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RELATIONSHIPS BETWEEN PLANT LIFE-FORMS AND MICROCLIMATE IN SOUTHEASTERN MICHIGAN

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INTRODUCTION

Raunkiaer's well known system of plant life-form classification shows relationships between relative importance of certain life-form classes and major world climatic zones. Recent investigations have shown that there are also differences in life-form distribution related to climatic variations within the larger "phytoclimates." Several reviews (Adamson 1939; Cain 1950; Cain & Castro 1959) have summarized our understanding of these life-form concepts.

Relationships between life-forms and microclimate, however, have not been intensively investigated. Cain (1950) suggests that "Although life-form spectra have been employed mostly for general climatic analysis, there are enough studies available to suggest that they may be even more useful for the analysis of climatic variants and microclimates." The limited data available in the literature provide enough evidence that life-form distribution varies with differences in topography and microclimate to warrant further investigation of the subject.

The possible indicator significance of variations in community life-form composition also have received little attention. Whittaker (1954) points out that "composition of vegetation in terms of life-forms and growth-forms may indicate position along local gradients." Furthermore, the fact that a plant's life-form represents, in theory, a fundamental adaptation to environment makes community life-form composition of greater potential value than community species composition for use as an indicator of site (microenvironmental) conditions.

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This study was an intensive investigation of the vegetation and microclimates of north- and south-facing (henceforth referred to as north and south) slopes on the E. S. George Reserve in southeastern Michigan. The data obtained were used to demonstrate relationships between Raunkiaerian life-forms and microclimate and to illustrate the value of community life-form data as indicators of habitat conditions.

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REVIEW OF THE LITERATURE

Physiognomy has long been an important feature in the description and analysis of vegetation. Early physiognomic systems were primarily descriptive and did not attempt to express environmental relationships. However, under the influence of Darwin's ideas, systems developed which sought not only to be descriptive but also to express relationships between physiognomic characters of the plant and its environment (DuRietz 1932). Warming's (1884) "biological life-form system" was the first of a series which culminated with publication of Raunkiaer's life-form system in 1904.

Cain (1950) has reviewed the bases of life-form systems and has pointed out that such systems have no relation to phylogenetic systems of classification but are based on the architecture or structural adaptations of the plant. However, phylogenetic considerations cannot be removed entirely for certain groups may be hereditarily disposed toward a certain life-form (Cain 1950). Numata & Asano (1956) point out such a case in the abundance of geophytes among monocots.

Of the many life-form systems only that of Raunkiaer has achieved any degree of universal acceptance (DuRietz 1932). This classification, originally limited to flowering plants, was based on the degree of protection afforded the perennating tissue during the unfavorable season. Five classes, each with subdivisions, were established: 1) *Phanerophytes* (buds 25 cm or more above the substratum); 2) *Chamaephytes* (buds in the first 25 cm above the soil surface); 3) *Hemicryptophytes* (buds at or in the soil surface); 4) *Cryptophytes* (buds hidden under the soil or in muck or under water); 5) *Therophytes* (annuals). The entire classification, with subdivisions, is discussed in Cain & Castro (1959).

Raunkiaer's system has been used widely in floristic (Ennis 1928; McDonald 1937) and vegetational studies. Raunkiaer himself presented the first vegetational analyses. Using a "normal spectrum", showing the percent representation of each life-form in the world flora, as a standard, Raunkiaer showed that there were four main phytoclimates each characterized by an increase in the percentage of a life-form over its percentage in the "normal spectrum." These were: a *Phanerophytic* climate of the warm, humid tropics; a *Therophytic* climate of warm, arid desert regions; a *Hemicryptophytic* climate of middle latitude deciduous and coniferous forest regions; and a *Chamaephytic* climate of cold areas.

Numerous other vegetational studies have supported and amplified Raunkiaer's conclusions. These have been reviewed in detail (Adamson 1939; Cain 1950; Cain & Castro 1959).

Recent studies have shown variations in community life-form composition related to climatic gradients. Buell & Wilbur (1948) and Buell & Cantlon (1951) showed an increase in the importance of protected life-forms in forest stands along the prairie border in Minnesota as opposed to forest stands further east. This trend appeared to be related to climatic data showing the prairie border to have a colder, drier climate than the area to the east. Stern & Buell (1951) found an increase in chamaephytes, hemicryptophytes, and cryptophytes and a decrease in phanerophytes from the shortleaf pine communities of the New Jersey pine barrens to the jack pine communities of Minnesota, and suggested this trend was related to differences in climate between the mild Atlantic coastal plain and the more severe climate of Minnesota. Archard & Buell (1954) found a similar trend when comparing oak-pitch pine communities in southern and northern New Jersey. Cain *et al.* (1956) found that in Brazilian rain forest phanerophytes dominated to the virtual exclusion of other life-froms. As stands southward from the equator were sampled, phanerophytes diminished and there was a trend toward the hemicryptophyte dominance characteristic of temperate areas.

Several studies provide limited data on relationships between life-forms and the presumed or documented microclimates of north- and south-facing slopes in deciduous forest areas (Table 1). From the data it appears that phanerophytes and cryptophytes are more numerous on north-facing slopes whereas hemicryptophytes and therophytes predominate on south-facing slopes. The large number of cryptophytes on the north-facing bluff in North Carolina suggested a cryptophyte climate to Oosting (1942) (although no such category has yet been suggested) and he posed the question as to whether cryptophytes might regularly reach this degree of importance in such topographic situations in hemicryptophytic climatic areas. Miller & Buell's (1956) results deserve further comment. Although the presence spectra cited in Table 1 agree with other spectra, quantitatively-based spectra showed a greater proportion of cryptophytes on the southwest-facing slope.

TABLE 1. Presence-based life-form spectra from north- and south-facing slopes in eastern American deciduous forest.

Location	No. of Species	Ph	Ch	H	Cr	Th	Author
Piedmont, N. C.							
South-facing bluff........	45	26.6	0.0	51.1	4.4	17.8	Oosting, 1942
North-facing bluff.......	84	45.2	3.6	25.0	27.4	0.0	
Cushetunk Mt., N. J.							
South-facing slope.......	112	32.1	1.8	46.4	12.5	7.1	Cantlon, 1953
North-facing slope.......	86	41.8	1.2	41.8	15.2	0.0	
Itasca Park, Minn.							
Southwest-facing slope....	50	25.0	2.0	55.0	18.0	0.0	Miller &
Northeast-facing slope....	62	41.0	3.0	33.0	23.0	0.0	Buell, 1956
Southeastern Michigan							
South-facing slope.......	94	25.5	2.1	57.5	8.5	6.4	Cooper,
North-facing slope.......	89	35.9	1.1	49.5	13.5	0.0	Prelim. invest.

Failure of the usual life-form spectrum to take into account the importance of plants in the community has long been recognized (Taylor 1918; Cain 1945). Quantitatively-based spectra, using density (Buell & Cantlon 1951), frequency (Cain 1945; Buell & Wilbur 1948), and coverage (Stern & Buell 1951; Archard & Buell 1954; Miller & Buell 1956) have been used to show variations in community life-form composition. Of these measures coverage seems the most promising (Cain & Castro 1959).

Leaf-size, an aspect of life-form, has also been utilized in vegetational analysis. Botanists have long been aware that, in general, leaf sizes of plants become smaller the more unfavorable (dry or cold) the environment. Raunkiaer (1916) was the first to make use of this generalization as an ecological tool. In formulating his leaf-size concept, Raunkiaer reflected the prevalent ideas of his day which assigned primary importance to relations between plants and their water supply. Many structural features such as covering of wax, thick cuticle, water storage tissue, and diminution of transpiring surface were assumed to enable plants to endure conditions causing excessive evaporation. Of these, leaf surface area best lent itself to statistical treatment. After examination of a large sample of the world flora, Raunkiaer enumerated seven leaf-size classes with limits set at points in the range of leaf sizes where natural limits seemed to fall. These were: *Aphyll* (leafless); *Leptophyll* (<25 mm^2); *Nanophyll* (<225 mm^2); *Microphyll* (<2025 mm^2); *Mesophyll* (<18225 mm^2); *Macrophyll* (<164025 mm^2); *Megaphyll* (>164025 mm^2).

Certain problems have limited the use of leaf-size data in vegetational analysis. Thoday (1931) objected to the idea that small leaves are an adaptation to extreme environments because in some plants large numbers of small leaves are the equivalent of small numbers of large leaves, resulting in no decrease in transpiring surface. Actually, transpiration per unit area may be increased as there is no interference by vapor layers over the numerous small leaves. Difficulties involved in determining area have also limited the use of leaf-size classes. Recently, Cain *et al.* (1956) showed that leaf areas determined by multiplying the product of leaf length and width by 2/3 introduced no real error in determination of leaf-size class in tropical species. This procedure was used in the present study (Cooper 1960b).

Vegetation studies using leaf-size data are not numerous. Withrow (1932) found upland and climax forests in the Cincinnati area were characterized by leaves of mesophyll size but that there were more microphylls in the upland forest than in the climax. Grassland, arid, and hydrophytic communities in the same area were predominantly microphyllous and she concluded that "with an increase in xerophytism there is a decrease in the percentage of large leaf-size classes and an increase in the smaller ones." Cuatrecasas (1934 in Dansereau, 1957) showed that in Colombia leaf size was greatly affected by altitude, no nanophylls being found below 3600 m and no macrophylls above this limit. Cannon (1921) found that there were no plants in arid south Australia with leaves larger than 1951 mm^2 and 90% had either nanophylls or microphylls. Cain *et al.* (1956) showed that in tropical rain forest there was a general decrease in leaf size with increasing distance from the equator. In true rain forest at the equator 68% of all species had mesophylls whereas further south in gallery rain forest only 24% of leaves were mesophylls and microphylls had increased to 54%.

No review of the extensive literature dealing with microclimates will be attempted as recent comprehensive reviews, at least up to the early 1950's, are available (Baum 1948, Wolfe *et al.* 1949; Cantlon 1953; Geiger 1957). However, as this study deals with the inter-related effects of topography and forest vegetation on microclimate and the role of microclimate in determining vegetational differences, one point must be made. Geiger (1957) has stressed the importance of the canopy to climatic conditions within the forest. As the upper surface of the canopy is the region where radiation interception occurs, it is thus impossible to compare the climate of an open area with that of the forest trunk space, because the "trunk space climate" is a result of an entirely different set of meteorological circumstances. Thus, the "trunk space area" of the forest is a distinctive microclimate. As will be shown, the data of the present study suggest some changes in the typical "trunk space climate" which topographic variations may produce.

THE STUDY AREA

The E. S. George Reserve, the site of this study, in located approximately 4.5 mi west of Pinckney and 23 mi northwest of Ann Arbor, in south-central Livingston County, Michigan. The Reserve is slightly less than 2 sq mi in area and has been fenced since 1928. The rugged glacial topography and the protection afforded instruments make the area ideal for microclimatic study. This study was confined to the Big Woods, the largest tract of woodland on the Reserve.

Physiography

The area is one of rolling glacial outwash topography, the primary land forms having originated during retreat of the Saginaw and/or Lake Erie lobes of the Cary substage of the Wisconsin glaciation. The topographic features of the Reserve uplands were probably formed during a period of rapid deterioration of the ice sheet as the esker- or kame-like formations, the large outwash plain, the numerous kettle holes, and the predominantly sandy texture of the soils suggest. Elevations vary from about 880 ft above sea level in the marshes of the southeastern portion to over 990 ft at several locations in the Big Woods. Local relief may exceed 80 ft, particularly along the sides of the main esker in the Big Woods. Due to the sandy soil, drainage of the uplands is good. In areas of pronounced local relief it may be excessive.

Vegetation and Land-use History

The pre-settlement forest of southwestern Livingston County, including the Reserve, appears to have been similar in species composition to that of today. Oaks, predominantly black and white, and hickories were the trees cited most frequently by the team which surveyed the area in 1825. "Prairie" (a term apparently used for grass-dominated lowlands), marsh, and tamarack swamp were mapped as occupying lowland sites much as they do today.

The original vegetation of the Reserve has been greatly altered by man. Logging, agriculture, grazing, and fire have dissected the upland forest and all that remain are isolated, more or less altered, stands. Present vegetation of the Reserve consists of approximately equal parts marsh and swamp, old fields, and second growth oak and oak-hickory woodland. Marshes and swamps occur slightly above and below the 900 ft contour. The old fields, now dominated by blue-grasses (*Poa compressa* L., *P. pratensis* L.) and forbs, are confined chiefly to the level uplands. The woodlands generally occupy uplands which, because of their irregular topography, were unsuitable for agriculture.

There is no actual written history of the Reserve, but Cantrall (1943) found that most of the farmlands now included in the Reserve were cleared by 1870. The presence and age of old-growth species such as sassafras and bigtooth aspen, in addition to the sprout origin of many oaks, indicate that extensive logging took place in the period 1860-1900. Also, all of the woodlands were heavily grazed during the period of farming. After 1900 agriculture gradually diminished and the land was virtually abandoned by 1926 when it came into the possession of the late E. S. George. Administration has been by the University of Michigan since 1930. Since that time the fence has minimized human disturbance, and no fire, lumbering, or cultivation has taken place. However, a deer herd has been maintained on the Reserve and the magnitude of the browsing effects of the deer is a debatable question. There is no doubt that in the past they have retarded return of forest to the open fields (Evans & Cain 1952), but since the herd was cut to 25 animals per square mile in the early 1950's succession seems to have accelerated.

SOILS

The upland soils of the Reserve are gray-brown podzolics and show horizon development characteristic for this great soil group. Parent materials are predominantly coarse-textured glacial outwash. Being water-laid deposits, parent materials are commonly bedded and may include lenses of gravel, sand, and even silt and clay. The soils are classified for the most part as sandy loams, loamy sands, or sands. The Livingston County soil survey (Wheeting & Bergquist 1923) shows the greater part of the upland soils of the Reserve to be Bellefontaine sandy loam with small areas of Miami loam in the southern portion. The poorly-drained soils, generally below the 900 ft contour, are either Carlisle muck, Greenwood peat, or Rifle peat.

Veatch (1953) described a number of soil types in the Big Woods ranging in texture from a fine sandy loam to a sand. The great diversity in soil units is due in part to the heterogeneous glacio-fluvial parent material and in part to the numerous topographic irregularities of the area. For example, Cooper (1960a) has shown that the differences in the microclimates of the north and south slopes appear to be major factors in producing different profiles of weathering on these slopes. Soils with more silt and clay in the B horizon, the Bellefontaine series, are found on south slopes, whereas more weakly-developed profiles, possibly to be classified as Coloma or Plainfield, are formed on many north slopes.

REGIONAL CLIMATE

The climate of southeastern Michigan is typical of humid, microthermal regions and is of the Koeppen Dbf type. There is a well-defined winter with considerable snow alternating with an equally well-defined summer. Spring and fall are generally short in duration. Precipitation is well-distributed throughout the year; summer, however, is usually the season of maximum rainfall.

No records of solar radiation are taken on the Reserve. However, data for East Lansing, Mich., approximately 40 mi to the northwest, are available (Crabb 1950; U. S. Dept. of Commerce 1957). The smoothed annual curve for East Lansing (Crabb 1950) is lower than comparable curves for most other U. S. stations. Crabb suggests this is due to the large amounts of moisture contributed to the atmosphere by the surrounding Great Lakes. Furthermore, the annual curve shows a spring plateau, related to moisture added to the atmosphere by the freshly ice-freed Great Lakes, and twin summer peaks (Crabb 1950). During 1957 there were two spring plateaus (March 12—April 9 and April 23—May 14) and the second summer peak was the higher, rather than the first as is usual.

An 8-yr record of local temperature and rainfall is provided by a weather station located on the Reserve. The average annual temperature, as indicated by data from this station, is 46.9° F. (All temperatures henceforth referred to are in °F). The average maximum is 56.8° and the average minimum 37.1°. January (23.6°) and February (25.5°) are the coldest months and annual lows are usually recorded in either of these months. The 8-yr low, -9.5°, occurred in February, 1958, after this study was concluded. July has the highest average temperature (70.7°), although the annual high may occur anytime during June-September. The all-time high is 97.8°.

The average annual temperature during 1957 was 46.0°, the average maximum temperature was 55.9°, and the average minimum temperature was 36.2°. The similarity between these values and the 8-yr means indicated that 1957 was a year with no major temperature irregularities. However, January was the coldest month on record, with lows for all temperature records up to that time being recorded.

