UPPER ATMOSPHERIC CONTROLS, SURFACE CLIMATE, AND PHYTOGEOGRAPHICAL IMPLICATIONS IN THE WESTERN GREAT LAKES REGION

By

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ABSTRACT

UPPER ATMOSPHERIC CONTROLS, SURFACE CLIMATE, AND PHYTOGEOGRAPHICAL IMPLICATIONS IN THE WESTERN GREAT LAKES REGION

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This research is an investigation of the linkage between atmospheric circulation, surface climate, and plant geographical distributions in the upper Middle West, U.S.A. Ecophysiological studies of the vegetation transition from tall-grass prairie in the south and west through a zone of deciduous forests to the mixed coniferous-deciduous forest in the northeast suggest that summer season moisture stress is the environmental parameter which limits the distribution of the major vegetation associations. This examination incorporates research methods designed to identify the surface weather patterns and associated upper atmospheric wind flow for days when a gradient in plant moisture stress exists across the western Great Lakes Region. A water balance approach is used to combine estimates of potential evapotranspiration calculated on a daily basis and precipitation receipts to produce a surrogate measure of plant moisture stress. Significant findings of this research are a demonstration that modal patterns of upper atmospheric circulation are associated with surface moisture stress patterns that coincide with the vegetation transitions and the implication that phytogeographic boundaries may be set not only by rare events, but also by the gradual accumulation of a frequently occurring environmental stress pattern.

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Chapter I

INTRODUCTION

The western Great Lakes region has been the site of a considerable number of research efforts dealing with both the patterns and controls of the distribution of natural vegetation. The transition from the tall-grass Prairie Peninsula through oak-hickory and beech-maple or maple-basswood deciduous forests into the mixed coniferous-deciduous Hemlock-White Pine-Northern Hardwoods Forest region has been well documented (Figure 1). Within this broad transition, differences in the composition of local communities have been attributed to many different but sometimes interrelated factors. These include either natural (Komarek, 1965; and Komarek, 1968) or anthropogenic fire (Gleason, 1913; Sauer, 1950; Stewart, 1953; and Stewart, 1963), topography (Wells, 1965; Wells, 1970a; and Wells, 1970b), edaphic factors (Fuller, 1923; Cowles, 1928; Norton and Smith, 1932; Kucera, 1952; and McAndrews, 1967), the survival of relic species in favorable habitats (Davis, 1977), or the differential migration rates of some taxa (Wright, 1968; and Davis, 1976). Thus the exact location of the vegetation transition is site specific, but the broad pattern of vegetational change is related to climatic patterns that result from the general atmospheric circulation. Davis has concluded that "the general configuration of the prairie-deciduous forest ecotone in the upper Middle West is determined largely by climate" (Davis, 1977).

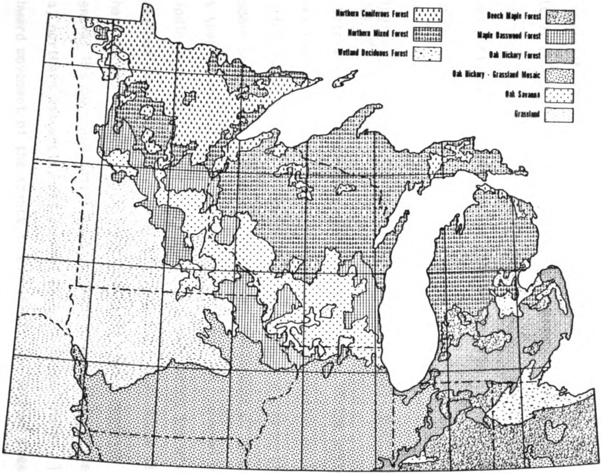

Figure 1. Generalized Vegetation Patterns of the Upper Middle West. Source: Kuchler, 1964.

An eco-physiological approach to plant geography is concerned with the relationships between environmental influences and the physiology of plants. The important physiochemical factors determining the habitat for natural vegetation have been identified as heat (temperature), water (hydrature), and chemical or mechanical factors (Walter, 1973). In a regional analysis of plant distributions the climatic factors, energy and moisture, become the factors of primary interest. This study combines an eco-physiological analysis of the vegetation in the western Great Lakes region with a synoptic analysis of the then identified climatic controls.

