sagittifolius	4	3	8	3	3	1			1
Athyrium filix-femina		1		2	3	1	0	5	2
Botrychium virginianum		1				1	1	2	3
Brachyelytrum erectum			1	2	1	1	2	2	3
Carex albursina						2			1
Carex pensylvanica	26	42	22	16	10		1	2	6
Carex plantaginea			1		2				
Caulophyllum thalictroides								2	4
Chimaphila umbellata	6	6	12	6	1	1			

Table 3 Average frequency values based upon nine 300-unit intervals along the northern continuum.

Species	Continuum Intervals								
	300 -600	600 -900	900 -1200	1200 -1500	1500 -1800	1800 -2100	2100 -2400	2400 -2700	2700 -3000
Circaea alpina					2		4	4	3
Circaea quadrisulcata		2		2		3	2	2	2
Claytonia caroliniana							5	6	11
Claytonia virginica								2	28
Clintonia borealis	2	1	7	9	16	6	18	10	13
Comandra richardsiana	3	3	1	1					
Convolvulus spithamaeus	3	3	3	2	1	1			
Coptis groenlandica	1		2	2	3	1	13	2	2
Coreopsis palmata	2	2							
Cornus canadensis	3	17	8	8	6	4	16	4	1
Cynoglossum boreale			2						
Desmodium glutinosum			4	1	3	1	3	1	
Dicentra cucullaria								15	49
Diervilla lonicera	14	22	26	22	13	4	3		
Dryopteris disjuncta					1		4	6	3
Dryopteris phegopteris							1	2	1
Dryopteris spinulosa			1	1	3	6	12	16	13
Epifagus virginiana									2
Epigaea repens	6	8	2	2		1			
Erythronium americanum						10		14	35
Euphorbia corollata	4	9	2						
Fragaria virginiana	8	6	18	13	5	2	2		
Galium triflorum		1	6	8	13	8	9	14	12
Gaultheria procumbens	37	26	39	28	20	6	4	1	
Geranium maculatum	1	1	17	6	8	1	7	2	4
Goodyera pubescens			2	1	1				
Helianthemum canadense	3	1							
Helianthus occidentalis	2	4	2						

Species	Continuum Intervals								
	300 -600	600 -900	900 -1200	1200 -1500	1500 -1800	1800 -2100	2100 -2400	2400 -2700	2700 -3000
Hepatica aculiloba				1		2	1	2	12
Hepatica americana		2	11	3	10	4	1	5	
Hieracium canadense			2						
Hydrophyllum virginianum								4	2
Impatiens capensis								1	3
Laportea canadensis							1	4	1
Lathyrus ochroleucus				3					
Lathyrus venosus	1		3	2	1				
Linnaea borealis	1	6	7	5	2	1	2		
Lycopodium annotinum				1		1	7	1	1
Lycopodium clavatum	1	3		2	3	1		1	
Lycopodium complanatum	2	1		2					
Lycopodium lucidulum					1	3	11	11	2
Lycopodium obscurum	6	8	2	7	14	6	10	6	2
Lysimachia quadrifolia	12	2	2	2					
Maianthemum canadense	51	46	42	56	63	26	43	43	26
Melampyrum lineare	6	1	2	3					
Mitchella repens			10	12	14	13	9	8	5
Mitella diphylla				2	2	1	3	10	12
Mitella nuda							1	2	1
Monarda fistulosa	3	3	1	1					
Moneses uniflora					2				
Onoclea sensibilis				1	1		2		
Oryzopsis asperifolia	7	9	38	17	35	18	10	5	5
Osmorhiza claytoni			1	1	3	1	3	15	30
Osmunda cinnamomea				2					
Osmunda Claytoniana			1	1	4	3	1	1	1
Oxalis montana							6	2	

Species	Continuum Intervals								
	300 -600	600 -900	900 -1200	1200 -1500	1500 -1800	1800 -2100	2100 -2400	2400 -2700	2700 -3000
Panax quinquefolius									2
Pedicularis canadensis		3							
Pedicularis lanceolata	1		6						
Phyrma leptostachya			1	1			1	1	2
Polygala paucifolia	6	12	12	12	7	2			
Polygonatum pubescens	7	9	3	6	12	6	8	9	17
Potentilla simplex	15	2		1	1				
Prenanthes alba	1	1	5	2	1	1			
Pteridium aquilinum	38	34	63	45	38	23	8	2	1
Pyrola elliptica	3	1	7	6	4	1	1	2	2
Pyrola rotundifolia	2	1	4	3	3	1		1	
Pyrola secunda	1	6	9	6	3	4	2	2	
Sanguinaria canadensis						1	1	1	13
Sanicula gregaria		1	1	1	2		2	1	1
Schizachne purpurascens	3	1	2	1	3			1	
Smilacina racemosa	5	10	15	5	13	5	7	2	14
Smilacina stellata	2	6	2						
Smilax ecirrhata	1	2							
Smilax herbacea	1	2		1					
Smilax tamnoides var. hispida			3	3	2		1		
Solidago flexicaulis	1						1	2	
Solidago speciosa	7								
Streptopus roseus		1	7	6	14	10	10	24	12
Thalictrum dioicum			1	1	10	2	4	2	

Species	Continuum Intervals								
	300-600	600-900	900-1200	1200-1500	1500-1800	1800-2100	2100-2400	2400-2700	2700-3000
Trientalis borealis	16	11	14	27	27	20	17	13	13
Trillium grandiflorum		1		5	11	8	9	7	23
Uvularia grandiflora			2	2	3		2	4	11
Uvularia sessilifolia	9	3	16	11	20	11	13	7	8
Vaccinium angustifolium	62	31	27	16	13	3			
Viola canadensis						2	1	4	7
Viola cucullata		1	4	3	5	1	4	7	4
Viola incognita		1	2	1					
Viola pensylvanica								1	3
Viola pubescens		1	4	3	2	1	1	6	10
Waldsteinia fragaroides	23	38	36	20	35	18	4	3	1

Table 4

Average frequency values based upon
nine 300-unit intervals along
the southern continuum

Species	Continuum Intervals							
	300 -600	600 -900	900 -1200	1200 -1500	1500 -1800	1800 -2100	2100 -2400	2400 -2700
Actea sp.				1	1	5	2	3
Adiantum pedatum		1	2	6	8	6	12	13
Agrimonia gryposepala			3	1	2	1		
Allium tricoccum			1	2	2	4	5	10
Amorpha canescens	30	4	1	1				
Amphicarpa bracteata	17	20	14	28	16	22	13	6
Anomone cylindrica	3			1				
Anomone quinquefolia	10	20	12	9	12	12	13	5
Anomonella thalictroides		1		1	4	1		5
Apocynum androsaemifolium	7	6	5	6	4	2		
Aquilegia canadensis	2		1	1		1		
Aralia nudicaulis	4	2	16	16	16	14	7	3
Aralia racemosa			1	2	3	2	1	1
Arenaria lateriflora		2	3		2		1	1
Arisaema atrorubens		2	1	12	11	15	23	22
Asarum canadense						1	5	4
Aster macrophyllus			2	7	6	13	4	
Aster shortii	3	4	1	3	1	3	3	4
Athyrium filix-femina	1	4	4	8	13	6	6	9
Botrychium virginianum		10	13	5	7	12	8	18
Brachyelytrum erectum				6	10	9	5	3
Campanula rotundifolia		10						
Carex albursina					1		5	8
Carex pensylvanica	7	18	21	6	14	18	4	

Table 4 Average frequency values based upon nine 300-unit intervals along the southern continuum. (Data not available for any stands in the ninth interval.)

Species	Continuum Intervals							
	300 -600	600 -900	900 -1200	1200 -1500	1500 -1800	1800 -2100	2100 -2400	2400 -2700
Caulophyllum thalictroides				3	2	4	8	11
Ceanothus americanus	4			2				
Circaea quadrisulcata	1	20	31	18	24	26	20	22
Claytonia virginica							4	36
Conopholis americana						1	2	
Convolvulus spithamaeus	3							
Cryptotaenia canadensis		1		3	2	5	8	2
Cypripedium calceolus var. pubescens				2	1	1		
Cystopteris bulbifera							4	
Cystopteris fragilis		1			1	1	3	4
Dentaria laciniata								11
Desmodium glutinosum		12	22	41	22	15	8	4
Desmodium nudiflorum			6	6	5	2		
Dicentra cucullaria							1	21
Diervilla lonicera			1	2	5			
Dryopteris spinulosa				2			1	
Erythronium albidum				4			6	20
Erythronium americanum								8
Eupatorium rugosum		2	1	3	2	2		2
Euphorbia corollata	36	1	1	2	1			
Floerkea proserpinacoides								8
Fragaria virginiana	16	15	3	7	6	4	1	
Galium aparine		16	13	20	9	11	14	49
Galium circaezans		1			3	3		
Galium concinnum		29	22	32	22	28	14	8
Galium triflorum	1	1	2	3	4	3	1	2

Species	Continuum Intervals							
	300 -600	600 -900	900 -1200	1200 -1500	1500 -1800	1800 -2100	2100 -2400	2400 -2700
Geranium maculatum	8	40	48	60	38	42	24	13
Geum canadense		6	18	8	8	7	3	5
Goodyera pubescens		1			1			
Hackelia virginiana					3			
Helianthemum canadense	17							
Helianthus strumosus	27	3	8	14	5	4		
Hepatica acutiloba					1	8	18	14
Hieracium canadense		3						
Hydrophyllum virginianum				1	1	8	14	30
Hystrix patula			2	2	2	4	1	2
Impatiens sp.			3	8	2	7	8	17
Isopyrum biternatum								3
Lactuca biennis		1	5	1	1	3	1	1
Laportea canadensis				1		2	1	13
Lathyrus ochroleucus	4	3		1	1	2		
Lathyrus venosus	4	3		1	1	1		
Lysimachia quadrifolia	1		4	2	3	1		
Maianthemum canadense		1	2	2	2	3		
Mitella diphylla		1		1	1	1	8	3
Monarda fistulosa	14	4	3	4	1			
Orchis spectabolis				1	1	2	1	1
Osmorhiza claytoni		12	19	26	23	31	24	13
Osmorhiza longistylis		1	4	6	4	3	4	9
Osmunda cinnamomea				1			3	
Osmunda claytoniana			1	4	6	2	2	1
Panicum latifolium			1	1	2	1		
Prietaria pensylvanica		10	2	1	6	3	4	2
Phlox divaricata								13

Species	Continuum Intervals							
	300 -600	600 -900	900 -1200	1200 -1500	1500 -1800	1800 -2100	2100 -2400	2400 -2700
Phryma leptostachya	1	20	23	16	18	13	7	1
Pilea pumila					3			
Podophyllum peltatum		2	8	22	9	8	16	18
Polemonium reptans				1	1	1	1	3
Polygonatum pubescens	14			1	2	5	14	5
Polyminia canadensis								8
Potentilla simplex	8	3	6	3	3	2	1	
Prenanthes alba	3	3	4	5	3	5	3	2
Pteridium aquilinum	16	4	12	14	13	11		
Pteretis pensylvanica								3
Pyrola elliptica		3	5	3	16	2	1	
Ranunculus abortivus	1		2	2	2	4	2	1
Ranunculus septentrionalis						1	2	4
Sanguinaria canadensis		2		6	11	18	24	33
Sanicula gregaria		3	6	14	7	24	13	10
Smilacina racemosa	12	33	40	39	38	24	23	28
Smilacina stellata	20	8	9	1	1	1		
Smilax ecirrhata	1	2	2	3	1	5	1	5
Smilax herbacea	2	1	3	2	2	4	2	1
Smilax tamnoides var. hispida					1	2	1	
Solidago flexicaulis								5
Solidago speciosa	4							
Solidago ulmifolia		2	1	11	4	10	10	2
Taenidia integerrima	1			3				
Thalictrum dioicum			1	8	9	6	13	2
Trillium flexipes			5	3	2	4	10	2
Trillium grandiflorum					7	7	4	2
Tovara virginiana							1	2

Species	Continuum Intervals							
	300 -600	600 -900	900 -1200	1200 -1500	1500 -1800	1800 -2100	2100 -2400	2400 -2700
Trillium recurvatum						1	4	18
Triosteum perfoliatum		1		3		1	1	1
Uvularia grandiflora		3		14	28	22	14	21
Veronicastrum virginicum			1	2	2	1		
Vicia americana	3	2				1		
Viola cucullata	5	16	8	10	8	18	10	25
Viola pubescens		1		2	3	17	18	32
Viola sagittata	2	2	3					

blossom in any but the most pioneer woods. Apocynum frequently reproduces vegetatively by means of roots when growing in the open, and this may occassionally be observed in very pioneer stands. More commonly, however, the stems of this plant are found as weak, small, non-flowering individuals. Presumably these arise from seeds that have blown into the forest and are unable to maintain themselves for any appreciable period.

Presenting a somewhat similar appearance in more climax stands is Impatiens capensis. While the data indicate that this is a climax species, most such individuals do not blossom and are depauperate in appearance when compared with others growing in moist sunny sites. In marked contrast to its normal appearance in maple woods is its vigor in gap phases in such woods. When several trees are felled in such a stand Impatiens grows in profusion to a height of five feet or more, and its chasmogamous flowers are conspicuous.

2. Life History Characteristics

When the species lists had been compiled, as described in a previous section of this paper, each species was classified with reference to 23 life history characteristics. These determinations were coded according to the scheme in figure 5 and the coded characteristics are presented in tables 5 and 6 for the northern and southern continua, respectively.

Figure 5

Life history characteristics and

code used for computations

1 Life form
- 1 Therophyte
- 2 Chamaephyte
- 3 Hemicryptophyte
- 4 Cryptophyte

2 Root system
- 1 Fibrous
- 2 Fascicled
- 3 Tuberous
- 4 Tap

3 Depth of roots
- 1 Indifferent
- 2 A_1 horizon

4 Overwintering organ
- 1 Bulb
- 2 Corm
- 3 Stem bud
- 4 Seed
- 5 Rhizome
- 6 Crown bud
- 7 Root bud

5 Overwintering organ depth
- 1 A_0 horizon
- 2 A_1 horizon
- 3 Indifferent
- 4 Aerial

6 Vegetative reproduction
- 1 Roots
- 2 Rhizome
- 3 Stolon
- 4 Absent
- 5 Detached part

7 Longevity
- 1 Winter annual
- 2 Biennial
- 3 Herbaceous perennial
- 4 Woody perennial
- 5 Annual

8 Canopy type
- 1 Lacking
- 2 Umbrella-like
- 3 Prostrate
- 4 Basal
- 5 Cauline

9 Leaf type
- 1 Simple
- 2 Compound

10 Leaf size (leaflet equals leaf)
- 1 Leptophyll
- 2 Nanophyll
- 3 Microphyll
- 4 Mesophyll

11 Leaf size (compound leaf equals leaf)
- 1 Leptophyll
- 2 Nanophyll
- 3 Microphyll
- 4 Mesophyll
- 5 Macrophyll

12 Photosynthetic season
- 1 Vernal
- 2 Growing season
- 3 Evergreen
- 4 Winter
- 5 None

13 Aerial stem type
- 1 Deliquescent
- 2 Excurrent
- 3 Reclining
- 4 Acaulescent
- 5 Twining

14 Pollination mechanism
1 Insect
2 Wind
3 Insect, bird, and cleisto-
4 Water -gamous
5 Cleistogamous and insect
6 Insect plus bird
1/3/5/6 All insect
3/5 All cleistogamous

15 Blooming season
1 Pre-vernal
2 Vernal
3 Aestival
4 Autumnal
5 Growing season

16 Seed or fruit dispersal mechanism
1 Fleshy
2 Explosive plus elaiosome
3 Elaiosome
4 Stick-tight
5 Explosive
6 Small and light
7 Plumed
8 Winged
9 No special method

17 Season of fruit ripening
1 Vernal
2 Aestival
3 Autumnal
4 Growing season

18 Season of flower bud formation
1 Current growing season
2 Previous growing season

19 Turrill's extended scheme
1 Deciduous shrubs
2 Perennial herbs or subshrubs, partially woody at base, and aerial parts dying back, but not to ground level
3 Grasses and grass-like plants

19 (continued)
4 Perennial herbs and subshrubs with runners, or sprawling or herbaceous or suffructicose stems
5 Rosette plants
6 Perennial herbs dying down yearly, with perennating buds on more or less thick stock at ground level
7 Geophytes
8 Annual herbs
9 Herbaceous twining plants, generally dying down each year
0 Evergreen shrubs

20 Taxomomy
1 Unstable
2 Intermediate
3 Stable

21 Spines
1 Plants armed with spines, thorns, etc.
2 Plants not so armed

22 Nutrition
1 Obligate autotroph
2 Partial autotroph
3 Parasite

23 Flower height
1 Below 18 inches
2 Above 18 inches

Table 5

Life history characteristics of northern species coded according to key in figure 5

Species	Life History Characteristics																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Actaea pachypoda	4	1	2	5	2	4	3	2	2	3	4	2	2	1	3	1	2	2	7	2	2	1	2
Adiantum pedatum	4	1	2	5	2	2	3	2	2	2	4	2	4	4	3	5	2	2	7	3	2	1	1
Allium tricoccum	4	1	2	1	2	2	3	4	1	4	4	1	4	1	3	9	3	1	7	3	2	1	1
Anemone cylindrica	3	1	2	5	2	4	3	4	2	3	3	2	2	1	3	8	2	1	6	3	2	1	1
Anemone quinquefolia	4	1	2	5	2	2	3	2	2	2	3	3	2	1	1	9	2	2	7	2	2	1	1
Apocynum androsaemifolium	3	1	2	7	3	1	3	5	1	3	3	2	1	1	3	8	3	1	6	2	2	1	2
Aquilegia canadensis	3	4	1	5	1	4	3	5	2	3	3	2	1	6	2	9	2	2	6	1	2	1	1
Aralia nudicaulis	3	1	2	5	1	2	3	2	2	3	4	2	2	1	3	1	2	2	6	3	2	1	1
Aralia racemosa	3	1	1	5	2	4	3	5	2	4	5	2	1	1	3	1	3	1	6	3	2	1	2
Arctostaphylos uva-ursi	2	1	1	3	4	3	4	3	1	2	2	3	3	1	2	1	3	2	0	1	2	1	1
Arenaria lateriflora	3	1	2	5	2	2	3	5	1	2	2	2	1	1	2	3	2	1	6	3	2	1	1
Arisaema atrorubens	4	1	2	2	2	2	3	2	2	4	4	2	2	1	2	1	3	2	7	1	2	1	1
Asarum canadense	3	1	2	5	2	2	3	2	1	4	4	2	4	5	2	3	1	2	6	1	2	1	1
Aster macrophyllus	3	1	1	5	2	2	3	4	1	4	4	3	2	1	3	8	3	1	5	1	2	1	2
Aster sagittifolius	3	1	2	6	1	4	3	5	1	3	3	2	2	1	3	8	2	1	6	1	2	1	2
Athyrium filix-femina	4	1	2	5	2	2	3	5	2	1	4	2	4	4	3	5	2	1	7	1	2	1	1
Botrychium virginianum	4	2	1	6	2	4	3	2	2	2	4	2	2	4	3	7	2	1	6	3	2	1	1
Brachyelytrum erectum	3	1	2	5	3	2	3	5	1	4	4	2	2	2	3	9	3	1	3	2	2	1	1
Carex albursina	3	1	2	5	2	2	3	4	1	4	4	3	2	2	3	9	2	2	3	3	2	1	1
Carex pensylvanica	4	1	2	5	1	3	3	5	1	3	3	3	2	2	2	9	2	2	3	1	2	1	1
Carex plantaginea	3	1	2	5	1	2	3	4	1	4	4	3	2	2	2	9	2	2	3	3	2	1	1
Caulophyllum thalictroides	4	1	2	5	2	2	3	5	2	3	4	2	1	1	2	1	3	2	7	3	2	1	2
Chimaphila umbellata	3	1	1	7	2	1	4	5	1	3	3	3	2	1	3	7	3	1	0	3	2	1	1
Circaea alpina	4	1	2	5	2	2	3	5	1	3	3	2	1	1	3	5	2	1	7	3	2	1	1
Circaea quadrisulcata	4	1	2	5	2	2	3	5	1	4	4	2	1	1	3	4	3	1	7	3	2	1	1

Species	Life History Characteristics																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Claytonia caroliniana	4	1	2	2	2	4	3	5	1	3	3	1	2	1	1	5	1	2	7	3	2	1	1
Claytonia virginica	4	1	2	2	2	4	3	5	1	3	3	1	2	1	1	5	1	2	7	2	2	1	1
Clintonia borealis	4	1	2	5	2	2	3	4	1	4	4	2	4	1	3	1	2	2	7	3	2	1	1
Comandra richardsiana	4	1	1	5	2	2	3	5	1	2	2	2	1	1	3	9	2	1	7	3	2	2	1
Convolvulus spithamaeus	3	1	1	7	2	1	3	5	1	3	3	2	3	1	3	9	2	1	6	2	2	1	1
Coptis groenlandica	3	1	2	5	2	2	3	2	1	3	3	3	4	1	1	9	2	2	5	3	2	1	1
Coreopsis palmata	3	1	1	5	1	2	3	5	1	3	3	2	1	1	3	8	2	1	6	3	2	1	2
Cornus canadensis	3	1	2	5	2	2	3	2	1	3	3	3	2	1	3	1	2	1	4	1	2	1	1
Cynoglossum boreale	3	4	2	6	1	4	3	5	1	4	4	2	1	1	3	4	2	1	6	3	2	1	2
Desmodium glutinosum	3	1	2	5	2	2	3	2	2	3	5	2	2	1	3	4	3	1	6	2	2	1	2
Dicentra cucullaria	4	1	2	2	2	5	3	4	2	2	4	1	4	1	1	3	1	2	7	3	2	1	1
Diervilla lonicera	2	1	1	3	5	1	4	5	1	3	3	2	1	1	3	9	2	2	1	3	2	1	1
Dryopteris disjuncta	4	1	2	5	2	2	3	2	2	2	4	2	4	4	3	5	2	1	7	3	2	1	1
Dryopteris phegopteris	4	1	2	5	3	2	3	2	2	2	4	2	4	4	3	5	2	1	7	3	2	1	1
Dryopteris spinulosa	3	1	2	5	2	2	4	5	2	2	4	3	4	4	3	5	3	1	4	1	2	1	1
Epifagus virginiana	1	2	1	4	2	4	5	1	1	1	1	5	1	5	3	7	2	1	8	3	2	3	1
Epigaea repens	2	4	1	3	4	4	4	3	1	3	3	3	3	1	1	1	1	2	0	2	2	1	1
Erythronium americanum	4	1	2	1	2	2	3	4	1	4	4	1	4	1	2	3	1	2	7	3	2	1	1
Euphorbia corollata	4	4	1	6	2	4	3	5	1	3	3	2	1	1	3	5	2	1	7	1	2	1	2
Fragaria virginiana	3	1	2	5	2	3	3	4	2	3	4	2	4	1	2	1	2	2	4	1	2	1	1
Galium triflorum	3	1	2	5	2	3	3	3	1	3	3	2	1	1	3	4	2	1	6	3	2	1	1
Gaultheria procumbens	3	1	1	5	2	2	4	2	1	3	3	3	2	1	3	1	3	1	0	3	2	1	1
Geranium maculatum	3	1	2	5	2	2	3	5	1	4	4	2	1	1	2	5	2	2	6	3	2	1	2
Goodyera pubescens	3	2	2	5	2	2	3	4	1	3	3	3	4	1	3	7	3	1	5	3	2	1	1
Helianthemum canadense	3	4	1	7	1	1	3	5	1	2	2	2	1	3	3	9	2	1	2	2	2	1	1
Helianthus occidentalis	3	1	1	5	2	2	3	4	1	3	3	2	2	1	3	9	3	1	6	2	2	1	2
Hepatica acutiloba	3	1	2	5	1	4	3	4	1	3	3	3	4	1	1	3	1	2	5	2	2	1	1
Hepatica americana	3	1	2	5	1	4	3	4	1	3	3	3	4	1	1	3	1	2	5	2	2	1	1
Hieracium canadense	3	1	1	5	2	4	3	5	1	3	3	2	1	1	3	8	2	1	6	1	2	1	2

Species	Life History Characteristics																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Hydrophyllum virginianum	3	1	2	5	2	2	3	4	1	4	4	2	1	1	3	9	2	2	6	3	2	1	1
Impatiens capensis	1	1	2	4	1	4	5	5	1	4	4	2	2	3	4	5	2	1	8	1	2	1	2
Laportea canadensis	4	1	2	5	2	2	3	5	1	4	4	2	2	2	3	9	3	1	7	3	1	1	2
Lathyrus ochroleucus	3	1	2	5	2	2	3	3	2	3	4	2	5	1	3	5	2	1	9	3	2	1	2
Lathyrus venosus	3	1	2	5	2	2	3	3	2	3	4	2	5	1	3	5	2	1	9	1	2	1	2
Linnaea borealis	2	1	1	3	4	4	4	3	1	2	2	3	3	1	3	4	2	1	4	3	2	1	1
Lycopodium annotinum	2	1	1	3	4	2	4	5	1	1	1	3	3	4	3	7	3	1	4	1	2	1	1
Lycopodium clavatum	2	2	2	3	4	3	4	5	1	1	1	3	2	4	3	7	2	1	0	1	2	1	1
Lycopodium complanatum	2	2	2	3	4	2	4	2	1	1	1	3	1	4	3	7	2	1	0	1	2	1	1
Lycopodium lucidulum	2	1	2	3	4	2	4	5	1	1	1	3	3	4	3	7	3	1	4	2	2	1	1
Lycopodium obscurum	2	1	1	3	4	2	4	5	1	1	1	3	1	4	3	7	3	1	4	2	2	1	1
Lysimachia quadrifolia	3	1	1	5	3	2	3	5	1	3	3	2	2	1	3	9	3	1	6	2	2	1	1
Maianthemum canadense	3	1	2	5	2	2	3	5	1	4	4	2	2	1	2	1	2	2	6	2	2	1	1
Melampyrum lineare	1	1	2	4	1	4	5	5	1	2	2	2	1	1	3	3	3	1	8	1	2	1	1
Mitchella repens	2	1	1	3	4	4	4	3	1	2	2	3	3	1	3	1	3	2	4	3	2	1	1
Mitella diphylla	3	1	2	5	2	2	3	5	1	4	4	2	2	1	2	9	1	2	6	2	2	1	1
Mitella nuda	3	1	2	5	1	2	3	4	1	3	3	2	2	1	3	9	2	2	6	3	2	1	1
Monarda fistulosa	3	1	2	5	2	4	3	5	1	3	3	2	2	1	3	9	3	1	6	1	2	1	2
Moneses uniflora	3	1	2	5	2	2	4	4	1	2	2	3	4	1	3	7	2	1	7	3	2	1	1
Onoclea sensibilis	4	1	2	5	2	2	3	5	2	4	4	2	4	4	3	7	3	2	6	3	2	1	1
Oryzopsis asperifolia	4	1	1	5	3	2	3	5	1	3	3	2	2	2	3	9	2	1	3	3	2	1	1
Osmorhiza claytoni	3	4	2	6	2	4	3	5	2	3	4	3	1	1	3	4	3	1	5	3	2	1	2
Osmunda cinnamomea	3	1	2	5	2	2	3	5	2	3	5	2	4	4	2	7	2	2	6	2	2	1	2
Osmunda claytoniana	3	1	2	5	2	2	3	5	2	3	5	2	4	4	3	7	2	2	6	2	2	1	2
Oxalis montana	3	1	1	5	2	2	3	4	2	2	3	3	4	5	3	5	3	2	5	3	2	1	1
Panax quinquefolius	4	2	2	5	2	4	3	2	2	4	3	2	1	1	2	1	2	2	7	3	2	1	1
Pedicularis canadensis	3	1	2	5	2	2	3	5	1	3	3	2	2	1	2	9	2	1	6	2	2	1	1
Pedicularis lanceolata	3	1	2	5	2	2	3	5	1	3	3	2	2	1	3	9	2	1	6	2	3	1	1

Species	Life History Characteristics																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Phryma leptostachya	3	1	1	5	2	4	3	5	1	4	4	2	1	6	3	4	3	1	6	3	2	1	2
Polygala paucifolia	3	1	2	5	2	2	3	2	1	2	2	3	2	5	3	3	2	2	0	3	2	1	1
Polygonatum pubescens	4	1	2	5	2	2	3	5	1	4	4	2	2	6	3	1	2	2	7	3	2	1	1
Potentilla simplex	3	1	2	5	3	3	3	5	2	3	3	2	2	1	3	3	2	2	6	2	2	1	1
Prenanthes alba	3	4	1	5	2	4	3	5	1	4	4	2	2	1	4	8	3	1	6	3	2	1	2
Pteridium aquilinum	4	1	1	5	3	2	3	2	2	2	4	2	4	4	3	7	3	1	7	1	2	1	2
Pyrola elliptica	3	1	2	5	2	2	4	4	1	3	3	3	4	5	3	7	3	2	5	3	2	1	1
Pyrola rotundifolia	3	1	1	5	2	2	4	4	1	3	3	3	4	5	3	7	2	2	5	3	2	1	1
Pyrola secunda	3	1	2	5	2	2	4	4	1	3	3	3	2	5	3	7	3	2	5	3	2	1	1
Sanguinaria canadensis	4	1	2	5	2	2	3	2	1	4	4	2	4	1	1	3	1	2	7	3	2	1	1
Sanicula gregaria	3	1	2	5	2	4	3	5	2	3	4	3	1	1	3	4	3	1	6	3	2	1	2
Schizachne purpurascens	3	1	1	5	2	2	3	5	1	3	3	2	2	2	3	9	2	1	3	3	2	1	1
Smilacina racemosa	4	1	1	5	2	2	3	5	1	4	4	2	2	1	3	1	2	2	7	3	2	1	1
Smilacina stellata	4	1	2	5	2	2	3	5	1	4	4	2	2	1	3	1	2	2	7	3	2	1	2
Smilax ecirrhata	4	1	1	5	2	2	3	5	1	4	4	2	2	1	3	1	3	2	7	3	2	1	1
Smilax herbacea	4	1	1	5	3	2	3	5	1	4	4	2	4	1	2	1	3	2	9	1	2	1	2
Smilax tamnoides	4	1	1	5	4	2	4	5	1	4	4	2	5	1	3	1	3	2	2	3	1	1	2
Solidago flexicaulis	3	1	2	5	2	2	3	5	1	4	4	2	2	1	4	8	3	1	6	3	2	1	1
Solidago speciosa	3	1	1	6	2	4	3	5	1	4	4	2	2	1	4	8	3	1	6	2	2	1	2
Streptopus roseus	4	1	2	5	2	2	3	5	1	4	4	2	1	1	2	1	2	2	7	1	2	1	1
Thalictrum dioicum	3	1	2	5	1	4	3	5	2	2	3	3	1	2	2	9	2	2	6	3	2	1	1
Trientalis borealis	3	1	2	5	2	3	3	2	1	3	3	2	2	1	3	9	2	2	6	3	2	1	1
Trillium grandiflorum	4	1	2	5	2	4	3	2	2	4	4	2	2	3	5	3	2	2	7	1	2	1	1
Uvularia grandiflora	4	1	2	5	2	4	3	5	1	3	3	2	1	1	2	3	2	2	7	3	2	1	1
Uvularia sessilifolia	4	1	2	5	3	2	3	5	1	3	3	2	1	1	2	3	2	2	7	3	2	1	1
Vaccinium angustifolium	2	1	1	3	4	2	4	5	1	2	2	2	1	1	3	1	2	2	1	1	2	1	1
Viola canadensis	3	1	2	5	2	2	3	2	1	3	3	2	2	5	2	5	2	2	6	3	2	1	1
Viola cucullata	3	1	2	5	2	2	3	4	1	3	3	2	4	5	2	5	2	2	5	1	2	1	1
Viola incognita	3	1	2	5	2	2	3	4	1	3	3	2	4	5	2	5	2	2	5	2	2	1	1
Viola pensylvanica	3	1	2	5	2	2	3	5	1	3	3	2	2	5	2	5	2	2	5	3	2	1	1
Viola pubescens	3	1	2	5	2	2	3	5	1	3	3	2	1	5	2	2	2	2	5	2	2	1	1
Waldsteinia fragarioides	3	1	2	5	1	2	3	4	1	4	4	3	4	1	3	3	2	2	5	3	2	1	1