Several features of the annual march of temperature during 1957 are significant. The annual low (—6.5°) occurred during the third week of January. The two weeks with the greatest temperature range, March 10-16 (53.5°) and April 14-20 (53.7°) coincided with the weeks during which early spring and late spring (see page 35) began. A plateau in the curve during the weeks of March 24-April 14 marked an extended period of wintery weather interrupting the progress of spring. A rapid climb from April 14 to May 5 marked the advent of the growing season, but a plateau in this upward trend was caused by the annual cold rainy spell of mid-May. Both spring temperature plateaus were closely related to the corresponding plateaus in solar radiation. Another period of cool, rainy weather in late June and early July caused a recession in the steady rise of temperature to the annual July maximum.

Total annual precipitation averages 33.7 in. Perhaps slightly more falls during summer than in other seasons. With one exception no major differences between long-term precipitation patterns and those of 1957 occurred. July, however, was extremely wet, with most of the record July rainfall (5.1 in.) falling in the first 13 days of the month. Extended summer droughts, which often do not appear in monthly rainfall data, are an annual occurrence. Dry periods (with less than 0.1 in. of rain) of 22 days (July 24-August 14) and 24 days (September 23-October 16) occurred in the summer and fall of 1957.

Annual snowfall averages 41.5 in. and ranges from 26 to 53 in. The average total is evenly spread over the period from December 1-March 31, but in a given year heavy snow may occur in any of these months. Snowfall during 1956-57 was about 6 in. below average. However, the January total of 13.4 in. was the heaviest ever recorded for that month.

THE SEASONS ON THE GEORGE RESERVE

An important aspect of the climate of an area is the character and duration of each of its seasons. However, the seasonal behavior of a regional biota does not necessarily coincide with the seasons of the year as defined by calendar limits (Wolfe *et al.* 1949). Thus, climatic summaries based on monthly or calendar seasonal data are of little use in ecological studies. Since the phenological responses of a biota are correlated with certain sets of recurring climatic events rather than with arbitrary dates, attempts have been made to distinguish seasons on the basis of these regularly-occurring biotic events (Hopkins & Murray 1933, Wolfe *et al.* 1949).

Four biotic events are accepted as initiating the major seasons in deciduous forest communities. Spring begins with the first marked biological activity under and on top of the leaf litter; summer is initiated by canopy closure; fall commences with the first coloration of canopy foliage; and winter is marked by completion of leaf fall. Wolfe *et al.* (1949) point out that these major seasons often are marked by distinct subperiods of biological activity and propose the following 10 seasons: early, mid-, and late winter, early and late spring, early, mid-, and late summer, and early and late fall. This system was used in the present study.

As only one year's observations were available, the seasons on the Reserve during 1957 were delimited partly by phenological data and partly by seemingly clear-cut meteorological events. The following remarks give some important seasonal characteristics and indicate how each season was defined.

Mid-winter began on December 25, 1956, when a light snow fell and initiated a snow cover which remained on the ground in most areas until early March, 1957. This was the coldest season of the year when both the annual low (-6.5°) and the lowest average temperature (17.0°) were recorded. Snowfall also was the heaviest of any season, totalling 12.4 in. The beginning of late winter was January 29 when there was a slight relaxation in a long cold spell. Winter ended with a period of warm weather prior to the beginning of spring.

Early spring began with a series of warm, sunny days lasting from March 12 to 16. Maxima rose to 69.5° on March 14 and minima did not fall below freezing during the period. Much biotic activity, particularly on south slopes, was observed. Virtually all biological activity was arrested by a period of low temperatures and intermittent snow from March 19 to April 10. The initiation of vigorous growth and flowering activity by the plants of the study area on April 15 marked the beginning of late spring. The first herbaceous flowers (*Hepatica americana*) were found on April 15 and by the second week of late spring numerous other species were flowering throughout the Big Woods. The first 3 weeks of late spring were warm and sunny. The latter part of late spring was characterized by several extended periods of cold, rainy weather. Nineteen species were observed to flower during late spring.

Early summer began on June 2 when the canopy of the Big Woods had closed. Considerable vegetative and reproductive activity took place during this season, particularly within the forest herbaceous layer. Almost 1/2 (30) of the species whose initial flowering date was observed were first observed during early summer. Although the annual maximum of 92.3° was recorded on June 18, average maxima were slightly below those of mid-summer. With the exception of one near-freezing night in early June, minima averaged in the mid-50's. Almost 1/4 of the total annual rainfall occurred during early summer. The beginning of mid-summer (July 14) was not marked by any striking biological event. However, as the season was characterized by extreme drought conditions the date of the last heavy rain in early July was taken as the end of early summer. Only 1 in. of rain fell during mid-summer and little of this wet the soil within the forests. Drought conditions became extreme late in mid-summer and diurnal wilting was observed in several herbaceous plants on south slopes. Mid-summer was the hottest season of the year, having the highest average temperature (69.4°) and average maxima (81.2°). Only 10 species were observed to flower during this season. Late summer began on August 24 when rains of moderate intensity broke the drought of mid-summer. Late summer was a transition period between summer and fall. No species wre ŏbserved to flower in the woods, although considerable flowering activity occurred in the fields.

Early fall began on September 17 when the first coloration was observed in the canopy and the first browning took place in the field layer. This season was one of drought, the most severe of the year, with only 0.6 in. of rain falling. The first frost of the year occurred on September 27. Coloration of tree leaves progressed rapidly after this and the height of fall color was during the first two weeks of October. Late fall was poorly-defined biologically, but seemed to begin on October 17 when a heavy rain broke the drought of early fall. Although all canopy foliage was dead during this season, the oaks retained many of their leaves. Little biological activity (except the flowering of *Hamamelis virginiana*) was noted.

Early winter began on November 9 when the first snow of the year fell. The 5 days following the snowfall had, in addition to low maxima, minima well below freezing. Snow fall during early winter totalled 7.5 in. and the average temperature was only slightly above freezing. Early winter ended on December 28 when a light snow fell. This snow was followed by others and many sites on the Reserve remained covered through late February, 1958.

METHODS

North- and south-facing slopes were chosen as sites for this study because of the great environmental and vegetational differences shown for such slopes in other studies (Potzger 1939, Shanks & Norris 1950, Cantlon 1953). Microenvironmental and vegetational sampling was carried out from March 17 to November 3, 1957. Data were obtained from 17 slopes, 9 north-facing and 8 south-facing. Slopes ranged from 31-60% in angle and deviated not more than 20° from true north or true south. Vegetation was sampled on 16 of these slopes, but microenvironmental data were recorded for only 4 north and 4 south slopes. Topographic features and canopy dominants for all plots are summarized in Table 2.

Although efforts were made to minimize all variables with the exception of topographic orientation, they were not entirely successful. In addition to orientation, an important variable was the presence or absence of protection as afforded by a facing slope. Thus, 4 groups of slopes were available: protected north slopes, open north slopes, protected south slopes, and open south slopes. The following data summarize the specific topographic characteristics of the sample sites:

Protected north slopes (Stations 1, 5, 6, 10, 16). Station 1 was on the side of an esker facing into a kettle whereas Stations 5, 6, 10, and 16 were on the sides of kettles. Contours at all stations were concave.

Open north slopes (Stations 8, 11, 13, 15). Station 8 was on the side of a large kettle but, as the opposite side was over 500 ft distant, the facing slope offered no protection. Stations 11 and 15 were on the edge of an outwash fan and Station 13 was on the side of an esker. Contours at Stations 8 and 11 were concave and those at Station 13 were straight. Contours at Station 15 were slightly convex.

Protected south slopes (Stations 7, 14). Both of these stations were on the sides of kettles with concave contours.

Open south slopes (Stations 2, 3, 4, 9, 12, 17). These stations were all on the sides of eskers. Stations 2 and 12 actually faced into a large kettle but, as the opposite slope was approximately 500 ft distant, there was no real protection. Contours at Stations 2, 3, and 12 were essentially straight. At Stations 4 and 9 contours were slightly convex whereas at Station 17 contours were somewhat concave.

Although no historical data were available for the sample sites, it appeared that there had been no selective effects of grazing or lumbering on any slope or group of slopes. Thus, it was assumed that the

TABLE 2. Description of topographic and vegetational features of sample plots, E. S. George Reserve. (From Cooper 1960a).

Station	Slope %	Topographic position	Compass bearing	Leading canopy dominants
		North slopes		
1*	53	Side of esker	N 16° W	*Quercus alba, Q. velutina, Prunus serotina.*
5†	42	Side of kettle	N 10° W	‡
6†	36	Side of kettle	N 2° E	*Quercus alba, Prunus serotina Acer rubrum, Q. rubra.*
8†	60	Side of kettle	N 18° E	*Quercus rubra, Q. alba, Acer rubrum.*
10	54	Side of kettle	N 10° E	*Quercus alba, Q. rubra, Acer rubrum.*
11	50	Side of outwash fan	N 4° E	*Carya ovalis, Quercus alba, Q. velutina.*
13	40	Side of esker	N 10° W	*Carya ovalis, Quercus velutina, Q. alba.*
15	51	Side of outwash fan	N 2° E	*Quercus rubra, Q. velutina, Carya ovalis.*
16	52	Side of kettle	N 18° W	*Carya ovalis, Acer rubrum, Quercus alba.*
		South slopes		
2*	43	Side of esker	S 16° E	*Quercus velutina, Q. alba, Carya ovalis.*
3†	39	Side of esker	S 15° W	*Quercus velutina, Q. alba, Carya ovalis.*
4†	46	Side of esker	S 4° W	*Quercus velutina, Carya ovalis, Q. alba.*
7†	39	Side of kettle	S 7° W	*Quercus velutina, Prunus serotina, Q. alba.*
9	54	Side of esker	S 19° W	*Quercus velutina, Carya ovalis, Q. alba.*
12	50	Side of esker	S 14° E	*Quercus alba, Q. velutina, Q. rubra.*
14	41	Side of kettle	S 15° W	*Quercus velutina, Q. alba, Prunus serotina.*
17	31	Side of esker	S 20° W	*Quercus velutina, Carya ovalis, Q. alba.*

* Main station.
† Scattered stations.
‡ Not sampled.

microclimatic and vegetational differences recorded were the results of real habitat differences rather than the past cultural practices of man.

MICROCLIMATES

Microclimatic data were derived from two independent series of instruments. One series, the "scattered stations," consisted of 3 north and 3 south slopes located at various points in the Big Woods, and the other, the "main station," of instruments disposed at the top, middle, and bottom of the north- and south-facing sides of an east-west trending hogback (Table 2). Wooden thermometer holders in the middle of the slopes marked the locations of the scattered stations. Readings were taken at the scattered stations between 3:00 and 4:00 P.M. All readings, except soil moisture, were taken daily from March 31 to July 20, every other day from July 21 to September 14, and once weekly from September 15 to November 3. Soil moisture determinations were made once weekly from March 31 to November 3. Standard Weather Bureau instrument shelters, located 10 m apart on the horizontal, marked sampling locations at the main station. Readings here, except evaporation, were taken between 2:00 and 3:00 P.M. daily from March 17 to September 14 and once a week from September 15 to November 9. Evaporation data were gathered once a week from May 5 to October 24.

Light intensities at both the scattered and main stations and outside the Big Woods were recorded with a General Electric photocell having a range from 1-10,000 fc. Each reading was taken in the same place at each station. The meter was held 50 cm above the soil surface at an angle of 45° and oriented toward the south. Although field readings were recorded in foot candles, results were expressed as percentage of full light intensity recorded outside the Big Woods.

Maximum, minimum, and current air temperatures at the scattered stations were recorded with Six type maximum-minimum thermometers mounted under rotatable boards 10 and 50 cm above the soil. At the main station Casella hygrothermographs (Model 1040) were placed in the shelters at the top and bottom of each slope and thermographs (one Casella Model 760 and one Bendix-Friez Model 505) in the shelters at the middle of the slopes. The shelters were located so that the instrument recording elements were 50 cm above the soil. Only the maximum, minimum, and current temperatures obtained from the daily record were used in data analysis. In addition to the recording instruments, maximum-minimum thermometers were placed in the shelter and under boards 10 cm above the soil. Maximum, minimum, and current readings were taken from these.

Evaporation data were gathered at the main station only. Paired black and white Livingston porous-bulb atmometers were placed about 4 ft west of the instrument shelters. The bulbs were installed 50 cm above the soil on the usual field apparatus (Livingston 1935) with mercury and glass-wool valves to prevent backflow. Readings of total weekly evaporation in cc were taken by filling the reservoir bottle to a zero line. The field readings were multiplied by the supplied correction factor to give corrected values.

Current soil temperatures at the scattered stations were taken with a Weston probe thermometer (Model 2261) and at the main station with thermistors (Western Electric, Model 7A) embedded in fiberglas. The thermistor resistances were recorded with a Coleman Model 300 ohm meter. Correction coefficients were determined by means of a series of temperatures recorded at the installation sites with the probe thermometer. Readings at both sets of stations were taken at 2 cm and 20 cm below the soil surface. These depths approximated the A_1 and A_2 horizons.

Soil moisture values in the A_1 horizon at the scattered stations were determined by the gravimetric method. Composite samples, collected once a week, were oven dried, and soil moisture was expressed as percentage of oven-dry weight. Current soil moisture values at the main station were determined with fiberglas soil moisture units (Model 351) 2 cm and 20 cm below the soil surface. Resistance values were recorded with the Coleman meter. The fiberglas units were calibrated using field calibration of the area type (Reinhart 1953). Values were also expressed as percentage of oven-dry weight.

For most microclimatic factors, weekly averages seemed to express the trends of the data adequately. Thus, these values were used extensively in the analysis of data. As used in this study, average daily temperature is the sum of the daily maximum and daily minimum divided by two. Average weekly temperature is the sum of the weekly maxima and weekly minima divided by the number of readings. Average seasonal temperature is the sum of the seasonal maxima and minima divided by the number of readings. Temperatures, unless otherwise specified, are in °F.

VEGETATION

Vegetational sampling was carried out during July and August of 1957. On each of the 16 slopes sampled (Table 2) a plot 900 m², consisting of three tiers of three 100 m² plots, was laid out. Presence of all vascular plant species occurring in each subplot was recorded. Coverage of species in the field layer (within 4.5 feet of the ground) was determined by the line-intercept method. As plots were laid out on the horizontal, plant cover was recorded on the horizontal by means of two meter sticks arranged so that one was placed perpendicular to the horizontal and the other moved up or down along it until it was horizontal. The central 10 m of both diagonals of each of the subplots were measured with this device. Thus, 180 m of line-intercept data were available for each slope sample plot. The diameter at breast height of all trees over 1 in. d.b.h. and density of all shrubs and transgressives below 1 in. d.b.h. and over 4.5 ft high were determined in each subplot. In addition, the total canopy cover of species over 1 in. d.b.h. was determined by pacing the four 30 m across-slope boundaries of the 3 tiers of subplots. The life-form of all species encountered was determined from winter and summer field observation during a part of 1956 and all of 1957 and by consulting other life-form studies of similar areas (Ennis 1928, McDonald 1937). Voucher specimens of all species are deposited either in the Reserve herbarium or in the author's collection. Nomenclature is that of Fernald (1950). Representative leaves were chosen from the voucher specimens and their areas determined both by tracings on millimeter graph paper and by the 2/3 length times width rule of Cain *et al.* (1956). The entire species list, showing both life-forms and leaf-size, may be found in Cooper (1958).

RESULTS: MICROCLIMATES[1]

Because of the diversity of microenvironmental data recorded during the study, variations in each factor will be discussed independently. An attempt also will be made to summarize the cumulative effects of the various factors.

LIGHT

With respect to the light factor, three variables, intensity, quality, and duration are of ecological importance. Of these, only light intensity was assessed in this study.

From the pattern of variation in relative light intensity at the scattered stations (Fig. 1) several generalizations can be made concerning light conditions on the slopes. During the leafless season average relative light intensities exceeded 35% on south slopes and 25% on north slopes. However, the variation in the raw data was great, ranging from 8-100% on south slopes and from 6-95% on north slopes. As the canopy closed with the beginning of late spring, light intensities dropped rapidly. This decline continued until the first week in June when the forest canopy had completed development. At all times during the drop in light intensity, and during all of summer, light intensities on south slopes exceeded those on north slopes. With leaf abscission in the fall, light intensities on both slopes increased rapidly to the leafless season peaks.