Paleoecological Evidence of Climatic Control on the Vegetational History of the Upper Middle West

The Late-glacial and Holocene vegetational history of the western Great Lakes region demonstrates the importance of the climatic controls on vegetation in the region. A spruce forest, similar in composition to the modern boreal forest except with a larger percentage of temperate deciduous species and a lower percentage of pine species, covered much of the Middle West south of the Laurentide ice sheet during the Wisconsin glacial maximum (Wright, 1970). During Late-glacial and Holocene time, the southern margin of this spruce forest migrated from a position across central Missouri and Kansas to a location transecting northeast Minnesota, northern Wisconsin, and central Lower Michigan (Moran, 1973). The northward movement of the spruce forest across the western Great Lakes region immediately followed or may have occurred upon the ablating Laurentide ice sheet. By 8,000 BP, the southern margin of the boreal forest had migrated to "its most northern Holocene position" (Bernabo and Webb, 1977). Following the northward withdrawal of the spruce forest, between

11,000 and 9,000 BP a temperate deciduous forest succeeded quickly (Wright, 1970) but the forest composition soon changed as pine migrated into the region from eastern sources (Davis, 1976). Further redistribution of the western Great Lakes region forest geography resulted as "oak-dominated deciduous forests moved up from the south" (Bernabo and Webb, 1977). Subsequently, the composition of both the conifer-hardwood and deciduous forest formations continued to change as other arboreal species immigrated into the region (Davis, 1976; Bernabo and Webb, 1977).

As the boreal forest moved northward, openings of grassland were developing in the eastern Great Plains. Eastward expansion of the grasslands as early as 11,000 BP is evident from the fossil pollen record of eastern South Dakota (Watts and Bright, 1968). By 7,200 BP, the prairie had advanced to a position 75 miles east of its present location in central Minnesota (Wright, 1976). The simplified Holocene paleoclimatic reconstruction of warming and drying in the upper Middle West until about 7,200 BP, followed by gradual cooling until the present, is supported by the westward withdrawal of the grasslands during the period from 7,000 to 4,000 BP (Bernabo and Webb, 1977).

Compelling evidence that the migrations of the vegetation associations were cliseral movements can be inferred from the fact that the response to climatic change generally occurred in broad, organized patterns. The occurrence of relic species in favorable habitats, such as white spruce in the Black Hills of South Dakota or tamarack swamps in the driftless area of Wisconsin, also supports this concept of climatically controlled shifting vegetation belts (Dansereau, 1957).

The climatic control over the locations of both the prairie-deciduous forest ecotone and the deciduous/coniferous-hardwood forest ecotone in the western Great Lakes region is evident in the dynamic character of these vegetation transitions. During the Holocene, for example, the prairie-deciduous forest border migrated eastward until approximately 7,000 BP and then receded slightly westward (Figure 2). The most rapid eastward migration of grassland vegetation occurred during the period from 11,000 to 9,000 BP, immediately following "the distinct change from the Late-glacial climate to that of the Holocene period that occurred about 11,300 BP" (Webb and Bryson, 1972). Westward movement of the ecotone starting at approximately 7,000 BP was at a slower pace with the ecotone stabilizing at the current location about 2,000 BP. Changes in ecotone configuration during the last 2,000 years have been "relatively small and often localized" (Bernabo and Webb, 1977).

Northward movement of the deciduous/conifer-hardwood forest ecotone was also rapid during the early Holocene (Figure 3). Between 8,000 and 7,000 BP, the rate of migration slowed and the transition zone shifted eastward in Minnesota. In the next 3,000 years, the deciduous/conifer-hardwood forest ecotone moved slightly westward in Minnesota, in accordance with the shift in location of the prairie-deciduous forest ecotone. By 4,000 BP, the position of the deciduous/conifer-hardwood forest ecotone had stabilized at its present location (Bernabo and Webb, 1977). Subsequently, the composition of both the Deciduous Forest Formation and the Hemlock-White Pine-Northern Hardwoods Forest Formation has changed due to the migration patterns of individual species (Wright, 1968; and Davis, 1976) but the locations of the ecotones have shown little movement.