Table 6

Life history characteristics of southern species coded according to key in figure 5

Species	Life History Characteristics																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Actaea sp.	4	1	2	5	2	4	3	2	2	3	4	2	2	1	3	1	2	2	7	2	2	1	2
Adiantum pedatum	4	1	2	5	2	2	3	2	2	2	4	2	4	4	3	5	2	2	7	3	2	1	1
Agrimonia gryposepala	3	1	1	5	2	4	3	5	2	3	4	2	1	1	3	4	3	1	6	3	2	1	2
Allium tricoccum	4	1	2	1	2	2	3	4	1	4	4	1	4	1	3	9	3	1	7	3	2	1	1
Amorpha canescens	3	1	1	3	4	3	4	5	2	2	3	2	2	1	3	9	2	1	1	3	2	1	2
Amphicarpa bracteata	3	1	1	5	1	4	3	5	2	3	3	2	5	5	3	5	3	1	6	2	2	1	2
Anemone cylindrica	3	1	2	5	2	4	3	4	2	3	3	2	2	1	3	8	2	1	6	3	2	1	1
Anemone quinquefolia	4	1	2	5	2	2	3	2	2	2	3	3	2	1	1	9	2	2	7	2	2	1	1
Anemonella thalictroides	4	2	2	6	2	4	3	2	2	2	3	1	2	1	1	3	2	2	7	3	2	1	1
Apocynum androsaemifolium	3	1	1	7	3	1	3	5	1	3	3	2	1	1	3	8	3	1	6	2	2	1	2
Aquilegia canadensis	3	4	1	5	1	1	3	5	2	3	3	2	1	6	2	9	2	2	6	1	2	1	2
Aralia nudicaulis	3	1	2	5	1	2	3	2	2	3	4	2	2	1	3	1	2	2	6	3	2	1	1
Aralia racemosa	3	1	1	5	2	4	3	5	2	4	5	2	1	1	3	1	3	1	6	3	2	1	2
Arenaria lateriflora	3	1	2	5	2	2	3	5	1	2	2	2	1	1	2	3	2	1	6	3	2	1	1
Arisaema atrorubens	4	1	2	2	2	2	3	2	2	4	4	2	2	1	2	1	3	2	7	1	2	1	1
Asarum canadense	3	1	2	5	2	2	3	2	1	4	4	2	4	5	2	3	1	2	6	1	2	1	1
Aster macrophyllus	3	1	1	5	2	2	3	4	1	4	4	3	2	1	3	8	3	1	5	1	2	1	2
Aster shortii	3	1	2	6	2	4	3	5	1	3	3	2	1	1	4	8	3	1	6	2	2	1	2
Athyrium filix-femina	4	1	2	5	2	2	3	5	2	1	4	2	4	4	3	5	2	1	7	1	2	1	1
Botrychium virginianum	4	2	1	6	2	4	3	2	2	2	4	2	2	4	3	7	2	1	6	3	2	1	1
Brachyelytrum erectum	3	1	2	5	1	2	3	5	1	4	4	2	2	2	3	9	3	1	3	2	2	1	1
Campanula rotundifolia	3	1	2	5	2	2	3	5	1	3	3	2	2	1	3	9	2	1	6	1	2	1	1
Carex albursina	3	1	2	5	2	2	3	4	1	4	4	3	2	2	3	9	2	2	3	3	2	1	1
Carex pensylvanica	4	1	2	5	1	3	3	5	1	3	3	3	2	2	2	9	2	2	3	1	2	1	1
Caulophyllum thalictroides	4	1	2	5	2	2	3	5	2	3	4	2	1	1	2	1	3	2	7	3	2	1	2
Ceanothus americanus	2	1	1	3	4	2	4	5	1	3	3	2	1	1	3	5	2	1	1	1	2	1	1
Circaea quadrisulcata	4	1	2	5	2	2	3	5	1	4	4	2	1	1	3	4	3	1	7	3	2	1	1
Claytonia virginica	4	1	2	2	2	4	3	5	1	3	3	1	2	1	1	5	1	2	7	2	2	1	1
Conopholis americana	4	2	2	5	2	2	3	1	1	2	2	5	2	1	3	7	2	2	7	3	2	3	1

Species	Life History Characteristics																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Convolvulus spithamaeus	3	1	1	7	2	1	3	5	1	3	3	2	3	1	3	9	2	1	6	2	2	1	1
Cryptotaenia canadensis	3	1	2	5	2	4	3	5	2	3	4	2	1	1	3	5	2	1	6	3	2	1	1
Cypripedium calceolus var. pubescens	4	2	2	5	2	2	3	5	1	4	4	2	2	1	3	7	3	2	7	1	2	1	1
Cystopteris bulbifera	3	1	2	5	2	5	3	4	2	2	4	2	4	4	3	7	3	1	6	3	2	1	1
Cystopteris fragilis	4	1	2	5	2	2	3	5	2	2	3	2	4	4	3	7	2	1	6	1	2	1	1
Dentaria laciniata	4	1	2	5	2	2	3	2	1	3	3	1	2	1	1	9	1	2	7	1	2	1	1
Desmodium glutinosum	3	1	5	5	2	2	3	2	2	3	4	2	2	1	3	4	3	1	6	2	2	1	2
Desmodium nudiflorum	3	1	1	5	2	2	3	2	2	3	4	2	1	1	3	4	2	1	6	2	2	1	1
Dicentra cucullaria	4	1	2	2	2	5	3	4	2	2	4	1	4	1	1	3	1	2	7	3	2	1	1
Diervilla lonicera	2	1	1	3	4	1	4	5	1	3	3	2	1	1	3	9	2	2	1	3	2	1	1
Dryopteris spinulosa	3	1	2	5	2	2	4	5	2	2	4	3	4	4	3	5	3	1	4	1	2	1	1
Erythronium albidum	4	1	2	1	2	2	3	4	1	4	4	1	4	1	2	3	1	2	7	2	2	1	1
Erythronium americanum	4	1	2	1	2	2	3	4	1	4	4	1	4	1	2	3	1	2	7	3	2	1	1
Eupatorium rugosum	3	1	2	6	2	4	3	5	1	4	4	2	1	1	4	8	3	1	6	1	2	1	2
Euphorbia corollata	4	4	1	6	2	4	3	5	1	3	3	2	1	1	3	5	2	1	7	1	2	1	2
Floerkea proserpinacoides	1	1	2	4	1	4	5	3	2	2	2	1	2	5	1	3	1	1	8	3	2	1	1
Fragaria virginiana	3	1	2	5	2	3	3	4	2	3	4	2	4	1	2	1	2	2	4	1	2	1	1
Galium aparine	1	1	2	3	4	4	1	3	1	2	2	4	3	1	3	4	2	1	8	3	2	1	1
Galium circaezans	3	1	2	5	2	3	3	5	1	3	3	2	1	1	3	9	2	1	6	2	2	1	1
Galium concinnum	3	1	2	6	2	4	3	5	1	1	1	2	1	1	3	9	2	1	6	3	2	1	1
Galium triflorum	3	1	2	5	2	3	3	3	1	3	3	2	1	1	3	4	2	1	6	3	2	1	1
Geranium maculatum	3	1	2	5	2	2	3	5	1	4	4	2	1	1	2	5	2	2	6	3	2	1	2
Geum canadense	3	1	2	6	1	4	3	5	2	3	3	3	1	1	3	4	3	1	5	1	2	1	2
Goodyera pubescens	3	2	2	5	2	2	3	4	1	3	3	3	4	1	3	7	3	1	5	3	2	1	1
Hackelia virginiana	3	4	1	3	1	4	2	5	1	3	3	3	1	1	3	4	3	1	6	3	2	1	2
Helianthemum canadense	3	4	1	7	1	1	3	5	1	2	2	2	2	5	3	9	2	1	2	2	2	1	1
Helianthus strumosus	3	1	1	5	2	2	3	5	1	4	4	2	2	1	3	9	2	1	6	3	2	1	2
Hepatica acutiloba	3	1	2	5	1	4	3	4	1	3	3	3	4	1	1	3	1	2	5	2	2	1	1
Hieracium canadense	3	1	1	5	2	4	3	5	1	3	3	2	1	1	5	8	2	1	6	1	2	1	2
Hydrophyllum virginianum	3	1	2	5	2	2	3	5	1	4	4	2	1	1	3	9	2	2	6	3	2	1	1

Species	Life History Characteristics																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Hystrix patula	3	1	2	5	1	2	3	5	1	3	3	2	2	2	3	9	3	1	3	2	2	1	2
Impatiens sp.	1	1	2	4	1	4	5	5	1	4	4	2	2	3	4	5	2	1	8	2	2	1	2
Isopyrum biternatum	3	3	2	5	2	2	3	5	2	2	2	4	1	1	2	3	1	2	5	3	2	1	1
Lactuca biennis	3	1	2	3	1	4	2	5	1	4	4	3	2	1	3	8	3	1	5	2	2	1	2
Laportea canadensis	4	1	2	5	2	2	3	5	1	4	4	2	2	2	3	9	3	1	7	3	1	1	2
Lathyrus ochroleucus	3	1	1	5	2	2	3	3	2	3	4	2	5	1	3	5	2	1	9	3	2	1	2
Lathyrus venosus	3	1	1	5	2	2	3	3	2	3	4	2	5	1	3	5	2	1	9	1	2	1	2
Lysimachia quadrifolia	3	1	1	5	3	2	3	5	1	3	3	2	2	1	3	9	3	1	6	2	2	1	1
Maianthemum canadense	3	1	2	5	2	2	3	5	1	4	4	2	2	1	2	1	2	2	6	2	2	1	1
Mitella diphylla	3	1	2	5	2	2	3	5	1	4	4	2	2	1	2	9	1	2	6	2	2	1	1
Monarda fistulosa	3	1	2	5	2	4	3	5	1	3	3	2	2	1	3	9	3	1	6	1	2	1	2
Orchis spectabilis	4	2	2	5	2	4	3	5	1	4	4	2	2	1	3	7	3	2	7	3	2	1	1
Osmorhiza claytoni	3	4	2	6	2	4	3	5	2	3	4	3	1	1	3	4	3	1	5	3	2	1	1
Osmorhiza longistylis	3	4	2	6	2	4	3	5	2	3	4	3	1	1	3	4	3	1	6	1	2	1	1
Osmunda cinnamomea	3	1	2	5	2	2	3	5	2	3	5	2	4	4	2	7	2	2	6	2	2	1	2
Osmunda claytoniana	3	1	2	5	2	2	3	5	2	3	5	2	4	4	3	7	2	2	6	2	2	1	2
Panicum latifolium	3	1	2	6	1	2	3	5	1	3	3	3	1	2	5	9	4	1	3	3	2	1	1
Parietaria pensylvanica	1	4	2	4	1	4	5	5	1	3	3	2	2	2	3	7	3	1	8	3	2	1	1
Phlox divaricata	2	1	2	3	1	3	4	5	1	3	3	2	2	1	2	5	2	2	2	2	2	1	1
Phryma leptostachya	3	1	1	5	2	4	3	5	1	4	4	2	1	6	3	4	3	1	6	3	2	1	2
Pilea pumila	1	1	2	4	1	4	5	5	1	3	3	2	2	2	2	7	3	1	8	2	2	1	1
Podophyllum peltatum	4	1	2	5	2	2	3	2	1	4	4	2	1	1	2	1	3	2	7	3	2	1	1
Polemonium reptans	3	1	2	5	2	4	3	5	2	2	3	2	1	1	2	5	1	2	6	3	2	1	1
Polygonatum pubescens	4	1	2	5	2	2	3	5	1	4	4	2	2	6	3	1	2	2	7	3	2	1	1
Polyminia canadensis	3	1	2	5	2	2	3	5	1	4	4	2	2	1	3	9	3	1	6	3	2	1	2
Potentilla simplex	3	1	2	5	3	3	3	5	2	3	3	2	2	1	3	3	2	2	6	2	2	1	1
Prenanthes alba	3	4	1	5	2	4	3	5	1	4	4	2	2	1	4	8	3	1	6	3	2	1	2
Pteridium aquilinum	4	1	1	5	3	2	3	2	2	2	4	2	4	4	3	7	3	1	7	1	2	1	2
Pteretis pensylvanica	3	1	2	5	2	2	3	5	2	3	5	2	4	4	3	7	2	1	6	2	2	1	1
Pyrola elliptica	3	1	2	5	2	2	4	4	1	3	3	3	4	5	3	7	3	2	5	3	2	1	1
Ranunculus abortivus	3	1	2	6	1	4	3	5	1	3	3	2	1	1	2	9	2	2	6	1	2	1	1

Species	Life History Characteristics																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Ranunculus septentrionalis	3	1	2	6	2	3	3	5	2	3	3	2	1	1	2	9	2	2	6	2	2	1	1
Sanguinaria canadensis	4	1	2	5	2	2	3	2	1	4	4	2	4	1	1	3	1	2	7	3	2	1	1
Sanicula gregaria	3	1	2	5	2	4	3	5	2	3	4	3	1	1	3	4	3	1	6	3	2	1	2
Smilacina racemosa	4	1	1	5	2	2	3	5	1	4	4	2	2	1	3	1	2	2	7	3	2	1	1
Smilacina stellata	4	1	2	5	2	2	3	5	1	4	4	2	2	1	3	1	2	2	7	3	2	1	2
Smilax ecirrhata	4	1	1	5	2	2	3	5	1	4	4	2	2	1	3	1	3	2	7	3	2	1	1
Smilax herbacea	4	1	1	5	3	2	3	5	1	4	4	2	5	1	2	1	3	2	9	1	2	1	2
Smilax tamnoides	2	1	1	3	2	2	4	5	1	4	4	2	5	1	3	1	3	2	2	3	1	1	2
Solidago flexicaulis	3	1	2	5	2	2	3	5	1	4	4	2	2	1	4	8	3	1	6	3	2	1	1
Solidago speciosa	3	1	1	6	2	4	3	5	1	4	4	2	2	1	4	8	3	1	6	2	2	1	2
Solidago ulmifolia	3	1	2	6	2	2	3	5	1	4	4	2	1	1	4	8	3	1	6	2	2	1	2
Taenidia integerrima	3	4	1	6	2	4	3	5	2	3	3	2	1	1	3	9	2	1	6	3	2	1	2
Thalictrum dioicum	3	1	2	5	1	4	3	5	2	2	3	3	1	2	2	9	2	2	6	3	2	1	1
Tovara virginiana	4	1	2	5	2	2	3	5	1	4	4	2	2	1	3	5	3	1	7	3	2	1	2
Trillium flexipes	4	1	2	5	2	4	3	2	2	4	4	2	2	3	5	3	2	2	7	3	2	1	1
Trillium grandiflorum	4	1	2	5	2	4	3	2	2	4	4	2	2	3	5	3	2	2	7	1	2	1	1
Trillium recurvatum	4	1	2	5	2	4	3	2	2	4	4	2	2	3	5	3	2	2	7	2	2	1	1
Triosteum perfoliatum	3	1	1	6	2	2	3	5	1	4	4	2	2	1	3	1	2	1	6	3	2	1	2
Uvularia grandiflora	4	1	2	5	2	4	3	5	1	3	3	2	1	1	2	3	2	2	7	3	2	1	1
Veronicastrum virginicum	4	1	1	5	2	2	3	5	1	3	3	2	2	1	2	9	2	1	7	3	2	1	2
Vicia americana	3	1	2	5	2	2	3	5	2	2	4	2	5	1	3	5	2	1	6	1	2	1	1
Viola cucullata	3	1	2	5	2	2	3	4	1	3	3	2	4	5	2	5	2	2	5	1	2	1	1
Viola pubescens	3	1	2	5	2	2	3	5	1	3	3	2	1	5	2	2	2	2	5	2	2	1	1
Viola sagittata	3	1	1	5	2	2	3	4	1	2	2	2	4	5	2	5	2	2	5	1	2	1	1

As explained previously, these coded values, together with those in tables 3 and 4, were punched in IBM cards and a series of "sums of average frequencies" was tabulated for each characteristic. The numerous tables in the appendix contain these sums and, in addition, indicate the number of species which contributed to each sum.

3. Conversion of Curves From Absolute to Relative Basis

If quadrat frequency values are accepted as being indicative of density, then the sums of average frequencies as contained in these tables represent the numbers of individuals which exhibit a particular life history characteristic. These values, then, are on an absolute basis.

If a certain characteristic has no value in enabling plants to grow under the influence of certain environmental conditions, the number of plants possessing that characteristic may be expected to occur as a more or less constant proportion of the total vegetation. No effect of selective action by the environment is evident. Any trend shown by the sums of average frequencies is only apparent because the total sum of average frequencies for all species is different in each of the nine continuum intervals. Plants possessing a trait with no true survival value may show a very definite trend on an absolute basis because there is a definite trend for the whole population.

A considerable difference may exist between the apparent trend on an absolute basis and the trend on a relative

basis as is shown in figure 6. Consequently all sums of average frequencies have been expressed as percentages of the total sums for the whole population, which are presented in the appendix. The relative values are included in the tables of the appendix and it is with these that the remainder of this presentation will be concerned.

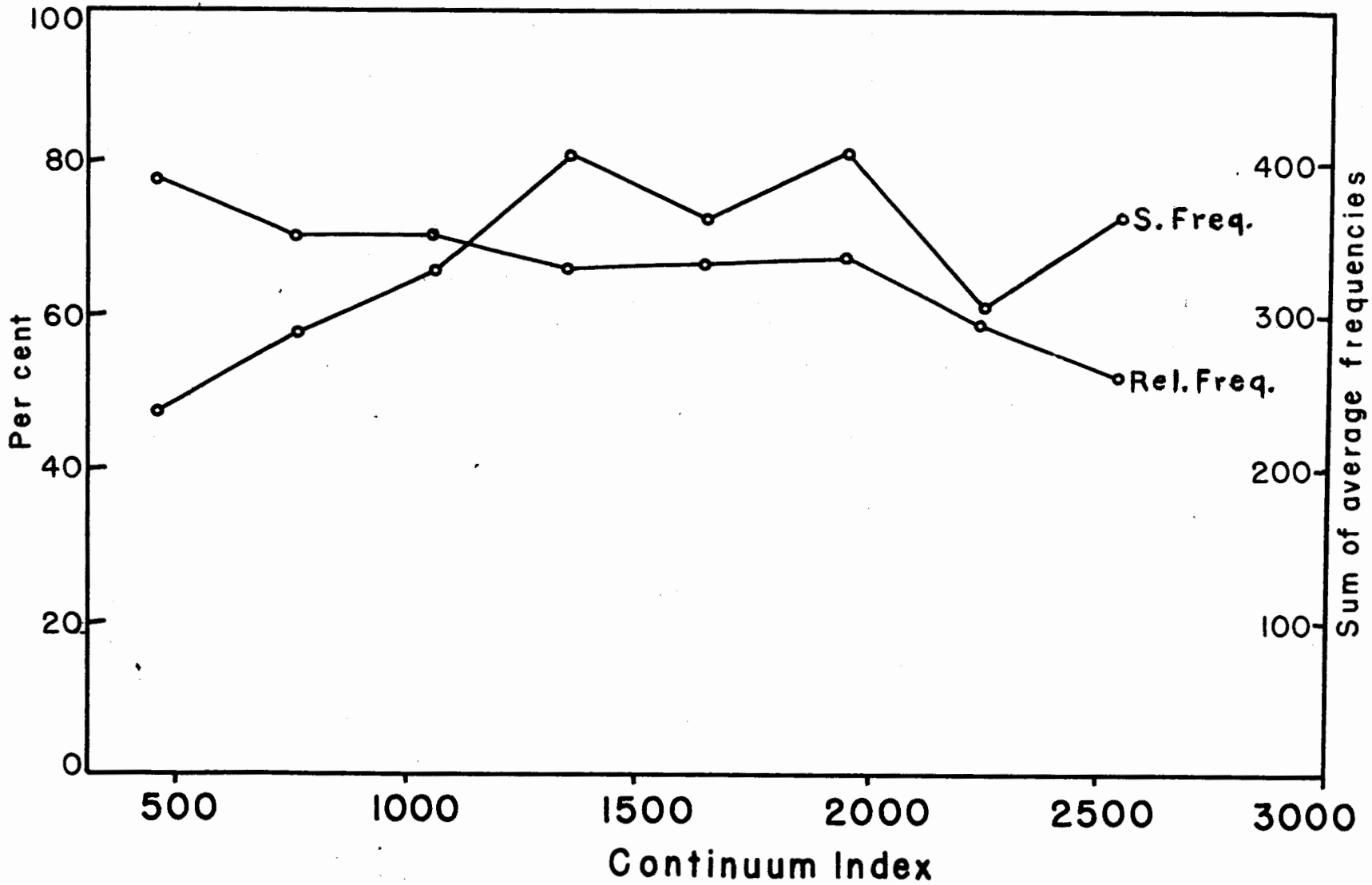
4. Determination of Significance of Curves

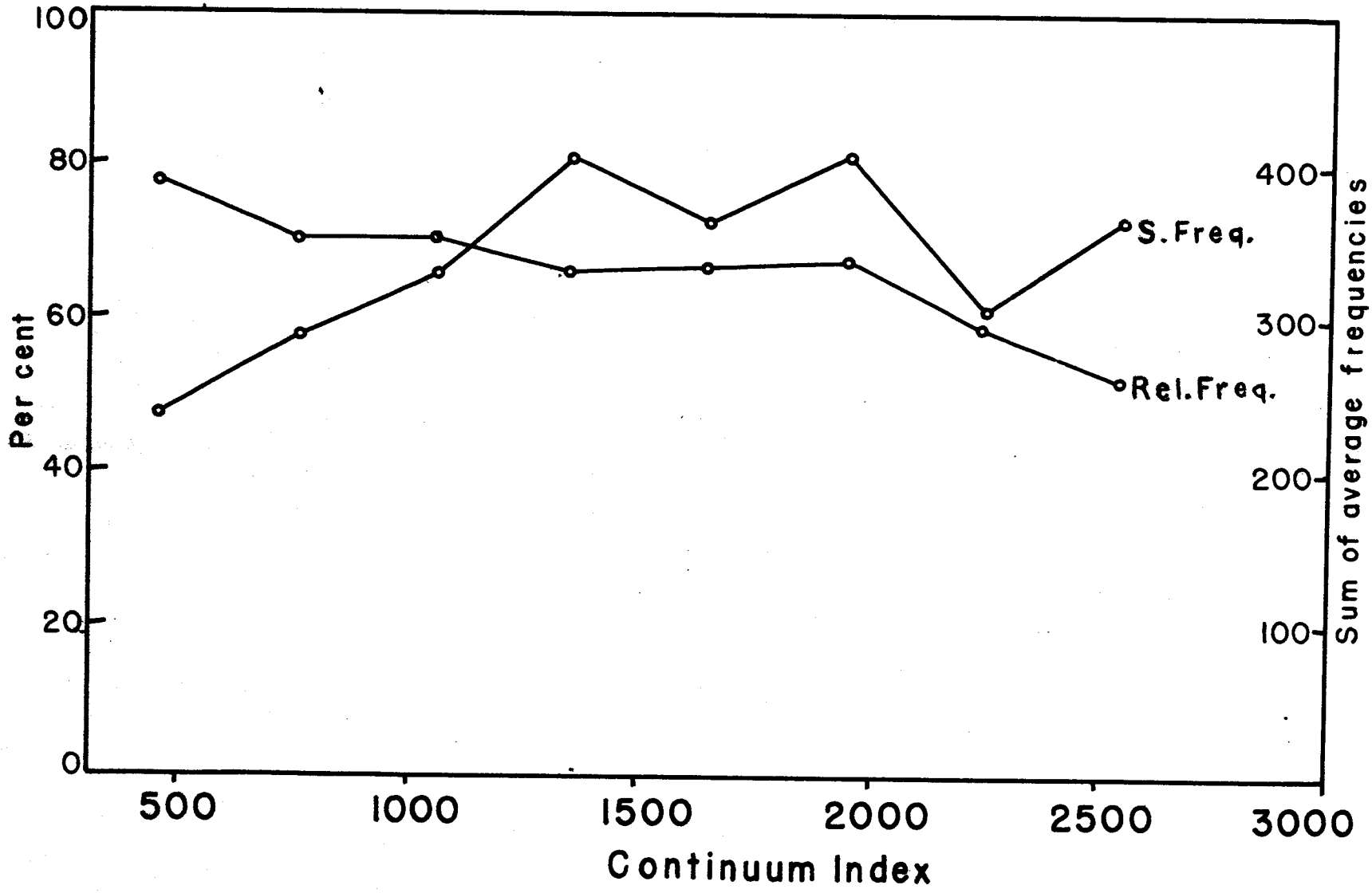
The curves which resulted from the use of this procedure number more than two hundred. Almost a complete gradual transition from definitely pioneer to obviously climax trends may be found among the mass of data. Not all of these trends are comparable in significance. An attempt to asses the validity of the apparent trends was made by means of a method described by Snedecor (1946, pp. 388-392). Briefly, this method consists of measuring the reduction in the sum of squares of deviations about a horizontal straight line, passing through the mean, when the data are fitted to another straight line or to a curve of higher degree.

Tests of significance at the five per cent level distinguished the curves which exhibit no apparent deviation from a horizontal straight line through the mean. It is concluded that the characteristics which show such a curve are varying at random as a more or less constant proportion of the total population. If this assumption is true, then these traits are not of great value in enabling plants to flourish under the environmental conditions characterizing

Figure 6

Cauline canopy along the southern continuum, showing different trends on absolute and relative bases


100
80
60
40
20
0
Per cent
400
300
200
100
Sum of average frequencies
S. Freq.
Rel. Freq.
500
1000
1500
2000
2500
3000
Continuum Index


100
80
60
40
20
0
Per cent
400
300
200
100
Sum of average frequencies
S. Freq.
Rel. Freq.
500
1000
1500
2000
2500
3000
Continuum Index

any one portion of the continuum. In table 7 these characteristics are listed as showing "no trend".

5. Evaluation of Significant Curves

The remaining curves deviate significantly from a horizontal straight line. They, therefore, appear to be of more importance under certain environmental conditions than under others. These curves may be separated more or less readily, by inspection and by the significance test, into three groups, namely, pioneer and climax monotopes and bell-shaped curves. These three types of curve are distinguished in table 7.

In an attempt to determine the extent of occurrence of these characteristics in the population, the three groups have been subdivided according to whether the mean is high (above 20 per cent) or low (below 20 per cent). In figures 7 through 10 are presented representatives of these seven types of curves.

Life form spectra show definite trends, as do leaf size spectra. These will be considered in more detail in the next section.

Tap roots appear to be a pioneer trait and tuberous roots are climax, although they, as well as fascicled roots, are by no means common among forest herbs.

A very definite trend is found for root depth. Many pioneer plants have their roots growing in more than one soil

Table 7

Classification of relative average frequency curves for life history characteristics. High curves have means greater than 20 per cent. Curves along northern and southern continua are represented by "N" and "S", respectively.