In general, the shapes of the curves were the same on both slopes. This seemed to indicate that variations due to cloudy days, which would tend to raise relative light values, were similar on both slopes. However, the period of canopy closure in early late spring was an important exception. The curve of relative light intensity on north slopes diminished continuously from the week of April 21 until the beginning of summer. On south slopes, on the other hand, the continuous decline did not begin until the week of April 28 and the greatest difference in relative light intensity (16%) between the slopes occurred during this week. Thus, the effects of canopy closure were

[1] All original microclimatic data are included in Vol. 2 of Cooper (1958).

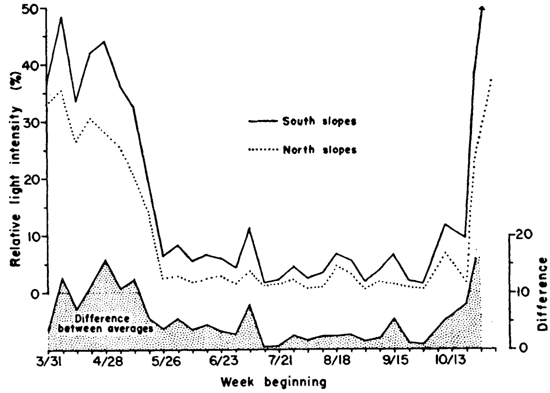

FIG. 1. Weekly average mid-afternoon relative light intensity (% of light in the open) at scattered stations. Each value is an average of the weekly averages at the 3 north or 3 south slopes.

first felt on north slopes and relative light values declined most rapidly on those slopes.

Data from the main station (Table 3) generally were similar to those from the scattered stations, but they show in addition the variations in light intensity occurring from top to bottom of the slopes. The seasonal averages show that, with the exception of early fall, light intensity was always greatest at the top of the south slope and diminished downslope. The pattern on the north slope was not as clear. In spring, early summer, and late summer, relative light values decreased from slope top to bottom. However, in midsummer and fall, values were highest in the middle of the north slope. These changes may be due to the variable effects of dense canopy in relation to the position of the sun. Despite these variations, the bottom of the north slope always had the lowest intensities recorded.

TABLE 3. Seasonal average relative light intensity (percentage of light in the open) at the main station.

Season	South top	South middle	South bottom	North top	North middle	North bottom
Early spring	55.3	52.2	52.3	35.7	33.5	32.5
Late spring	43.7	43.4	38.4	25.6	23.8	20.3
Early summer	8.0	7.6	5.5	1.8	1.7	1.3
Mid-summer	6.1	5.1	4.0	0.7	1.0	0.7
Late summer	9.2	6.3	6.0	1.4	1.3	1.1
Early fall	12.3	10.0	13.0	3.2	3.4	2.7
Late fall	57.3	56.2	44.9	13.8	15.5	13.9
Average	27.4	25.8	23.4	11.7	11.5	10.4

Analysis of light intensities during the period of canopy closure at the main station showed variations in the amounts of high-intensity light at various positions on the slopes. These differences were due to the differential effects of canopy closure on the slopes. At the bottom of the north slope, light intensity first passed under 10% on May 9 and it remained permanently under this level after May 20. At the top and middle of the north slope intensities did not pass under the 10% level for the remainder of the growing season until May 24. On the south slope the first day under 10% at the top and bottom of the slope was May 26 and, in the middle of the slope, May 28. All stations passed more or less permanently below 10% on June 6. Thus, there was a longer period of low light intensity during the growing season on the north slope as there was a period of almost one month during which intensities fell below 10% on the north slope while remaining well above this level on the south slope. During summer no values over 10% of full light occurred on the north slope. However, on the south slope such readings were recorded between 8 and 13 times. The maximum relative light intensity recorded during summer on the south slope ranged from 22.7-36.3% whereas on the north slope it never exceeded 6.7%.

AIR TEMPERATURE

Variations in air temperature within forests and on north and south slopes have been investigated more intensively than variations in any other microclimatic factor. The present study also gave the greatest share of attention to temperature phenomena.

AVERAGE TEMPERATURE

Average air temperature data were useful to summarize gross differences between the slopes and to approximate general temperature patterns during the period of the study.

South slopes had higher average air temperatures throughout the entire growing season as data from the 50 cm level at the scattered stations show (Fig. 2). The differences between the slopes were least in the first two weeks of late spring before the canopy had closed. In this period more radiation penetrated to the surface on the north slope than during any other season. With canopy closure, air temperatures on the south slopes were consistently higher than those on north slopes. The greatest difference was during mid-summer when averages were 7-8° higher on the south slopes. During late summer and fall temperatures were almost uniformly 2-4° higher on south slopes. The two major dips in the curves, one in mid-May and the other in late June and early July, were due to periods of cool, rainy weather which affected both slopes uniformly.

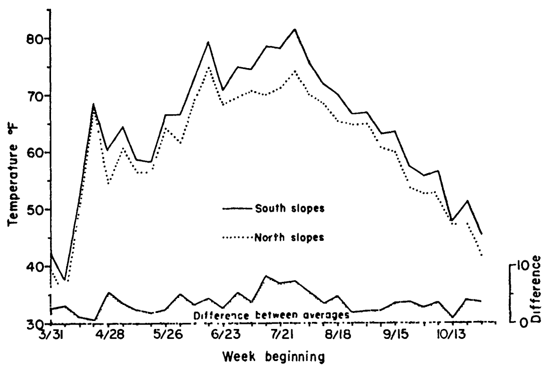

FIG. 2. Weekly average air temperature at the 50 cm level at scattered stations. Averages computed as in Fig. 1.

Average seasonal temperature data from the 10 cm and 50 cm levels at the main station (Table 4) show that temperatures at both levels on the south slope generally exceeded those on the north slope during the entire growing season. During spring, temperatures were higher close to the ground on both slopes but the gradient was always steepest on the south slope, averaging 4-5° in early spring and 3-4° in late spring. During summer, temperatures continued warmest near the ground on the south slope and at the top of the north slope. Gradients were generally less than in spring except at the top of the south slope where the increase was 5°. Temperatures at the middle and bottom of the north slope were, with one exception, slightly higher at 50 cm than at 10 cm. Thus, temperature conditions characteristic of a mature forest were found only during summer and only at the lower stations on the north slope. The data further show that, in general, the highest average temperatures occurred at the top of the south slope and that temperatures diminished slightly downslope whereas the lowest averages consistently were recorded at either the middle or bottom of the north slope.

TABLE 4. Seasonal average temperatures at 10 cm and 50 cm levels at main station.

Season	South top	South middle	South bottom	North top	North middle	North bottom
Early spring						
10 cm	40.3	40.1	*	*	36.2	36.5
50 cm.	36.1	36.0	35.7	35.3	35.2	34.6
Late spring						
10 cm.....	62.7	62.5	62.1	60.0	58.7	59.1
50 cm	59.1	59.1	58.9	58.4	58.4	58.0
Early summer						
10 cm... . . .	69.9	70.4	69.9	68.1	66.4	66.9
50 cm.. . .	67.9	67.8	67.6	67.3	67.6	67.2
Mid-summer						
10 cm	75.0	72.9	71.8	69.9	68.9	69.4
50 cm...........	69.9	69.7	69.5	68.2	69.4	68.8
Late summer						
10 cm.....	67.1	66.1	66.7	64.3	63.1	63.0
50 cm.	64.4	64.5	64.2	63.6	63.9	63.5
Early fall						
10 cm...........	58.0	58.0	59.2	55.8	54.6	54.8
50 cm	54.0	54.1	53.7	53.4	53.2	52.6

* Insufficient data.

MAXIMUM TEMPERATURES

Although average temperatures were useful for illustrating general patterns, extremes of temperature (maxima and minima) showed greater variation and thus more clearly illustrated the differences between the air temperature regimes of the slopes.

The greatest and most consistent differences in air temperature between the slopes were in the maximum temperature area. Average weekly maxima and

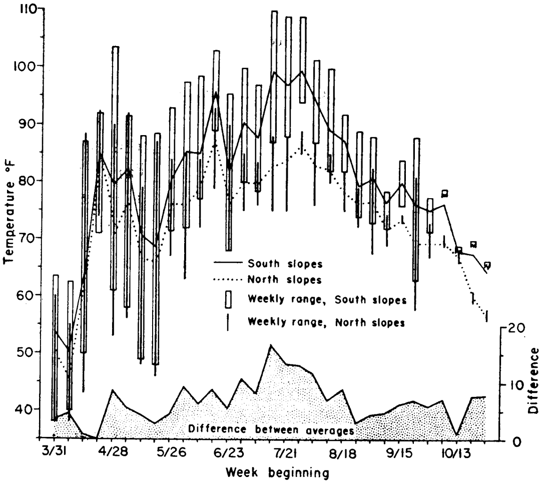

FIG. 3. Weekly average maximum air temperature and weekly range in maximum air temperature at 50 cm level at scattered stations. Averages computed as in Fig. 1.

ranges in maxima at the 50 cm level at the scattered stations (Fig. 3) showed that very different maximum temperature regimes characterized the slopes during the period of the study.

On north slopes maxima rose rapidly early in late spring and averaged in the 80's during the week of April 21. Maxima declined through the remainder of late spring, first under the influence of canopy development and then in response to the period of cool, cloudy weather in May. The greatest ranges in maxima on north slopes occurred during early late-spring. During summer two peaks of maxima occurred, one in June and the other in July. However, neither of these exceeded 90° and average maxima generally ranged between 75° and 85°. Ranges of maxima exceeded 90° only during the week of June 16.

On south slopes, however, average maxima were much higher throughout most of the growing season. During early late spring averages and ranges were very similar to those on north slopes. In the final weeks of late spring maxima declined but still averaged 3-5° higher than on north slopes. During summer, maxima were considerably higher than on north slopes with averages over 90° for half of the 12 weeks of early and mid-summer. Maxima exceeded 90° during every week of summer.

Thus, on north slopes maxima showed the most variation in spring before canopy closure and during the remainder of the growing season relatively stable conditions prevailed. On south slopes, however, there was the same period of high spring maxima, but this was followed by a period of even higher maxima during summer. These regimes were comparable to those of thinly-forested and cove stations at Neotoma Valley (Wolfe *et al.* 1949). The south slope regimes agreed with those of thinly forested stations where temperatures rose sharply to a spring maximum, leveled off, and then returned to or exceeded the spring maximum in late summer or early fall. North slope regimes, however, resembled those of deep coves where temperatures rose rapidly in early spring and then leveled off for the remainder of the growing season.

The least differences between the maximum temperature regimes of the slopes occurred during the first 2 weeks of late spring before canopy closure had taken place. Both slopes had average maxima of 85° during the week of April 21 and ranges on the north slope actually were greater than those on south slopes during this period. As all north slopes were located on the sides of kettles, this phenomenon may be related to temporary retention of heated air within the kettles. However, the effects of canopy closure were immediately manifested on the north slopes by a great reduction in the extremes of maximum temperature. The highest average maxima on north slopes occurred during the week of the summer solstice (June 16) when the sun was at its highest in the sky and was falling most directly on the north slopes. Differences between the slopes were greatest in mid-summer when the sun shone almost directly on the south slopes, but the combination of canopy and lowered angle of incidence produced less incoming radiation on the north slopes.

Maximum temperature conditions at the main station (Table 5) were similar to those at the scattered stations. However, because of the amieliorating effects of the instrument shelters, extremes at the 50 cm level were not as high as those recorded on the thermometers at comparable levels at the scattered stations. Wolfe *et. al.* (1949) found a similar situation with respect to minimum temperatures and showed that minima recorded within a standard shelter were consistently higher than those to which plant parts appeared to be exposed. The data of this study support a similar conclusion with respect to maximum temperatures. Despite these inadequacies, certain patterns in maximum temperature regimes can be drawn from the main station data. These patterns illustrate general maximum temperature regimes, and more important, maximum temperature gradients in the air layer near the ground during periods of occurrence of the "incoming radiation type" (Geiger, 1957).

During early spring, maxima were higher at all stations on the south slope, and the gradient between maxima at 50 cm and those at 10 cm was much greater on south slopes. This gradient amounted to 10° at the top of the south slope and was only half as great at the bottom of the north slope. With the transition to late spring, maxima rose abruptly on both slopes. Temperatures continued to increase toward the ground on both slopes, but the steepest gradients still were on the south slope. On the north slope the annual maximum of 96° occurred during the week of April 28. During this period of maximum solar radiation on the north slope, air at the bottom of the slope in the kettle became intensely heated, and thus un-

TABLE 5. Seasonal average maximum temperatures at 10 cm and 50 cm levels at main station.

Season	South top	South middle	South bottom	North top	North middle	North bottom
Early spring						
10 cm	55.5	54.1	*	*	47.7	49.0
50 cm	45.5	45.5	45.0	44.3	43.9	44.0
Late spring						
10 cm	78.0	77.8	77.6	73.0	71.7	73.3
50 cm	70.7	70.6	70.8	70.0	69.4	70.1
Early summer						
10 cm	81.2	82.3	81.5	77.7	75.4	76.4
50 cm	78.0	77.5	77.5	76.9	76.8	76.4
Mid-summer						
10 cm	90.0	86.0	84.3	80.1	79.0	79.9
50 cm	81.2	80.5	80.8	79.2	79.4	78.6
Late summer						
10 cm	77.8	75.9	77.4	72.3	71.1	70.7
50 cm	73.8	73.7	73.5	72.1	71.9	71.4
Early fall						
10 cm	73.6	74.4	77.2	69.9	68.5	68.3
50 cm	65.0	65.0	64.8	64.1	63.0	62.4

* Insufficient data.

stable. Small parcels of air were seen to escape up the sides of the kettle as minature "dust-devils" with leaves in their vortices. These also occurred on the south slope under the intense heating of early late spring. They were observed at no other time during the study at any location. On the north slope, increasing temperatures toward the ground were characteristic of the first 3 weeks of late spring. However, after canopy closure, temperatures in the air layer near the ground approached those of densely-forested areas and by the week of May 26 both the bottom and middle of the north slope had lower weekly maxima at 10 cm than at 50 cm.

During summer, maxima at 50 cm were confined to a relatively narrow range on both slopes. This condition was in contrast to the pattern at the scattered stations where maxima on south slopes rose to an annual high during mid-summer and may be explained by the modifying effect of the shelters on maximum temperature readings. The mid-summer peak was apparent at 10 cm and was particularly marked at the top of the south slope where an annual maximum of 102° was reached during the week of August 18. Maxima averaged higher near the ground at all south slope stations and at the top of the north slope throughout all of summer. At the bottom and middle of the north slope average maxima were, with one exception, greater at 50 cm than at 10 cm. Thus, during summer, maximum temperature stratification at the lower stations on the north slope was that of well-developed forests whereas on the south slope and at the top of the north slope a weak version of the incoming radiation type typically developed.

During early fall, maxima were similar to those of late summer with temperatures at 50 cm slightly higher on the south slope and those at 10 cm considerably greater. Maxima increased from 50 cm to 10 cm at all stations, but again gradients were greater on the south slope. The opening of the canopy during late fall allowed considerable heating of the south slope, but because of the lowering of the sun in the sky, this factor had little effect on the north slope. Thus, maxima were much higher on the south slope during this season, particularly at 10 cm.

MINIMUM TEMPERATURES

Minimum temperature regimes did not show the great variations characteristic of maximum temperature regimes. Limited observations at the main station indicated that the lowest minima generally occurred at the bottoms of the slopes and the highest at the tops. The lowest minimum recorded at any station was -5° at the bottom of the north slope during the weeks of January 4 and 11, 1958.

Average weekly minima and minimum temperature ranges at the scattered stations (Fig. 4) illustrate general conditions on the slopes. During spring, minima were consistently lower on the north slopes. The differences were greatest in early spring and became progressively less toward summer. No great differences in minima were found in summer and during 5 weeks, minima actually averaged higher on north slopes. The greatest ranges in minima on both slopes occurred during the first week of late spring. The first day of late spring (April 16) was preceded by 4 nights of sub-freezing temperature. April 14 and 15 were clear with maxima well into the 50's. On the night of April 15 the temperature failed to fall below freezing at any of the stations and sub-freezing temperatures were not recorded anywhere in the study area until 17 days later on the night of May 2. The accelerated period of plant activity marking the beginning of late spring seemed a response to this abrupt change in minimum temperature regime. The only other ranges of minimum temperature in excess of 25° occurred in early spring. During the remainder of the growing season no wide ranges in minima were recorded and there were no significant differences between ranges on north and south slopes.