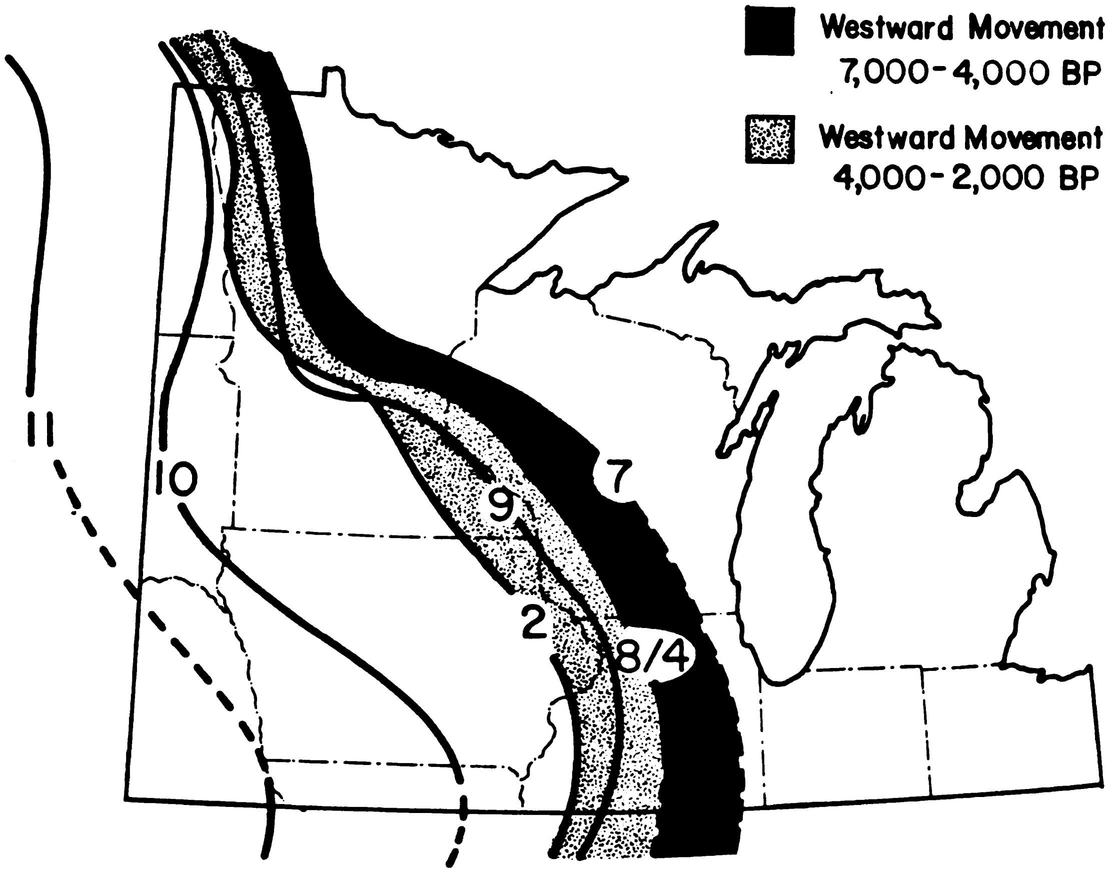

Figure 2. Isochrones (1000's of years) Showing the Holocene Movement of the Prairie-Deciduous Forest Ecotone.
Source: Bernabo and Webb, 1977.