Characteristic	Pioneer		Middle		Climax		No Trend
	High	Low	High	Low	High	Low	
Life Form							
Therophyte						S	N
Chamaephyte		N S					
Hemicryptophyte			N S				
Cryptophyte					N S		
Root System							
Fibrous			S				N
Fascicled						S	N
Tuberous						S	
Tap		N S					
Depth of Roots							
Indifferent	N S						
A_1 Horizon					N S		
Overwintering Organ							
Bulb						N S	
Corm						N S	
Stem Buds		N S					
Seeds						S	N
Rhizome			N S				
Crown buds				S			N
Root buds		N S					
Overwintering Organ Depth							
A_o Horizon				N S			
A_1 Horizon					N S		
Indifferent		N S					
Aerial		N S					
Vegetative Reproduction							
Roots		N S					
Rhizome			N		S		
Stolons		N S					
Absent					S	N	
Detached parts						S	
Longevity							
Winter annual						S	
Biennial							S
Herbaceous perennial			S		N		
Short-lived, woody		N S					
Annual						S	N

Characteristic	Pioneer		Middle		Climax		No
	High	Low	High	Low	High	Low	Trend
Canopy							
Lacking				S		N	
Umbrella-like			N S				
Prostrate				N			S
Basal			N			S	
Cauline	S						N
Leaf Type							
Simple	N						S
Compound					N		S
Leaf Size (lft = lf)							
Leptophyll				N S			
Nanophyll	N						S
Microphyll			N				S
Mesophyll					N S		
Leaf Size (cmpd lf = lf)							
Leptophyll				N S			
Nanophyll		N					S
Microphyll	N S						
Mesophyll			S		N		
Macrophyll				N			S
Photosynthetic Season							
Vernal						N S	
Growing Season	S						N
Evergreen			N	S			
Winter						S	
None				S		N	
Aerial Stem Type							
Deliquescent			S				N
Excurrent	N S						
Reclining				N		S	
Acaulescent					N	S	
Twining		S		N			
Pollination							
Insect	N		S				
Wind				S			N
Water				N S			
Cleistogamous and insect						N	S
Insect and bird						N	S
Insect,bird,& cleist.						N S	
All insect							N S
All cleistogamous							

Characteristic	Pioneer		Middle		Climax		No Trend
	High	Low	High	Low	High	Low	
Blooming Season							
Prevernal						N S	
Vernal					N S		
Aestival	N S						
Autumnal							N S
Growing Season							S
Prevernal and vernal					N S		
Seed of Fruit Dispersal							
Fleshy	N	S					
Explosive and elaiosome						N S	
Elaiosome						N S	
Stick-tights				S		N	
Explosive	S					N	
Small and Light				N S			
Plumed		S		N			
Winged		N					
No special method	N S						
All wind		S		N			
All elaiosome						N S	
All explosive	S					N	
Season of Fruit Ripening							
Vernal						N S	
Aestival	N S						
Autumnal			N S				
Growing season							S
Season of Flower Bud Formation							
Current season	N S						
Previous season					N S		
Turrill's Extended Scheme							
Deciduous shrub		N S					
Perennial herbs or sub-shrubs, partially woody at base, and aerial parts dying back, but not to ground level							N S
Grasses and grass-like				N S			
Perennial herbs and sub-shrubs with runners, or herbaceous or suffruct-icose stems.		S		N			
Rosette plants				N S			
Perennial herbs dying down yearly, with perennating buds on more or less thick stock at ground level.			N S				

Characteristic	Pioneer		Middle		Climax		No Trend
	High	Low	High	Low	High	Low	
Turrill's Scheme (cont.)							
Geophytes					N S		
Annuals						S	N
Herbaceous twiners		S		N			
Evergreen shrubs		N					
Taxonomy							
Unstable	N S						
Intermediate							N S
Stable					N S		
Spines							
Armed						N S	
Not armed	N S						
Nutrition							
Obligate autotroph							N S
Partial autotroph		N					
Parasite				S		N	
Flower Height							
Below 18 inches					N S		
Above 18 inches	N S						

Figure 7

Examples of pioneer characteristics with high mean (indifferent root depth along northern continuum) and with low mean (deciduous shrubs along northern continuum)

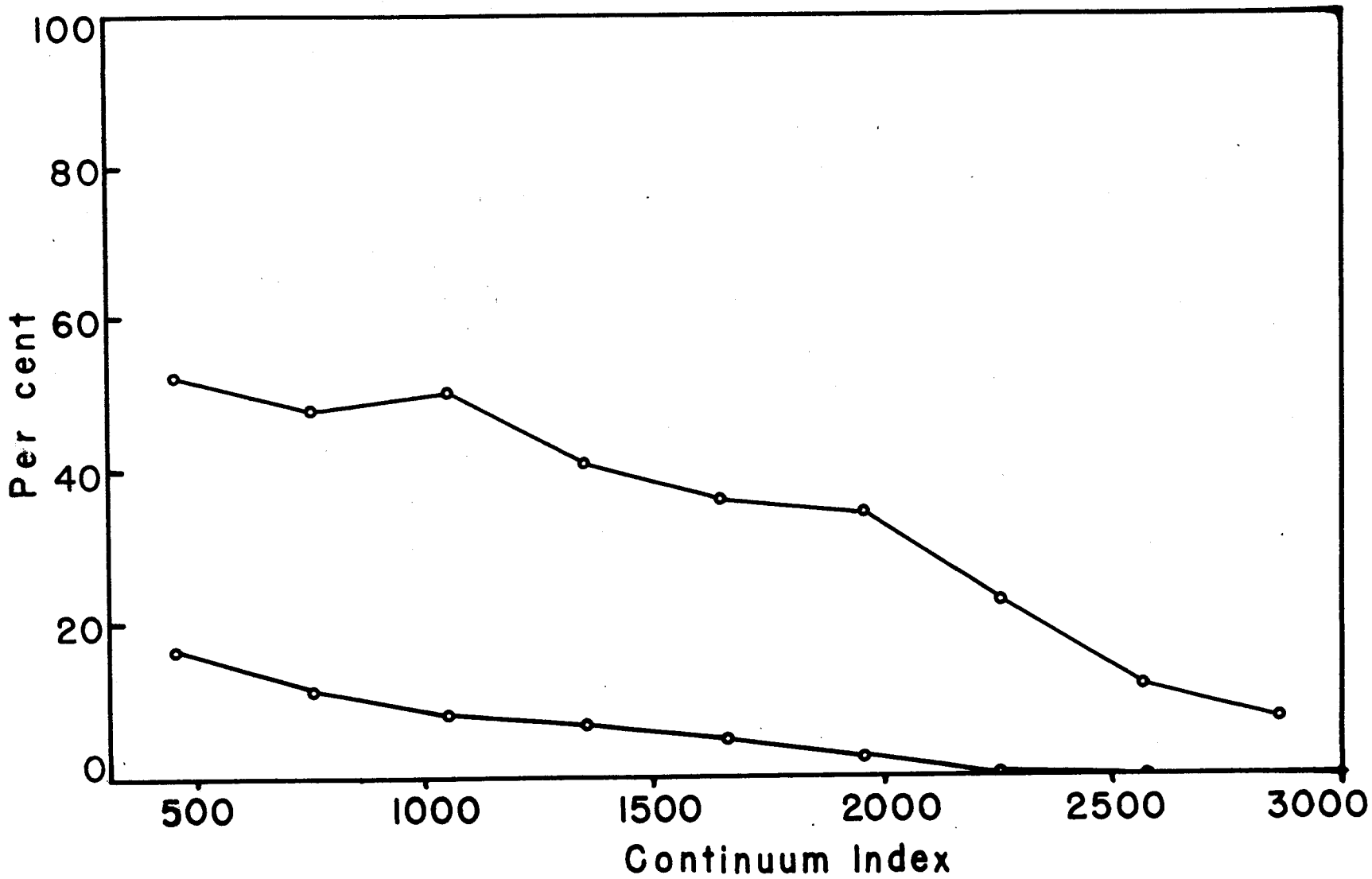

100
80
60
40
20
0
Per cent
500
1000
1500
2000
2500
3000
Continuum Index

Figure 8

Examples of characteristics of intermediate vegetation with high mean (hemicryptophytes along southern continuum) and with low mean (evergreens along southern continuum)

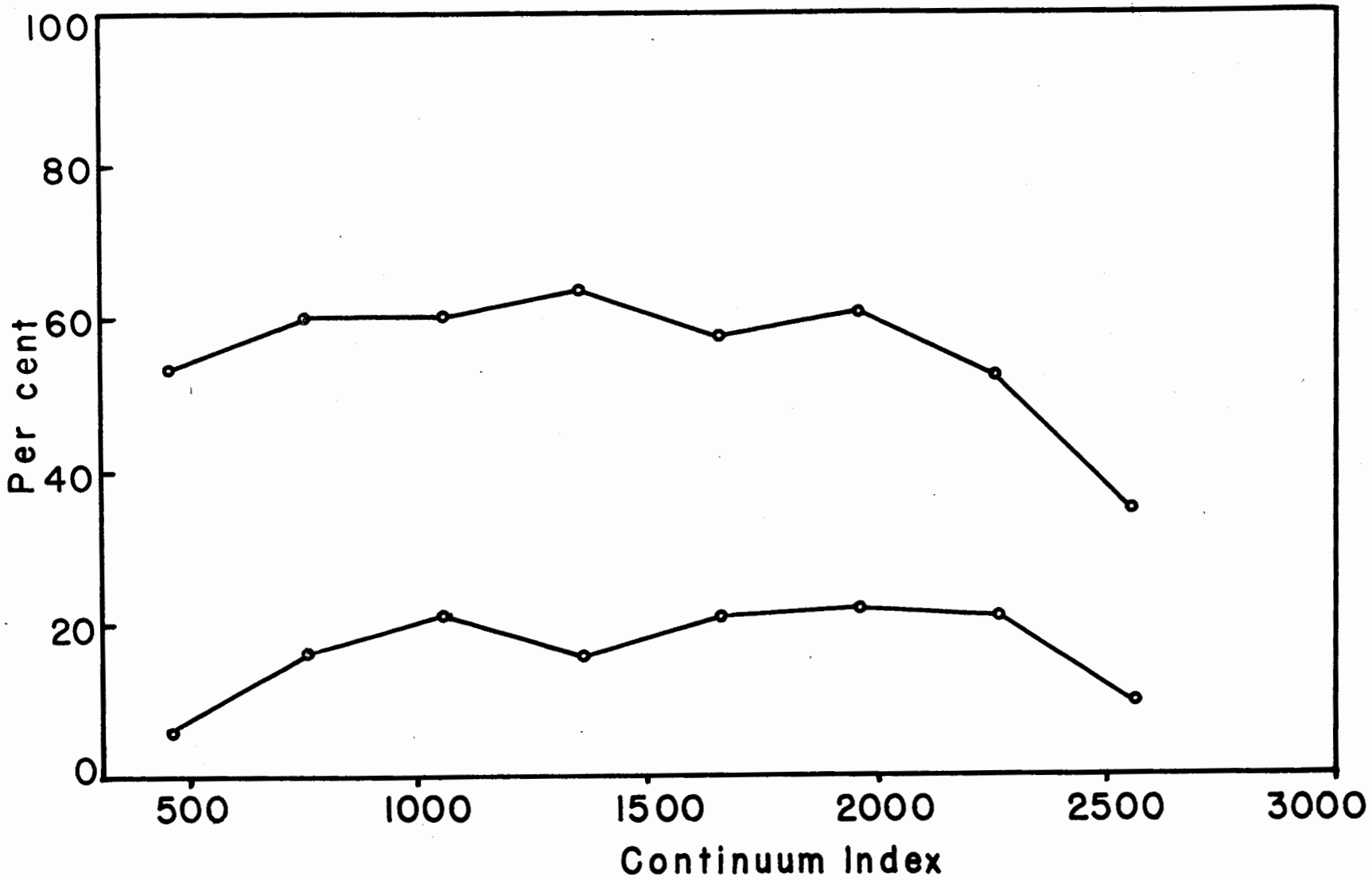

100
80
60
40
20
0
Per cent
500
1000
1500
2000
2500
3000
Continuum Index

Figure 9

Examples of climax characteristics with high mean (flower buds formed during previous growing season along southern continuum) and with low mean (explosive seed dispersal along northern continuum)

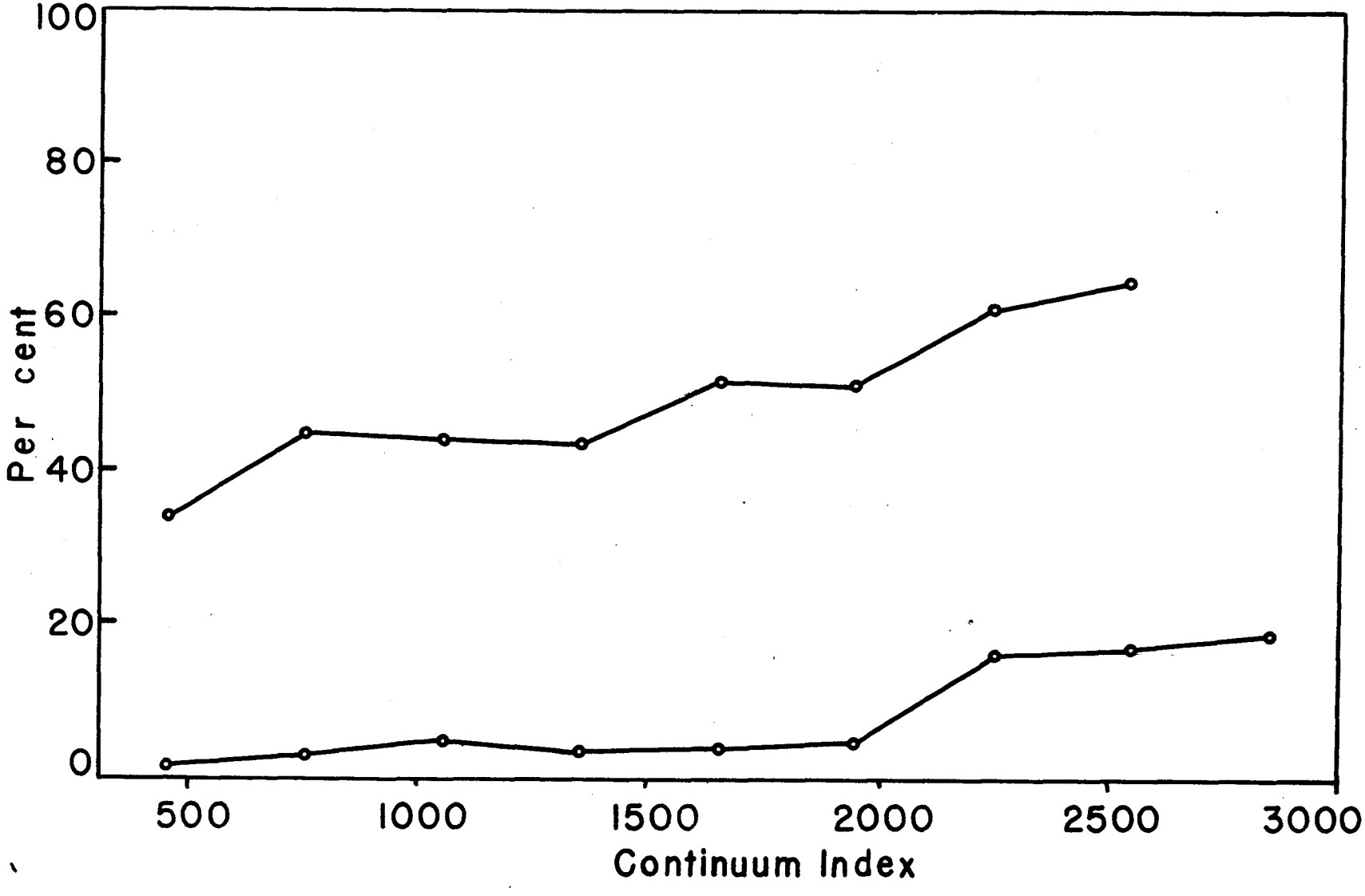
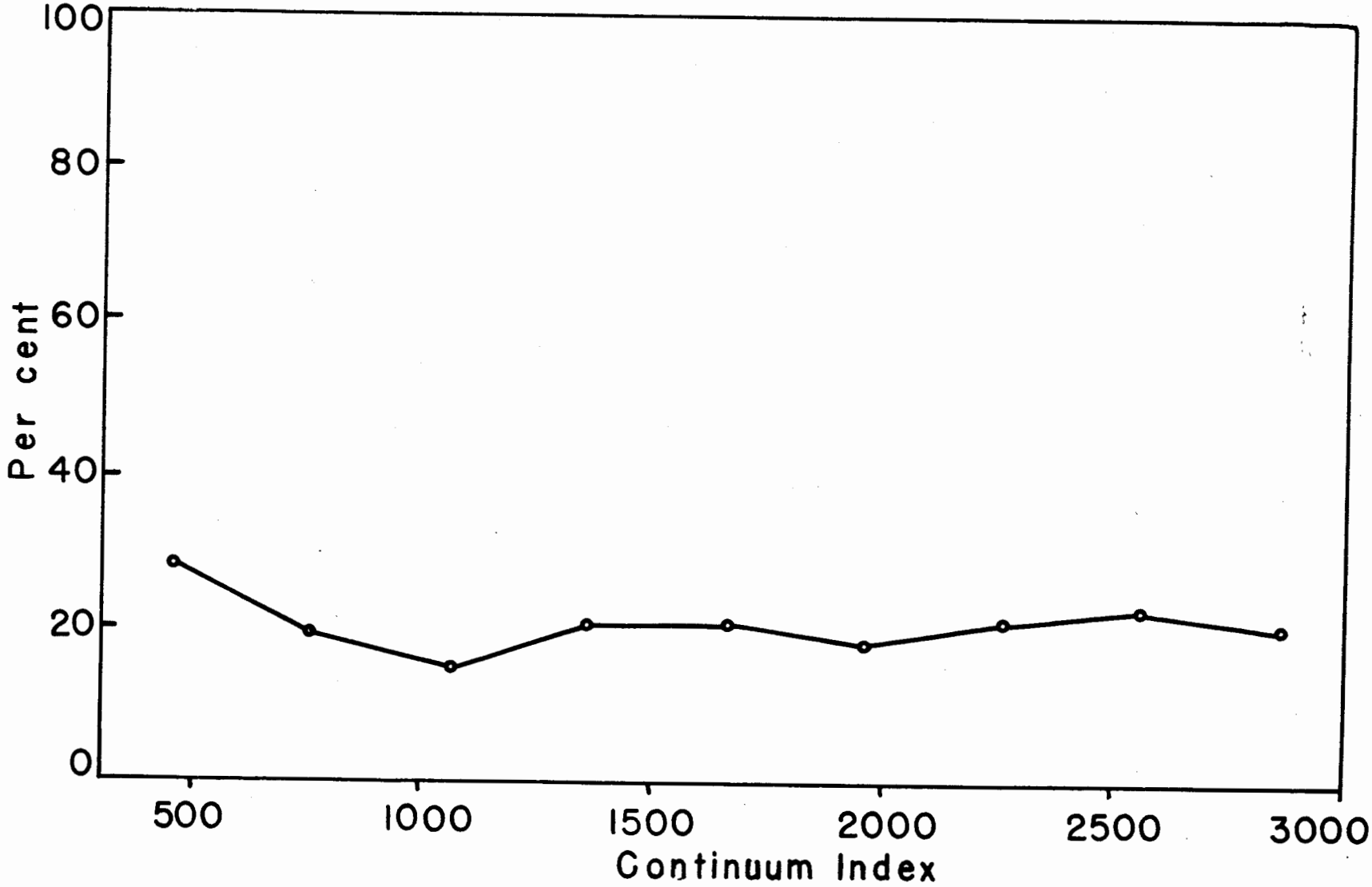

100
80
60
40
20
0
Per cent
500
1000
1500
2000
2500
3000
Continuum Index

Figure 10

An example of a characteristic exhibiting "no trend" (intermediate taxonomy along northern continuum)


100
80
60
40
20
0
Per cent
500
1000
1500
2000
2500
3000
Continuum Index

horizon. Climax plants, on the other hand, normally have roots only in the A_1 horizon. The depth of this horizon is greater in more climax stands, but this is not considered to be the determining factor. It is believed that the roots of most climax plants would be confined to this soil layer even where it is fairly shallow.

Bulbs and corms are exclusively climax overwintering organs within the limits of the present investigation. Root buds and stem buds, on the other hand, are characteristically pioneer in occurrence. An exception to this last statement is caused by the inclusion of Galium aparine, a climax winter annual, in the stem bud category for the southern continuum. Since this species is actively growing during the winter its active terminal bud should not be considered an overwintering organ. A separate category should have been erected for this species. Had this been done the curve for southern stem buds would also show a pioneer trend and is so shown in table 7. Rhizomes as overwintering organs are more important in the intermediate portion of the continua.

In comparable manner, pioneer plants frequently overwinter with aerial buds, or if by means of subterranean organs, these buds are found in different soil horizons. Intermediate species, on the other hand, tend to overwinter with buds located in the A_0 horizon to a greater extent than either the pioneer or climax species. Climax vegetation characteristically overwinters with buds in the A_1 horizon.

Vegetative reproduction by stolons and root buds are clearly pioneer traits while the special types included under "detached parts" are climax. As indicated by the "vegetative reproduction absent" curves, vegetative reproduction is least evident among climax vegetation. The trend is quite pronounced in the northern continuum. In the southern continuum, however, there is only a slight trend in the importance of vegetative reproduction after an abrupt initial decline.

The trends for longevity require some explanation. Only one winter annual, Galium aparine, is included and since this is a climax plant the trend is a climax one. Only two biennials are included, namely Hackelia virginiana and Lactuca biennis, and the values are too low and too irregular to show any pronounced trend. Certainly biennials are much more common in unforested sites. While the annuals included in this study constitute a climax group of species there are certainly other annuals, not included, which might have caused the trend to be reversed. As with biennials, annuals are characteristically pioneer plants. Short-lived woody plants are generally the same species included under the headings of chamaephyte and stem buds as overwintering organs, and therefore show the same pioneer trend.

Canopy lacking is another characteristic with a paucity of species. Only Conopholis americana is included in the southern list. According to Percival (1931) this species is

parasitic only upon Quercus borealis. Certainly the average frequency curve for this species matches the importance curve for red oak. In the northern list only one species, Epifagus virginiana, appears and this, of course, follows the climax trend of Fagus americana. With the exception of cauline canopies along the southern continuum the canopy trends are not particularly striking. What the significance of this trend may be is not known.

No significant trend is apparent in the case of simple versus compound leaves along the southern continuum. A slightly discernible trend may exist, and if so, it follows that of the northern continuum. In the northern continuum a definite trend exists. While simple leaves are more common throughout the continuum than compound leaves, they are less important among climax vegetation and among pioneer plants. The effect of this situation is discussed further in connection with leaf size spectra, in the next section of this paper.

Many investigators have referred to the commonness of vernal photosynthetics in climax forests. It is interesting to note that such plants are rather uncommon in the beech woods of Britain while they are conspicuous in the Quercus robur stands. According to Salisbury (1916) the shade cast by the beeches in winter and early spring is much denser than that cast by the oak, so dense, in fact, that there is not enough light for the vernal species. Evergreens, although

less common in the southern continuum, are most important in the intermediate portions of both continua. This characteristic of the vegetation is rather prominent in the northern pine woods. Galium aparine and Isopyrum biternatum are the only winter photosynthetics included in the species lists and these are both climax species. Aplectrum hyemale is another such plant, but was not sufficiently common to be included. The general tendency of climax vegetation to carry on photosynthesis during seasons other than summer is rather striking. Many of the climax species here included under the category "growing season" actually carry on most of their food manufacturing during the spring as noted by Hesselman (1904) and Salisbury (1916).

On the whole the trends shown for aerial stem type are more impressive than are those for canopy type. As with this latter series, nothing is known of its possible significance.

Various groupings of pollination mechanisms were necessary because of the difficulty of assessing the relative importance of the various agencies when a certain species is known to effect pollination in more than one way. For example, Wildman (1950) has shown that Asarum may produce seed without the aid of insects. The determination of such relative importance for each species would require prolonged and detailed observation and experimentation over a number of years and in various sites. Most species are here considered to be dependent upon insects for pollination. It is

of interest that those plants which depend only upon insects are more common in the pioneer stages of the continua. The tendency of climax species to be adapted to more than one pollinating agent is more conspicuous in the northern continuum, although such species do not constitute the majority of the climax vegetation. A very definite climax trend along the northern continuum is apparent when all species bearing cleistogamous flowers are grouped.

The prevernal and vernal flower displays in climax stands are well known. The majority of the pioneer forest herbs, in contrast, are aestival blossomers. Autumnal-flowering species are more characteristic of open sites and show no trend in the forest.

Many seed dispersal mechanisms are in evidence among forest herbs. Fleshy fruits are more important in the pioneer stages as are those plants for which no special method has been discovered. Plants which rely upon wind for the transportation of their seeds are more important in the southern pioneer stands and in the northern pine stands. In both of these communities there may be a fair amount of wind. Pronounced, yet distinctly different, are the trends for stick-tights. Along the southern continuum these are most important in the white oak woods while along the northern continuum they are less important but definitely a more prominent feature of the climax vegetation than of any other portion of the continuum. In similar manner the curves for

explosive seed dispersal are radically different. In the north a climax trend is apparent, while along the southern continuum this is a pioneer characteristic.

Along both the northern and southern continua elaiosomes are much more characteristic of the seeds of climax plants than of those from pioneer vegetation. It should be pointed out that except for various published accounts bearing upon experiments with a few species, little is known concerning the degree to which ants are effective in transporting these seeds. Sernander conducted such experiments with the seeds of a large number of European species and gives a full account of them. Many of these species have conterparts in the forests of Wisconsin and the seeds of these have been compared. Other species which have seeds provided with similar structures were also included in this category.

It is of further interest to inquire of the presence of ants in the climax forests. As yet little is known of this subject with regard to the forests of Wisconsin, although an investigation of this subject is being planned. Talbot (1934) conducted such an investigation in the Chicago region and found that while more ants are found in oak woods, the hypogeic forms reach a peak of importance in the climax beech-maple stands, being found most commonly in dead logs. The two commonest species in the maple woods were Lasius niger alienus americanus and Aphaenogaster fulva aquia picea,

while Formica fusca subaenescens was found in some numbers. Gates (1941) offered seeds of Trillium grandiflorum to Lasius niger and these were promptly carried away. In like manner Robertson (1897) found that Formica fusca removed seeds of Trillium recurvatum, Sanguinaria canadensis, Erythronium albidum and Uvularia grandiflora when these were offered. Whether the Aphaenogaster barbara which Sernander found instrumental in transporting the seeds of various European species is comparable to Aphaenogaster fulva is not known.

Vernal fruit ripening is almost exclusively a climax characteristic. This follows from the similar trend shown by prevernal and vernal blossoming. Most forest herbs ripen their seeds during the aestival season, and this is more characteristic of the pioneer vegetation. Autumnal fruit ripening curves peak in the intermediate forest stages.

Of considerable interest is the fact that the majority of climax plants develop well-formed flower buds during the previous growing season. As mentioned previously, these embryonic flowers are well enough developed to permit species identification, although this is rarely necessary since the underground parts of most of the forest herbs are quite distinctive. Although the climax trend is conspicuous along both continua it is probably worth noticing that in the more pioneer portions the values for the northern

continuum are considerably higher than for the comparable values in the south.

As was mentioned in an earlier section, Turrill's extended scheme is not admirably adapted to the present purposes because it allows for the placing of a species into more than one subdivision. Certain categories are worthy of note, however, as these are rather distinct and do show definite trends. For example, deciduous shrubs and evergreen shrubs are clearly pioneer in occurrence. When combined, these are generally equivalent to chamaephytes which show a similar trend. Geophytes are, of course, similar to the cryptophytes of Raunkaier and show a comparable climax trend. Grasses and grass-like plants are found to be more important in the intermediate portions of both continua. Such plants are not abundant in the forest.

In an attempt to eliminate some of the difficulty inherent in Turrill's scheme, the presence or absence of spines and similar structures was erected as a separate characteristic. The presence of such structures is found to be a climax characteristic, although always a very minor feature of the vegetation. One exception to this statement, and the reason for a climax trend, is Laportea canadensis. Had the scope of this study included such plants as the various species of Rubus an entirely different, and more valid, trend would no doubt have resulted.

It has long been noted that pioneer plants tend to be unstable taxonomically, exhibiting many variants. Such a trend has been found in the present study for both continua. An opposite trend is shown for taxonomically stable vegetation, while no apparent trend is evident for intermediate taxonomic stability.

Almost all plants included in this investigation are obligate autotrophs. Only one partial autotroph, Commandra richardsiana, was included and the resulting curve is therefore of the pioneer type. As mentioned in connection with the characteristic of canopy lacking, Conopholis americana is the only parasite included in the southern series. In northern Wisconsin the occurrence of the higher parasitic and saprophytic plants in climax forests is conspicuous. Although Epifagus virginiana was the only one of these which was included in the present study, others do occur. Among these may be mentioned Monotropa uniflora, M. hypopithys, and Coralorhiza maculata.

Finally, the species were classified into two groups depending upon whether their flowers are normally borne higher or lower than a height of eighteen inches above the ground. The resulting trends show that low height of flowers is a climax characteristic. Along the southern continuum this trend is one of the most conspicuous of the whole series of curves, rising from 32.4 per cent in the pioneer interval to 84.1 per cent in the climax.

6. Life Form and Leaf Size Spectra

Various investigators have presented comparison of the floras of different regions on the basis wherein each species occurring within a region carries equal weight. This is the floristic approach. Inasmuch as many of these regions have extended throughout political subdivisions, such as countries and states (e.g. Ennis 1928, MacDonald 1937), they usually include more than one floristic province or region of relatively uniform flora (Dansereau 1951). To be more effective, these studies should be restricted to one such province, as has been attempted by Ewer (1932) for four regions in Illinois and by Jones for Merriam's life-zones on the Olympic Peninsula (1936) and Mount Rainier (1938).

An even more important improvement in the technique, however, is the construction of life form spectra based upon the vegetation instead of the flora of such a floristic province. According to this method each species is weighted in proportion to its commonness. Such weighting is accomplished by the use of quantitative data such as presence, frequency, and density. Inasmuch as density determinations are particularly time-consuming and difficulties are encountered in the interpretation of what constitutes one plant, this measure of commonness has been little used in this connection. The species are grouped according to life form and, within each group, the quantitative values are summed. These sums are then expressed as percentages of

the total sum of such values for all species. Buell and Wilbur (1948) have shown that considerable differences exist between spectra based on flora and vegetation.

As Cain (1950) has pointed out, this technique has two important applications, the comparison of the communities constituting a successional series (e.g. Dansereau and Gille 1949), and the comparison of equivalent communities in different regions. For this latter purpose he points out that since the climax community is in equilibrium with the regional climate, this terminal stage should be the one used for such comparisons.

In figures 11 and 12 are presented the life form spectra for the various intervals along the southern and northern continua. These are based upon the frequency data discussed in the preceeding pages of this paper, and the values are presented in the first table of the appendix. A similar pattern is evident in both series of spectra. In general, chamaephytes decrease in importance, as do the hemicryptophytes. Even more pronounced, however, is the tendency of cryptophytes to increase greatly in importance in the climax forests.