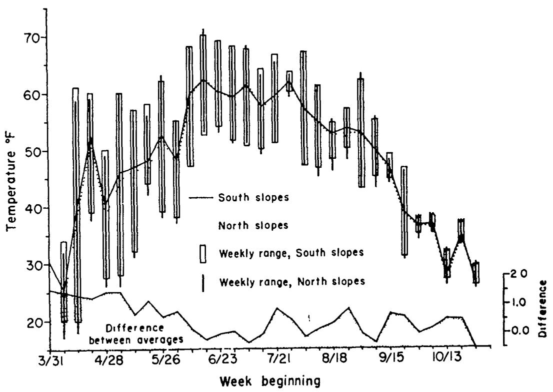

FIG. 4. Weekly average minimum air temperature and weekly range in minimum air temperature at 50 cm level at scattered stations. Averages computed as in Fig. 1.

Despite the small differences in minimum temperature regimes at the main station certain patterns were found. Here also minima showed most variation during the early growing season. During early spring and the first weeks of late spring there was a consistent tendency for the highest minima to be recorded at the top or middle of the south slope and for minima to diminish down slope. On the north slope during this period a similar progression was observed and the lowest minima at all stations almost always were recorded at the bottom of this slope. However, during the last three weeks of late spring, presumably under the influence of the developing canopy, variations in minima became negligible. Minimum temperature variations in summer were slight. In fact, the diurnal low often was recorded at stations on the south slope, a circumstance probably associated with the thinner south slope canopy which permitted the escape of greater amounts of outgoing radiation at night than did the thicker canopy of the north slope. In fall, patterns were similar to those of summer, with little marked difference between the slopes. During late fall there was a trend toward lower minima on the north slope indicating a transition to winter conditions.

The consistent presence of the lowest weekly minima at the bottom of the north slope during the first 3 weeks of late spring may be explained in terms of cold air drainage patterns. In the evening the soil and low vegetation on the sides of the kettle above this station radiated heat and temperatures dropped within the lower layers of air. This cooled air flowed down the sides of the kettle replacing warm air which occupied the kettle during the day. As cold air accumulated in the kettle a "cold air lake" was formed. When the level of this lake passed the level of the instruments at the bottom of the north slope, a marked drop in temperature was registered. Thermograph charts during this period often recorded this phenomenon, and abrupt drops in temperature of 4-8° between 7:40 and 8:35 P.M. were not uncommon. The abrupt drop was always preceded by a slight rise in temperature associated with the forcing upward by the cold air of warm air which had filled the kettle during the late afternoon. The cessation of this pattern during the last part of late spring was due to a decrease in nocturnal outgoing radiation associated with canopy closure.

Minima were most often recorded during the hours of early dawn when the "outgoing radiation type" (Geiger, 1957) had developed. A condition often associated with nocturnal minima is the development of a temperature reversal, or inversion, near the ground.

Comparison of minima from the 10 cm and 50 cm levels at the main station indicated that pronounced inversions were recorded during early spring and the first weeks of late spring (Table 6). During the first 3.5 weeks of late spring inversions occurred at all stations. On the south slope and at the top of the north slope 10 cm minima averaged about one degree

TABLE 6. Comparison of occurrence and magnitude of inversions during late spring at main station.

Temperature difference between 10 and 50 cm	South top	South middle	South bottom	North top	North middle	North bottom
April 16-May 9						
0.1-1.0	1	1	0	0	0	0
0.0	3	3	5	8	0	1
−0.1-1.0	10	14	8	11	2	9
−1.1-2.0	8	6	10	5	9	9
−2.1-3 0	1	0	1	0	9	4
−3.1 plus	1	0	0	0	4	1
Mean	−1.2°	−1.0°	−1.2°	−0.8°	−2.4°	−1.6°
Nights with inversions (%)	83%	83%	79%	67%	100%	100%
May 10-June 1						
2.1-3.0	2	1	1	0	0	0
1.1-2.0	5	1	1	5	0	2
0.1-1.0	12	8	5	12	0	6
0.0	4	10	15	6	5	3
−0.1-1.0	0	3	1	0	13	9
−1.1-2.0	0	0	0	0	4	3
−2.1-3.0	0	0	0	0	1	0
Mean	1.1°	0.3°	0.3°	0.9°	−1.0°	−0.3°
Nights with inversions (%)	0%	13%	4%	0%	78%	52%

below those at 50 cm whereas at the middle and bottom of the north slope 10 cm minima were 2.4° and 1.6° respectively below those at 50 cm. Thus, early in late spring, before the canopy and low plant cover had fully developed, inversions occurred on both slopes.

On May 10 an abrupt change occurred in the pattern and distribution of inversions. From this date through the close of late spring and throughout the remainder of the growing season inversions rarely were recorded on the south slope and at the top of the north slope. In fact, minima were generally higher at 10 cm than at 50 cm. At the lower stations on the north slope inversions continued to form but they were lower in magnitude than during the first part of late spring. An explanation for this shift in appearance of inversions may lie in the development of the ground layer vegetation on the slopes. A low plant cover spreads out the region of daytime heat absorption and the region of heat loss at night (Geiger, 1957), and a dense cover can hold cold air above it by the interference of its vegetative parts. Thus, on the south slope where the ground layer was better developed the low vegetation acted as a buffer zone for night-time extremes in temperature and prevented inversions from forming. On the north slope, however, the sparser ground layer was ineffective in this role and a weak inversion typically developed. During summer, the lowest average minima at 50 cm at the main station actually occurred on the south slope. At this level there was no protection from the low plant cover and, because of the thinner canopy on this slope, heat exchange with the air outside the forest took place more freely than on the north slope. Thus, on the average, minima at 50 cm on the north slope were higher than those at comparable levels on the south slope.

WIND

No detailed data on wind variations in the study area were collected. However, several limited observations illustrated variations in the climate of the slopes at the main station related to differences in wind direction and velocity.

A brief study of wind variability at the main station was carried out on May 4, 1957.[2] Measurements of maximum, minimum, and average velocities and of wind direction at mid-day were taken at 4 stations on both slopes. Due to the direction of the wind, from the north-northwest, wind speeds were higher at each station on the north slope than at corresponding stations on the south slope. Velocities were highest at the slope tops and decreased down slope. The lowest velocities were recorded at the bottom of the south slope. The data also showed that wind speeds were considerably lower at 10 inches above the ground than at 5 ft, particularly at the slope bottoms.

There was evidence that such modified wind patterns appeared to exert some effect on daytime temperature regimes on the slopes (Table 7). On calm summer days, for example, the incoming radiation type was well-developed at all stations, particularly on the south slope. Intense solar radiation heated the air layer near the ground and, as there was little air movement to cool these sites, temperatures near the ground were extremely high. However, on days when there was a recognizable wind from the south or southwest, the incoming radiation type was not as strongly developed. The bottom and middle stations on the south slope appeared to be least affected by the wind, whereas the two stations most affected were those at the tops of the slopes.

TABLE 7. Average mid-afternoon air temperature at 10 cm and 50 cm levels on clear, calm days and clear, windy days during summer at the main station.

Station	AIR CALM[a]		WIND FROM SOUTH OR SOUTHWEST[b]	
	10 cm	50 cm	10 cm	50 cm
South top.......	84.5	81.1	79.4	78.9
South middle....	83.6	80.3	79.9	78.5
South bottom....	83.4	80.6	80.9	78.9
North top.......	80.2	79.2	78.3	78.3
North middle....	78.9	79.4	76.6	78 4
North bottom....	79.1	78.4	77.1	77.6

[a] Average of 7 days.
[b] Average of 4 days.

[2] The author is indebted to E. W. Bierly and J. S. Marshall for collecting these data and to Dr. A. N. Dingle for permission to use them.

EVAPORATION

Evaporative water loss from soil and plant surfaces is an important microclimatic factor. Despite the fact that evaporation is dependent on other physical phenomena (radiation, air movement, etc.) it is a useful measure of the environmental differences between various sites. The instrument measuring water loss integrates evaporation-influencing factors and, in this respect, behaves as a plant by responding to the sum of factors rather than to each individually.

The fact that evaporation was greatest on the south slope throughout the study was shown by cumulative data from black and white bulb atmometers (Table 8). In fact, evaporation from white bulbs on the south slope exceeded that from black bulbs on the north slope. Evaporation for the season took place in a straight-line fashion, each 4-week increment approximately equalling that of the previous period. There was no evidence of a reversal to winter conditions with diminished evaporation because measurements were concluded before the cool, rainy weather of late fall and winter began.

TABLE 8. Total evaporation and evaporation factors at main station, May 5-October 24, 1957.

Station	Total evaporation (cc)	Factor
North slope		
Bottom: White bulb.......	1457	1.00
Black bulb.......	1601	1.00
Middle: White bulb.......	1629	1.12
Black bulb.......	1800	1.12
Top: White bulb.......	1803	1.24
Black bulb.......	1965	1.23
South slope		
Bottom: White bulb.......	2044	1.41
Black bulb.......	2430	1.52
Middle: White bulb.......	2168	1.49
Black bulb.......	2694	1.68
Top: White bulb.......	2225	1.53
Black bulb.......	2722	1.70

The general pattern of water loss through the growing season was similar for each of the locations sampled. During late spring evaporation dropped sharply due to canopy closure and attendant lowering of solar radiation and air movement within the trunk-space area. Several periods of accelerated evaporation occurred. These were related to periods of clear, warm weather. The most marked of these was during mid-summer when little rain fell and weeks were characterized by a high percentage of cloudless, sunny days. From this mid-summer peak, evaporation fell off through the remainder of the summer and increased during the dry fall when trees began to lose their leaves. Although water loss patterns were similar at all locations, total loss was considerably higher on the south slope and there was a pattern of highest evaporation at the top of each slope and least at the bottom.

Using the atmometer pair at the bottom of the north slope as a standard, evaporation factors were established for the various locations (Table 8). These data show the differences both between slopes and with position on the slopes. Total black and white bulb evaporation both increased by approximately 12.5% increments up the north slope. The similarity between the precentage increases was probably due to the low levels of light intensity occurring throughout most of the growing season on the north slope. On the south slope, however, white bulb evaporation was much greater than on the north slope, varying from 1.4 to 1.5 times as great from slope bottom to top. Black bulb evaporation was also much greater and showed a similar increase from bottom to top of slope. However, black-bulb values were higher than their white-bulb counterparts, a fact probably explained by the greater solar radiation received on the south slope.

SOIL TEMPERATURE

Because of the equipment used, soil temperatures recorded in this study were obtained at only one time during the diurnal period. Such data have certain limitations. Muttrich (1880, in Li 1926) showed that these data were not a safe basis for the calculation of mean soil temperatures and that they could be used only on a comparative basis (as in the present study). Thus, maximum and minimum daily temperatures would be more desirable for describing annual and diurnal temperature regimes.

Furthermore, the comparative value of the mid-afternoon readings obtained in this study is complicated by the different diurnal temperature regimes which characterized the slopes. A short study of diurnal soil temperature patterns at the main station on May 4, 1957, showed that maxima in the A_1 horizon were attained earlier on the south slope (1:00 to 2:15 P.M.) and later (2:30 to 3:45 P.M.) on the north slope. In the A_2 horizon, temperatures rose continually during the afternoon and maxima at this depth on both slopes were not reached until late in the afternoon. Thus, by sampling soil temperature between 2:00 and 4:00 P.M., temperatures slightly below diurnal maxima were recorded in the A_2 horizon on both slopes and in the A_1 horizon on south slopes. Only A_1 horizon readings on north slopes approximated maxima for the day at those locations. Despite these limitations, the data obtained were useful in contrasting soil temperature regimes on the slopes.

The general trend of soil temperatures in the A_1 and A_2 horizons was shown by average weekly temperatures from the scattered stations (Fig. 5). South slopes were characterized by warmer soil temperature regimes than north slopes. In early spring temperatures in the A_1 horizon exceeded 50° on south slopes while remaining at or below freezing on north slopes. Soil temperatures rose rapidly on both slopes during late spring. The greatest temperature range in the A_1 horizon on both slopes occurred during the first week of late spring. During the next 2 weeks, before the canopy had fully developed, maxima reached 73° on south slopes and 69° on north slopes. Increase in temperature in the A_2 horizon lagged behind that in the A_1, the lag being greater on north slopes. The A_1 and A_2 horizons on south slopes and the A_1 horizon on north slopes all reached their spring maxima during the first 2 weeks of early spring whereas the A_2 horizon on north slopes did not reach its spring maximum until the last week of late spring.

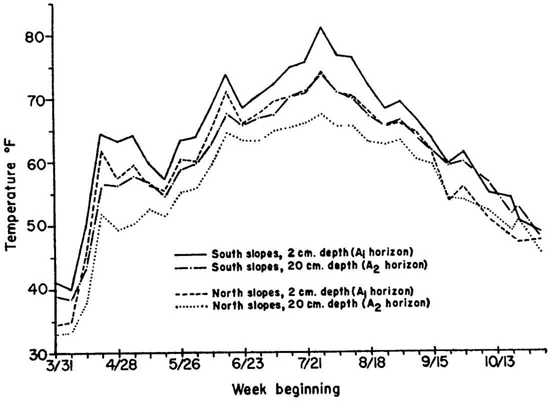

FIG. 5. Weekly average mid-afternoon soil temperature in A_1 and A_2 horizons at scattered stations (from Cooper 1960a). Averages computed as in Fig. 1.

Annual maxima were reached in both horizons and on both slopes during mid-summer. Maxima were higher on south slopes and temperatures averaged 3-6° higher at similar depths on south slopes throughout most of summer. Differences in soil temperature diminished through late summer and early fall and were least in fall when there was an approach to the winter type of temperature profile with warmer temperatures deeper in the soil.

Seasonal average soil temperatures from the main station showed the variations due to slope position (Table 9). Seasonal soil temperatures in both the A_1 and A_2 horizons were always highest on the south slope. Furthermore, during practically every season values decreased progressively from a high at the top of the south slope to a low at the bottom of the north slope. Differences between the slopes were greatest during late spring when values were 10-12° higher on the south slope than at similar stations on the north slope. Other seasons of major difference were early spring and mid-summer when comparable values were 8-10° and 6-7° higher on the south slope. Differences between the slopes were least in fall when, due to the lag effect, temperatures on the north slope were dropping proportionately slower than those on the south slope.

TABLE 9. Seasonal average soil temperatures in the A_1 and A_2 horizons at the main station.

Season	South top	South middle	South bottom	North top	North middle	North bottom
Early spring						
A_1	43.3	43.6	41.2	34.4	33.5	33.4
A_2	38.5	38.6	37.6	33.4	32.6	33.1
Late spring						
A_1	65.0	64.9	61.7	53.2	52.2	51.2
A_2	55.5	55.5	53.6	48.9	48.3	47.4
Early summer						
A_1	70.7	69.1	67.7	64.3	64.2	63.5
A_2	64.9	64.2	63.2	60.6	60.1	59.2
Mid-summer						
A_1	76.2	75.2	72.7	69.6	68.3	67.0
A_2	70.1	68.7	67.2	65.8	65.3	64.5
Late summer						
A_1	68.2	67.5	68.2	65.6	65.2	63.7
A_2	65.6	64.8	64.1	62.8	62.4	62.1
Early fall						
A_1	60.3	60.8	60.4	57.9	57.2	56.5
A_2	58.5	58.3	57.2	56.4	56.0	56.0
Late fall						
A_1	50.0	48.7	50.2	49.0	48.5	48.7
A_2	50.8	50.7	49.5	49.3	48.7	50.0

TABLE 10. Distribution of mid-afternoon A_1 horizon soil temperatures at the main station in various temperature intervals during selected seasons.