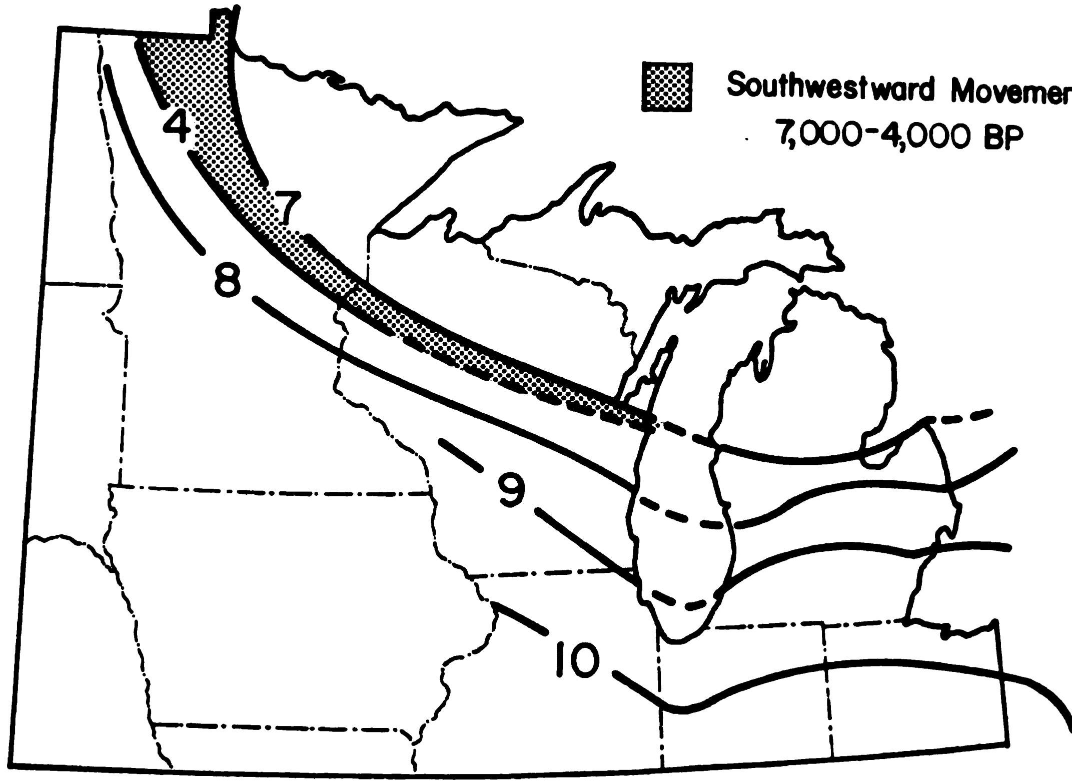

Figure 3. Isochrones (1000's of years) Showing the Holocene Movement of the Conifer-Hardwood/Deciduous Forest Ecotone. Source: Bernabo and Webb, 1977.

Ecoclimatology and the Western Great Lakes Region

Reconstructed Holocene vegetation patterns and the inferred relationship between vegetation and climatic variables have been primary sources of evidence used by paleoclimatologists to identify the changes in atmospheric circulation during the last 10,000 years. Traditionally, biogeographers and ecological climatologists have attempted to explain the location of ecotones using static meterological parameters and a major problem was the circular reasoning of using vegetation transitions as a basis for recognizing climatic boundaries and then concluding that the ecotone exists because of a climatic gradient. Early researchers attempted to relate mean annual values of measurable parameters (temperature and/or precipitation) to vegetation zones (Koppen, 1936). Others compared isorithms of mean annual climatic statistics to the range of an individual species (Good, 1925; and Salisbury, 1926). In the western Great Lakes region, static meteorological parameters have been analyzed to argue that the Prairie Peninsula has a unique climate and that its natural tall-grass prairie vegetation can be considered climax (Transeau, 1935). The climatic transition on the northeastern margin of the central North American grassland has been described through the use of mean monthly and seasonal meteorological data (Borchert, 1950). Borchert summarized the climatic gradients which correlate with the transition from prairie to forest as being "characterized by (1) a relatively steep gradient of winter snowfall and snow cover and (2) a small but abrupt increase in frequency of days with rain in summer and an accompanying increase in cloud cover and relative humidity" (Borchert, 1950). Acknowledging the causative relationship between atmospheric circulation patterns and surface climate, Borchert also examined the mean monthly streamlines of wind flow at the gradient level (about 500 meters above the surface). He concluded that the areas of grassland vegetation have a continental airflow at least half of the year (Borchert, 1950).