In northern Wisconsin, therophytes are almost entirely absent. In southern Wisconsin, on the other hand, they constitute a more important phase of the vegetation. The high value for therophytes in the climax interval is due primarily to the increasing importance of Floerkea proserpinacoides,

Figure 11

Life form spectra

along the southern continuum

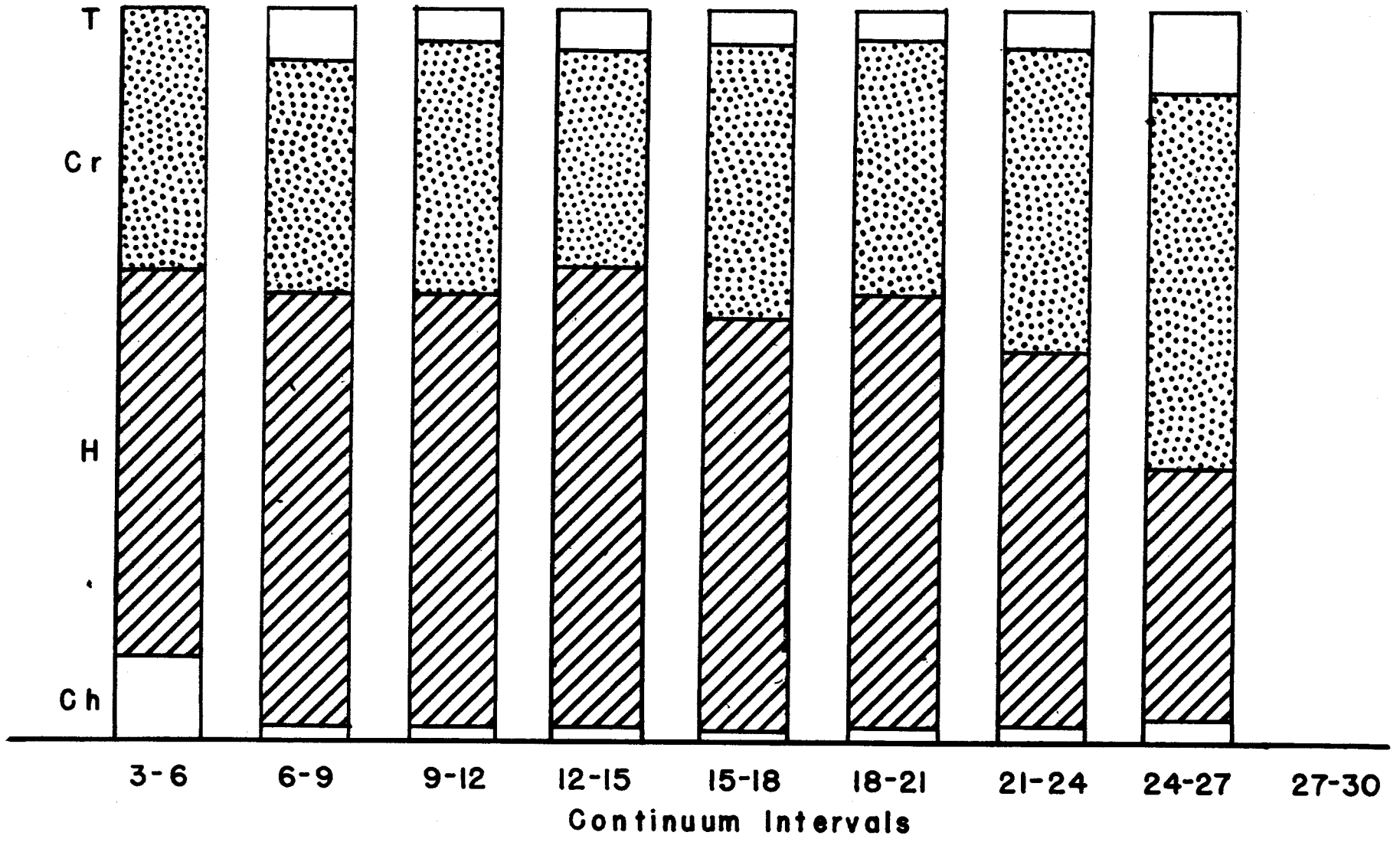
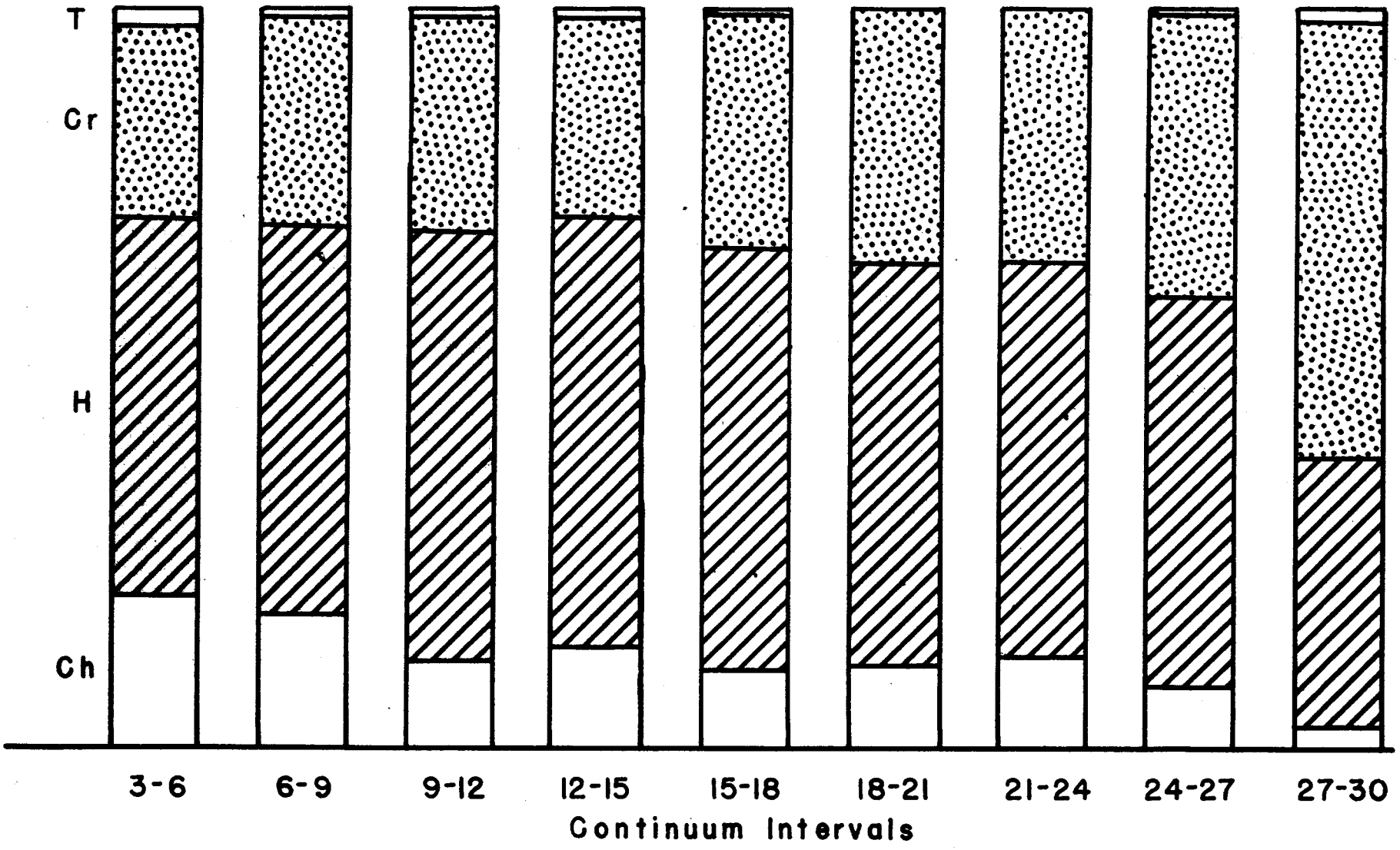

T
Cr
H
Ch
3-6
6-9
9-12
12-15
15-18
18-21
21-24
24-27
27-30
Continuum Intervals

Figure 12

Life form spectra

along the northern continuum


T
Cr
H
Ch
3-6
6-9
9-12
12-15
15-18
18-21
21-24
24-27
27-30
Continuum Intervals

Galium aparine, and Impatiens capensis. It should be noted that the first two of these species, like many of the climax cryptophytes, are not present in the aestival aspect. It is essential, therefore, that climax stands be sampled in late spring before these plants die down and after the later growing species become evident. If this precaution is not followed, a faulty spectrum is likely to result.

An example of this situation is seen in Oosting (1942). The author attempted to compile a life form spectrum as an afterthought, after gathering his data during the autumn. The resulting spectrum contains no therophytes, but consists of 92.3 per cent hemicryptophytes and 7.7 per cent cryptophytes. Most of the vernal species are cryptophytes and they were missed entirely.

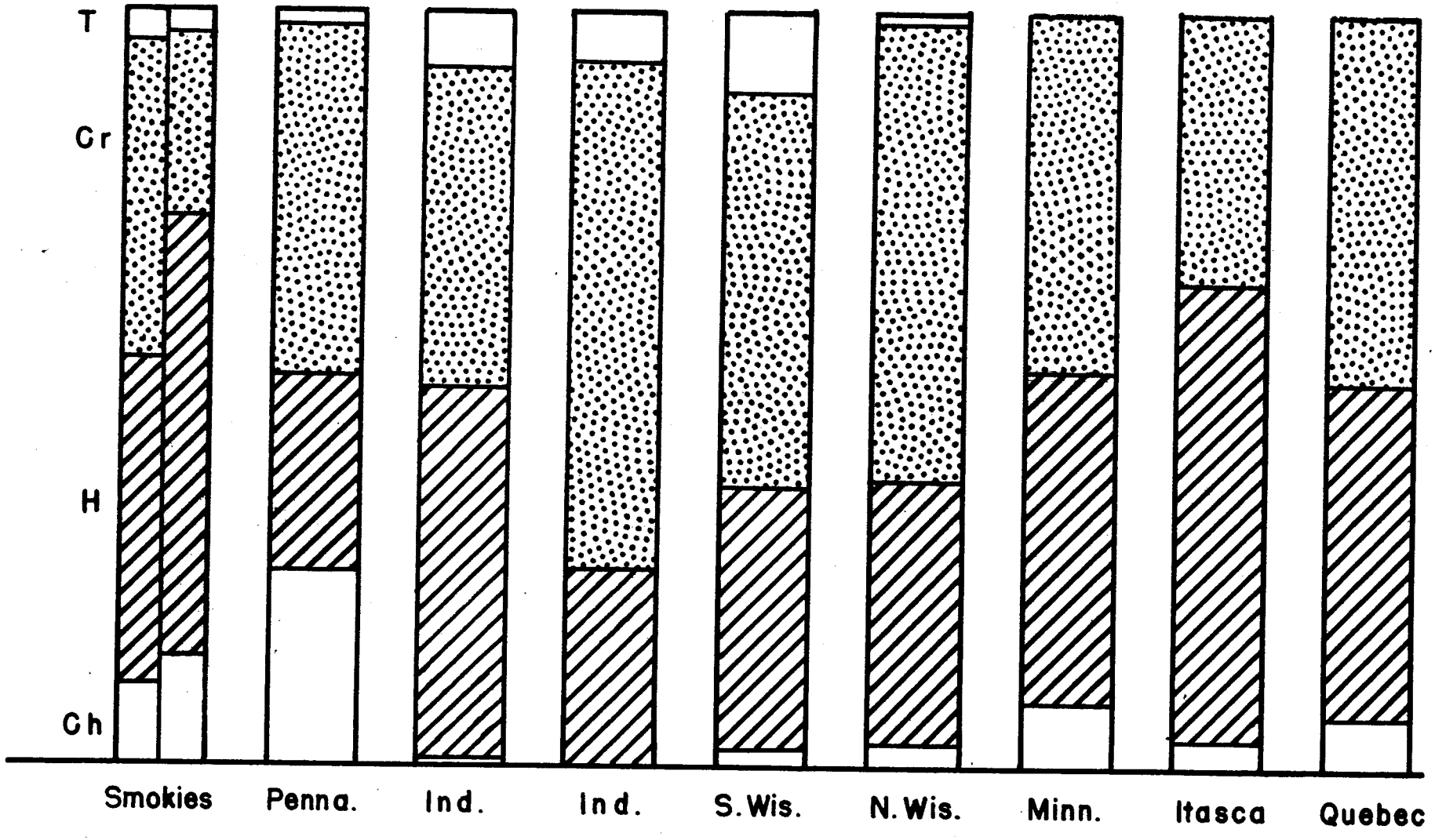
The conclusion must therefore be accepted that comparison of the life form spectra of different regions should be based upon studies of comparable communities and the study should be conducted at such a season that all important species are in evidence.

Raunkaier (1934) was the first to use frequency as a basis for the determination of life form spectra. A few investigators have since followed his example. The results of such studies, along with others constructed from data in the literature, are presented in figure 13.

Cain (1945) presents two spectra for the cove hardwoods in the Great Smoky Mountains. The spectrum for the vernal

Figure 13

Comparison of nine life form spectra of climax vegetation within the eastern deciduous forest


T
Cr
H
Ch
Smokies
Penna.
Ind.
Ind.
S.Wis.
N.Wis.
Minn.
Itasca
Quebec

aspect is based upon the average frequency in ten stands, each stand having been sampled by means of ten one-square-meter quadrats. His spectrum for the aestival aspect was based upon nine stands, with ten six-square-meter quadrats per stand. Different stands were used for the two seasonal studies. Both spectra are included in figure 13 for purposes of comparison. The considerable decrease in percentage of cryptophytes in the aestival spectrum is readily apparent.

Lutz's (1930) frequency data for a beech-hemlock stand in northwestern Pennsylvania, based upon 118 quadrats, each one meter square, were also used. The species were assigned to the various life forms according to the determinations of Dansereau (1943). Vernal species are lacking from this Pennsylvania list.

Potzger and Friesner (1940) presented the results of studies of 8 beech-maple stands in central Indiana. Each stand was sampled in the spring, summer, and fall by means of ten one-square-meter quadrats. From their data a life form spectrum has been prepared as follows. The average frequency values, where present, for the three seasons were averaged for each species. Since the life forms of certain species vary from one region to another, MacDonald's (1937) life form determinations were used for classifying these species into the proper groups. The average frequency values of each group were added and the sum was expressed as a

percentage of the total for all species.

Esten (1932) erected permanent quadrats in a beech-maple stand at Turkey Run State Park, Indiana. Twenty-five quadrats, one meter square, were used, and were revisited throughout the growing season. Actual frequency values are not given in her tables, the species being assigned to the five frequency classes of Raunkaier (0-20, 20-40, 40-60, 60-80, 80-100 per cent). In order to construct a life form spectrum based on frequency, the intermediate frequency values of 10, 30, 50, 70, and 90 per cent were assigned to the classes. Since the life form of each species was given in her tables, the plants were grouped and the spectrum calculated in the same manner as previously described.

The fifth and sixth spectra presented in figure 13 are duplicates of the climax spectra of figure 11 for the southern Wisconsin continuum and of figure 12 for the northern Wisconsin continuum.

Daubenmire (1936) presents frequency and density values in Minnetonka Woods, Minnesota, based upon 100 quadrats, each $\frac{1}{4}$ x 4 meters in size. These species were assigned to life form classes according to the Wisconsin determinations. Calculation of the spectra proceeded as before. This investigator states that these quadrat data were obtained during the last half of July in order to include vernal and later species. Unfortunately, such vernal species as Claytonia, Dicentra, and Erythronium were evidently missed entirely. As a result,

the cryptophyte portion of the spectrum is probably too small.

The eighth spectrum in figure 13 is drawn from the table presented by Buell and Wilbur (1948). Their data are derived from a study of ten climax stands in the Itasca Park region of Minnesota. In each stand 40 quadrats, ¼ x 4 meters were used. Only the aestival aspect was sampled and consequently what vernal cryptophytes occur there were missed. None appear on their species list.

Dansereau (1943) lists the species occurring in 180 stands of the sugar maple grove of southern Quebec. For each of the 346 species the life form and percentage of occurrence, in one 200-meter-square quadrat per stand, is also given. While no mention of season of study appears, a constancy value of 35 per cent for Erythronium indicates that at least many stands were sampled in the vernal aspect. Proceeding as before, the species were grouped into the various life form classes and their constance values summed and expressed as percentages of the total for all species.

These life form spectra have been arranged more or less in accordance with what seems to constitute a climatic gradient. Various considerations must be taken into account in any attempt to interpret the seeming trends depicted. As described above, the various spectra are based upon both constancy and frequency, and for the determination of frequency various sizes, shapes, and numbers of quadrats were used. An even more important consideration is the consider-

able divergence of opinion among the investigators with regard to the life form class to which a particular species belongs. Many seemingly obvious mistakes have been made in this manner as is evidenced by the various published lists, and the present study is probably no exception. There is certainly honest room for doubt in the case of intermediate species and the choice rests with the individual investigator. An extreme example is Taylor's (1918) system of including all species with rhizomes among the cryptophytes (Ennis 1928). As pointed out by Buell and Wilbur (1948), certain species alter their life form from one region to another. Studies conducted at various seasons of the year further confound the attempt to discern trends.

In general, if allowance is made for this seasonal variation by increasing the cryptophyte portion, it would appear from the data that cryptophytes reach a peak of importance in the climax forests of the prairie-forest border region and decrease in relative importance to the east and south. Hemicryptophytes exhibit an opposite trend, while chamaephytes and therophytes are variable in importance and constitute a minor element throughout. It should be borne in mind that the spectra are based upon relative values. As such they do not necessarily reflect variations in the absolute numbers of the members of a particular life form class.

As Cain (1950) has noted, there is no proof that life-forms are of value for the survival of plants in various

climates. They may, however, show such a correlation, especially when comparable phases of the vegetational complex are compared. It may well be that comparison of pioneer vegetation would yield more positive results than the climax.

Raunkaier (1934) devised a system of leaf size classes for the classification of the plants of one life form. Only a few attempts to use this scheme have since been made (Esten 1934, Withrow 1934) and these have been upon a floristic basis. As in these two studies, no attempt was made in the present investigation to use leaf size classes within a particular life form type. All species being studied were utilized without reference to life form.

As mentioned previously in this paper, Esten (1932) considered the leaflet of a compound leaf to be equivalent to a simple leaf, while Withrow (1932) preferred the alternative of equating the whole compound leaf to a simple leaf. In the present study both systems have been used.

The four resulting series of leaf size spectra along the continua are presented in figures 14 to 17, with the larger leaf sizes nearer the bottom of the columns. In general, there is evident a trend toward the dominance of larger leaves in the climax portions of the continua, regardless of whether a compound leaf is considered a leaf or many leaves. A similar trend was found by Withrow (1934) in comparing four kinds of vegetation in the Cincinnati region, namely, xerophytic (Opuntia, et cetera), prairie,

Figure 14

Leaf size spectra along the southern continuum based upon equivalence of leaflet and simple leaf

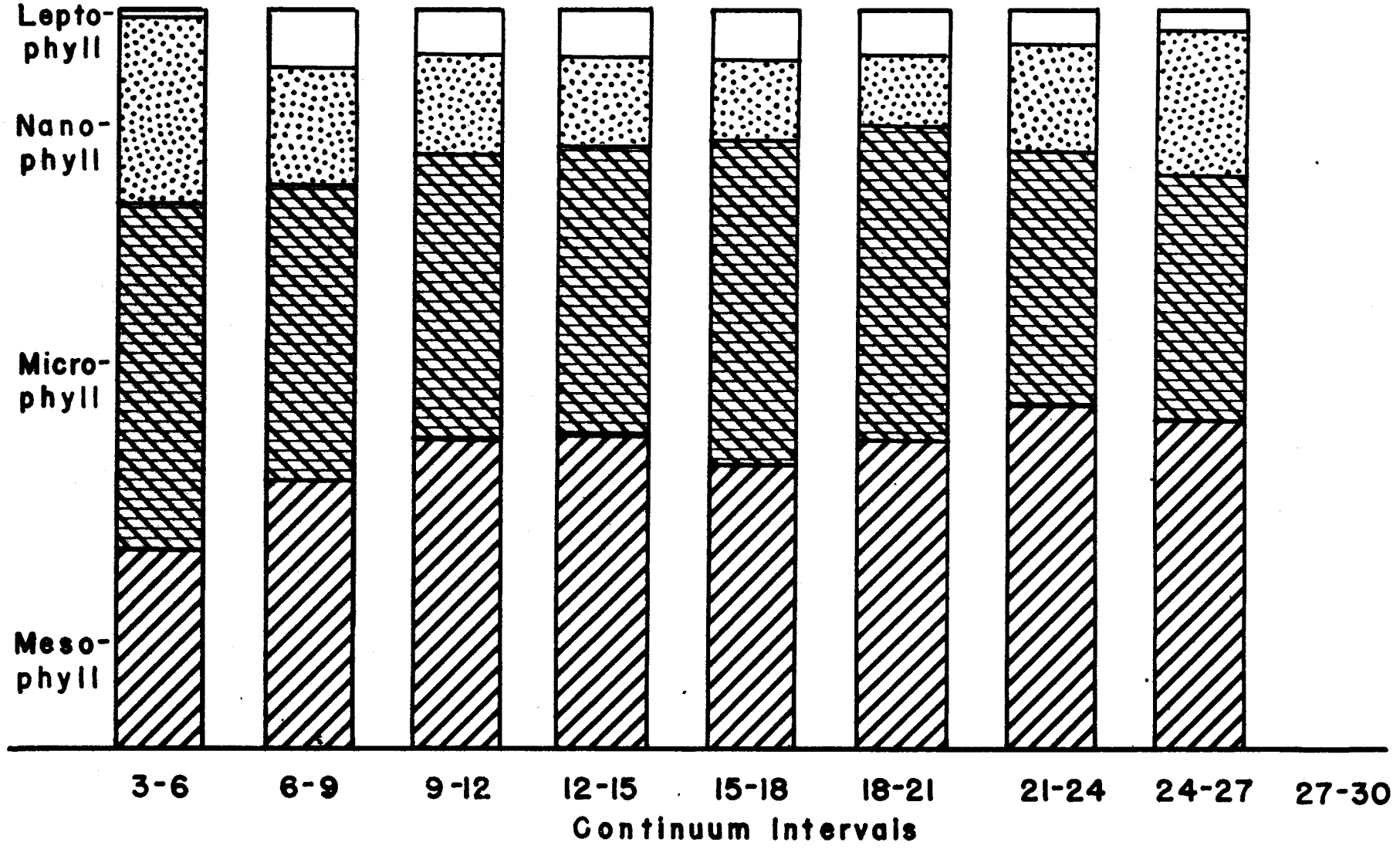

Lepto-
phyll
Nano-
phyll
Micro-
phyll
Meso-
phyll
3-6
6-9
9-12
12-15
15-18
18-21
21-24
24-27
27-30
Continuum Intervals

Figure 15

Leaf size spectra along the northern continuum based upon equivalence of leaflet and simple leaf

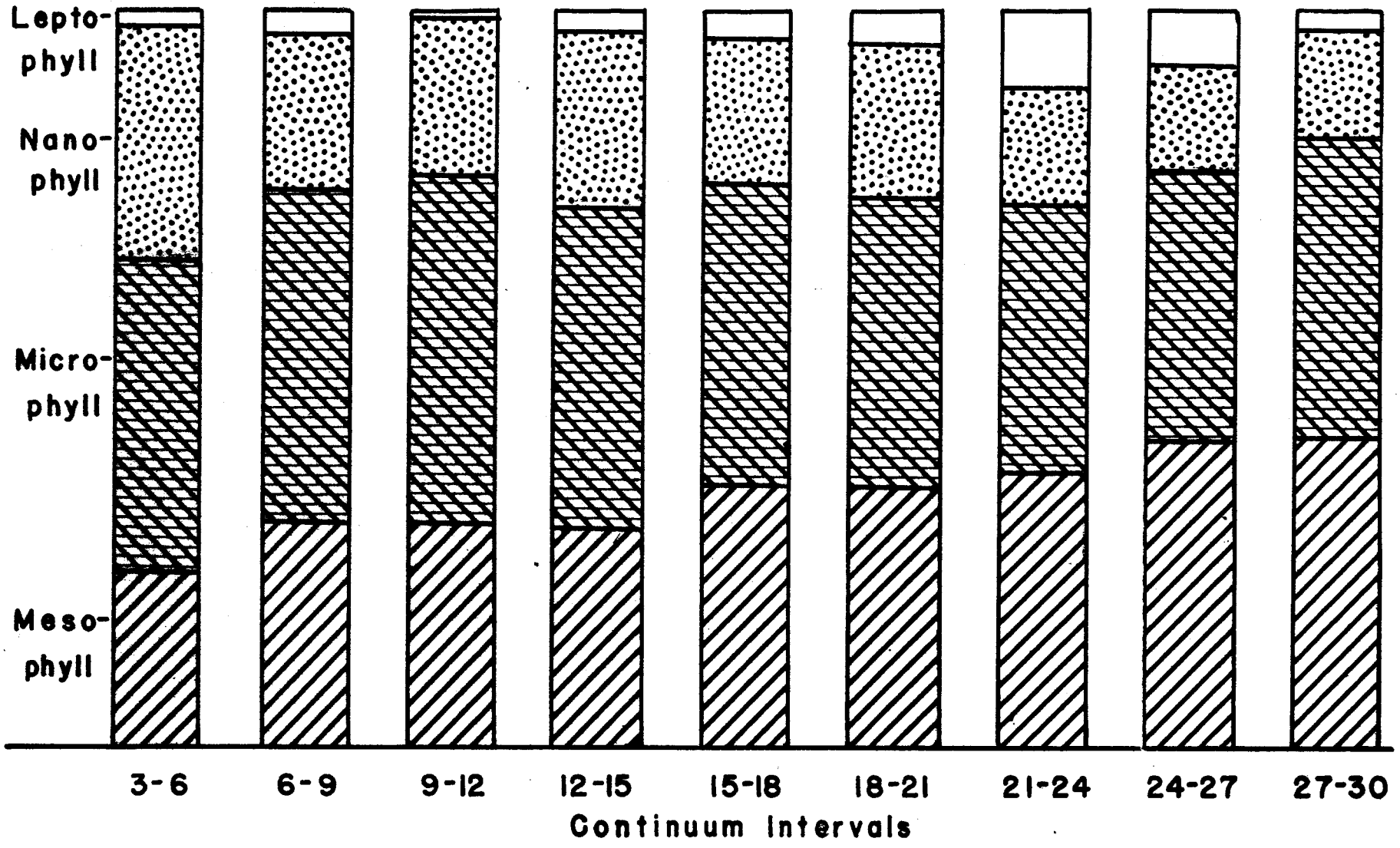

Lepto-
phyll
Nano-
phyll
Micro-
phyll
Meso-
phyll
3-6
6-9
9-12
12-15
15-18
18-21
21-24
24-27
27-30
Continuum Intervals

Figure 16

Leaf size spectra along the southern continuum based upon the non-equivalence of leaflets and simple leaves

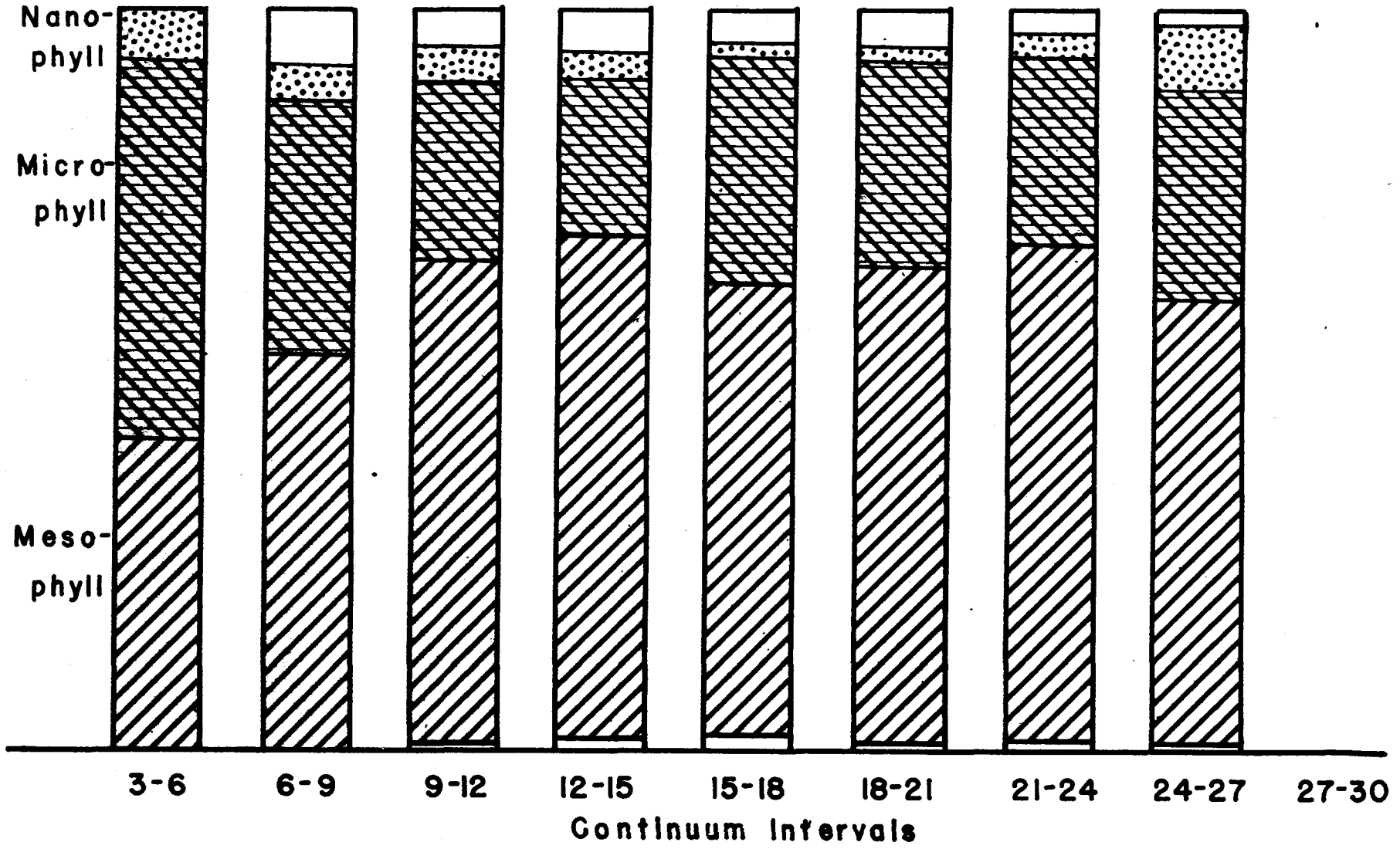
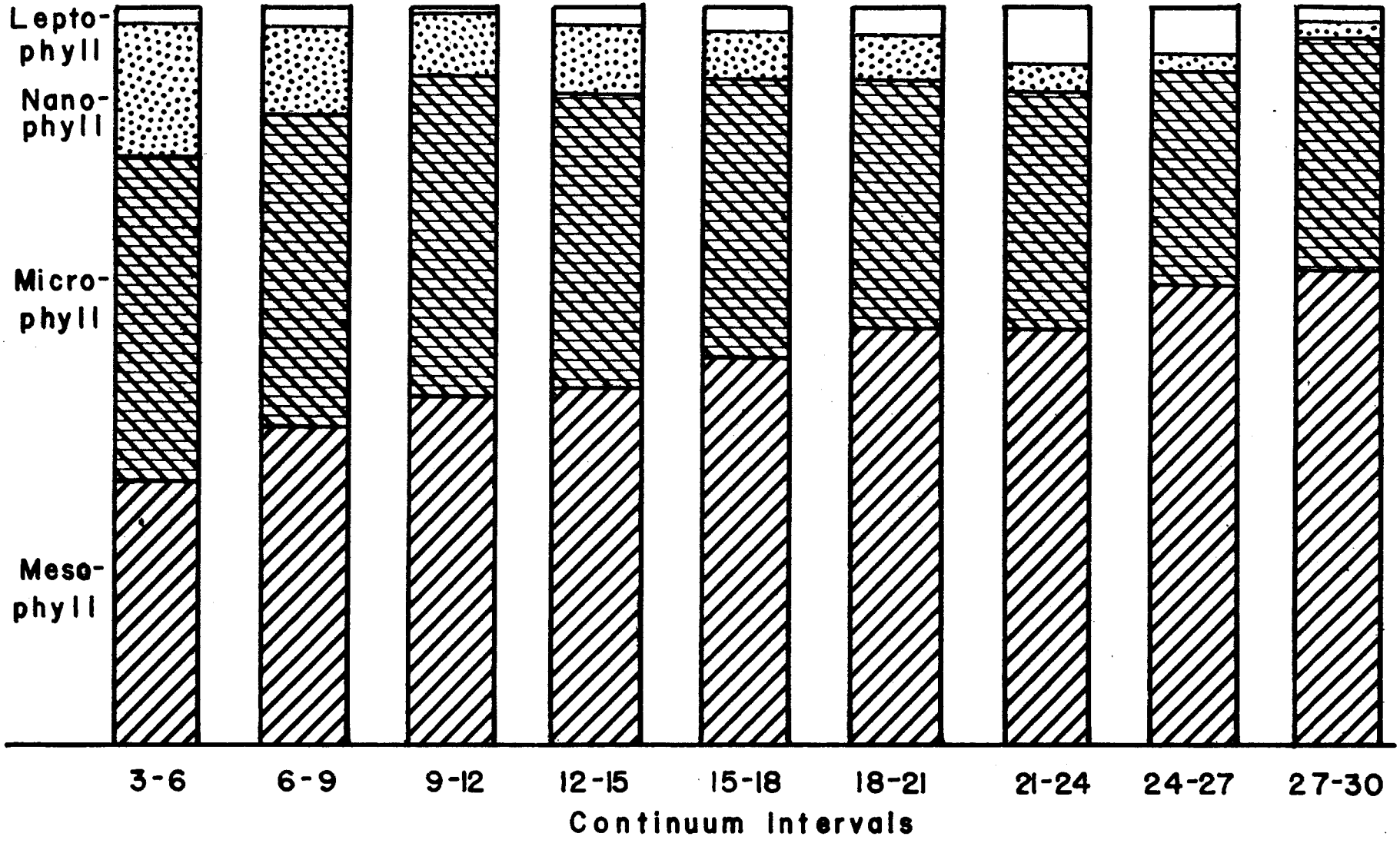

Nano-
phyll
Micro-
phyll
Meso-
phyll
3-6
6-9
9-12
12-15
15-18
18-21
21-24
24-27
27-30
Continuum Intervals

Figure 17

Leaf size spectra along the northern continuum based upon the non-equivalence of leaflets and simple leaves


Lepto-
phyll
Nano-
phyll
Micro-
phyll
Meso-
phyll
3-6
6-9
9-12
12-15
15-18
18-21
21-24
24-27
27-30
Continuum Intervals

pin oak forest, and beech-maple climax forest. She found, for example, 5.9, 26.6, 51.9, and 56.1 per cent mesophylls, respectively, in these four sites.