Temperature interval	NUMBER OF DAYS					
	South top	South middle	South bottom	North top	North middle	North bottom
			Early spring			
— 32.0	0	0	0	1	10	11
32.1 - 40.0	10	9	11	25	16	15
40.1 - 48.0	12	10	13	0	0	0
48.1 - +	4	7	2	0	0	0
			First four weeks of late spring			
32.1 - 40.0	0	0	0	2	2	3
40.1 - 48.0	2	1	2	5	5	6
48.1 - 56.0	2	3	3	13	12	18
56.1 - 64.0	7	8	11	7	8	0
64.1 - 72.0	7	5	10	0	0	0
72.1 - 80.0	8	9	1	0	0	0
80.1 - +	1	1	0	0	0	0
			Mid-summer			
60.1 - 68.0	0	0	1	19	17	24
68.1 - 76.0	21	24	34	21	23	16
76.1 - 84.0	19	16	5	0	0	0

That there were four periods of major differences in soil temperatures at the main station can be shown by weekly average A_1 horizon values from the top of the south slope and bottom of the north slope (Fig. 6). The first period of difference was in early spring when the soils of the south slope had thawed and warmed whereas the soil at the bottom of the north slope remained frozen. Although data for this season were incomplete, over one-half of all readings on the south slope were above 40° whereas no readings this high were recorded on the north slope (Table 10). Conversely, temperatures of freezing and below were recorded regularly at the middle and bottom of the north slope, and not at all on the south slope. The first 4 weeks of late spring marked the second, and greatest, period of difference in soil temperature. During this season, before canopy closure, temperatures in the soil rose rapidly on both slopes. However, temperatures on the south slope rose higher and fluctuated more than those on the north slope (Table 10). Almost half of the temperatures recorded on the south slope during this period were over 64° whereas no temperatures of this magnitude were recorded on the north slope.

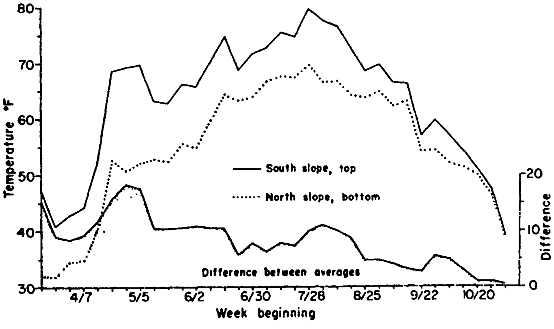

FIG. 6. Weekly average mid-afternoon soil temperature in A_1 horizon at top of south slope and bottom of north slope at main station.

The other periods of difference occurred during periods of high air temperature and low rainfall in mid-summer and early fall. The differences during mid-summer were particularly striking (Table 10). At the upper stations on the south slope almost half of the temperatures recorded were over 76°, whereas less than one-quarter of the readings at the upper stations on the north slope were of this magnitude. Furthermore, the lowest temperature recorded at the top of the south slope during this period was 71° whereas the highest temperature recorded at the bottom of the north slope was 72°. Thus, there was practically no overlap between soil temperature ranges at these two stations. Examination of the temperature distributions (Table 10) showed that the stations topographically-intermediate between these two extremes had intermediate temperature distributions.

Although no quantitative measurements were made, observations during the winters of 1957 and 1958 indicated that different temperature conditions prevailed in the surface soils of the slopes during this season (Cooper 1960a). Winter snow covers were seldom of long duration on south slopes. Snow usually melted soon after falling and there was seldom any great accumulation. North slopes, on the other hand, had a more or less continuous snow cover throughout most of mid-winter. The surface soils on south slopes underwent numerous cycles of freezing and thawing, particularly on warm, sunny days, whereas the soil remained frozen continuously under the snow cover of north slopes. Even after snow had melted in early spring the soils of some north slopes remained frozen several weeks longer than soils on south slopes. By March 31, 1957, for example, no frost was found in any south slope soil, whereas frost was still encountered as late as April 4 and April 17 on two north slopes.

SOIL MOISTURE

As would be expected, there were differences between the soil moisture regimes of the slopes. Average weekly values from the scattered stations showed that north slopes had higher amounts of moisture in the A_1 horizon throughout almost the entire growing season (Fig. 7). With the exception of one week, average values were always lower on south slopes. There was an abundance of soil moisture on both slopes during all of spring. There was a rapid decline in soil moisture during early summer but the heavy rains of the last two weeks of this season raised levels again. Mid-summer was a period of extreme soil-moisture depletion with little or no rain falling during this period of annual maximum temperatures. Even during this period of drought soil moistures were higher on north slopes. Heavy rains in late summer raised soil moisture levels slightly, but these reserves were rapidly depleted by a long period of drought (22 days) during early fall. With the beginning of late fall soil-moisture values began to return to the high levels of winter and early spring.

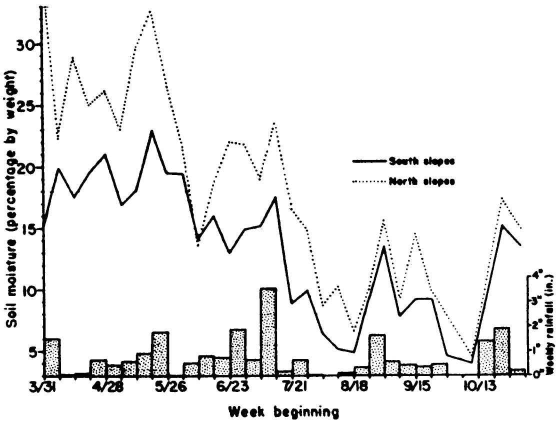

FIG. 7. Weekly mid-afternoon soil moisture (per cent by weight) in A_1 horizon at scattered stations (from Cooper 1960a). Averages computed as in Fig. 1.

The mid-summer drought when many plants, particularly those of south slope field layers, were still active vegetatively and reproductively, appeared to be of importance to plant distributions in the study area. During this lengthy dry period soil moistures probably dropped close to the permanent wilting point on both slopes. The drop was more marked on south slopes and this, coupled with the high air temperatures and evaporation rates of these sites, undoubtedly has been important in limiting the distribution of species with higher moisture requirements on south slopes. The mid-summer moisture stress of these sites was indicated by the fact that several species (*Amphicarpa bracteata, Lysimachia quadrifolia, Monarda fistulosa,* and *Phryma leptostachya*) underwent brief mid-afternoon wilting several times during the week of August 11-17. These conditions were in marked contrast to those of north slopes. When soil-moisture conditions became critical during mid-summer on those sites, maximum temperatures were low enough so that the great evaporation stress of south slopes was not present. Wolfe *et al.* (1949) called attention to a similar situation with regard to maximum temperature variations between cliff and forest habitats at Neotoma. Furthermore, many late-aestival and autumnal flowering species of the south slopes carried on their entire reproductive cycle during the period of extreme moisture stress in late summer or fall whereas on north slopes more species were vegetatively and reproductively active during spring when there was abundant moisture in the soil.

Seasonal percentages at the main station (Table 11) supported the generalizations derived from the scattered station data. During early spring there was a large amount of moisture in the soil on both slopes. More moisture was present in the A_2 horizon during early spring than during any other part of the growing season. Soil moistures at all stations remained relatively high during late spring and early summer but during mid-summer values averaged lower than any other season except early fall. During these dry periods values at each station, with the possible exception of the bottom of the north slope, undoubtedly approached the permanent wilting point. At the bottom of the north slope during the drying cycles moisture values in the A_1 horizon were higher than at other stations. This was due to the lower soil temperatures, air temperatures, and evaporation rates at this site. Also, the heavy litter layer prevented a considerable amount of direct evaporative water loss from the soil.

The pattern of daily soil-moisture values in the A_1 horizon at the top of the south slope and the

TABLE 11. Seasonal average soil moisture (percentage by weight) in A_1 and A_2 horizons at the main station.

Season	South top	South middle	South bottom	North top	North middle	North bottom
Early spring						
A_1	25.0	22.6	19.6	23.0	22.5	19.8
A_2	7.8	8.7	11.0	14.2	12.2	9.9
Late spring						
A_1	22.8	21.5	20.0	23.4	20.0	20.3
A_2	8.0	9.1	9.8	13.2	8.8	8.3
Early summer						
A_1	19.9	15.8	16.4	17.9	20.8	23.4
A_2	7.6	8.5	8.0	9.7	8.0	8.4
Mid-summer						
A_1	8.7	8.4	8.9	9.1	12.8	15.5
A_2	4.8	4.7	4.1	5.2	6.0	5.7
Late summer						
A_1	20.7	16.9	17.2	16.7	20.2	19.1
A_2	5.0	5.2	5.9	6.2	4.8	7.5
Early fall						
A_1	8.8	7.4	10.1	7.5	11.4	12.3
A_2	3.6	3.1	2.8	3.6	3.5	3.7
Late fall						
A_1	31.8	25.0	24.3	25.9	33.5	42.4
A_2	10.8	9.2	10.1	23.0	10.5	12.4

bottom of the north slope (Fig. 8) showed a further difference between the soil-moisture regimes of the slopes obscured by the seasonal, or even weekly, averages. During late spring and early summer four well-developed cycles of wetting and drying (A, B, C, and D) occurred at the top of the south slope. These cycles were poorly developed at the bottom of the north slope. There was one cycle of drying during summer and one in fall. These extended cycles, marking the periods of summer and fall drought, occurred on both slopes but were more severe on the south slope. Thus, even during late spring and early summer, when soil-moisture levels were the most favorable of any season, repeated cycles of drying took place on the south slope. These cycles of high moisture stress, developing in response to periods of low rainfall and high temperature, probably were a significant habitat difference between the slopes.

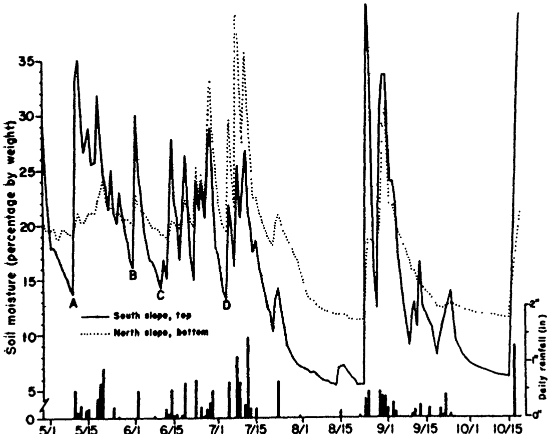

FIG. 8. Daily mid-afternoon soil moisture in A_1 horizon at top of south slope and bottom of north slope at main station (from Cooper 1960a).

Soil-moisture regimes in the A_2 horizon operated through a smaller range and fell much lower during dry periods than did soils of the A_1 horizon. The high values of early spring were never fully replenished until the heavy rains of fall after the end of the growing season. Variations in intensity, interception by the canopy and litter, and retention of water in the surface layers of the soil combined to limit the effectiveness of summer rains in wetting the A_2 horizon. For example, a heavy rain (0.65 in.) fell during the morning of July 22. Moistures in the A_1 horizon were raised more than 20% at several stations, but in the A_2 horizon the greatest increase was 2.4% and several stations showed no increase at all. During the second and third weeks of September there was no moisture increase in the A_2 horizon despite 4 moderate rainfalls and 2 showers. Moisture was lost continuously through the 2-week period while 3 cycles of wetting and drying took place in the A_1 horizon. Thus, plants having their major root activity in the A_2 horizon must be able to operate on a low moisture budget throughout most of the growing season. As mentioned, the effects of this lower moisture budget were not as great on north slopes.

SUMMARY OF MICROCLIMATES

The major differences between the microclimates of the slopes are summarized (Table 12) by average values for major microenvironmental factors for the period March 31—September 14, 1957 (the period of most intensive instrumentation).

Most of the differences between the slopes may be related to basic differences in their solar radiation budgets. Differences in visible radiation (relative light intensity) may be taken as indications of differences in total solar radiation budgets (Table 12). Relative light intensity was greatest on south slopes, averaging over 5% higher than on north slopes. Furthermore average intensities were highest at the top and middle of the south slope (21.8% and 21.5%) and diminished to a low of 9.3% at the bottom of the north slope.

The greater net solar radiation budget of the south slopes, interacting with vegetation, produced higher air and soil temperatures, higher evaporation rates, and lower soil moisture values on south slopes than on north slopes (Table 12). Average air temperatures were higher on south slopes throughout most of the year and different maximum air temperature

TABLE 12. Averages of weekly values for principal microenvironmental factors at scattered and main stations. March 31-September 14, 1957.

Factor	SCATTERED STATIONS		MAIN STATION					
	South slopes	North slopes	South top	South middle	South bottom	North top	North middle	North bottom
Relative light intensity (%)	15.6	10.3	21.8	21.5	18.8	11.3	10.5	9.3
Maximum air temp., 50 cm (°F)	81.8	75.0	73.2	72.9	72.9	72.0	71.7	71.6
Maximum air temp., 10 cm (°F)	83.5	75.6	81.9	80.7	80.2	75.9	74.4	75.3
Minimum air temp., 50 cm (°F)	51.3	50.7	51.8	52.0	51.6	51.6	52.3	51.5
Minimum air temp., 10 cm (°F)	52.3	51.5	54.7	54.6	54.2	54.5	53.4	53.2
Evaporation (cc)	*	*	113.4	112.3	101.3	81.9	75.0	66.7
Soil temp., A_1 (°F)	65.9	61.9	67.6	67.0	64.8	60.0	59.8	57.9
Soil temp., A_2 (°F)	61.3	56.9	61.3	60.6	59.3	56.4	55.9	55.2
Soil moisture, A_1 (% by weight)	14.5	19.6	15.1	13.0	13.0	15.3	16.4	18.2

* Not sampled.

regimes characterized the slopes. Maximum air temperatures averaged almost 7° higher at 50 cm and 8° higher at 10 cm on south slopes at the scattered stations. Average maxima at both levels at the main station were highest at the top of the south slope and declined to lows at the middle and bottom of the north slope. Soil temperatures in the A_1 horizon averaged 4° higher on south slopes at the scattered stations and such temperatures averaged almost 10° higher at the top of the south slope than at the bottom of the north slope at the main station. Similar differences were observed in the A_2 horizon. Evaporation rates at the main station averaged 50-70% greater on the south slope than at the bottom of the north slope. Soil moisture levels were somewhat variable, but in general average values were lower on south slopes than on north slopes.

In summary, the microclimates varied from warm and dry, with relatively wide extremes, on south slopes, to cooler, more moist, and less variable on north slopes. Whereas south slopes had a xeric microclimate, north slopes were more mesic. Furthermore, xeric characteristics were best expressed at the top of south slopes and more mesic conditions were best expressed at bottoms of north slopes. Stations topographically intermediate between these extremes showed correspondingly intermediate microclimates.

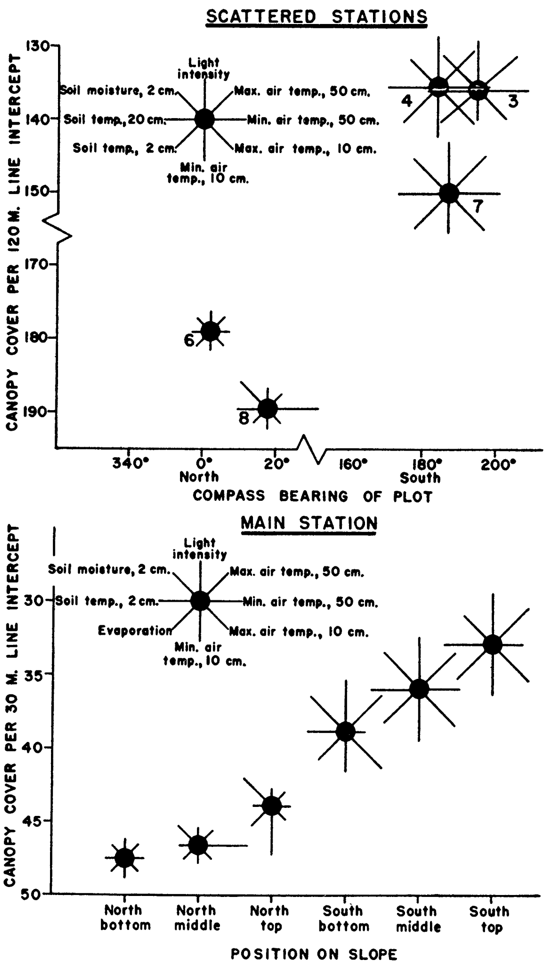

FIG. 9. Scatter diagrams showing relationships between slope and slope position, canopy cover, and microclimatic averages at scattered and main stations. See text for explanation.