It is of interest to note the effect on these spectra caused by variations in the curves for simple and compound leaves. For example, along the northern continuum, compound leaves constitute a climax characteristic and consequently the series of spectra based upon compound leaves is distorted to some extent when converted to spectra based upon leaflets.

If the values obtained in these various studies are compared for climax stands, little variation is found. In figure 18 the three climax spectra which treat the compound leaf as a unit are compared. In the same figure the three spectra using the leaflet as a leaf are presented along with a fourth. This latter spectrum was constructed on the basis of the constancy values given by Dansereau (1943) for the sugar maple grove of southern Quebec. The species were assigned to leaf size classes on the basis of the determinations for the Wisconsin spectra and by reference to herbarium specimens for the additional species.

On the basis of the spectra presented there seems to be little value in the comparison of the climax herbaceous vegetation of the different portions of the deciduous forest. Either system of treating compound leaves may be selected, but should be used only for comparison with other spectra based upon the

Figure 18

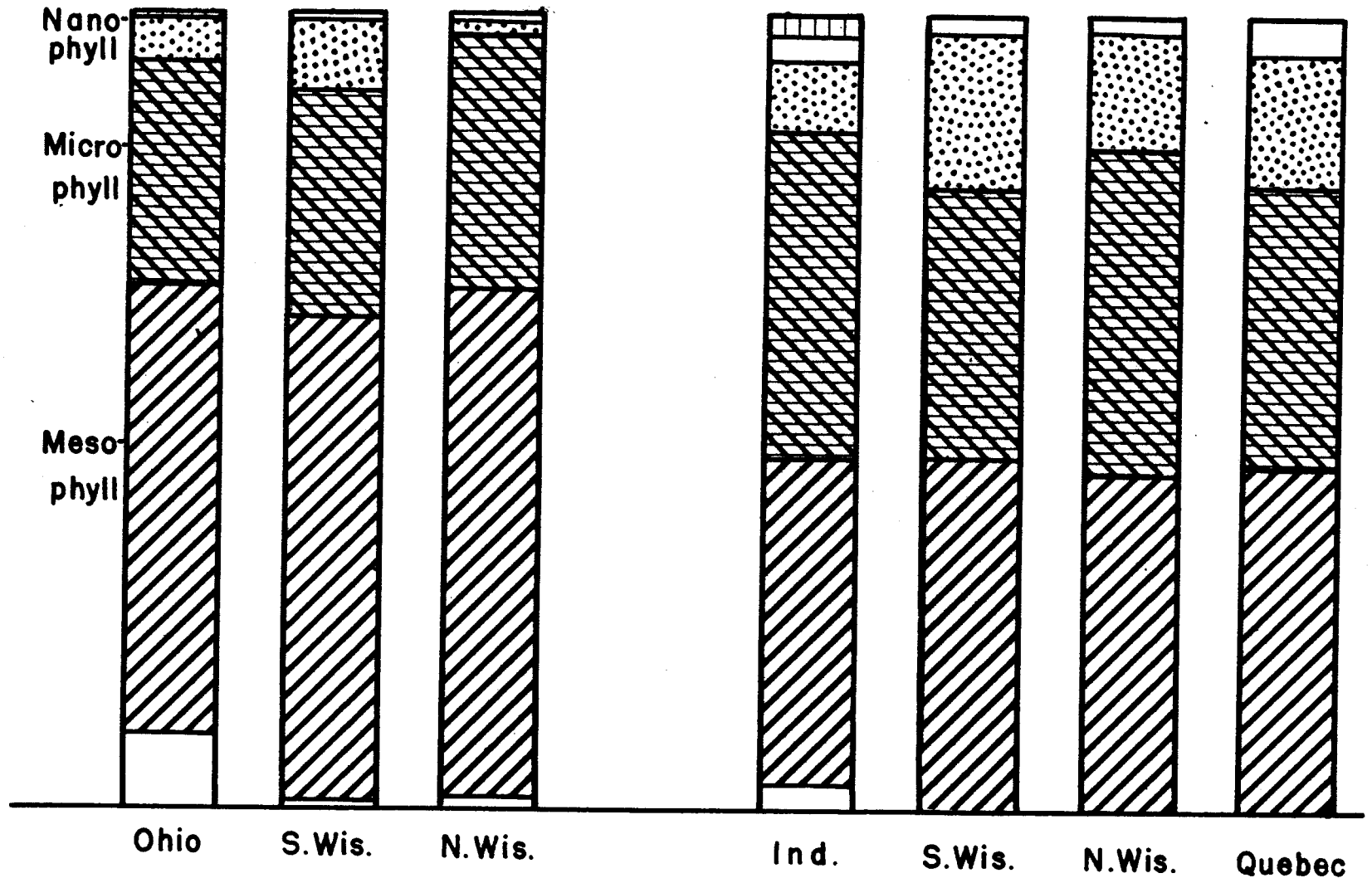
Two comparison series of leaf size spectra for climax vegetation within the eastern deciduous forest.

Unlabelled classes are:

At top: (vertically lined) Aphyllous

(unshaded) Leptophyll

At bottom: (unshaded) Macrophyll


Nano-
phyll
Micro-
phyll
Meso-
phyll
Ohio
S.Wis.
N.Wis.
Ind.
S.Wis.
N.Wis.
Quebec

same treatment. Leaf size classes are of value, however, in comparing the several plant communities within one region.

III. PHYSIOLOGICAL CHARACTERISTICS

The studies described in part II of this paper have been concerned with life history and morphological characteristics. Various physiological characteristics have also been studied in some detail. Because the nature of the determinations is quantitative the treatment of data was necessarily different.

A. Methods

This study is based upon the assumption that the truest picture of the autecological characteristics of a species may be obtained by studying that species where it is growing under the influence of the environmental conditions which favor maximum development. For this purpose the average frequency curves described in a previous section of this paper were used for the selection of species. Since the field data were obtained in various forest stands located near Madison the average frequency curves were those based on the southern Wisconsin continuum.

For the wilting studies, ten species were selected in each continuum interval, with the exception of the 600-900 interval, in which only six species were found to reach optimum development. Thus 76 different species are included. The species selected within any one interval are among those which reach optimum development within that interval and are the ten which have the highest average frequencies there.

This method of species selection would have resulted in the inclusion of Claytonia virginiana, Dicentra cucullaria and Erythronium albidum in the 2400-2700 continuum interval. Inasmuch as these species die down before the forest canopy has reached its maximum density, they are not considered to be representative of the true shade vegetation. Consequently these three species are excluded.

Since, as Livingston and Brown (1912) have shown, the water content of leaves declines during the day and increases at night, the weights of fully turgid leaves are best determined early in the morning during a period preceeded by a normal amount of precipitation. Eight forest stands, each representative of a different continuum interval, were selected. Each stand consisted essentially of undisturbed forest, but included small portions which has been recently cut. These stands were visited between the hours of four and seven o'clock (standard time) on consecutive mornings in early June. The presence of abundant dew on grass outside the stands served as additional assurance that the plants being studied were near full turgidity. The species studied in any stand are the ten which peak in the continuum interval to which that stand belongs.

A triple-beam balance was erected on a log or stump in the woods and sheltered from the wind. A sample of leaves from one of the ten species was collected from several individuals and weighed immediately. The leaves were then placed on logs, or other exposed positions and allowed to

wilt, while samples of the other species were collected in like manner. When wilting was unmistakably evident the leaves were reweighed. They were later returned to the laboratory for determination of the oven-dry weight. In most instances only the leaves were weighed, but in those cases (e.g. Galium concinnum) where the removal of enough leaves to give an adequate sample would have been so time consuming that some water loss would occur before the weighing, a minimum of stems was included. Such species are indicated by an asterisk in the table

Three additional species: Fragaria virginiana, a pioneer species, Viola pubescens, a climax species, and Geranium maculatum, a species which reaches optimum development near the middle of the continuum, but which occurs commonly throughout, were similarly sampled in all of the stands in which they occurred.

For the chlorophyll studies, five of the species used in each interval for the wilting studies, were chosen. These are the five with highest average frequency values which could be found growing undisturbed in the normal shade of the stand visited and also in portions of that stand which had recently been cut in light logging operations. Examination of the rhizomes and other underground parts of these plants were made in all cases where possible to insure that the herbs had been growing there before the canopy had been opened.

Eighty sets of leaf samples, consisting of leaves from forty species growing undisturbed in the shade and from forty series of plants of the same species which were undisturbed except for the recent removal of the tree canopy above them, were gathered in the same stands as were used in the wilting studies. Within each series ten samples were removed from as many leaves by means of a cork borer, each sample having an area of 65.0 mm^2. The larger veins were avoided. The ten samples were pooled and the chlorophyll was extracted quantitatively in acetone and then transferred quantitatively to ethyl ether. Determinations of the total chlorophyll content were made by means of the Evelyn photoelectric colorimeter, using a 660 filter, thus obviating the necessity of removing the carotinoid pigments.

The oven-dry weight of ten duplicate samples was also determined for each shade series.

After the chlorophyll content had been determined for all forty species, 15 cc. portions of the chlorophyll solutions of the shade series were simultaneously exposed to bright sunlight for a period of six minutes in test tubes placed on white paper. The total chlorophyll content was then redetermined.

B. Results

In table 8 are presented the values obtained for each of the 76 species studied. This table also serves to indicate the species studied and the continuum interval in which each reaches optimum development. In the first column

Table 8

Species studied, arranged in continuum intervals of optimum development, with values obtained for the characteristics desbribed in the text. Values in first two columns for species marked with one asterisk are based upon samples which included stems or woody stipes. Wintergreen species are denoted by two asterisks.

Columns 5 and 6 contain values expressed as percentages of the chlorophyll contents of the original shade series of leaves.

Intervals and Species	Water lost before wilting %	Percent dry matter %	Dry weight of shade series mg	Chlorophyll in shade series ug	Chlorophyll in sun series %	Chlorophyll after photo-destruction %	Chlorophyll per mg. dry leaf ug/mg
300-600							
Antennaria sp.	18.6	17.7					
Apocynum androsaemifolium	21.3	19.4					
Comandra umbellata	15.7	19.1					
Euphorbia corollata	20.9	21.6	21.9	80	107.5	57.5	3.6
Fragaria virginiana	21.7	24.0	27.2	90	90.0	62.2	3.3
Helianthus strumosus	20.2	16.4	24.1	93	111.8	44.1	3.9
Polygonatum canaliculatum	18.8	18.3					
Potentilla simplex	12.4	22.1					
Pteridium aquilinum*	24.0	22.7	30.2	90	90.0	75.5	3.0
Smilacina stellata	26.1	18.8	26.7	146	80.8	67.8	5.5
600-900							
Anemone quinquefolia	23.0	19.3	27.8	114	96.5	26.0	4.1
Gaylussacia baccata	20.0	25.9	30.2	87	103.4	77.0	2.9
Goodyera pubescens**	22.1	8.4					
Hieracium canadense	21.2	21.4	29.5	95	95.0	67.4	3.2
Parietaria pensylvanica	15.5	20.2	21.1	87	89.7	58.6	4.1
Vaccinium angustifolium*	21.7	28.2	31.3	90	101.1	68.9	2.9
900-1200							
Agrimonia gryposepala	18.0	17.5					
Aralia nudicaulis	18.1	14.5					
Arenaria lateriflora	8.3	17.8	15.3	118	89.0	44.1	7.7
Carex pensylvanica**	30.6	26.7	25.9	93	107.5	80.6	3.6
Circaea quadrisulcata	13.8	10.2	16.0	64	76.6	53.1	4.0
Geum canadense	18.4	17.3					

Intervals and Species	Water lost before wilting %	Percent dry matter %	Dry weight of shade series mg	Chlorophyll in shade series ug	Chlorophyll in sun series %	Chlorophyll after photo-destruction %	Chlorophyll per mg. dry leaf ug/mg
900-1200 (continued)							
Lactuca biennis	9.2	7.8					
Lysimachia quadrifolia	17.2	14.1					
Phryma leptostachya	12.0	14.2	13.8	90	92.2	63.3	6.5
Smilacina racemosa	21.4	16.6	15.5	105	74.3	74.3	6.8
1200-1500							
Amphicarpa bracteata	5.9	9.9	10.6	78	96.2	48.7	7.4
Cypripedium calceolus	15.4	11.9					
Desmodium glutinosum	13.5	14.0	12.2	90	95.6	54.4	7.4
Eupatorium rugosum	9.8	11.1					
Galium concinnum*	21.9	34.9					
Geranium maculatum	9.5	19.4	34.7	121	96.7	43.8	3.2
Podophyllum peltatum	14.4	19.8	31.3	144	76.4	91.0	4.6
Prenanthes alba	9.8	10.9	15.5	125	69.6	42.2	8.1
Taenidia integerrima	3.5	19.4					
Veronicastrum virginicum	7.7	26.3					
1500-1800							
Aralia racemosa	6.5	19.7					
Athyrium filix-femina	12.9	16.7	19.0	146	82.9	65.8	7.7
Brachyelytrum erectum	15.4	19.6					
Galium triflorum	4.5	14.7					
Hackelia virginiana	12.5	14.9					
Osmunda claytoniana*	17.1	23.2	19.0	121	108.3	43.8	6.4
Panicum latifolium	16.3	19.0					
Pyrola elliptica**	12.1	19.5	20.2	90	92.2	71.1	4.5
Trillium grandiflorum	15.2	12.5	14.5	121	62.8	59.5	8.4
Uvularia grandiflora	14.7	20.1	20.1	125	72.0	57.6	6.2

Intervals and Species	Water lost before wilting %	Percent dry matter %	Dry weight of shade series mg	Chlorophyll in shade series ug	Chlorophyll in sun series %	Chlorophyll after photo-destruction %	Chlorophyll per mg. dry leaf ug/mg
1800-2100							
Actaea pachypoda	8.7	17.0	17.0	110	50.0	41.8	6.5
Aster macrophyllus	11.1	12.1	17.7	121	89.3	76.0	6.8
Galium circaezans	9.9	17.1	13.4	100	72.0	64.0	7.5
Hystrix patula*	16.9	20.1					
Maianthemum canadense	14.9	17.3					
Osmorhiza claytoni	6.1	13.0	12.2	97	57.7	53.6	7.9
Ranunculus abortivus	16.5	17.3					
Sanicula gregaria	8.1	13.8	15.3	128	78.1	36.3	8.4
Smilax herbacea	12.8	16.0					
Smilax tamnoides	12.0	16.1					
2100-2400							
Arisaema atrorubens	5.6	9.5	12.8	126	39.7	19.0	9.9
Asarum canadense	7.3	12.0	17.1	110	84.5	78.2	6.4
Cryptotaemia canadensis	8.1	13.7					
Hepatica acutiloba**	7.1	22.2	28.1	144	62.5	79.2	5.1
Menispermum	7.3	8.1					
Mitella diphylla	9.0	16.2					
Osmunda cinnamomea*	14.3	17.6					
Polygonatum pubescens	8.0	10.9					
Thalictrum dioicum	3.4	10.0	8.7	90	71.1	23.3	10.4
Trillium flexipes	8.0	12.0	16.9	153	52.3	29.4	9.2

Intervals and Species	Water lost before wilting %	Percent dry matter %	Dry weight of shade series mg	Chlorophyll in shade series ug	Chlorophyll in sun series %	Chlorophyll after photo-destruction %	Chlorophyll per mg. dry leaf ug/mg
2400-2700							
Adiantum pedatum*	3.3	22.1					
Botrychium virginianum	3.0	14.4					
Galium aparine**	3.1	14.2	10.8	86	74.4	25.6	8.0
Hydrophyllum virginianum	2.3	12.9	16.4	135	60.7	18.5	8.2
Impatiens capensis	1.9	2.9					
Laportea canadensis	1.6	12.3					
Sanguinaria canadensis	3.7	12.4	17.5	103	18.4	12.6	5.9
Trillium recurvatum	8.0	9.8					
Viola cucullata	5.7	5.1	14.5	128	53.9	43.0	8.8
Viola pubescens	3.7	11.1	16.0	116	30.2	50.0	7.3

is shown the percentage of water lost before wilting became apparent. These values were calculated by dividing the difference between the fully turgid weight and the weight at wilting by the difference between the fully turgid weight and the oven-dry weight. Within each continuum interval the arithmetic mean was calculated for the ten species and the resulting values plotted in figure 19. This curve shows a pronounced decrease from the pioneer to the climax portions of the continuum. The pioneer plants lose approximately 20 per cent of their total water content before they wilt while the climax species show signs of wilting when they have lost 3.5 per cent of their total water.

These results agree remarkably well with the observations of Maximov (1938). In comparing extreme sun plants with extreme shade species he found values of 25 to 30 per cent for the heliophytes and 2 to 3 per cent for the sciophytes. Since the present study is concerned with a narrower range of environmental conditons, the values might be expected to exhibit less variation. The extreme susceptibility of some climax species to wilting is easily observed in the field by picking Impatiens, Laportea, and Sanguinaria.

The amount of oven-dry matter in the leaves was calculated as a percentage of the fully turgid weight. These values are presented in the second column of the table. The average value for each continuum interval was plotted against the continuum index and the resulting curve is shown in figure 20. Again, the values are found to decrease from

Figure 19

Per cent water content lost before wilting.

Averages of ten species per interval.

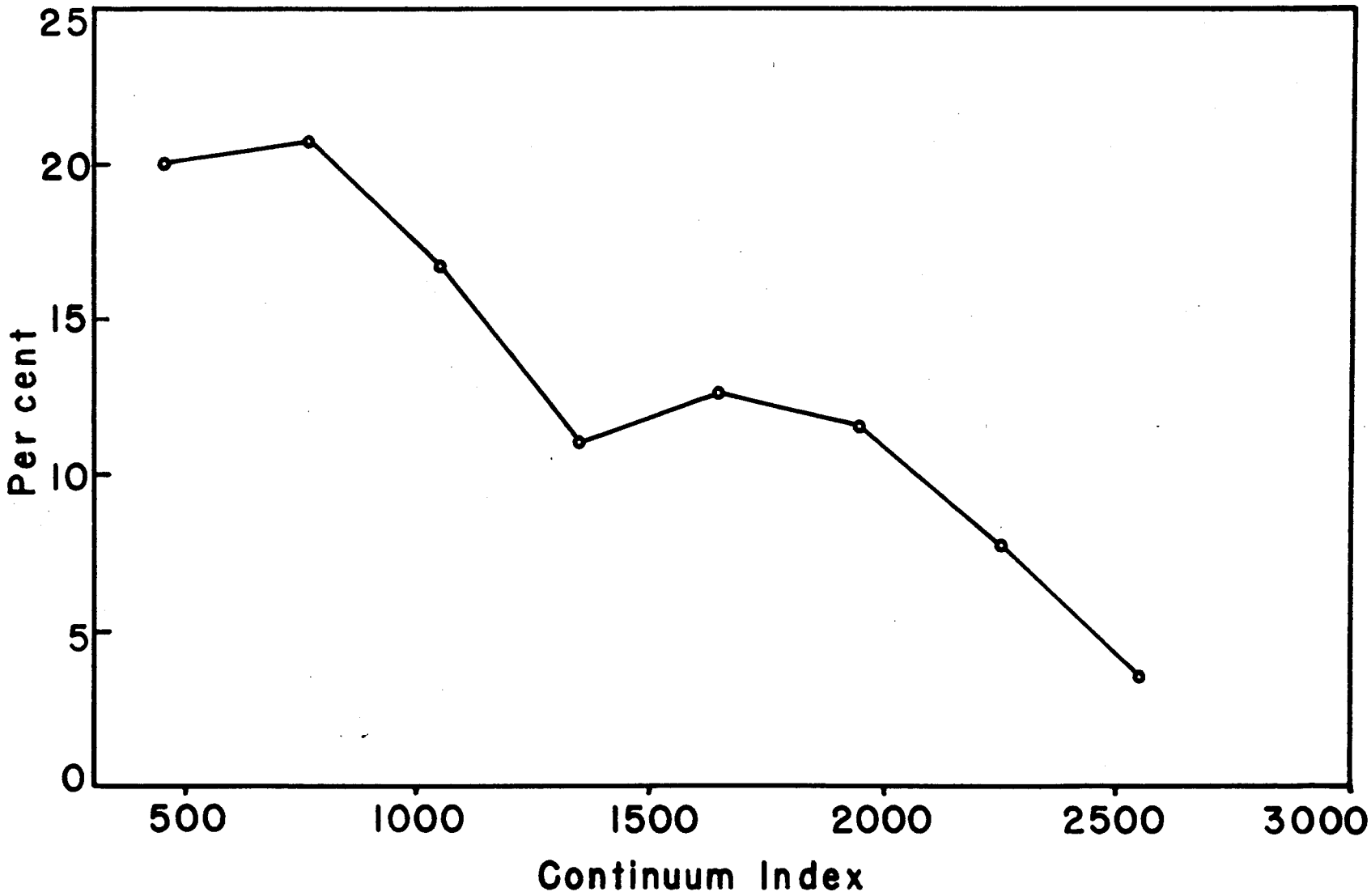
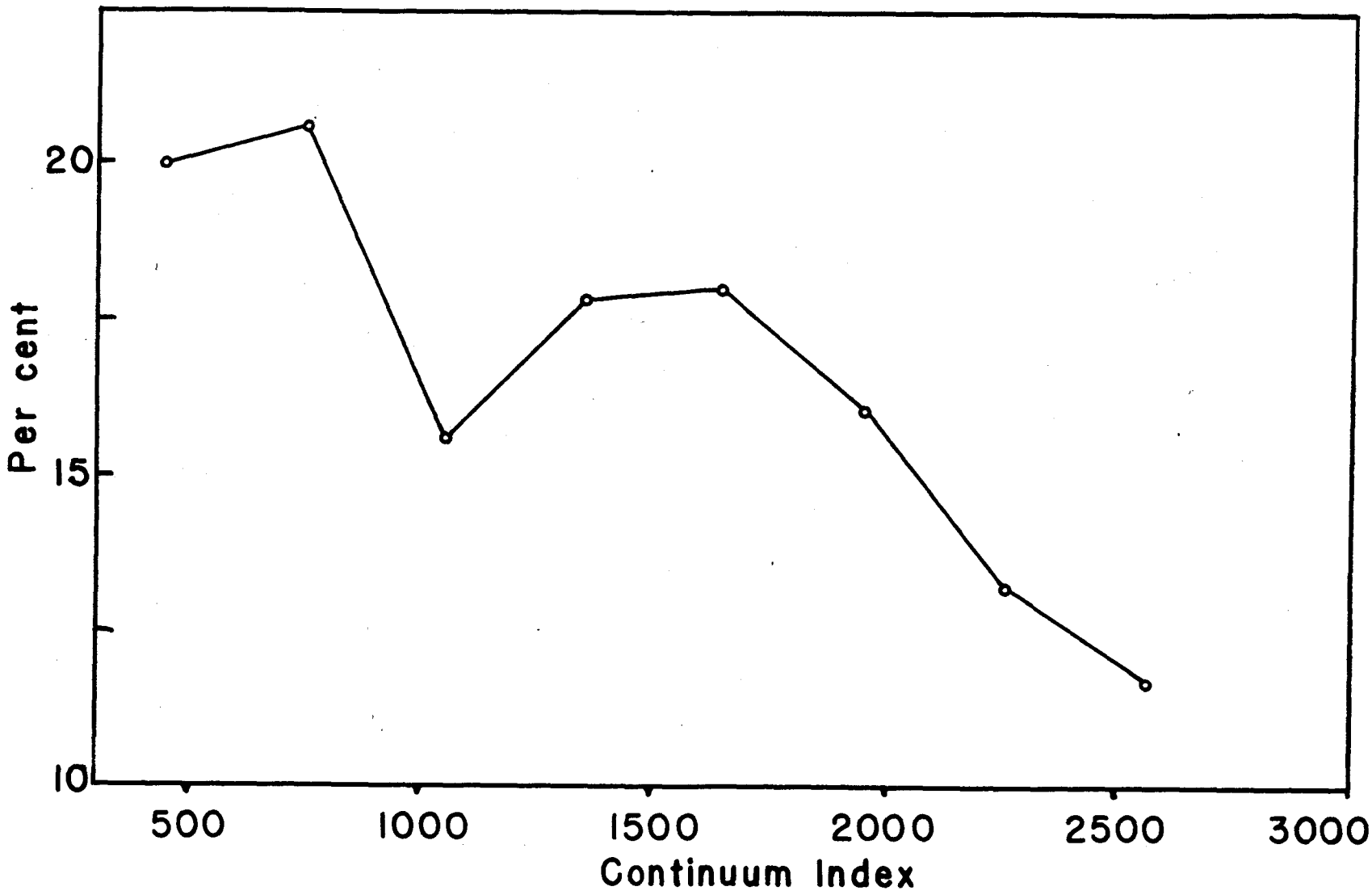

25
20
15
10
5
0
Per cent
500
1000
1500
2000
2500
3000
Continuum Index

Figure 20

Oven-dry weight of leaves as per cent of turgid weight. Averages of ten species per interval.


Per cent
20
15
10
500
1000
1500
2000
2500
3000
Continuum Index

the pioneer species to the climax species. A difference of approximately 67 per cent occurs between the two ends of this curve. These results agree with those of Géneau (1892) and of Lubimenko (1908) in that they show considerably less dry matter in the shade species.

Much interest has been attached to the question of ecotypes or population segregates versus environmental effects on plants of a homogeneous population. In the present study no attempt is made to consider this question in detail. However, variations in two characteristics have been studied for three species in an attempt to determine the validity of a basic assumption. This problem concerns the advisability of obtaining the data from plants growing under optimum environmental conditions.

Fragaria virginiana is a distinctly pioneer species as is shown by its average frequency curve. That optimum development of this species lies outside the range of the forest continuum is strongly suspected. The decrease from 23 to 4 per cent in water loss before wilting is a most pronounced trend (figure 21). Similar, but less marked, is the curve for proportion of oven-dry matter in the leaves (figure 22). Obviously, then, a considerable difference might result in the values obtained throughout the present study if the species were sampled under environmental conditions other than optimum.

Viola pubescens, a climax species, shows a similar

Figure 21

Per cent water content lost before wilting

for three representative species:

Fragaria virginiana

Geranium maculatum

Viola pubescens

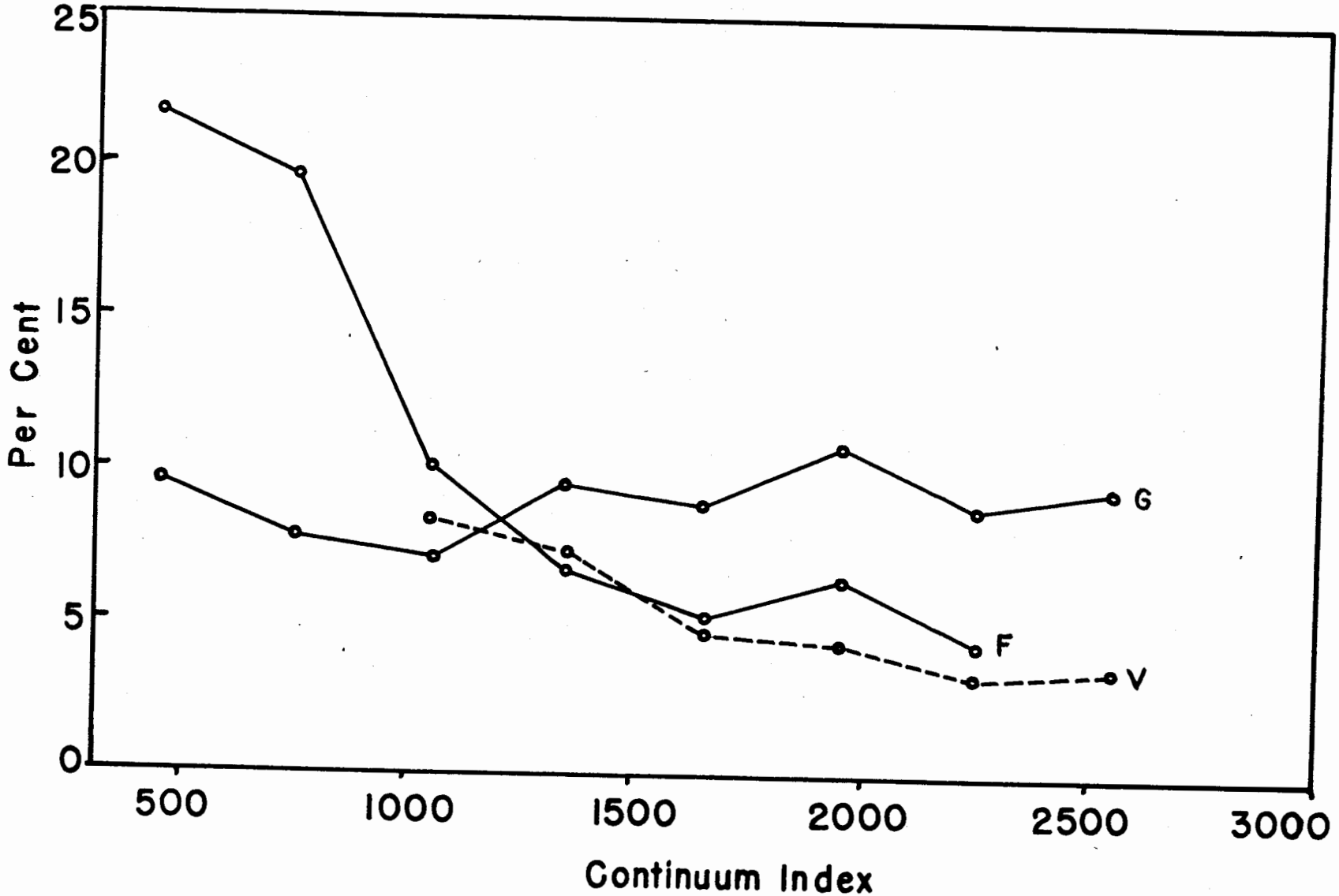

25
20
15
10
5
0
Per Cent
500
1000
1500
2000
2500
3000
Continuum Index
G
F
V

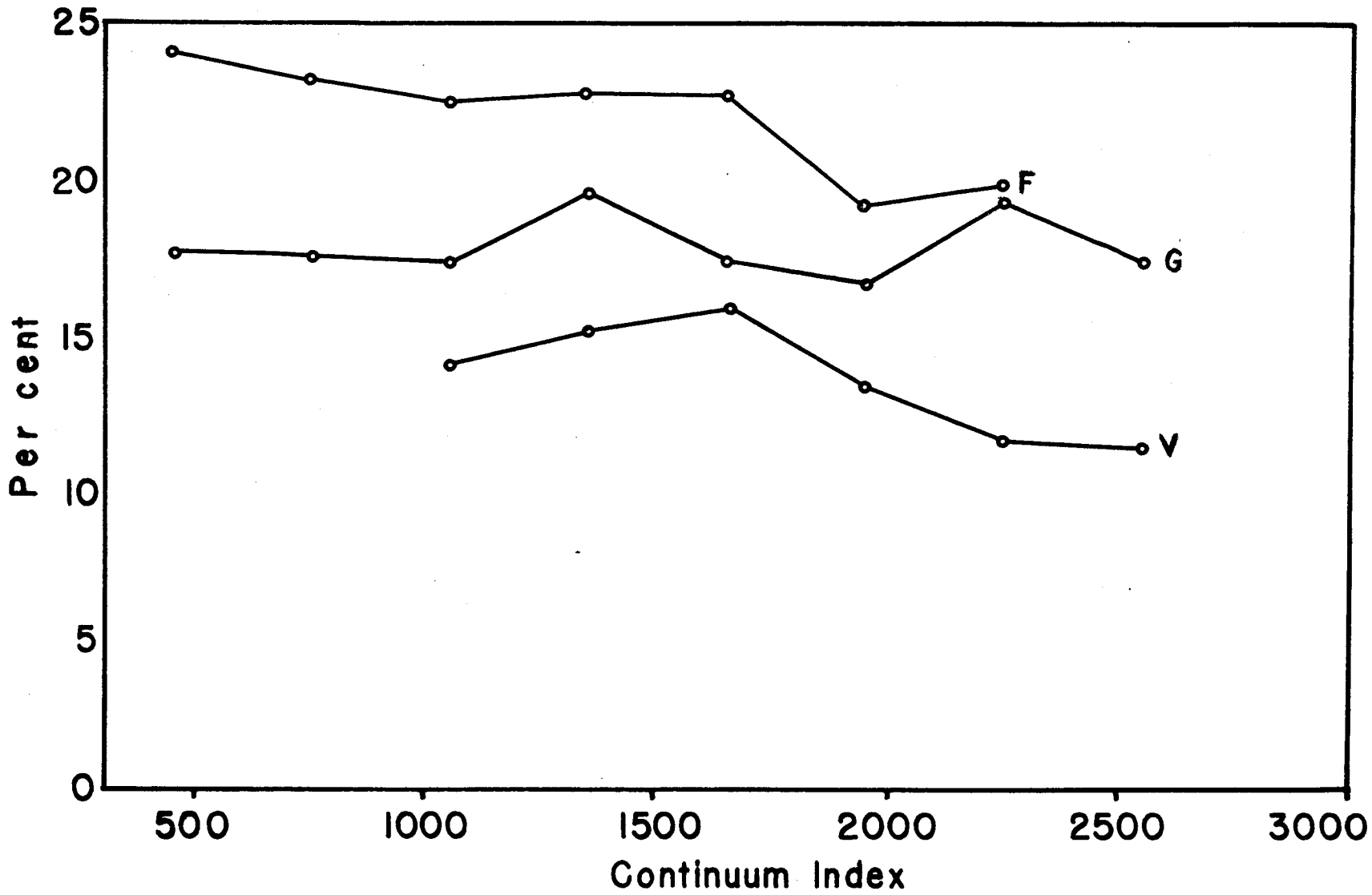
Figure 22

Oven-dry weight of leaves as per cent of turgid weight for three representative species:

Fragaria virginiana

Geranium maculatum

Viola pubescens


25
20
15
10
5
0
Per cent
F
G
V
500
1000
1500
2000
2500
3000
Continuum Index

curve for water loss before wilting. In the case of dry matter content, however, the downward trend is preceeded by a slight rise. If this rise is significant, it may be the resultant of an interplay of variations in such characteristics as photosynthetic, respiration, and assimilation rates.

Geranium maculatum was chosen as an example of a very ubiquitous species, for, while its average frequency curve shows a pronounced peak in the 1200-1500 interval of the continuum, it occurs in 92 of the 96 stands which constitute the base of this study. The two curves for this species are alike in that no definite trend is apparent.

Results similar to those in figure 22 are obtained in the case of oven-dry matter per unit area, as determined on the basis of five species per continuum interval (figure 23).

A difference of approximately 50 per cent between the pioneer and climax species is apparent. Géneau (1892), comparing the leaves of sun and shade individuals of four species of herbs, found an average difference of 51.5 per cent for this same character.

The table also includes the results of the other studies with five species per continuum interval. In the fourth column of this table is shown the amount of chlorophyll, in micrograms, present in the shade leaves of each species, each series consisting of ten 65.0mm.^{2} samples from as many leaves. Arithmetic means of these values are plotted in figure 24. Although there is considerable variation, it

Figure 23

Oven-dry matter in 6.5 $cm.^2$ leaf samples of shade series. Averages of five species per interval.

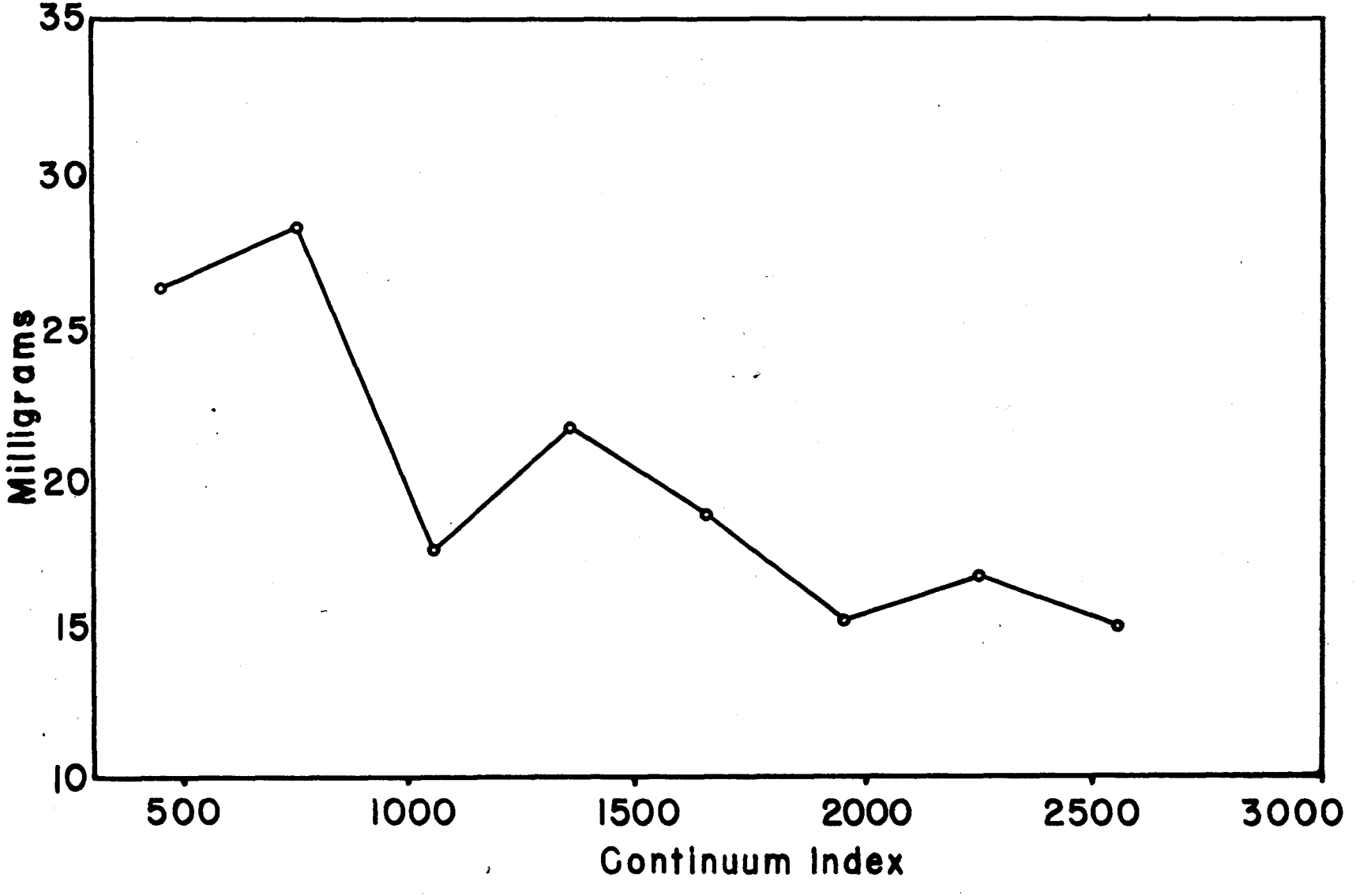
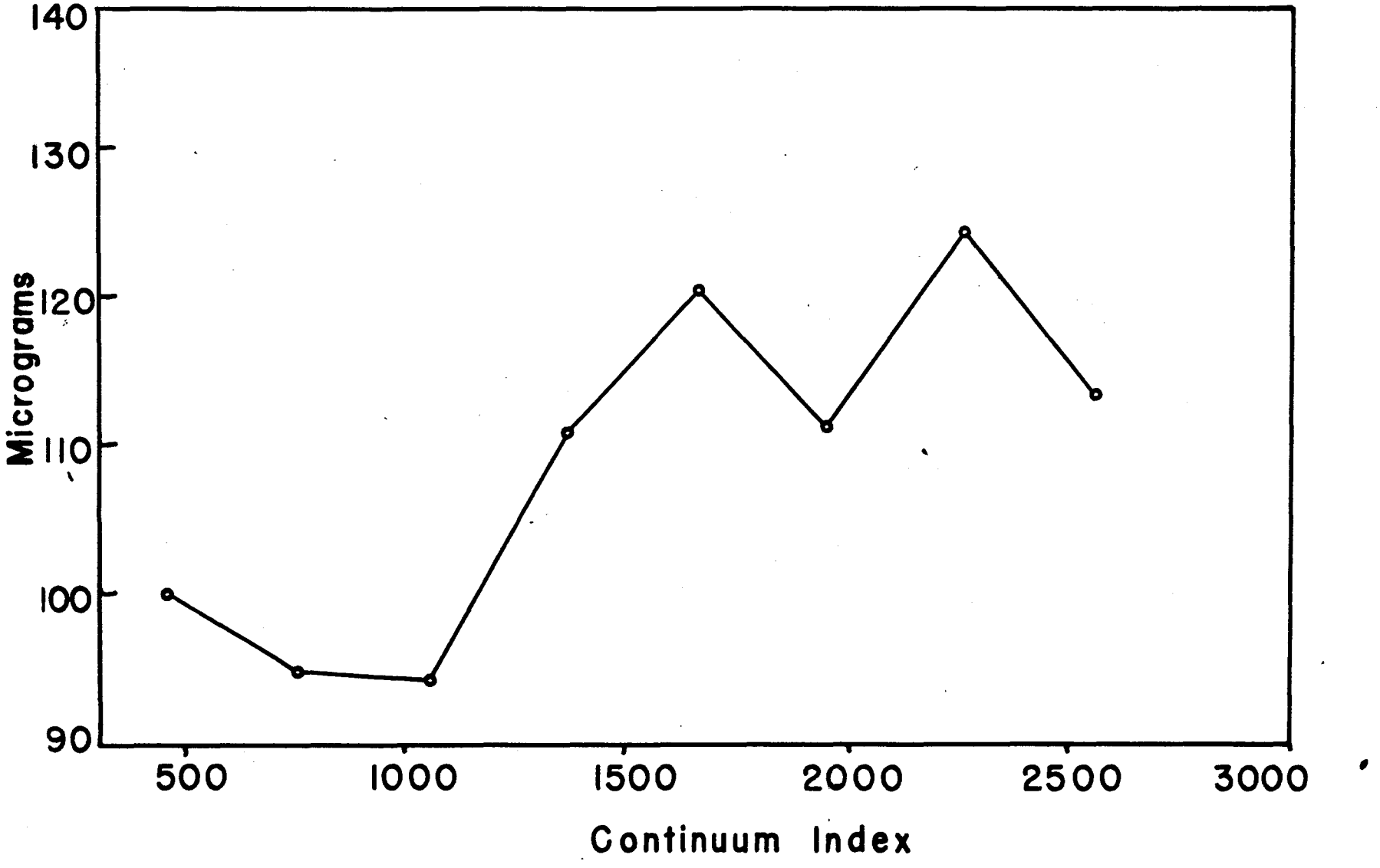

35
30
25
20
15
10
Milligrams
500
1000
1500
2000
2500
3000
Continuum Index

Figure 24

Chlorophyll content per 6.5 cm.^{2} leaf samples of shade series. Averages of five species per interval.


140
130
120
110
100
90
Micrograms
500
1000
1500
2000
2500
3000
Continuum Index

is readily apparent that the climax species contain more chlorophyll than do the pioneer species.

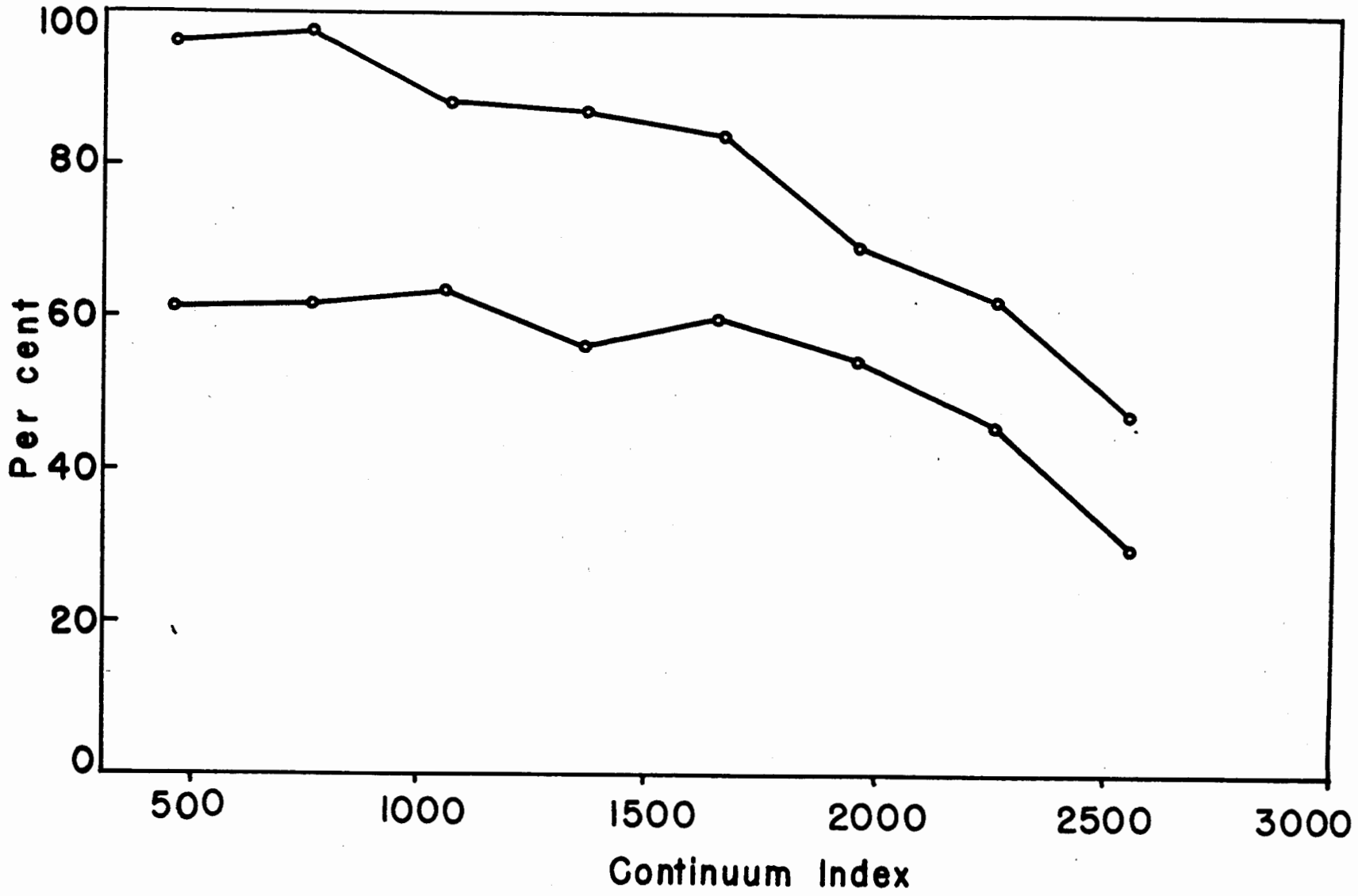
An extreme difference between pioneer and climax species is shown in the case of the chlorophyll content of sun versus shade individuals (figure 25). Those species which show optimum development in the pioneer portion of the continuum retain approximately 96 per cent of their chlorophyll content when the tree canopy is removed, while the chlorophyll content of the climax species is reduced by one half. This is easily observed in the field in the leaves of such species as Sanguinaria canadensis and Viola pubescens, which assume a pronounced yellow color in sites where the canopy has been removed.

Examination of underground parts in all cases where possible was undertaken to ensure that the plants growing in bright sunlight had been there before the cutting and thus could be considered genetically similar to the replicates still growing in shade. Observed differences between these replicates, therefore, are resultants of environmental change. As early as 1904, Boodle showed that leaves are plastic; i.e. similar young leaves become mature sun leaves if grown in bright sunlight, or develop into characteristic shade leaves if grown in shade.

Decolorization of chlorophyll by bright sunlight is twice as rapid in the case of climax species as it is in pioneer species (figure 25). Since no determinations were made of chlorophyll a : b ratios, it is not known whether

Figure 25

Chlorophyll content of sun series as a percentage of that in shade series (upper curve). Percentage of chlorophyll retained in ether solutions of shade series after exposure to bright sunlight. Averages of five species per interval.


100
80
60
40
20
0
Per cent
500
1000
1500
2000
2500
3000
Continuum Index

this considerable difference is due to variation in quantities of chlorophyll b . However, since chlorophyll b is said to be much more susceptible to photo-oxidation than chlorophyll a (Strain 1949), and to be present in greater proportion to a in shade leaves (Rabinowitch 1945), this assumption seems reasonable.

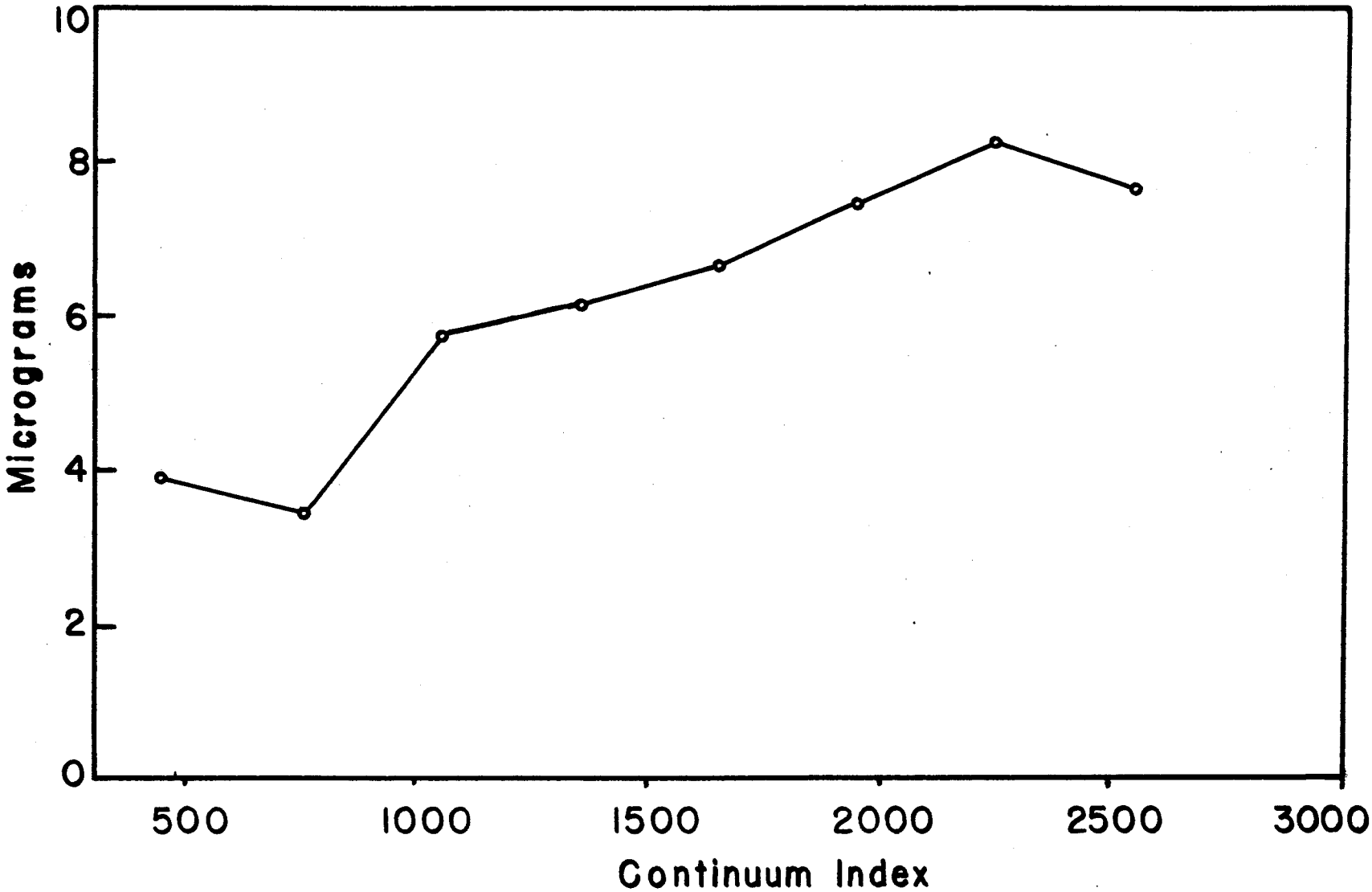
While the curves in figure 25 are alike the values for the ether solutions are noticeably lower. This difference might be expected from the remark of Rabinowitch (1945) that chlorophyll is less stable to light in vitro than in vivo.

The average amounts of chlorophyll per unit of dry matter contained in the shade series is shown in figure 26 Although the trend is conspicuous, it is not believed that these values necessarily indicate a greater efficiency of the chlorophyll of pioneer species. Since much of the food synthesized in the leaves may be translocated to other parts of the plant, and since no measure was available regarding the amount of food translocated, it seems best to resist any tendency to draw such conclusions. Hesselman (1904) has shown that while most species have high photosynthetic rates in the spring, the measured rate drops, frequently to zero, in the case of forest herbs as a dense forest canopy closes above them. This measured rate seems to be the excess above the compensation point.

An additional item of interest is the osmotic pressure of cell sap. No determinations of this characteristic were

Figure 26

Amount of chlorophyll per milligram of dry leaf matter in shade series. Averages of five species per interval.


10
8
6
4
2
0
Micrograms
500
1000
1500
2000
2500
3000
Continuum Index

made in this study. However, twenty-five species for which sufficient data are available to yield average frequency curves, are included in the tables of osmotic pressure determinations made by Harris (1934). Within each continuum interval the osmotic pressures shown in table 9 were averaged for the species which reach optimum development there. Two of the intervals lack species entirely. From the curve plotted in figure 27 a decreasing trend is readily apparent, even though so few species are included.

There is no assurance, in this case, that the determinations were made on samples gathered in sites of optimum development. Descriptions of collection sites are given in Harris' tables, however, and any determinations based upon specimens from obviously non-optimum sites were not included in calculating the average osmotic pressure of a particular species.