The data suggested that the microclimates studied constituted a microenvironmental gradient. That such a gradient exists can be shown by the use of scatter diagrams (Fig. 9). In these diagrams topographic and vegetational features are used for the graph axes. Each point represents a station sampled and the radiating lines represent 8 major environmental factors. The length of each line is determined from the range of values of the yearly averages for each factor. The shortest line represents a value in the lowest 1/4 of the range with lengths increasing for values in the second, third, and highest quarters. Soil moisture values are reversed, with low soil moisture values being placed in the highest quarter and high values in the lowest.

These figures show that the north slopes are characterized by predominantly short radiating lines whereas south slopes have long lines for almost every factor. At the main station, the bottom of the north slope has all short radiating lines indicating low (or narrow) yearly averages. The number of long lines, indicating increasing xerism, increases up the north slope and also up the south slope with the middle and top of the south slope having almost all long lines. Thus, the method gives a visual representation to the variation in the microclimates in addition to indicating their gradient relationships.

RESULTS: VEGETATION[3]

Just as a knowledge of the regional climate is necessary for an interpretation of specific microclimates, the regional biological spectrum is basic to an understanding of variations in community life-form composition. The biological spectrum for the entire Reserve flora was hemicryptophytic, as were spectra for other communities on the Reserve, in that they showed an increase of over twice the number of hemicrypfophytes and cryptophytes in the normal spectrum at the expense of phanerophytes and chamaephytes (Table 13). Such spectra are characteristic of temperate regions with an unfavorable season represented by a cold winter. Differences between field and forest communities with respect to percentages of phanerophytes, hemicryptophytes, and therophytes merely reflect differences in the physiognomy of these types. Cryptophytes were less important in the upland areas than in the total flora because of the absence of hydro- and helophytes in these habitats.

The greatest differences in vegetation at the study sites were found in a comparison of the grouped slopes (see page 18). Because of the limited num-

[3] For the raw data and other vegetational correlations see Cooper, 1958.

TABLE 13. Presence-based life-form spectra for certain upland communities on the E. S. George Reserve.

Community	No. spp.	Ph	Ch	H	Cr	Th
Total Reserve flora (Cooper, 1958)	567	16.5	1.4	56.0	15.0	11.1
Old field (Evans and Cain, 1952)	90	8.9	2.2	64.5	11.1	13.3
Upland forest (Cooper, 1958)						
West Woods	100	30.0	1.0	55.0	13.0	1.0
Southwest Woods	97	33.0	0.0	51.5	14.5	1.0
Big Woods	219	23.2	1.8	59.8	11.4	4.6
Normal Spectrum (Raunkiaer, 1934)	1000	46.0	9.0	26.0	6.0	13.0

bers of slopes in each group, statistical comparisons were not made. Only the most evident differences are discussed. Stations 12 and 13 were eliminated from these comparisons as their central tiers contained old roadways and thus were somewhat disturbed.

There were several gross vegetational differences between the groups of slopes. Despite the fact that there were no great differences in total numbers of species within the groups, the total number of hemicryptophyte species was lowest on protected north slopes (53) and open north slopes (55) increasing to 56 on protected south slopes and 59 on open south slopes. Phanerophytes were most numerous on both protected north slopes and protected south slopes (31 on each) and least abundant on open north slopes (27) and open south slopes (26). Total vegetative cover was greatest on protected north slopes, averaging 21,767 cm/120 m, diminishing to 20,153 cm on open north slopes and 19,729 cm on protected south slopes. Total cover was least on open south slopes, averaging 17,826 cm/120 m. Of this total cover, by far the greatest percentage was phanerophytic. Phanerophyte cover values were greatest on protected north slopes (20,480 cm/120 m), diminishing to 17,960 cm on open north slopes and 17,831 cm on protected south slopes, and were least on open south slopes (14,810 cm).

There were also differences in the field layers of the grouped slopes. Total field layer cover averaged 3064 cm/180 m on protected north slopes, increasing to 4158 cm on open north slopes, 5305 cm on protected south slopes, and 6427 cm on open south slopes. Total hemicryptophyte cover was lowest (967 cm/180 m) on protected north slopes and averaged 3 times as great (2974 cm) on open south slopes. Open north slopes and protected south slopes had intermediate values. Field layer phanerophyte cover averaged least (894 cm/180 m) on open north slopes and most on protected south slopes (2472 cm). Values on protected north slopes and open south slopes were 1202 cm and 1925 cm respectively.

Certain variations within life-form subclasses were also evident. Canopy cover (total cover of meso- and megaphanerophytes) averaged 175 m/120 m on protected north slopes, 159 m on open north slopes, 158 m on protected south slopes, and 135 m on open south slopes. Comparable basal areas for the grouped slopes were 26.2, 26.7, 20.6, and 21.4 $ft^2/900\ m^2$. Total microphanerophyte cover also was greatest on protected north slopes (21.8 m/120 m) and least on open south slopes (0.4 m). Values on open north slopes and protected south slopes were intermediate, being 14.5 m and 3.6 m respectively. Among hemicryptophytes, protohemicryptophytes had, on the average, 10 times greater cover value on open south slopes than on protected north slopes. Rosette hemicryptophyte cover was greatest on open north slopes (349 cm/180 m) and protected north slopes (331 cm), diminishing to 66 cm on protected south slopes and 37 cm on open south slopes. There were no clear patterns with respect to distributions of true nanophanerophytes, chamaephytes, geophytes[4] and therophytes.

The differences in field layer life-form distributions suggested that there might also be shifts in life-form dominance from the bottoms to the tops of the grouped slopes. As each plot consisted of 3 tiers of 3 100 m^2 plots, data were available from the top, middle, and bottom of each slope. From these data trends in life-form composition at different slope positions were analyzed.

Each group of slopes had a characteristic distribution of field-layer life-forms. On protected north slopes total cover in the field layer increased toward the slope tops. Relative cover of hemicryptophytes was greatest in the middle of the slopes where relative values of geophytes and nanophanerophytes were least. Geophytes and hemicryptophytes were of about equal importance at the bottoms of these slopes and hemicryptophytes increased in relative value upslope. Open north slopes showed an opposite pattern, total field-layer cover decreasing toward slope tops. Hemicryptophytes were of greatest relative importance at the slope bottoms and decreased in importance upslope, whereas geophytes and nanophanerophytes had greatest relative values at slope tops and decreased in importance downslope. Thus, the 2 groups of north slopes showed almost reverse trends.

On open south slopes field-layer cover increased greatly toward slope tops. Hemicryptophytes had almost twice the relative value at the tops of the slopes as at the bottoms and nanophanerophytes decreased in importance toward the slope tops. Geophytes had rather constant relative coverage but decreased upslope in relation to hemicryptophytes. Protected south slopes showed the same general trends, but in a less marked fashion.

From these data it is possible to generalize that, within the field layer, in situations where hemicryptophytes increase in relative importance geophytes and woody field-layer species decrease.

Despite differences in degree of protection afforded the slopes and variations in topographic outline it was possible to demonstrate certain contrasts between all north slopes as opposed to all south slopes. Distribution of species in life-form classes and presence-

[4] As geophytes were the only class of cryptophytes represented, the term geophyte is used when referring to the cryptophyte life-form.

based life-form spectra showed that there were no significant (Mann-Whitney U Test, Siegel 1956) differences between the distribution of life-forms in the total floras of the north and south slopes. There were slightly more species on south slopes, an average of 105 to 102. There was an average of 30 phanerophytes on north slopes and 27 on south slopes. Hemicryptophytes were more numerous on south slopes, an average of 60 to 54. However, the wide ranges in the values negated these small differences.

Analysis of total cover values for each life-form class (Fig. 10) and coverage-based life-form spectra for the entire plot vegetation showed that there were differences in the importance of certain life-forms on the slopes. There was a significantly greater total vegetative cover (5% level) and cover of phanerophytes (5% level) on north slopes and a significantly greater cover of hemicryptophytes (1% level) on south slopes. There were no significant differences in the distribution patterns of other life-form classes.

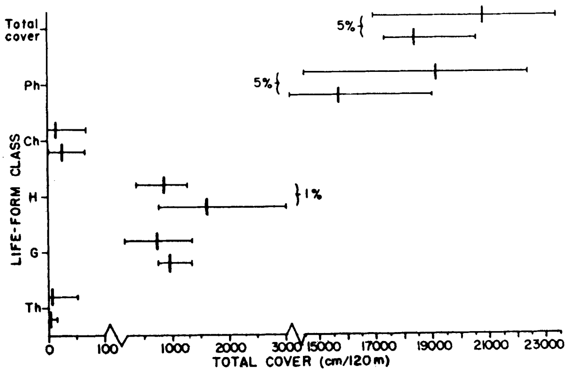

FIG. 10. Total cover of each life-form class in total vegetation of slopes. Upper line of pair indicates north slopes, lower line south slopes. Horizontal line indicates the range of values and vertical bar the mean value. Per cent values refer to significance levels using the Mann-Whitney U Test (Siegel 1956). Ph=phanerophytes; Ch=chamaephytes; H=hemicryptophytes; G=geophytes; Th=therophytes.

Spectra constructed from the total flora of sample plots, however, are too general to be sensitive. They include members of different strata which, in maturity, are responding to different sets of microenvironmental factors. Cantlon (1953) showed that vegetational differences between slopes, in conjunction with microclimatic differences, increased with proximity to the soil surface. Thus, an analysis of the field-layer (forest floor) vegetation, which is established under, and responds to, the microclimatic conditions near the ground, should yield the greatest differences between the structure of the vegetation of the slopes. In addition, when studies exclude the tree layer and are based on coverage, the overwhelming influence of the trees is escaped and other differences become more apparent.

There were no significant differences either in distribution of species in life-form classes or in presence-based life-form spectra for the slope field layers. The distributions and spectra were virtually identical to those for total plot floras as almost all canopy and understory species were represented by reproduction in the field layer.

However, total cover values for each life-form class (Fig. 11) and coverage-based life-form spectra showed that there were differences between the slopes. There was a significantly greater total field-layer cover (1% level), cover of nanophanerophytes (5% level) and hemicryptophytes (1% level) on south slopes. There were no significant differences with respect to cover of chamaephytes, geophytes, or therophytes.

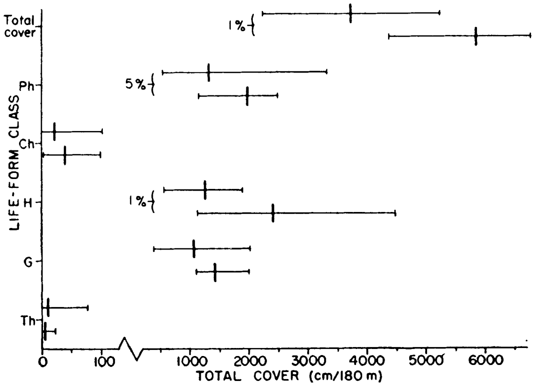

FIG. 11. Total cover of life-form classes in field-layer vegetation. Explanation and abbreviations as in Fig. 10.

Thus, the gross structure of the vegetation on the slopes was different. On the north slopes there was a greater total plant cover and cover of phanerophytes (trees and shrubs) but a more poorly-developed field layer. On the south slopes there was less tree and shrub cover but greater field-layer cover. Within the field layer, cover of nanophanerophytes and hemicryptophytes was greater on south slopes than on north slopes.

Analysis of the distribution patterns of the subclasses of the 5 major life-form classes brought out further differences between the slopes. Among phanerophytes (Fig. 12), there was a significantly greater diversity of species and significantly greater cover (1% level) of meso- and megaphanerophytes on north slopes. Breakdown of data for trees (meso- and megaphanerophytes) showed that although there were no differences in total number of stems or in stems of smaller size classes (Table 14), there were significantly more large trees (over 18 in. d.b.h.) on north slopes. The total basal area averaged 5 ft more per 900 m^2 on the north slopes and this difference was significant at the 1% level. The tree of mean diameter was also significantly larger (5% level) on the north slopes. Although there was no significant difference in the number of microphanerophyte species or stems on the slopes, this life-form had a somewhat significantly greater cover on north slopes (10% level). There was great variability in the distribution of microphanerophytes on north slopes as the deviations in Figure 12 indicate. The heavy cover at several stations (1, 10, 11) was produced by a dense growth of *Hamamelis virginiana* whereas on other north slopes cover was contributed by more widely-spaced saplings, small trees, and Hamamelis. On south slopes cover was uniformly low and was mostly of scattered saplings and individuals of Amelanchier.

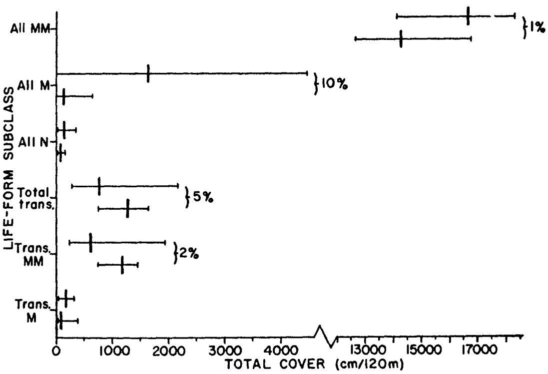

FIG. 12. Total cover of phanerophyte subclasses. Explanation as in Fig. 10. MM=meso- and megaphanerophytes; M=microphanerophytes; N=nanophanerophytes.

TABLE 14. Density and basal area (per 900 m^2) of meso- and megaphanerophytes.

Plot	Total stems over 1 in. d.b.h.	Stems over 18 in. d.b.h.	Basal area (ft^2)	Tree of mean diam. (in.)
		North slopes		
1..........	70	2	30.7	9.0
6..........	62	4	26.4	9.0
8..........	83	4	27.5	7.7
10..........	49	3	22.9	9.4
11..........	57	0	23.4	8.7
13..........	73	1	23.3	7.6
15..........	48	4	29.1	11.0
16..........	105	3	24.7	6.6
Mean.......	68	2.6[a]	26.0[b]	8.6[c]
		South slopes		
2..........	71	1	21.7	7.6
3..........	82	0	19.2	6.6
4..........	74	0	18.8	7.0
7..........	80	0	20.8	6.9
9..........	95	0	24.0	6.8
12..........	62	1	19.7	8.0
14..........	67	1	20.3	7.4
17..........	62	2	23.3	8.4
Mean.......	74	0.6[a]	21.0[b]	7.3[c]

[a] Difference significant at 2% level.
[b] Difference significant at 1% level.
[c] Difference significant at 5% level.
Other difference not significant.

Of the field-layer phanerophytes (Fig. 12), some were true nanophanerophytes and thus natural elements of the field layer whereas others were transgressives which eventually will exceed the nanophanerophyte class. There was no significant difference in the number of species or total cover of true nanophanerophytes on the slopes. As the small cover values indicate, this life-form was not significant in the total field-layer vegetation. However, cover of all transgressives was significantly greater on south slopes. Breakdown of this phanerophyte reproduction showed the source of difference to be within reproduction of the meso- and megaphanerophyte classes. These life-forms had significantly greater cover (2% level) on south slopes whereas there was no significant difference in cover of microphanerophyte reproduction. Thus, whereas conditions favored germination and establishment of tree reproduction on south slopes, conditions on north slopes appeared to be such that a greater number of individuals reached maturity and those that matured grew to larger sizes. Mortality on south slopes seemed to occur between the seedling and sapling stages.

Analysis of the herbaceous element of the field layer showed further differences between the slopes (Fig. 13). There were greater numbers of protohemicryptophytes and these had a significantly greater cover value (1% level) on south slopes. There were no significant differences, either in number of species or cover, of semi-rosette hemicryptophytes. However, rosette hemicryptophytes had significantly more cover (1% level) on north slopes. Thus, the differences between the hemicryptophyte populations of the slopes are due to the considerably greater dominance of protohemicryptophytes on south slopes.