Table 9

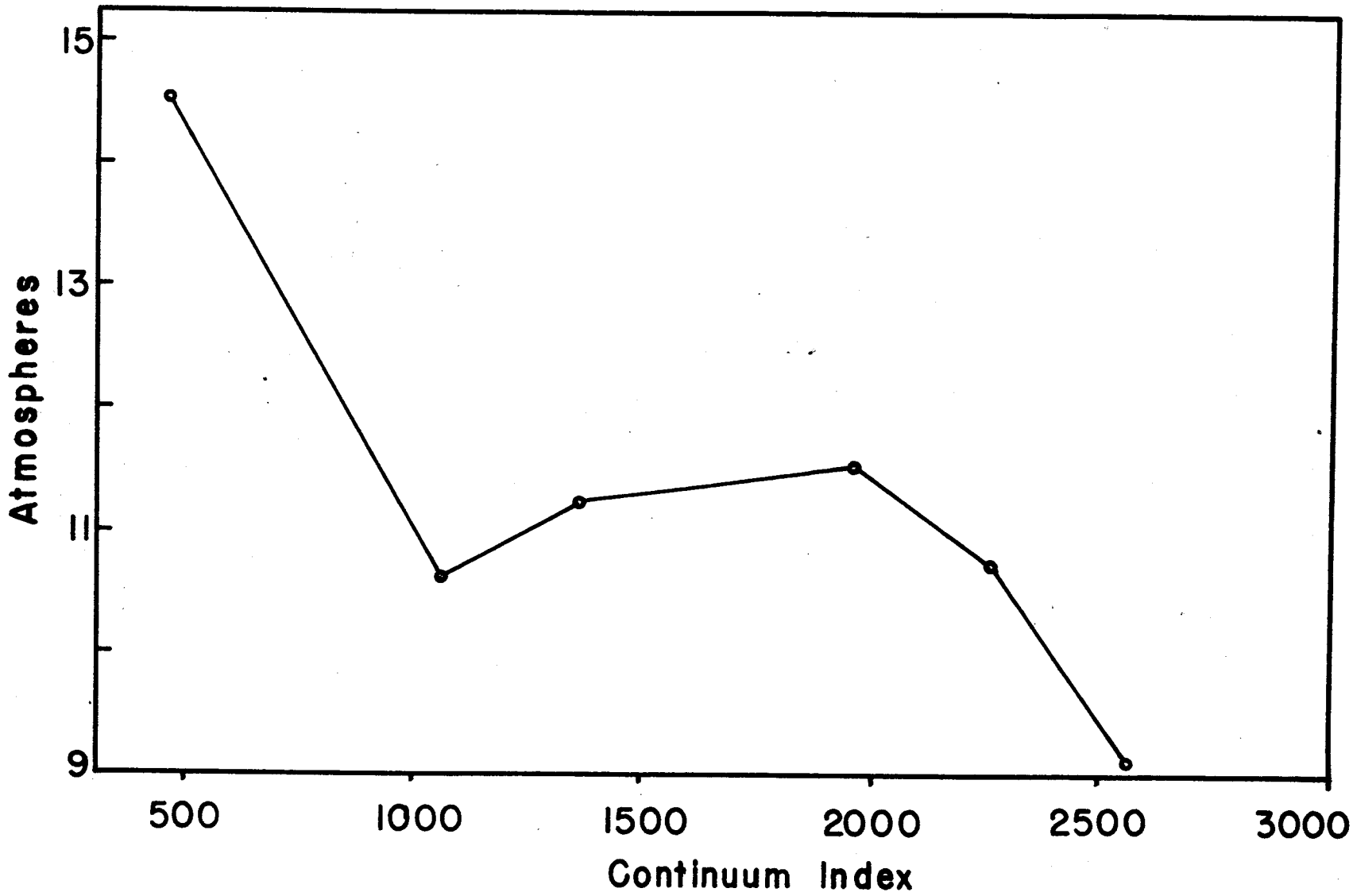
Average osmotic pressures of 25 species (after Harris 1934) arranged according to the continuum interval within which each species reaches a peak of importance

	Average Osmotic Pressure
300- 600	
Monarda fistulosa	12.5
Pteridium aquilinum	18.7
Smilacina stellata	12.2
600- 900	
900-1200	
Agrimonia gryposepala	10.6
Circaea quadrisulcata	6.7
Geum canadense	12.9
Lactuca biennis	12.8
Lysimachia quadrifolia	8.0
Smilacina racemosa	12.6
1200-1500	
Amphicarpa bracteata	10.2
Aralia nudicaulis	16.7
Desmodium nudiflorum	8.7
Geranium maculatum	9.3
1500-1800	
1800-2100	
Actaea pachypoda	12.0
Aster macrophyllus	6.4
Ranunculus abortivus	14.8
2100-2400	
Arisaema atrorubens	9.3
Cryptotaenia canadensis	10.9
Thalictrum dioicum	11.9
2400-2700	
Galium aparine	8.9
Impatiens capensis	5.7
Osmorhiza longistylis	13.5
Ranunculus septentrionalis	12.4
Tovara virginiana	5.4
Viola cucullata	8.6

Figure 27

Osmotic pressure of cell sap expressed from leaves (data from Harris 1934).

Averages of 3, 6, 4, 3, 3, 6 species, reading from left.


15
13
11
9
Atmospheres
500
1000
1500
2000
2500
3000
Continuum Index

IV. DISCUSSION AND CONCLUSIONS

Climax adaptation values as assigned to various tree species by Curtis and McIntosh (1951) may as readily be assigned to the various species of forest herbs. This value expresses the degree to which the complex of physiological and morphological attributes of a particular species approaches that of the climax vegetation. That climax vegetation exhibits definite features which are different from those of more pioneer forests has been demonstrated in the present investigation.

Climax forests are characterized by low light, abundant and constant moisture, and mature soil conditions. The species which reach optimum development under these conditions show great taxonomic stability. Their flower buds are formed during the previous growing season and the floral display is therefore not greatly effected by vagaries of the current weather conditions.

These climax species blossom before the dense shade of summer falls upon them and they tend to disperse their seeds by specialized means, including a conspicuous relationship with ants. A majority of them are of small stature (many are acaulescent) and their roots are largely confined to the rich organic soil horizon. Various specialized devices for vegetative reproduction and overwintering are characteristic. They overwinter under the protection afforded by subterranean

conditions.

Photosynthesis is carried on at all seasons of the year, but is most important during seasons other than summer when shade is very intense. Climax plants have larger and thinner leaves and lower osmotic pressures. Their leaves contain more chlorophyll and this chlorophyll is more subject to photo-destruction than that of pioneer plants. Wilting becomes obvious after only a small portion of their water content has been lost.

Many climax species are exacting in their demands upon the environment and consequently are not found in appreciable numbers outside of the climax stands. The competitive struggle so evident among pioneer vegetation is by no means as apparent among the climax herbs. Most of the aggressive species are light-demanding and consequently are excluded by the dense shade of maple woods. Having low compensation points, and avoiding the dense shade by blossoming and photosynthesizing at times of the year when most other plants are inactive, these plants are able to flourish.

The high degree of integration of the climax community is exhibited by the tendency toward parasitism and saprophytism. That many climax species form mycorrhizal associations has been shown elsewhere. Sunlight falling upon a climax community at any time of the year is utilized by at least some of the vegetation. A greater amount of the incoming energy is thus retained. Many climax species are

long-lived and this energy is thus stored over long periods. The remains of these plants are utilized by the parasites and saprophytes and there is thus a greater and more prolonged utilization of the incoming energy.

Pioneer plants, on the other hand, are less stable taxonomically. They blossom during the summer and many rely upon insects for pollination. Their seeds and fruits ripen during the summer and many of these are fleshy or are dispersed through the agency of wind, both effective means for wide dissemination. Since their flower buds are formed during the current growing season the number of flowers is variable with weather conditions.

Woody tendencies are in evidence, but many are short-lived. These plants are tall, with leaves arranged above each other for a considerable distance along the stem. Some of them are twining plants. Their roots are not confined to the thin humus-rich upper layers of soil, but penetrate to considerable depths in many species. Tap roots are in evidence. The tendency to reproduce vegetatively by means of stolons, which meet less resistence than do rhizomes, and by means of adventitious buds upon roots, are noteworthy characteristics. Overwintering is accomplished in a variety of strata, aerial as well as at the soil surface and at various depths below it.

Pioneer vegetation exhibits smaller and thicker leaves and higher osmotic pressures. They contain more oven-dry

matter than do climax plants. There is less chlorophyll in the leaves and this is not conspicuously subject to destruction by strong sunlight. With the exception of certain evergreen species, pioneer plants exhibit no tendencies to photosynthesize at seasons other than summer. Wilting does not become apparent until a considerable amount of water has been lost by the plants.

Agressive competition is everywhere apparent in pioneer forests. The vegetation is dense, tall, some species are climbing upon others, reproduction by vegetative means as well as by seeds is common. Roots penetrate to various depths of the soil and condequently tend to avoid those of other species. Except for evergreens, they all carry on photosynthesis during the summer months exclusively, and light is at a premium during this season.

There are thus seen to be two extreme types of vegetation within the forest complex. Intermediates between these may be characterized by the degree to which they exhibit the characteristics of the extremes. As stated previously, the characteristics which have been investigated here constitute only a portion of the complex of morphological and physiological attributes which combine to characterize a phase of the vegetation and to enable plants possessed of these traits to exist under various environmental conditions.

Whether or not the particular autecological characteristics which have been the subject of this study actually

are the most important ones is not known. Certainly other characteristics may be equally as important as many that have been investigated. Furthermore, it is impossible to say whether all those characteristics for which definite trends have been shown really have survival value. At any rate, the results of this investigation do serve to show the existence of such trends and their characteristics. In this way it may form the springboard for future intensive investigations of the individual characteristics.

In the meantime there is a great need for detailed life history studies such as those being conducted by Perttula, Salisbury, Tamm, and previously, by Holm. As Blackman and Rutter (1946) have said, "....there is an absence of accurate and comprehensive information on the autecology of any individual woodland plant." Only when such knowledge is at hand can a true understanding of the interrelationships of the vegetational complex be attained.

V. SUMMARY

In order to determine the relative importance and variations in occurrence of many elements in the complex of morphological and physiological attributes of forest herbs this study was based upon the two upland forest continua which have been described in Wisconsin. By means of frequency values based upon twenty ¼ milacre quadrats per stand in 116 northern Wisconsin communities and in 96 stands located in the southern part of the state, variations in importance were determined for all herb species in nine equal-sized intervals along the two continua. The 114 commonest species within each continuum were selected for further study.

These species were classified with regard to twenty-three life history characteristics. These characteristics were weighted according to the importance of the species possessing them, using IBM techniques. The resulting values were converted so that they represent the proportion of the total vegetation which exhibits a particular trait.

Additional studies were conducted with regard to various physiological characteristics of 76 important species within the southern continuum.

Each continuum represents a gradient from pioneer upland forests with high light, variable moisture, and immature soil conditions to climax forests characterized by low light,

abundant and constant moisture, and mature soil conditions. The plants which reach optimum development under climax conditions are taxonomically stable. Their flower buds are formed during the previous growing season and the floral display is therefore not greatly effected by vagaries of the current weather conditions.

These climax species blossom before the dense shade of summer falls upon them and they tend to disperse their seeds by specialized means, including a conspicuous relationship with ants. A majority of them are of small stature (many are acaulescent) and their roots are largely confined to the rich organic soil horizon. Various specialized devices for vegetative reproduction and overwintering are characteristic. They overwinter under the protection afforded by subterranean conditions.

Photosynthesis is carried on at all seasons of the year, but is most important during seasons other than summer when shade is very intense. Climax plants have larger and thinner leaves and lower osmotic pressures. Their leaves contain more chlorophyll and this chlorophyll is more subject to photo-destruction than that of pioneer plants. Wilting becomes obvious after only a small portion of their water content has been lost.

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APPENDIX

In this appendix are included the values for all life history characteristics curves. These are arranged in nine columns with headings which identify the continuum intervals (multiply by 100). On each page, or series of pages, are listed the values for one set of life history characteristics, the name of which follows a number in parentheses to correspond with the code. The subdivisions of each characteristic are listed at the left margin and the letter in parentheses following these headings indicates whether the values are for the northern or southern continuum. All of the categories for the northern continuum are listed first, followed by those for the southern continuum.

Within each subdivision there are three lines of figures. The first, "S freq.", series are the sums of average frequencies. The second, "Rel. freq.", series are the relative sums of average frequencies by means of which the trends are determined. These were obtained by dividing the values in the preceeding series by those appearing in the table below. The third line shows the number of species which contributed to the sums of average frequencies. These may be compared with the total numbers of species in the various intervals as shown in the following table.

Table of Totals

		3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
North-	S freq.	459	457	651	549	591	311	362	373	506
ern	S no.sp.	51	58	64	70	63	57	60	67	61
South-	S freq.	299	403	462	605	537	591	510	692	---
ern	S no.sp.	37	58	59	80	80	80	71	71	---

(1) Life form

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Therophyte (N)									
S freq.	6	1	2	3	-	-	-	1	5
Rel. freq.	1.3	.2	.3	.5	-	-	-	.3	1.0
No. sp.	1	1	1	1	-	-	-	1	2
Chamaephyte (N)									
S freq.	96	79	76	72	60	33	43	27	10
Rel. freq.	20.9	17.3	11.6	13.1	10.2	10.6	11.9	7.2	2.0
No. sp.	8	7	6	10	7	9	7	5	4
Hemicryptophyte (N)									
S freq.	239	249	380	322	339	170	197	203	191
Rel. freq.	52.1	54.5	58.4	58.7	57.4	54.7	54.4	54.4	37.7
No. sp.	30	34	45	44	40	33	30	35	27
Cryptophyte (N)									
S freq.	117	128	193	151	192	108	122	142	300
Rel. freq.	25.5	28.0	29.6	27.5	32.5	34.7	33.7	38.1	59.3
No. sp.	11	16	12	14	16	15	23	26	28
Therophyte (S)									
S freq.	-	26	18	29	20	21	26	76	
Rel. freq.	-	6.4	3.9	4.8	3.7	3.6	5.1	11.0	
No. sp.	-	2	3	3	4	3	3	4	
Chamaephyte (S)									
S freq.	34	4	2	5	6	2	1	13	
Rel. freq.	11.4	1.0	.4	.8	1.1	.3	.2	1.9	
No. sp.	2	1	2	3	2	1	1	1	
Hemicryptophyte (S)									
S freq.	159	240	276	384	305	356	265	241	
Rel. freq.	52.9	59.6	59.7	63.4	56.7	60.2	51.9	34.8	
No. sp.	25	37	37	48	48	48	40	38	
Cryptophyte (S)									
S freq.	106	133	166	187	206	212	218	362	
Rel. freq.	35.5	33.0	35.9	30.9	38.4	35.9	42.7	52.3	
No. sp.	10	18	17	26	26	28	27	28	

(2) Root system

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Fibrous (N)									
S freq.	444	435	644	541	586	309	361	370	499
Rel. freq.	96.7	95.2	98.9	98.5	99.2	99.4	99.7	99.2	98.6
No. sp.	47	53	60	66	61	55	59	65	58
Fascicled (N)									
S freq.	3	5	2	5	4	2	1	3	7
Rel. freq.	.7	1.1	.3	.9	.7	.6	.3	.8	1.4
No. sp.	2	3	1	3	2	2	1	2	3
Tap (N)									
S freq.	14	9	15	7	3	2	-	-	-
Rel. freq.	3.1	2.0	2.3	1.3	.5	.6	-	-	-
No. sp.	4	4	5	3	2	2	-	-	-
Fibrous (S)									
S freq.	240	364	418	551	482	523	450	609	
Rel. freq.	80.3	90.3	90.5	91.1	89.8	88.5	88.2	88.0	
Fascicled (S)									
S freq.	-	12	13	9	14	17	11	24	
Rel. freq.	-	3.0	2.8	1.5	2.6	2.9	2.2	3.5	
No. sp.	-	3	1	4	5	5	3	3	
Tuberous (S)									
S freq.	-	-	-	-	-	-	-	3	
Rel. freq.	-	-	-	-	-	-	-	.4	
No. sp.	-	-	-	-	-	-	-	1	
Tap (S)									
S freq.	59	27	31	44	40	43	35	26	
Rel. freq.	19.7	6.7	6.7	7.3	7.4	7.3	6.9	3.8	
No. sp.	5	5	6	7	6	5	4	4	

(3) Depth of Roots

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Indifferent (N)									
S freq.	242	220	328	227	216	109	85	47	41
Rel. freq.	52.7	48.1	50.4	41.3	36.5	35.0	23.5	12.6	8.1
No. sp.	25	24	24	23	18	17	14	14	10
A_1 Horizon (N)									
S freq.	217	237	323	321	372	202	284	326	465
Rel. freq.	47.3	51.9	49.6	58.7	63.5	65.0	76.5	87.4	91.9
No. sp.	26	34	40	47	45	40	46	53	51
Indifferent (S)									
S freq.	182	88	108	129	92	95	41	35	
Rel. freq.	60.9	21.8	23.4	21.3	17.1	16.1	8.0	5.1	
No. sp.	20	16	20	24	21	20	10	8	
A_1 Horizon (S)									
S freq.	117	315	354	476	445	496	469	657	
Rel. freq.	39.0	78.2	76.6	78.5	82.9	83.9	92.0	94.9	
No. sp.	17	42	39	56	59	60	61	63	

(4) Overwintering Organ

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Bulb (N)									
S freq.	-	-	-	-	-	10	-	14	37
Rel. freq.	-	-	-	-	-	3.2	-	3.8	7.3
No. sp.	-	-	-	-	-	1	-	1	2
Corm (N)									
S freq.	-	-	-	-	1	1	11	28	97
Rel. freq.	-	-	-	-	.2	.3	3.0	7.5	19.2
No. sp.	-	-	-	-	1	1	2	4	4
Stem bud (N)									
S freq.	96	79	74	69	60	33	42	27	10
Rel. freq.	20.9	17.3	11.4	12.6	10.2	10.6	11.6	7.2	2.0
No. sp.	8	7	6	9	7	9	6	5	4
Seed (N)									
S freq.	6	1	2	3	-	-	-	1	5
Rel. freq.	1.3	.2	.3	.5	-	-	-	.3	1.0
No. sp.	1	1	1	1	-	-	-	1	2
Rhizome (N)									
S freq.	324	352	543	462	520	261	305	286	323
Rel. freq.	70.6	77.0	83.4	84.2	88.0	83.9	84.3	76.7	63.8
No. sp.	35	43	50	55	50	40	50	54	46
Crown bud (N)									
S freq.	15	13	13	4	6	3	4	17	34
Rel. freq.	3.3	2.8	2.0	.7	1.0	1.0	1.1	4.6	6.7
No. sp.	3	3	4	2	2	3	2	2	3
Root bud (N)									
S freq.	18	12	19	11	4	3	-	-	-
Rel. freq.	3.9	2.6	2.9	2.0	.7	1.0	-	-	-
No. sp.	4	4	3	3	3	3	-	-	-
Bulb (S)									
S freq.	-	-	1	6	2	4	11	38	
Rel. freq.	-	-	.2	1.0	.4	.7	2.2	5.5	
No. sp.	-	-	1	2	1	1	2	3	

(4) Overwintering Organ

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Corm (S)									
S freq.	-	2	1	12	11	15	28	79	
Rel. freq.	-	.5	.2	2.0	2.0	2.5	5.5	11.4	
No. sp.	-	1	1	1	1	1	3	3	
Stem bud (S)									
S freq.	34	21	20	26	19	16	16	63	
Rel. freq.	11.3	5.2	4.3	4.3	3.5	2.7	3.1	9.1	
No. sp.	2	3	4	5	5	3	3	3	
Seed (S)									
S freq.	-	10	5	9	11	10	12	27	
Rel. freq.	-	2.5	1.1	1.5	2.0	1.7	2.4	3.9	
No. sp.	-	1	2	2	3	2	2	3	
Rhizome (S)									
S freq.	193	295	345	440	410	440	372	413	
Rel. freq.	64.5	73.2	74.7	72.7	76.3	74.4	72.9	59.7	
No. sp.	27	41	39	55	57	59	51	47	
Crown bud (S)									
S freq.	45	69	83	106	80	104	71	72	
Rel. freq.	15.0	17.1	18.0	17.5	14.9	17.6	13.9	10.4	
No. sp.	5	11	11	14	12	13	10	12	
Root bud (S)									
S freq.	27	6	5	6	4	2	-	-	
Rel. freq.	9.0	1.5	1.1	1.0	.7	.3	-	-	
No. sp.	3	1	1	1	1	1	-	-	

(5) Overwintering Organ Depth

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
A_0 Horizon (N)									
S freq.	69	100	103	77	106	48	31	36	48
Rel. freq.	15.0	21.9	15.8	14.0	17.9	15.4	8.6	9.7	9.5
No. sp.	7	8	10	9	8	6	9	11	10
A_1 Horizon (N)									
S freq.	206	224	347	318	326	176	235	279	424
Rel. freq.	44.8	49.0	53.3	57.9	55.2	56.6	64.9	74.8	83.8
No. sp.	29	36	41	43	41	37	38	45	41
Indifferent (N)									
S freq.	88	54	121	79	95	54	33	18	18
Rel. freq.	19.2	11.8	18.6	14.4	16.1	17.4	9.1	4.8	3.6
No. sp.	7	7	5	7	5	5	4	5	5
Aerial (N)									
S freq.	96	79	80	75	64	33	63	40	16
Rel. freq.	20.9	17.3	12.3	13.7	10.8	10.6	17.4	10.7	3.2
No. sp.	8	7	8	11	9	9	9	6	5
A_0 Horizon (S)									
S freq.	48	73	99	108	103	118	92	125	
Rel. freq.	16.0	18.1	21.4	17.9	19.2	20.0	18.0	18.1	
No. sp.	6	7	13	14	14	15	13	13	
A_1 Horizon (S)									
S freq.	185	313	334	467	416	467	411	566	
Rel. freq.	61.6	77.7	72.3	77.1	77.4	78.9	80.6	81.8	
No. sp.	25	47	40	59	60	61	55	57	
Indifferent (S)									
S freq.	32	13	27	25	13	6	3	1	
Rel. freq.	10.7	3.2	5.8	4.1	2.4	1.0	.6	.1	
No. sp.	4	3	4	4	5	4	2	1	
Aerial (S)									
S freq.	34	4	2	5	5	-	4	-	
Rel. freq.	11.3	1.0	.4	.8	.9	-	.8	-	
No. sp.	2	1	2	3	1	-	1	-	

(6) Vegetative Reproduction

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Roots (N)									
S freq.	32	34	45	33	17	7	3	-	-
Rel. freq.	7.0	7.4	6.9	6.0	2.9	2.3	.8	-	-
No. sp.	5	5	4	4	4	4	1	-	-
Rhizome (N)									
S freq.	332	331	485	409	463	244	297	284	338
Rel. freq.	72.3	72.4	74.5	74.5	78.3	78.5	82.0	76.1	66.8
No. sp.	33	37	39	45	41	39	43	48	42
Stolon (N)									
S freq.	70	65	60	67	59	31	29	30	31
Rel. freq.	15.3	14.2	9.2	12.2	10.0	10.0	8.0	8.0	6.1
No. sp.	6	6	4	6	6	4	4	4	3
Absent (N)									
S freq.	25	27	61	40	52	29	33	59	137
Rel. freq.	5.4	5.9	9.4	7.3	8.8	9.3	9.1	15.8	27.1
No. sp.	7	10	17	15	12	10	12	14	15
Detached part (N)									
S freq.	-	-	-	-	-	-	-	15	49
Rel. freq.	-	-	-	-	-	-	-	4.0	9.7
No. sp.	-	-	-	-	-	-	-	1	1
Roots (S)									
S freq.	27	6	6	8	9	2	-	-	
Rel. freq.	9.0	1.5	1.3	1.3	1.7	.3	-	-	
No. sp.	3	1	2	2	2	1	-	-	
Rhizome (S)									
S freq.	139	205	258	354	300	319	309	391	
Rel. freq.	46.5	50.9	55.8	58.5	55.9	54.0	60.6	56.5	
No. sp.	18	31	29	42	41	43	37	37	
Stolon (S)									
S freq.	62	42	33	20	30	31	9	19	
Rel. freq.	20.7	10.4	7.1	3.3	5.6	5.2	1.8	2.7	
No. sp.	5	6	5	5	5	6	5	3	

(6) Vegetative Reproduction

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Absent (S)									
S freq.	71	150	165	223	198	239	187	261	
Rel. freq.	23.7	37.2	35.7	36.9	36.9	40.4	36.7	37.7	
No. sp.	11	20	23	31	32	30	27	30	
Detached part (S)									
S freq.	-	-	-	-	-	-	5	21	
Rel. freq.	-	-	-	-	-	-	1.0	3.0	
No. sp.	-	-	-	-	-	-	2	1	

(7) Longevity

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Herbaceous perennial (N)									
S freq.	308	337	500	424	493	259	300	323	476
Rel. freq.	67.1	73.8	77.0	77.2	83.2	83.3	82.9	86.6	94.1
No. sp.	37	45	50	53	48	42	49	56	53
Woody perennial (N)									
S freq.	145	119	149	122	98	52	62	49	25
Rel. freq.	31.6	26.1	22.9	22.2	16.6	16.7	17.1	13.1	4.9
No. sp.	13	12	13	16	15	15	11	10	6
Annual (N)									
S freq.	6	1	2	3	-	-	-	1	5
Rel. freq.	1.3	.2	.3	.5	-	-	-	.3	1.0
No. sp.	1	1	1	1	-	-	-	1	2
Winter annual (S)									
S freq.	-	16	13	20	9	11	14	49	
Rel. freq.	-	4.0	2.8	3.3	1.7	1.9	2,7	7.1	
No. sp.	-	1	1	1	1	1	1	1	
Biennial (S)									
S freq.	-	1	5	1	4	3	1	1	
Rel. freq.	-	.2	1.1	.2	.7	.5	.2	.1	
No. sp.	-	1	1	1	2	1	1	1	
Herbaceous perennial (S)									
S freq.	265	369	432	565	491	563	480	602	
Rel. freq.	88.6	91.5	93.5	93.4	91.4	95.3	94.1	87.0	
No. sp.	35	53	52	71	71	74	64	65	
Woody perennial (S)									
S freq.	34	7	7	10	22	4	3	13	
Rel. freq.	11.4	1.7	1.5	1.6	4.1	.7	.6	1.9	
No. sp.	2	2	3	5	3	2	3	1	
Annual (S)									
S freq.	-	10	5	9	11	10	12	27	
Rel. freq.	-	2.5	1.1	1.5	2.0	1.7	2.4	3.9	
No. sp.	-	1	2	2	3	2	2	3	

(8) Canopy Type

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Lacking (N)									
S freq.	-	-	-	-	-	-	-	-	2
Rel. freq.	-	-	-	-	-	-	-	-	.4
No. sp.	-	-	-	-	-	-	-	-	1
Umbrella-type (N)									
S freq.	128	119	176	186	175	101	108	75	127
Rel. freq.	27.9	26.1	27.1	33.9	29.6	32.5	29.8	20.1	25.1
No. sp.	9	10	9	11	13	15	17	18	16
Prostrate (N)									
Sfreq.	12	15	28	32	30	23	20	22	17
Rel. freq.	2.6	3.3	4.3	5.8	5.1	7.4	5.5	5.9	3.4
No. sp.	4	3	5	6	4	4	3	2	2
Basal (N)									
S freq.	53	89	161	108	126	74	56	78	106
Rel. freq.	11.6	19.5	24.8	19.7	21.3	23.8	15.5	20.9	20.9
No. sp.	8	11	14	12	12	12	11	15	13
Cauline (N)									
S freq.	266	234	286	223	260	113	178	198	254
Rel. freq.	58.0	51.2	44.0	40.6	44.0	36.3	49.2	53.1	50.2
No. sp.	30	34	36	41	34	26	28	32	29
Lacking (S)									
S freq.	-	-	-	-	-	1	2	-	
Rel. freq.	-	-	-	-	-	.2	.4	-	
No. sp.	-	-	-	-	-	1	1	-	
Umbrella-like (S)									
S freq.	30	56	97	142	118	122	136	161	
Rel. freq.	10.0	13.9	21.0	23.4	21.9	20.6	26.7	23.3	
No. sp.	3	10	10	13	14	16	13	15	
Prostrate (S)									
S freq.	9	23	15	25	15	17	15	59	
Rel. freq.	3.0	5.7	3.2	4.1	2.8	2.9	2.9	8.5	
No. sp.	3	4	2	4	4	4	2	3	

(8) Canopy Type

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Basal (S)									
S freq.	26	37	22	34	41	49	55	106	
Rel. freq.	8.7	9.2	4.8	5.6	7.6	8.3	10.8	15.3	
No. sp.	4	5	6	7	8	6	10	7	
Cauline (S)									
S freq.	234	287	328	404	363	402	302	366	
Rel. freq.	78.2	71.1	71.0	66.7	67.5	68.0	59.2	52.9	
No. sp.	27	39	41	56	54	53	45	46	

(9) Leaf Type

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Simple (N)									
S freq.	372	395	519	411	453	233	269	281	362
Rel. freq.	81.1	86.5	79.9	74.8	76.6	74.9	74.3	75.3	71.5
No. sp.	45	49	52	53	44	44	41	47	42
Compound (N)									
S freq.	87	62	132	138	138	78	93	92	144
Rel. freq.	19.0	13.6	20.3	25.1	23.3	25.1	25.7	24.7	28.5
No. sp.	6	9	12	17	19	13	19	20	19
Simple (S)									
S freq.	180	271	283	339	323	365	294	467	
Rel. freq.	60.2	67.2	61.2	55.9	60.1	61.7	57.6	67.5	
No. sp.	23	35	35	46	49	46	40	41	
Compound (S)									
S freq.	119	132	179	266	214	226	216	225	
Rel. freq.	39.8	32.7	38.7	43.9	39.8	38.2	42.3	32.5	
No. sp.	14	23	24	34	31	34	31	30	

(10) Leaf size (leaflet equals leaf)

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Leptophyll (N)									
S freq.	9	13	2	14	21	12	37	24	9
Rel. freq.	2.0	2.8	.3	2.5	3.6	3.9	10.2	6.4	1.8
No. sp.	3	4	1	5	4	5	4	5	5
Nanophyll (N)									
S freq.	143	95	142	129	112	61	54	63	104
Rel. freq.	31.2	20.8	21.9	23.5	19.0	19.6	14.9	16.9	20.6
No. sp.	9	10	10	11	10	10	11	11	9
Microphyll (N)									
S freq.	200	210	312	243	247	121	137	123	196
Rel. freq.	43.6	46.0	48.0	44.2	41.8	38.9	37.8	35.4	38.7
No. sp.	27	31	39	38	33	26	27	30	25
Mesophyll (N)									
S freq.	107	139	195	163	211	117	134	154	197
Rel. freq.	23.3	30.4	30.0	29.7	35.7	37.6	37.0	41.3	38.9
No. sp.	12	13	14	16	16	16	18	21	22
Leptophyll (S)									
S freq.	1	33	26	40	35	34	20	17	
Rel. freq.	.3	8.2	5.6	6.6	6.5	5.7	3.9	2.5	
No. sp.	1	2	2	2	2	2	2	2	
Nanophyll (S)									
S freq.	78	63	60	67	56	53	73	132	
Rel. freq.	26.1	15.6	13.0	11.1	10.4	9.0	14.3	19.1	
No. sp.	6	11	9	10	10	11	12	12	
Microphyll (S)									
S freq.	141	163	178	242	238	256	179	237	
Rel. freq.	47.2	40.4	38.5	39.9	44.3	43.3	35.1	34.2	
No. sp.	20	27	28	39	39	35	27	25	
Mesophyll (S)									
S freq.	79	144	198	256	208	248	238	306	
Rel. freq.	26.4	35.7	42.8	42.2	38.7	41.9	46.6	44.2	
No. sp.	10	18	20	29	29	32	30	32	

(11) Leaf size (compound leaf equals leaf)