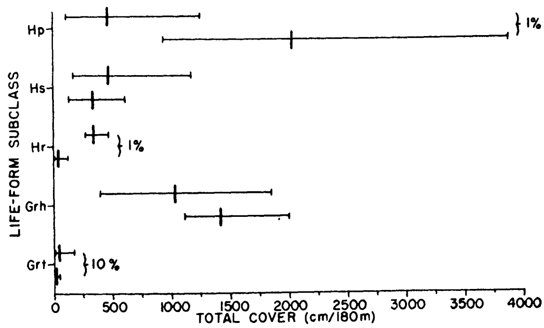

FIG. 13. Total cover of hemicryptophyte and geophyte subclasses. Explanation as in Fig. 10. Hp=protohemicryptophytes; Hs=semi-rosette hemicryptophytes; Hr=rosette hemicryptophytes; Grh=rhizome geophytes; Grt=root tuber geophytes.

There were no great differences in the number of species or cover values of geophytes, chamaephytes, or therophytes. Although there was no significant difference in total geophyte or rhizome geophyte cover, there was a somewhat significantly greater cover (10% level) of root-tuber geophytes on north slopes. As only 2 species were involved, this relationship seems of questionable importance. Only 4 chamaephytes were encountered in this study and, in terms of coverage, these were an insignificant component of the vegetation. This is in keeping with other life-form studies of eastern American deciduous forest. Therophytes were irregularly distributed and were not found to be more important on south slopes, either in number of species or cover. Other workers (Oosting 1942, Cantlon 1953, Miller & Buell 1956) found more therophytes on south than north slopes and related this condition to the lack of light and open ground on north slopes. Although there often were more therophytes in stands with low canopy cover this relationship was by no means consistent. Their presence seemed more related to available disturbed or open ground, regardless of slope orientation.

As previously indicated, there are few studies dealing with the distribution of Raunkiaerian leaf-size classes within a single vegetation type. The data of this study offered an opportunity to analyze variation in distribution of leaf-size classes within a large community and to relate this variation, where possible, to habitat variation.

Analysis of leaf-sizes in the Big Woods showed that 58% of the species were microphylls. Nanophylls (19.7%) and mesophylls (18.4%) were of secondary importance and the larger-sized leaves, macrophylls and megaphylls, were absent. Other woodland communities on the Reserve showed very similar patterns. These distributions were similar to those of other deciduous forests and to that reported for temperate gallery rain forest by Cain *et al.* (1956). There was a definite shift toward a greater percentage of small leaves, leptophylls and nanophylls, in the old-field community studied by Evans & Cain (1952).

Analysis of the entire plot vegetation showed several differences in leaf-size classes on the slopes. On a species basis, only differences in presence of nanophylls were significant, as this size class was more abundant on south slopes. However, total cover (Fig. 14, top) of leptophylls and microphylls was significantly greater (1% level and 10% level respectively) on south slopes. Total cover of mesophylls was significantly greater (2% level) on north slopes. The greater mesophyll cover on north slopes was directly related to the greater tree dominance on those slopes as virtually all trees had mesophylls. Although there were significantly more nanophyllous species on south slopes, there were no differences in cover values for this class.

Proportions in the field layer were somewhat different. Here leptophylls, microphylls, and mesophylls all had significantly greater cover (1%, 2%, and 10% levels respectively) on the south slopes (Fig. 14, bottom). The greater cover of mesophylls in the field layer on south slopes as opposed to their greater coverage in the total vegetation of north slopes was related to the similar shift in dominance of phanerophytes. The greater cover of mesophylls in the field layer on south slopes was due to the greater cover of transgressives on the south slopes, as these transgressives were virtually all reproduction of the mesophyll-class trees.

Those life-forms confined to the herbaceous synusia (Fig. 15) had a more definite pattern of difference between the slopes. Among these species, leptophylls and microphylls again had significantly greater cover on south slopes (both 1% level). However, herbaceous mesophylls had significantly greater cover (1% level) on north slopes. Thus, there was a greater importance of herbaceous species with small leaves on south slopes whereas herbaceous species with larger leaves were a more prevalent element on north slopes.

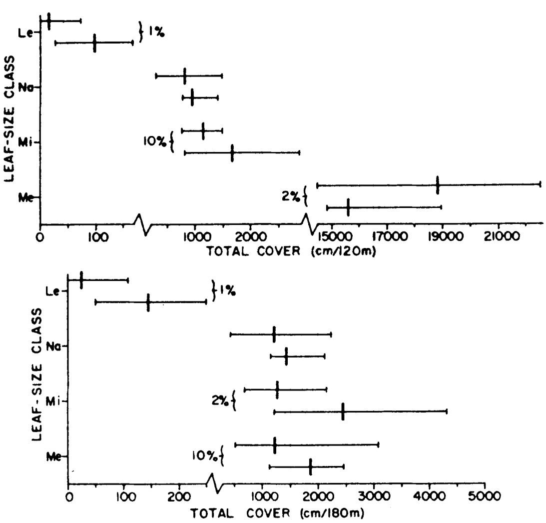

FIG. 14. Total cover of leaf-size classes in total vegetation (above) and field-layer vegetation (below). Explanation as in Fig. 10. Le=leptophylls; Na=nanophylls; Mi=microphylls; Me=mesophylls.

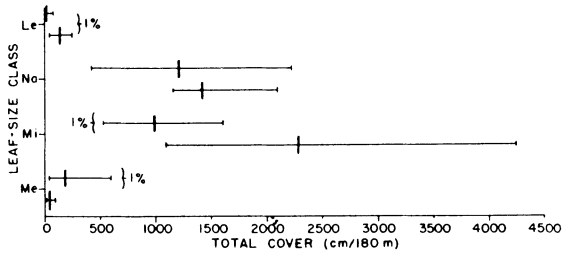

FIG. 15. Total cover of leaf-size classes among herbaceous species. Explanation as in Fig. 10, abbreviations as in Fig. 14.

There were no great variations in dominance of leaf-size classes at different slope positions. Leptophyll cover averaged the least at the bottoms of the north slopes and the most at the tops of the south slopes. These trends, however, were not significant. Herbaceous mesophylls showed a reverse pattern, having the greatest cover at bottoms of north slopes, but these trends also were not significant. Microphyll cover increased up the north slope and was significantly greater (10% level) at the top of the south slope than at the bottom.

RELATIONSHIPS BETWEEN LIFE-FORMS AND MICROCLIMATE

Several approaches to the interrelations of vegetational and microclimatic data were possible. The most direct was correlation of variations in life-form distribution with variations in single factors of the microclimate. However, as the variations in light, air and soil temperature, evaporation, and soil moisture formed a gradient of change from a mesic to a xeric extreme, each vegetational feature would show the same general relationships with each of the individual microclimatic factors. Thus, another approach seemed desirable.

As the presence of a plant on a given site is generally determined by a complex of environmental factors rather than by one factor alone (Billings 1952), the differences in vegetation between sites (on a compositional or structural basis) may be regarded as due to the sum of the environmental differences between the sites. Thus, a method which gathered together the differences in the several environmental features at each site and expressed these as one cumulative value seemed a logical means of expressing the total environmental differences among the sites studied.

Such a combination of data, termed the Microenvironmental Index, was used in this study. The Index was computed in the same manner as a Hybrid Index (Anderson 1949). Base figures used in computation were averages for environmental factors for the period March 31 to September 14, 1957. A total range of 10 was used, with mesic features such as low light intensities, low temperatures, low evaporation rates, and higher soil moistures assigned values near zero and xeric features assigned values near 10. In assigning final values, the mesic extreme of a given factor was assigned a value of 0 and the xeric extreme a value of 10. Intermediate values were placed along a scale in their proper position between the extremes and assigned Index values by comparison with the scale of 10 equal units. Ten factors for each set of data were used, making a total possible Index range from 0-100. Thus, values near 100 indicated xeric microenvironments whereas values near zero indicated more mesic conditions.

Microenvironmental Indices for both the scattered and main stations are shown in Table 15. At the scattered stations high Indices were characteristic of the south slopes and lower values occurred on the north slopes. At the main station Indices were highest at the top of the south slope and declined to a low at the bottom of the north slope. These values corresponded very closely to the positions of the dots in the scatter diagrams (Fig. 9) and offered a sort of numerical corroboration of the conclusions drawn from them.

Several limitations exist on the data available for comparison. Indices for the scattered and main stations cannot be compared because of the differences in the types of instrumentation (maximum temperature, e.g.) and in factors recorded (evaporation at the main station only). Furthermore, the north slope at the main station was a protected north slope and the south slope was an open slope. Thus, any correlations of microclimatic data for different slope positions with vegetational changes were limited to correlations of vegetational data from protected north slopes and open south slopes with microclimatic data from the main station.

TABLE 15. Computation of Microenvironmental Indices for scattered and main stations.

A. Scattered Stations	South Slopes			North Slopes		
	3	4	7	5	6	8
Max. Air Temp., 50 cm....	8.8	10.0	7.7	0.5	1.1	0.0
Min. Air Temp., 50 cm....	8.6	10.0	8.1	6.3	0.0	10.0
Range, Air Temp., 50 cm..	9.0	10.0	7.8	1.7	2.8	0.0
Max. Air Temp., 10 cm....	7.0	10.0	9.8	0.0	0.5	1.0
Min. Air Temp., 10 cm....	3.6	10.0	5.7	0.0	0.4	2.2
Range, Air Temp., 10 cm..	6.6	9.0	10.0	0.0	0.5	0.2
Light Intensity...........	8.8	10.0	8.0	3.0	0.0	1.2
Soil Temp., 2 cm.........	8.8	10.0	9.8	0.0	0.8	2.4
Soil Temp., 20 cm........	9.5	10.0	8.7	0.9	0.0	3.0
Soil Moisture, 2 cm.......	7.7	6.8	10.0	0.0	2.3	5.2
Microenvironmental Index.	78.4	95.8	85.6	12.4	8.4	25.2

B. Main Station	South Slope			North Slope		
	Top	Middle	Bottom	Top	Middle	Bottom
Max. Air Temp., 50 cm....	10.0	8.1	8.2	2.2	0.6	0.0
Min. Air Temp., 50 cm....	4.2	6.0	1.0	0.8	10.0	0.0
Range, Air Temp., 50 cm..	9.3	8.1	10.0	5.4	0.0	8.4
Max. Air Temp., 10 cm....	10.0	8.5	7.9	2.2	0.0	1.2
Min. Air Temp., 10 cm....	10.0	9.0	6.3	8.5	1.6	0.0
Evaporation.............	10.0	9.8	7.4	3.2	2.2	0.0
Light Intensity...........	10.0	9.6	7.5	1.7	0.9	0.0
Soil Temperature, 2 cm....	10.0	9.4	6.9	2.2	2.0	0.0
Soil Temperature, 20 cm...	10.0	9.0	6.7	2.1	1.0	0.0
Soil Moisture, 2 cm.......	6.1	10.0	9.9	5.6	3.3	0.0
Microenvironmental Index.	89.6	87.5	71.8	33.9	21.6	9.6

Gross vegetational features correlated rather well with the Microenvironmental Index. Total field layer cover increased greatly in the more xeric microenvironments. Field layer cover averaged 3064 cm and 4158 cm on protected and open north slopes respectively, increasing to 5305 cm on protected south slopes and 6427 cm on open south slopes. Total cover also increased from an average of 696 cm at the bottom, to 1174 cm at the middle, and 1193 cm at the top of protected north slopes and from 1765 cm at the bottom of open south slopes to 2135 cm and 2527 cm at the middle and top of these slopes.

Relative cover of hemicryptophytes (Table 16) showed a general increase in more xeric microclimates. Although the variations at the extremes were considerable, intermediate stations showed some deviations. Relative cover of geophytes (Table 16) appeared to be greatest in areas with low Index values (mesic) and to decrease as Index values increased. The variation at the extremes, however, was not as great as with hemicryptophytes. Thus, although the

TABLE 16. Relative coverage of herbaceous life-forms in relation to Microenvironmental Indices on grouped slopes. H=hemicryptophytes; G=geophytes; Le= leptophylls; Mi=microphylls; Me=mesophylls; MiH=hemicryptophytes with microphylls; MeG=geophytes with mesophylls.

Station	Index* value	RELATIVE COVERAGE OF: H	G	Le	Mi	Me	MiH	MeG
Protected north slopes	10.4	35.3	25.8	0.1	51.2	7.0	45.8	3.3
Open north slopes	25.2	42.3	34.5	0.9	34.9	8.8	30.9	1.4
Protected south slopes	85.6	27.5	24.4	1.6	48.7	3.1	46.8	1.3
Open south slopes	87.1	45.9	23.4	4.5	62.1	0.8	60.1	0.3
Protected north slopes								
Bottom	9.6	26.7	27.5	0.0	54.0	10.0	45.8	8.4
Middle	21.6	44.2	23.8	0.1	59.2	6.5	54.8	2.9
Top	33.9	33.6	26.5	0.1	43.1	6.5	38.7	1.7
Open south slopes								
Bottom	71.8	28.2	21.8	7.0	53.2	1.6	51.4	0.9
Middle	87.5	44.9	28.0	3.7	57.3	0.4	56.4	0.2
Top	89.6	57.4	21.3	4.6	68.0	0.9	64.8	0.1

* Index values from Table 15.

patterns were by no means linear, relative cover of hemicryptophytes and geophytes showed more or less reverse trends with values for hemicryptophytes greatest on xeric sites and those for geophytes greatest on more mesic sites.

Herbaceous leaf-size classes also showed variations in relation to shifts in microclimate (Table 16). Relative coverage of herbaceous leptophylls and microphylls increased with higher Index values whereas relative coverage of herbaceous mesophylls was greatest in sites with lower Index values. These changes were evident both in data from the grouped plots and in data showing variation with slope position. Again, although the relationships were not linear, the trends and the variations at the extremes were clear.

In summarizing, there was a trend toward a lower relative coverage of geophytes and herbaceous plants with mesophylls as microclimates became more xeric. Hemicryptophytes and plants with leptophylls and microphylls increased in relative coverage as microclimates became more xeric.

These generalizations are shown by the fact that relative coverage of geophytes with mesophylls decreased in xeric microclimates (Table 16). Relative coverage of microphyllous hemicryptophytes showed a reverse trend, increasing on xeric sites. These variations showed less irregularity than did relationships between Index values and entire life-form or leaf-size classes.

Data as yet undiscussed suggest another approach which is of interest not only in this study but also on a wider basis within the deciduous forest formation. In southeastern Michigan and nearby areas, mesic forests (usually the Beech-Maple type) are characterized by an herbaceous stratum in which the hemicryptophyte and geophyte life-forms are of almost equal importance. In the most mesic situations this equality may be demonstrated on a species-presence basis whereas on a coverage basis geophytes may outrank hemicryptophytes in importance, particularly in spring. The more xeric environments (Oak-Hickory woodlands, for example) have a much greater number of hemicryptophytes with geophytes constituting a minor portion of the vegetation. These generalizations are supported by life-form spectra from several regional forest communities (Table 17) which show a progression in presence-based spectra from an approximate 1:1 ratio of hemicryptophytes to geophytes in the Beech-Maple forest to a ratio of about 5:1 in the Oak-Hickory stand. Frequency-based spectra from the same communities showed similar trends.

TABLE 17. Presence-based life-form spectra for field-layer vegetation from various communities showing variation in hemicryptophyte:geophyte ratio.

Community and location	Ph	Ch	H	G	Th	H/G ratio	Author
Beech-Maple Turkey Run, Ind.	*	*	50.0	40.6	9.4	1.23	Esten, 1932
Beech-Maple Warrens Woods, Mich.	42.9	1.4	28.6	22.9	4.3	1.25	Cain, 1935
Maple-Beech Haven Hill, Mich.	26.6	0.0	40.0	30.0	3.3	1.33	Cain & Castro, 1959
Oak-Hickory-Maple Ann Arbor, Mich.	*	*	54.6	36.4	9.1	1.50	Cooper, unpbl.
Oak-Hickory George Reserve, Mich.	23.2	1.8	59.8	11.4	4.6	5.20	Cooper, 1958

* Not sampled.

An example of succession in the deciduous forest region, from grassy fields to the *Aceretum* climax in the St. Lawrence lowland (Dansereau 1957), reveals a similar pattern. Here, the hemicryptophyte: geophyte ratio decreased from 11.9 in the xeric consolidation *Poaetum,* to 7.0 in the *Solidaginetum,* 2.0 in the *Betuletum,* and 1.1 in the sugar maple climax forest. It is interesting to note that the *Aceretum saccharophori tsugosum* quasiclimax, which has a slightly lower hemicryptophyte:geophyte ratio than the climax, is characterized by Dansereau as having narrower extremes of temperature and humidity than the climax.