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Leptophyll (N)									
S freq.	9	12	2	12	18	11	28	19	7
Rel. freq.	2.0	2.6	.3	2.2	3.0	3.5	7.7	5.1	1.4
No. sp.	3	3	1	4	3	4	3	4	4
Nanophyll (N)									
S freq.	85	55	59	53	38	19	11	8	5
Rel. freq.	18.5	12.0	9.1	9.6	6.4	6.1	3.0	2.1	1.0
No. sp.	7	7	6	7	5	4	2	1	1
Microphyll (N)									
S freq.	206	197	287	222	225	102	122	106	161
Rel. freq.	44.9	43.1	44.2	40.4	38.1	32.8	33.7	28.4	31.8
No. sp.	25	29	34	31	27	23	23	26	21
Mesophyll (N)									
S freq.	159	193	302	259	305	176	200	237	330
Rel. freq.	34.7	42.3	46.5	47.1	51.6	56.6	55.2	63.5	65.2
No. sp.	16	19	22	26	26	25	31	34	33
Macrophyll (N)									
S freq.	-	-	1	3	5	3	1	3	3
Rel. freq.	-	-	.2	.5	.8	1.0	.3	.8	.6
No. sp.	-	-	1	2	2	1	1	2	2
Leptophyll (S)									
S freq.	-	29	22	32	22	28	14	8	
Rel. freq.	-	7.2	4.8	5.3	4.1	4.7	2.7	1.2	
No. sp.	-	1	1	1	1	1	1	1	
Nanophyll (S)									
S freq.	19	20	19	20	11	12	17	61	
Rel. freq.	6.4	5.0	4.1	3.3	2.0	2.0	3.3	8.8	
No. sp.	2	3	3	1	2	2	3	4	
Microphyll (S)									
S freq.	153	137	112	131	167	164	129	197	
Rel. freq.	51.2	34.0	24.2	21.6	31.1	27.7	25.3	28.5	
No. sp.	18	22	22	29	30	26	20	20	

(11) Leaf size (compound leaf equals leaf)

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Mesophyll (S)									
S freq.	127	217	307	415	328	383	344	421	
Rel. freq.	42.5	53.8	66.4	68.5	61.0	64.7	67.4	60.8	
No. sp.	17	32	31	46	45	49	44	43	
Macrophyll (S)									
S freq.	-	-	2	7	9	4	6	5	
Rel. freq.	-	-	.4	1.2	1.7	.7	1.2	.7	
No. sp.	-	-	2	3	2	2	3	3	

(12) Photosynthetic season

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Vernal (N)									
S freq.	-	-	-	-	-	10	5	37	125
Rel. freq.	-	-	-	-	-	3.2	1.4	9.9	24.7
No. sp.	-	-	-	-	-	1	1	4	5
Growing season (N)									
S freq.	299	246	387	331	370	190	229	231	275
Rel. freq.	65.2	53.9	59.4	60.2	62.6	61.1	63.2	61.9	54.3
No. sp.	33	40	41	44	38	32	38	41	39
Evergreen (N)									
S freq.	160	211	264	218	221	111	128	105	104
Rel. freq.	34.9	46.2	40.7	39.7	37.4	35.7	35.4	28.2	20.6
No. sp.	18	18	23	26	25	24	21	22	16
None (N)									
S freq.	-	-	-	-	-	-	-	-	2
Rel. freq.	-	-	-	-	-	-	-	-	.4
No. sp.	-	-	-	-	-	-	-	-	1
Vernal (S)									
S freq.	-	1	1	7	6	5	16	119	
Rel. freq.	-	.2	.2	1.2	1.1	.8	3.1	17.2	
No. sp.	-	1	1	3	2	2	4	8	
Growing season (S)									
S freq.	282	321	354	487	414	446	374	454	
Rel. freq.	94.3	79.6	76.6	80.5	77.1	75.5	73.3	65.6	
No. sp.	35	47	46	64	62	64	52	52	
Evergreen (S)									
S freq.	17	65	94	91	108	128	104	67	
Rel. freq.	5.7	16.1	20.4	15.0	20.1	21.7	20.4	9.7	
No. sp.	2	9	11	12	15	12	13	9	
Winter (S)									
S freq.	-	16	13	20	9	11	14	52	
Rel. freq.	-	4.0	2.8	3.3	1.7	1.9	2.7	7.5	
No. sp.	-	1	1	1	1	1	1	2	

(12) Photosynthetic season

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
None (S)									
S freq.	-	-	-	-	-	1	2	-	
Rel. freq.	-	-	-	-	-	.2	.4	-	
No. sp.	-	-	-	-	-	1	1	-	

(13) Aerial Stem Type

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Deliquescent (N)									
S freq.	118	91	128	103	122	51	71	96	109
Rel. freq.	25.7	19.9	20.7	18.8	20.6	16.4	19.6	25.7	21.5
No. sp.	12	18	20	20	16	12	14	16	17
Excurrent (N)									
S freq.	248	261	337	301	314	157	169	158	227
Rel. freq.	54.0	57.1	51.8	54.8	53.1	50.5	46.7	42.4	44.9
No. sp.	26	26	25	24	25	23	23	28	25
Reclining (N)									
S freq.	14	17	22	22	18	20	29	20	8
Rel. freq.	3.1	3.7	3.4	4.0	3.0	6.4	8.0	5.4	1.6
No. sp.	4	3	4	5	4	6	4	3	3
Acaulescent (N)									
S freq.	77	86	158	114	134	83	92	101	162
Rel. freq.	16.8	18.8	24.3	20.8	22.7	26.7	25.4	27.1	32.0
No. sp.	7	10	13	17	16	16	18	20	16
Twining (N)									
S freq.	2	2	6	9	3	-	1	-	-
Rel. freq.	.4	.4	.9	1.6	.5	-	.3	-	-
No. sp.	2	1	2	4	2	-	1	-	-
Deliquescent (S)									
S freq.	82	161	213	283	243	283	222	226	
Rel. freq.	27.4	39.9	46.1	46.8	45.2	47.9	43.5	32.7	
No. sp.	10	21	23	29	29	28	22	25	
Excurrent (S)									
S freq.	144	149	184	207	189	197	157	251	
Rel. freq.	48.2	37.0	39.8	34.2	35.2	33.3	30.8	36.3	
No. sp.	16	21	24	34	33	34	29	31	
Reclining (S)									
S freq.	3	16	13	20	9	11	14	49	
Rel. freq.	1.0	4.0	2.8	3.3	1.7	1.9	2.7	7.1	
No. sp.	1	1	1	1	1	1	1	1	

(13) Aerial Stem Type

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Acaulescent (S)									
S freq.	40	49	39	64	76	71	102	165	
Rel. freq.	13.4	12.2	8.4	10.6	14.2	12.0	20.0	23.8	
No. sp.	5	10	9	12	12	12	16	12	
Twining (S)									
S freq.	30	29	17	32	21	32	16	7	
Rel. freq.	10.0	7.2	3.7	5.3	3.9	5.4	3.1	1.0	
No. sp.	5	5	2	4	5	5	3	2	

(14) Pollination

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Insect (N)									
S freq.	361	332	506	415	445	231	248	246	353
Rel. freq.	78.6	72.6	77.7	75.6	75.3	74.3	68.5	66.0	69.8
No. sp.	39	40	44	44	39	34	34	36	35
Wind (N)									
S freq.	29	43	28	21	29	6	11	26	41
Rel. freq.	6.3	9.4	4.3	3.8	4.9	1.9	3.0	7.0	8.1
No. sp.	2	2	6	5	6	4	5	6	5
Insect, bird, and cleistogamous (N)									
S freq.	-	-	-	-	-	-	-	1	3
Rel. freq.	-	-	-	-	-	-	-	.3	.6
No. sp.	-	-	-	-	-	-	-	1	1
Water (N)									
S freq.	47	48	67	64	68	48	70	56	39
Rel. freq.	10.2	10.5	10.3	11.6	11.5	15.4	19.3	15.0	7.7
No. sp.	4	6	4	10	9	10	12	12	11
Cleistogamous and insect (N)									
S freq.	15	25	42	39	35	20	24	34	51
Rel. freq.	3.3	5.5	6.4	7.1	5.9	6.4	6.6	9.4	10.7
No. sp.	5	9	7	8	7	8	7	10	7
Insect and bird (N)									
S freq.	7	9	8	10	14	6	9	10	19
Rel. freq.	1.5	2.0	1.2	1.8	2.4	1.9	2.5	2.7	3.8
No. sp.	1	1	3	3	2	1	2	2	2
All insects (N)									
S freq.	383	366	556	464	494	257	281	291	426
Rel. freq.	83.4	80.1	85.4	84.5	83.6	82.6	77.6	78.0	84.2
No. sp.	45	50	54	55	48	43	43	49	45
All cleistogamous (N)									
S freq.	15	25	42	39	35	20	24	35	54
Rel. freq.	3.3	5.5	6.4	7.1	5.9	6.4	6.6	9.4	10.7
No. sp.	5	9	7	8	7	8	7	11	8

(14) Pollination

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Insect (S)									
S freq.	217	293	346	471	387	434	362	517	
Rel. freq.	72.6	72.7	74.9	77.9	72.1	73.4	71.0	74.7	
No. sp.	27	45	42	58	59	58	48	51	
Wind (S)									
S freq.	7	28	27	25	47	43	33	30	
Rel. freq.	2.3	6.9	5.8	4.1	8.8	7.3	6.5	4.3	
No. sp.	1	2	5	7	8	7	7	6	
Insect, bird, and cleistogamous (S)									
S freq.	-	-	3	8	2	7	8	17	
Rel. freq.	-	-	.6	1.3	.4	1.2	1.6	2.5	
No. sp.	-	-	1	1	1	1	1	1	
Water (S)									
S freq.	17	20	32	40	38	28	39	48	
Rel. freq.	5.7	5.0	6.9	6.6	7.1	4.7	7.6	6.9	
No. sp.	2	5	5	7	6	6	8	6	
Cleistogamous and insect (S)									
S freq.	41	42	30	43	43	60	47	74	
Rel. freq.	13.7	10.4	6.5	7.1	8.0	10.2	12.6	10.7	
No. sp.	4	5	4	4	4	5	5	5	
Insect and bird (S)									
S freq.	17	20	24	18	20	19	21	6	
Rel. freq.	5.7	5.0	5.2	3.0	3.7	3.2	4.1	8.7	
No. sp..	3	1	2	3	2	3	2	2	
All insect (S)									
S freq.	275	255	403	540	452	520	438	614	
Rel. freq.	92.0	88.1	87.2	89.3	84.2	88.0	85.9	88.7	
No. sp.	34	51	49	66	66	67	56	59	
All cleistogamous (S)									
S freq.	41	42	33	51	45	67	55	91	
Rel. freq.	13.7	10.4	7.1	8.4	8.4	11.3	10.8	13.2	
No. sp.	4	5	5	5	5	6	6	6	

(15) Blooming season

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Pre-vernal (N)									
S freq.	27	15	33	37	35	16	24	38	134
Rel. freq.	5.9	3.3	5.1	6.7	5.9	5.1	6.6	10.2	26.5
No. sp.	3	3	4	5	3	5	6	7	6
Vernal (N)									
S freq.	100	109	140	135	158	76	106	142	176
Rel. freq.	21.8	23.9	21.6	24.6	26.7	24.4	29.3	38.1	34.8
No. sp.	7	13	13	17	15	14	14	18	17
Aestival (N)									
S freq.	323	332	473	3756	397	218	231	190	193
Rel. freq.	70.4	72.7	72.8	68.2	67.2	70.1	63.8	50.9	38.1
No. sp.	38	41	46	47	44	37	39	40	37
Autumnal (N)									
S freq.	9	1	5	2	1	1	1	3	3
Rel. freq.	2.0	.2	.8	.4	.2	.3	.3	.8	.6
No. sp.	3	1	1	1	1	1	1	2	1
Pre-vernal and vernal (N)									
S freq.	127	124	173	172	193	92	130	180	310
Rel. freq.	27.7	27.1	26.6	31.3	32.7	29.6	35.9	48.3	61.3
No. sp.	10	16	17	22	18	19	20	25	23
Pre-vernal (S)									
S freq.	10	23	12	16	28	39	60	125	
Rel. freq.	3.3	5.7	2.6	2.6	5.2	6.6	11.8	18.1	
No. sp.	1	3	1	3	4	4	5	7	
Vernal (S)									
S freq.	43	104	109	161	150	182	179	235	
Rel. freq.	14.4	25.8	23.6	26.6	27.9	30.8	35.1	34.0	
No. sp.	8	13	14	19	19	21	22	23	
Aestival (S)									
S freq.	236	262	330	397	345	342	247	300	
Rel. freq.	78.9	65.0	71.4	65.5	64.2	57.8	48.4	43.4	
No. sp.	25	37	38	52	51	49	40	35	

(15) Blooming season

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Autumnal (S)									
S freq.	10	11	10	30	12	27	24	32	
Rel. freq.	3.3	2.7	2.2	5.0	2.2	4.6	4.7	4.6	
No. sp.	3	4	5	5	5	5	4	6	
Growing season (S)									
S freq.	-	-	1	1	2	1	-	-	
Rel. freq.	-	-	.2	.2	.4	.2	-	-	
No. sp.	-	-	1	1	1	1	-	-	
Vernal and pre-vernal (S)									
S freq.	53	127	121	177	178	221	239	360	
Rel. freq.	17.6	31.5	26.2	39.2	33.1	37.4	46.8	52.0	
No. sp.	9	16	15	22	23	25	27	30	

(16) Seed or fruit dispersal

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Fleshy (N)									
S freq.	187	167	196	184	204	97	133	116	108
Rel. freq.	40.7	36.5	30.1	33.5	34.5	31.2	36.7	31.1	21.3
No. sp.	13	13	13	12	14	11	12	12	12
Explosive plus elaisome (N)									
S freq.	-	1	4	3	2	1	1	6	10
Rel. freq.	-	.2	.6	.5	.3	.3	.3	1.6	2.0
No. sp.	-	1	1	1	1	1	1	1	1
Elaisome (N)									
S freq.	59	60	79	62	87	56	31	60	152
Rel. freq.	12.9	13.1	12.2	11.3	14.7	18.0	8.6	16.1	30.0
No. sp.	5	8	6	10	7	8	7	10	8
Stick-tight (N)									
S freq.	1	10	22	19	23	14	22	34	47
Rel. freq.	.2	2.2	3.4	3.5	3.9	4.5	6.1	9.1	9.3
No. sp.	1	4	7	7	5	5	7	6	5
Explosive (N)									
S freq.	6	13	29	18	23	14	57	61	92
Rel. freq.	1.3	2.8	4.5	3.3	3.9	4.5	15.7	16.4	18.2
No. sp.	3	5	6	7	7	6	11	14	13
Small and light (N)									
S freq.	58	58	100	81	72	44	43	28	14
Rel. freq.	12.6	12.7	15.4	14.7	12.2	14.1	11.9	7.5	2.8
No. sp.	7	8	8	12	11	10	9	9	8
Plumed (N)									
S freq.	31	34	77	50	46	26	17	15	7
Rel. freq.	6.8	7.4	11.9	9.1	7.8	8.4	4.7	4.0	1.4
No. sp.	6	4	6	4	4	4	2	2	2
Winged (N)									
S freq.	2	2	-	-	-	-	-	-	-
Rel. freq.	.4	.4	-	-	-	-	-	-	-
No. sp.	1	1	-	-	-	-	-	-	-

(16) Seed or fruit dispersal

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
No special method (N)									
S freq.	117	114	144	132	134	59	58	53	76
Rel. freq.	25.5	24.9	22.1	24.0	22.7	19.0	16.0	14.2	15.0
No. sp.	16	15	17	17	14	12	11	13	12
All elaisomes (N)									
S freq.	59	61	83	65	89	57	32	66	162
Rel. freq.	12.8	13.3	12.7	11.8	15.1	18.3	8.8	17.7	32.0
No. sp.	5	9	7	11	8	9	8	11	9
All explosives (N)									
S freq.	6	14	33	21	25	15	58	67	102
Rel. freq.	1.3	3.0	5.1	3.8	4.2	4.8	16.0	18.0	20.2
No. sp.	3	6	7	8	8	7	12	15	14
All wind (N)									
S freq.	91	94	177	131	118	70	60	43	21
Rel. freq.	19.8	20.6	27.2	23.9	20.0	22.5	16.6	11.5	4.2
No. sp.	14	13	14	16	15	14	11	11	10
Fleshy (S)									
S freq.	55	67	85	113	93	92	86	93	
Rel. freq.	18.4	16.6	18.4	18.6	17.3	15.5	16.9	13.4	
No. sp.	6	10	10	13	13	14	12	20	
Explosive plus elaisome (S)									
S freq.	-	1	-	2	3	17	18	32	
Rel. freq.	-	.2	-	.3	.6	2.9	3.5	4.6	
No. sp.	-	1	-	1	1	1	1	1	
Elaisome (S)									
S freq.	8	11	14	31	58	64	88	160	
Rel. freq.	2.7	2.7	3.0	5.1	10.8	10.8	17.3	23.1	
No. sp.	1	5	3	6	8	9	11	14	
Stick-tight (S)									
S freq.	3	91	147	158	128	128	80	85	
Rel. freq.	1.0	22.6	31.8	26.1	23.8	21.7	15.7	12.3	
No. sp.	3	9	11	10	11	10	8	8	

(16) Seed or fruit dispersal

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Explosive (S)									
S freq.	84	93	83	132	91	111	88	139	
Rel. freq.	28.1	23.1	18.0	21.8	16.9	18.3	17.3	20.1	
No. sp.	10	11	8	13	11	11	11	11	
Small and light (S)									
S freq.	17	29	37	33	48	26	28	29	
Rel. freq.	5.7	7.2	8.0	5.5	8.9	4.4	5.5	4.2	
No. sp.	2	6	6	9	11	10	9	6	
Plumed (S)									
S freq.	20	21	19	37	21	38	21	16	
Rel. freq.	6.7	5.2	4.1	6.1	3.9	6.4	4.1	2.3	
No. sp.	5	7	7	8	7	7	5	6	
No special method (S)									
S freq.	112	90	77	99	95	115	101	138	
Rel. freq.	37.5	22.3	16.7	16.4	17.7	19.5	19.8	19.9	
No. sp.	10	9	14	20	18	18	14	15	
All elaisomes (S)									
S freq.	8	12	14	33	61	81	106	192	
Rel. freq.	2.7	2.9	3.0	5.4	11.4	13.7	20.8	27.7	
No. sp.	1	6	3	7	9	10	12	15	
All explosive (S)									
S freq.	84	94	83	134	94	128	106	171	
Rel. freq.	28.1	23.3	18.0	22.1	17.5	21.7	20.8	24.7	
No. sp.	10	12	8	14	12	12	12	12	
All wind (S)									
S freq.	37	50	56	70	69	64	49	45	
Rel. freq.	12.4	12.4	12.1	11.6	12.8	10.8	9.6	6.5	
No. sp.	8	14	13	17	18	17	14	12	

(17) Season of fruit ripening

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Vernal (N)									
S freq.	6	10	13	8	12	19	11	57	160
Rel. freq.	1.3	2.2	2.0	1.5	2.0	6.1	3.0	15.3	31.6
No. sp.	1	2	2	4	2	5	5	9	7
Aestival (N)									
S freq.	306	318	410	362	423	196	241	215	249
Rel. freq.	66.7	69.6	63.0	65.9	71.6	63.0	66.6	57.6	49.2
No. sp.	32	39	40	41	40	34	33	36	36
Autumnal (N)									
S freq.	147	129	228	179	156	96	110	101	97
Rel. freq.	32.0	28.2	35.0	32.6	26.4	30.9	30.4	27.1	19.2
No. sp.	18	17	22	25	21	18	22	22	18
Vernal (S)									
S freq.	-	3	-	12	14	29	66	164	
Rel. freq.	-	.7	-	2.6	2.6	4.9	12.9	23.7	
No. sp.	-	2	-	4	4	5	8	12	
Aestival (S)									
S freq.	199	255	257	313	295	312	255	343	
Rel. freq.	66.6	63.5	55.6	51.7	54.9	52.8	50.0	49.6	
No. sp.	24	32	29	40	39	41	33	31	
Autumnal (S)									
S freq.	100	145	204	279	226	249	189	185	
Rel. freq.	33.4	36.0	44.2	46.1	42.1	42.1	37.1	26.7	
No. sp.	13	24	29	35	36	33	30	28	
Growing season (S)									
S freq.	-	-	1	1	2	1	-	-	
Rel. freq.	-	-	.2	.2	.4	.2	-	-	
No. sp.	-	-	1	1	1	1	-	-	

(18) Season of flower bud formation

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Current growing season (N)									
S freq.	168	174	296	214	208	116	140	124	101
Rel. freq.	36.6	38.1	45.5	39.0	35.2	37.2	38.7	33.2	20.0
No. sp.	26	29	32	33	28	22	24	27	25
Previous growing season (N)									
S freq.	291	283	355	335	383	195	222	249	405
Rel. freq.	63.4	61.9	54.5	61.0	64.8	62.7	61.3	66.8	80.0
No. sp.	25	29	32	37	35	35	36	40	36
Current growing season (S)									
S freq.	199	225	259	344	262	291	198	245	
Rel. freq.	66.6	55.8	56.1	56.9	48.8	49.2	38.8	35.4	
No. sp.	22	35	35	44	43	40	31	32	
Previous growing season (S)									
S freq.	100	178	203	261	275	300	312	447	
Rel. freq.	33.4	44.2	43.9	43.1	51.2	50.8	61.2	64.6	
No. sp.	15	23	24	36	37	40	40	39	

(19) Turrill's extended scheme

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Deciduous shrubs (N)									
S freq.	76	53	53	38	26	7	3	-	-
Rel. freq.	16.6	11.6	8.2	6.9	4.4	2.2	.8	-	-
No. sp.	2	2	2	2	2	2	1	-	-
Perennial herbs or subshrubs, partially woody at base, and aerial parts dying back, but not to ground level (N)									
S freq.	3	1	3	3	2	-	1	-	-
Rel. freq.	.7	.2	.5	.5	.3	-	.3	-	-
No. sp.	1	1	1	1	1	-	1	-	-
Grasses and grass-like plants (N)									
S freq.	36	52	64	36	51	21	13	10	15
Rel. freq.	7.8	11.4	9.9	6.6	8.6	6.8	3.6	2.7	3.0
No. sp.	3	3	5	4	5	3	3	4	4
Perennial herbs and subshrubs with runners, or sprawling or herbaceous or suffructicose stems (N)									
S freq.	18	37	46	47	45	36	69	46	24
Rel. freq.	3.9	8.1	7.1	8.6	7.6	11.6	19.1	12.3	4.7
No. sp.	4	4	6	7	7	8	8	6	6
Rosette plants (N)									
S freq.	42	79	138	92	109	57	52	61	70
Rel. freq.	9.2	17.3	21.3	16.7	18.4	18.3	14.4	16.4	13.8
No. sp.	6	9	12	13	11	11	11	13	9
Perennial herbs dying down yearly, with perennating buds on more or less thick stock at ground level (N)									
S freq.	130	98	144	155	178	90	112	120	106
Rel. freq.	28.3	21.4	22.2	28.2	30.1	28.9	30.9	32.2	20.9
No. sp.	16	18	22	22	18	15	16	18	15
Geophytes (N)									
S freq.	84	78	133	117	148	89	108	133	286
Rel. freq.	18.3	17.1	20.5	21.3	25.0	28.6	29.8	35.7	56.5
No. sp.	9	13	10	11	14	13	19	23	25

(19) Turrill's extended scheme

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Annual herbs (N)									
S freq.	6	1	2	3	-	-	-	1	5
Rel. freq.	1.3	.2	.3	.5	-	-	-	.3	1.0
No. sp.	1	1	1	1	-	-	-	1	2
Herbaceous twining plants, generally dying down each year (N)									
S freq.	2	2	3	6	1	-	-	-	-
Rel. freq.	.4	.4	.5	1.1	.2	-	-	-	-
No. sp.	2	1	1	3	1	-	-	-	-
Evergreen shrubs (N)									
S freq.	62	56	65	52	31	11	4	2	-
Rel. freq.	13.5	12.3	10.0	9.5	5.2	3.5	1.1	.5	-
No. sp.	7	6	4	6	4	5	1	2	-
Deciduous shrubs (S)									
S freq.	34	4	2	5	5	-	-	-	
Rel. freq.	11.4	1.0	.4	.8	.9	-	-	-	
No. sp.	2	1	2	3	1	-	-	-	
Perennial herbs or subshrubs, partially woody at base, and aerial parts dying back, but not to ground level (S)									
S freq.	17	-	-	-	1	2	1	13	
Rel. freq.	5.7	-	-	-	.2	.3	.2	1.9	
No. sp.	1	-	-	-	1	1	1	1	
Grasses and grass-like plants (S)									
S freq.	11	20	40	31	45	46	22	16	
Rel. freq.	3.7	5.0	8.7	5.1	8.4	7.8	4.3	2.3	
No. sp.	2	2	4	5	6	5	5	4	
Perennial herbs and subshrubs with runners, or sprawling or herbaceous or suffructicose stems (S)									
S freq.	16	15	3	9	6	4	2	-	
Rel. freq.	5.4	3.7	.6	1.5	1.1	.7	.4	-	
No. sp.	1	1	1	2	1	1	2	-	

(19) Turrill's extended scheme

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Rosette plants (S)									
S freq.	7	42	60	57	67	99	79	93	
Rel. freq.	2.3	10.4	13.0	9.4	12.5	16.7	15.5	13.4	
No. sp.	2	8	7	7	9	8	8	7	
Perennial herbs dying down yearly, with perennating buds on more or less thick stock at ground level (S)									
S freq.	107	186	207	296	207	235	177	154	
Rel. freq.6	35.8	46.2	44.8	48.9	38.5	39.8	34.7	22.3	
No. sp.	18	27	27	34	33	35	28	29	
Geophytes (S)									
S freq.	97	103	129	174	182	177	201	339	
Rel. freq.	32.4	25.6	27.9	28.8	33.9	29.9	39.4	49.0	
No. sp.	8	14	14	23	22	24	23	25	
Annual herbs (S)									
S freq.	-	26	18	29	20	21	26	76	
Rel. freq.	-	6.4	3.9	4.8	3.7	3.5	5.1	11.0	
No. sp.	-	2	3	3	4	3	3	4	
Herbaceous twining plants generally dying down each year (S)									
S freq.	10	7	3	4	4	7	2	1	
Rel. freq.	3.3	1.7	.6	.7	.7	1.2	.4	.1	
No. sp.	3	3	1	3	3	3	1	1	

(20) Taxonomy

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Unstable (N)									
S freq.	175	184	228	175	158	85	100	91	82
Rel. freq.	38.1	40.3	35.0	31.9	26.7	27.3	27.6	24.4	16.2
No. sp.	15	17	16	20	16	14	12	14	13
Intermediate (N)									
S freq.	131	88	98	116	126	57	77	85	104
Rel. freq.	28.5	19.3	15.1	21.1	21.3	18.3	21.3	22.8	20.6
No. sp.	11	14	14	16	13	13	11	12	10
Stable (N)									
S freq.	153	185	325	258	307	169	185	197	320
Rel. freq.	33.3	40.5	49.9	47.0	51.9	54.3	51.1	52.8	63.2
No. sp.	25	27	34	34	34	30	37	41	38
Unstable (S)									
S freq.	113	95	87	99	91	108	72	95	
Rel. freq.	37.8	23.6	18.8	16.4	16.9	18.3	14.1	13.7	
No. sp.	14	18	16	19	18	19	14	12	
Intermediate (S)									
S freq.	70	72	84	141	105	133	130	191	
Rel. freq.	23.4	17.9	18.2	23.3	19.6	22.5	25.5	27.6	
No. sp.	9	12	14	20	21	22	20	20	
Stable (S)									
S freq.	116	236	291	365	341	350	308	406	
Rel. freq.	38.8	58.6	63.0	60.3	63.5	59.2	60.4	58.7	
No. sp.	14	28	29	41	41	39	37	39	

(21) Spines

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Plants armed with spines, thorns, etc. (N)									
S freq.	-	-	1	3	2	-	2	4	10
Rel. freq.	-	-	.2	.5	.3	-	.6	1.1	2.0
No. sp.	-	-	1	1	1	-	2	1	1
Plants not armed with spines, etc. (N)									
S freq.	459	457	648	546	589	311	360	369	496
Rel. freq.	100.0	100.0	99.8	99.4	99.7	100.0	99.4	98.9	98.0
No. sp.	51	58	63	69	62	57	58	66	60
Plants armed with spines (S)									
S freq.	-	-	-	1	1	4	2	13	
Rel. freq.	-	-	-	.2	.2	.7	.4	1.9	
No. sp.	-	-	-	1	1	2	2	1	
Plants not armed (S)									
S freq.	299	403	462	604	536	587	508	679	
Rel. freq.	100.0	100.0	100.0	99.7	99.7	99.2	99.6	98.1	
No. sp.	37	58	59	79	79	78	69	70	

(22) Nutrition

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Obligate autotroph (N)									
S freq.	456	454	650	548	591	311	362	373	504
Rel. freq.	99.3	99.3	99.8	99.8	100.0	100.0	100.0	100.0	99.6
No. sp.	50	57	63	69	63	57	60	67	60
Partial autotroph (N)									
S freq.	3	3	1	1	-	-	-	-	-
Rel. freq.	.6	.7	.2	.2	-	-	-	-	-
No. sp.	1	1	1	1	-	-	-	-	-
Parasite (N)									
S freq.	-	-	-	-	-	-	-	-	2
Rel. freq.	-	-	-	-	-	-	-	-	.4
No. sp.	-	-	-	-	-	-	-	-	1
Obligate autotroph (S)									
S freq.	299	403	462	605	537	590	508	692	
Rel. freq.	100.0	100.0	100.0	100.0	100.0	99.8	99.6	100.0	
No. sp.	37	58	59	80	80	79	70	71	
Parasite (S)									
S freq.	-	-	-	-	-	1	2	-	
Rel. freq.	-	-	-	-	-	.2	.4	-	
No. freq.	-	-	-	-	-	1	1	-	

(23) Flower Height

	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30
Below 18 inches (N)									
S freq.	372	360	475	431	481	257	317	327	449
Rel. freq.	81.0	78.8	73.0	78.5	81.4	82.6	87.6	87.7	88.7
No. sp.	36	44	46	53	49	48	47	50	44
Above 18 inches (N)									
S freq.	87	97	176	118	110	54	45	46	57
Rel. freq.	19.0	21.2	27.0	21.5	18.6	17.4	12.4	12.3	11.3
No. sp.	15	14	18	17	14	8	12	13	13
Below 18 inches (S)									
S freq.	97	239	263	330	371	385	390	582	
Rel. freq.	32.4	59.3	56.9	54.5	69.1	65.1	76.5	84.1	
No. sp.	18	34	32	45	50	49	48	49	
Above 18 inches (S)									
S freq.	202	164	199	275	166	206	120	110	
Rel. freq.	67.6	40.7	43.1	45.5	30.9	34.9	23.5	15.9	
No. sp.	19	24	27	35	30	31	23	22	

TITLE OF THESIS Interrelations of autecological characteristics of forest herbs

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