Data adapted from Potzger & Friesner (1940) showed shifts in relative importance of hemicryptophytes and geophytes on a seasonal basis in studies of the spring, summer and fall aspects of Beech-Maple and Oak-Hickory forests in southern Indiana. In the Beech-Maple woods, the hemicryptophyte: geophyte ratio increased from 1.1 in spring, to 3.3 in summer, and 2.7 in fall. In the Oak-Hickory woods, the ratio was 2.7 in spring, 4.6 in summer, and 4.8 in fall. Thus, hemicryptophytes were 2.5 times as important as geophytes, even in spring, in the drier Oak-Hickory forest.

From these data it appears that in the field layers of the most mesophytic deciduous hardwood stands, geophytes are of equal or greater importance than hemicryptophytes. As the environment becomes more xeric hemicryptophytes become increasingly dominant elements of the vegetation.

The data at hand offered an opportunity to test the ratio of hemicryptophytes to geophytes (H/G ratio) against known microclimatic data. When average H/G cover ratios from the 4 groups of slopes were plotted against Index values from the scattered stations (Fig. 16), the relationships were not particularly close. There was an overall increase in the ratio from 1.65 on protected north slopes to 2.13 on open south slopes, but the other slopes showed lower ratios. Average ratios from the top, middle, and bottom of protected north slopes and open south slopes, plotted against Index values from the main station, showed a similar relationship at the extremes. The ratio was 0.97 at the bottom of protected north slopes, and 2.69 at the top of open south slopes. There was considerable variation between. In general, however, on north slopes geophyte cover values more closely approximated those of hemicryptophytes. On south slopes, hemicryptophytes were of greater relative importance.

The importance of microphylls on south slopes and of mesophylls on north slopes suggested a refinement of the H/G ratio, termed the microphyllous hemicryptophyte:mesophyllous geophyte ratio. When this ratio was plotted against Index values the results were more clear-cut (Fig. 17). Average values from the grouped slopes increased from 22.7 on protected north slopes to 756 on open south slopes. Values at the bottom of protected north slopes averaged 41.6, increasing up the slopes to a maximum value of 844 at the top of open south slopes. Thus, broad-leaved geophytes were of great importance on mesic north slopes and smaller-leaved hemicryptophytes increased greatly in importance on the more xeric south slopes.

DISCUSSION

This study has shown that there are correlations between the distribution and importance of certain Raunkiaerian life-forms and small variations in local climate just as there are correlations between life-forms and the major climatic zones of the earth.

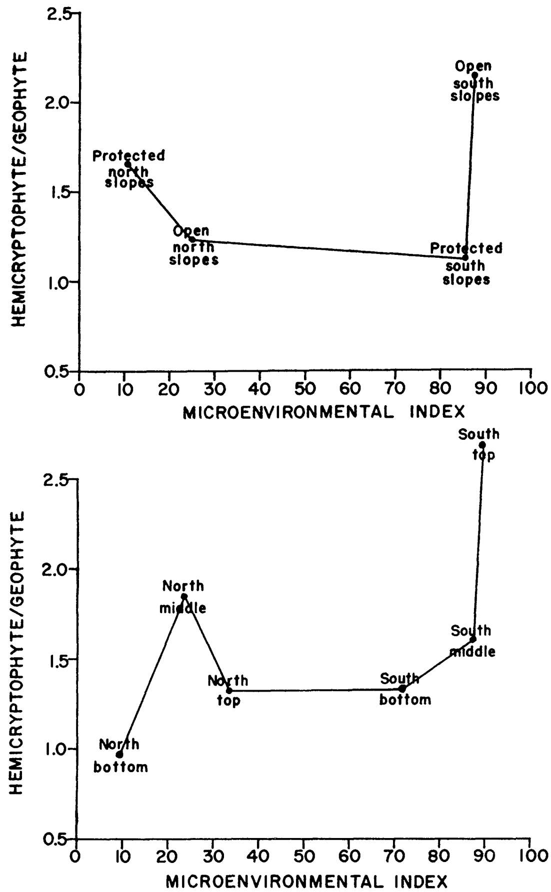

FIG. 16. Relationship between Microenvironmental Index and hemicryptophyte:geophyte ratio on protected and open north and south slopes and at top, middle, and bottom of protected north and open south slopes. Index values from Table 15.

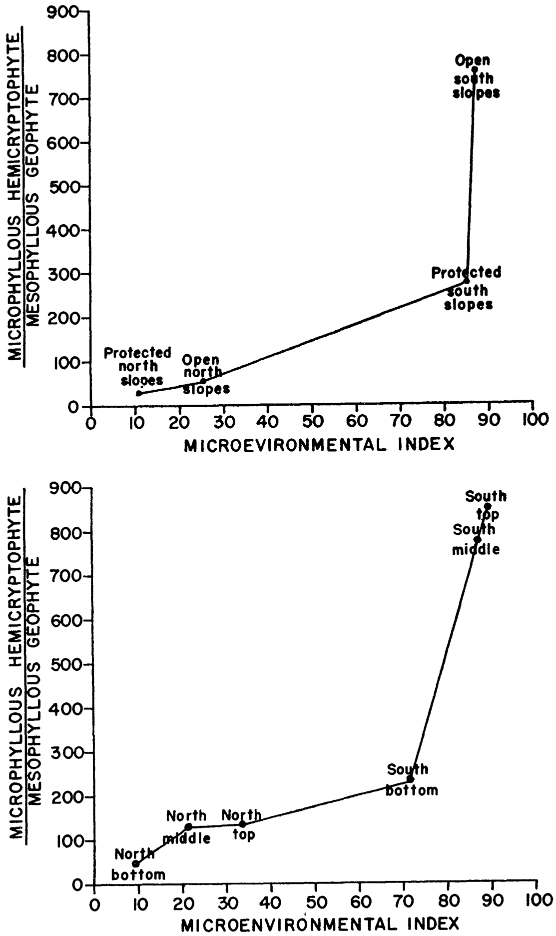

FIG. 17. Relationship between Microenvironmental Index and microphyllous hemicryptophyte:mesophyllous geophyte ratio on protected and open north and south slopes and at top, middle, and bottom of protected north and open south slopes. Index values from Table 15.

The differences in life-form distribution in the Big Woods appeared to be less (both qualitatively and quantitatively) than might be expected in other types of vegetation and situations. The marginal site qualities and history of disturbance prevailing throughout most of the George Reserve combined to limit the development of a rich deciduous forest flora. It would be anticipated that similar studies elsewhere, particularly in undisturbed mesophytic forest areas, would reveal greater contrasts than those reported here.

The microclimatic data of this study emphasize the importance of topography as a factor in producing variations in forest "trunk space" microclimates. In general, the microclimates of the trunk space on north slopes were similar to those reported for dense or mature forests whereas comparable microclimates on south slopes resembled those of than forests or open areas. These conclusions agree with those of Cantlon (1953) and the conclusions of similar studies (for which see Cantlon).

During most of the growing season the denser canopy and angle of slope combine to allow less solar radiation (as indicated by light regimes) to penetrate to the forest floor on north slopes. Only during early spring and the first weeks of late spring is the forest floor the active meteorological surface. The greatest daily and weekly ranges of temperature on north slopes occur during this period. These conditions are similar to those described for a dense Ohio beech forest (Christy 1952), for mesophytic forests in coves at Neotoma (Wolfe *et al.* 1949), and for oak-hickory forest in New Jersey (Sparkes & Buell 1955).

In contrast, south slopes received greater amounts of solar radiation throughout the entire growing season. Except in heavy shade, temperature stratification was, depending on the density of canopy, a weak to strong version of the incoming radiation type (Geiger 1957). Annual maxima here agreed more closely with maxima in the macroclimate as was shown for thin oak forests on southwest-facing slopes at Neotoma (Wolfe *et al.* 1949).

The data also show the more favorable moisture relations of the trunk-space climate on north slopes. The higher solar radiation and temperature conditions produce evaporation rates on south slopes roughly 50% greater than those on north slopes. Potzger (1939) found a comparable situation on a ridge in Indiana. The percentage reduction of evaporation on north slopes found in this study approaches the difference between evaporation in forested and open areas (Kucera 1954, Selleck & Schuppert 1957).

Soil moisture values fluctuated less and did not fall as low on north slopes as on south slopes. Cantlon (1953) suggested that this was true for the north slope he studied in New Jersey. Recently, Gilbert & Wolfe (1959) have shown that soil moisture values on lower northeast-facing slopes under mixed mesophytic forest do not fall as close to the permanent wilting point during summer droughts as do soils of southwest-facing slopes under mixed oak forest.

In view of the great microclimatic differences between the slopes the large differences in vegetation are not surprising. A comparison of these differences with those reported in other studies of the relations between life-forms and microclimate reveals certain similarities and differences.

Oosting (1942) and Cantlon (1953) showed that on the Piedmont of North Carolina and New Jersey phanerophytes and geophytes were more important elements of north slope floras as opposed to those of south slopes which were characterized by greater numbers of hemicryptophytes and therophytes. These conditions generally were true of the Big Woods on the George Reserve. Phanerophytes showed a greater dominance, both of the flora and vegetation, on north slopes whereas hemicryptophytes behaved similarly on south slopes. However, the studies of Oosting and of Cantlon dealt with the entire floras of the slopes and did not segregate the species by strata. In this study a treatment by strata showed that although meso- and megaphanerophytes had greater total cover values on north slopes their reproduction in the field layer was greater on south slopes.

On a world basis phanerophytes decrease in dominance with increasing climatic severity (generally extremes of temperature). This fact has been extended to the microclimatic level by Miller & Buell (1956) who concluded that in temperate regions a dominance of phanerophytes indicates a climate more "congenial" (showing less variation in extremes) for plant growth. The George Reserve data indicate that this is true only when the total vegetation of the slopes is considered. If the coverage of phanerophytes in the field layer of south slopes is compared with that of north slopes it might be concluded that the south slope microclimate was less variable in its extremes and thus was more favorable for plant growth. Such a conclusion is not warranted on the basis of the microclimatic data. Thus, statements that a dominance of phanerophytes indicates a microclimate with less variable extremes apparently are valid only in terms of the entire vegetation and not in terms of its component strata.

On a relative basis geophytes were more dominant on north slopes on the George Reserve. This fact is in agreement with the findings of Oosting (1942) and Cantlon (1953). However, Miller & Buell (1956) found that geophytes, on a coverage basis, were more important on south slopes near the prairie border region in Minnesota. They found this to be in accord with Raunkiaer's original hypothesis ascribing dominance of more-protected life-forms to those areas with the greatest climatic severity. There is a direct contradiction between these findings and those of the present study and of Oosting and Cantlon. In the deciduous forest region geophytes are more abundant (and dominant) in mesophytic forests characterized by greatly-moderated climatic extremes, whereas they are apparently more abundant on southwest-facing slopes characterized by wide climatic extremes near the prairie-border region. Furthermore, it is interesting that there should be a greater geophyte dominance on southwest-facing slopes when, as Miller & Buell point out, such slopes immediately to the west show floristic and vegetational affinities to the hemicryptophytic grasslands lying even further west.

These problems emphasize the need for intensive regional studies of life-form behavior. They also emphasize the potential danger in generalizing about life-form behavior in relation to microclimate from a limited number of slope samples. The variability of the data encountered in this study of 16 slopes indicates that before meaningful generalizations can be made an even larger series of slopes should be sampled.

This study also shows the need for quantitative data in the evaluation of localized variations in life-form behavior. Few, if any, of the correlations presented can be made on the basis of species presence alone. The limited nature of the demonstrated changes emphasizes the desirability of quantitative evaluation of the importance of a particular life-form in a given situation and the potential usefulness of statistical analyses for determining the validity of apparent trends.

SUMMARY

A study of the relationships between Raunkiaerian plant life-forms and microclimate on north and south slopes in the Big Woods of the George Reserve in southeastern Michigan was conducted during 1957.

Microclimatic instrumentation was carried out on 3 north and 3 south slopes ("scattered stations") and at the top, middle, and bottom of the north- and south-facing sides of a hogback ("main station") in the Big Woods of the Reserve. Light intensity, air temperature, wind movement, evaporation, and soil temperature and moisture were sampled. Vegetational data were obtained from a series of 16 sample plots placed on well-expressed slopes which deviated not more than 20° from true north or south.

Relative light intensity was greatest on south slopes and intensities generally diminished downslope. Average air temperature was highest on south slopes and, except during early summer, average temperatures on south slopes increased toward the ground. On north slopes, maximum air temperatures and the greatest ranges in maxima occurred during the first weeks of late spring. On south slopes, maxima rose to a late spring peak, leveled off, and continued to rise to an annual mid-summer maximum. Summer maximum temperature ranges were greatest on south slopes. Minimum air temperatures showed less variation than maxima. During spring, minima were lower on north slopes and the greatest growing season range in minima at all stations occurred during spring. In summer, minima were similar on both slopes. Air movement was greatest at slope tops and diminished downslope. At times, air movement limited development of the incoming radiation type. Evaporation was greatest at the top of the south slope and least at the bottom of the north slope. Soil temperatures were higher on south slopes throughout the growing season, with differences greatest in early spring. Annual maxima on both slopes were recorded in mid-summer. Differences between the slopes were least in late summer and fall. In winter, snow cover limited soil temperature fluctuations on north slopes but was seldom of any duration on south slopes. North slopes had higher soil moisture values than south slopes. Moisture was abundant on both slopes in spring but mid-summer and fall were seasons of soil moisture stress. On south slopes cycles of wetting and drying marked periods of adequate soil moisture whereas on north slopes these cycles were not as evident.

In summary, the microclimates of the slopes varied from a cool, moist (mesic) extreme at the bottom of north slopes to a warm, dry (xeric) extreme at the top of south slopes. Microclimatic conditions on north slopes resembled those of well-developed forests whereas those on south slopes were more similar to the microclimates of exposed areas.

The biological spectrum of the George Reserve was predominantly hemicryptophytic. Within the entire slope vegetation there was a greater phanerophyte cover on north slopes and hemicryptophyte cover on south slopes. In the field layer only, there was greater phanerophyte and hemicryptophyte cover on south slopes. There was a greater cover and basal area of meso- and megaphanerophytes on north slopes and a greater cover of microphanerophytes on north slopes. Transgressive nanophanerophytes had greater cover values on south slopes. Protohemicryptophytes had greater cover on south slopes and rosette hemicryptophytes had greater cover on north slopes. Differentiation of plots into protected and exposed north and south slopes showed that within the field layer relative coverage of hemicryptophytes increased in situations where relative coverage of phanerophytes and geophytes decreased.

The flora of the George Reserve was predominantly microphyllous. Within the slope vegetation there was greater leptophyll and microphyll cover on south slopes and greater mesophyll cover on north slopes. Within the field layer, leptophylls, microphylls, and mesophylls had greater cover on south slopes. However, in the herbaceous element of the field layer mesophylls had more cover on north slopes whereas leptophylls and microphylls still had greater cover on south slopes.

Correlations between life-form and microclimatic data were confined to the field-layer vegetation. A Microenvironmental Index, expressing the sum of the environmental characteristics of a given site, was used for correlation with vegetational data. Total field layer cover and relative cover of hemicryptophytes was greatest in xeric microenvironments. Relative cover of geophytes was greatest in more mesic sites. Herbaceous leptophylls and microphylls increased in relative cover in xeric sites whereas her-

baceous mesophyll cover was greatest in mesic micro-environments.

Data from deciduous forest communities suggested that a low hemicryptophyte:geophyte (H/G) ratio was characteristic of mesic sites and that this ratio increases as the environment becomes more xeric. Comparison of the H/G ratio with Index values showed that, in general, low ratios were associated with mesic sites and high ratios with xeric sites. A similar, but closer, relationship was shown for the ratio of microphyllous hemicryptophytes to mesophyllous geophytes.

The microclimatic data obtained agree with those of other studies and emphasize the importance of topography as a factor producing variations in forest microclimates in that the microclimates of north slopes resembled those of mature forests whereas comparable microclimates on south slopes resembled those of thin forests or open areas. The life-form data are in agreement with those of other deciduous forest reports but disagree with an example from the prairie-deciduous forest transition. The data show the danger in generalizing concerning life-form and microclimate relations from limited numbers of slope samples.

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