Studies dealing with the identification of Holocene climatic patterns and atmospheric circulation changes have utilized these ecoclimatological relationships. Based on the association identified between gradient level westerly circulation and the distribution of grassland vegetation in central North America, Borchert mapped the climatic regions of North America east of the Rocky Mountains as they may have existed during the period of "post-glacial, pre-historic expansion of the grassland" (Borchert, 1950). The congruence between air mass frequencies, the arctic frontal zone, and the boreal forest-tundra ecotone in northern Canada (Bryson, 1966) has also been used in an attempt to identify surface climatic patterns for three intervals in Late-glacial and post-glacial time (Lamb and Woodroffe, 1970). Estimates of atmospheric thickness (1000-500 mb height differences) based primarily on paleobotanical evidence have been used to reconstruct the mid-tropospheric circulation for the Wisconsin glacial maximum and six additional time periods during the Holocene (Lamb, 1971).

Other ecoclimatologists, following Borchert's lead, have studied the relationships between synoptic climatology (patterns of atmospheric circulation) and surface vegetation transitions. Since the lower atmosphere can be subdivided into relatively large, natural units, called air masses, whose physical properties are more or less uniform horizontally, most recent ecoclimatological studies have attempted to relate air mass frequencies to vegetation distributions. Differences of temperature, moisture content, and/or lapse rate between two air masses are the result of two major influences: (1) the source region and (2) the degree to which the air mass has been modified upon leaving the source region. Geographic differences in the frequencies of these air masses can be used to define climatic regions (Bryson, 1966) and, as a result, the identification and explanation of congruent biotic and climatic transition zones is possible (Bryson and Wendland, 1967). Bryson used monthly resultant surface wind streamlines and air mass frequencies defined by both the trajectory method and the partial collective method to show a congruence between the mean or modal position of the southern boundary of Arctic air and the vegetation transition between boreal forest and tundra (Bryson, 1966). Barry questioned the strength of this relationship between the summer position of the Arctic front and the forest-tundra ecotone in eastern Canada. Basing his analysis on the baroclinic structure of the atmosphere in middle and high latitudes, Barry identified the surface location of the southern boundary of Arctic air using the frontal location at the 850 mb level (Barry, 1967). In eastern Canada, the summertime location of this northern zone of baroclinicity is problematic because Arctic air masses can have either a continental or Atlantic source region. The width of the boreal forest-tundra ecotone in eastern Canada is very broad (Marr, 1948) and "it is noteworthy that in this region where the location of the front is, according to present results, uncertain, the forest boundary is replaced by an extensive forest-tundra ecotone" (Barry, 1967). A similar relationship to that found in North America by Bryson exists between the Arctic front, as defined from analysis of surface synoptic charts, and the taiga-tundra boundary in Eurasia (Krebs and Barry, 1970). Frontal boundary and ecotonal congruence have also been identified in western North America. The mean summer position of the southern boundary of Pacific Air as defined by equivalent potential temperature corresponds with the southern border of the extension of Pacific flora (the "Pacific Peninsula" or "Inland Empire") into the northwestern United States (Mitchell, 1976).

Attempts at describing the relationship between natural vegetation and mean frontal location have been primarily statistical in nature. Principle components analysis was used to show a strong correlation between the relative abundance of certain species in the boreal forest-tundra vegetation transition zone and air mass frequencies (Larsen, 1971). In addition, an index of tree growth based on the mean growth curve of black spruce has been used to define a theoretical location of the tree line which corresponds with the mean summer position of the Arctic frontal zone (Mitchell, 1973).

Ecoclimatology and Plant Physiology

Since biotic communities adjust competitively to the summation of physiological stresses created by environmental conditions, several ecological climatologists have attempted to identify, on a plant physiological basis, those environmental factors that are important in controlling the distribution of natural vegetation. Indicies of energy for plant development and plant moisture demand (potential evapotranspiration and the moisture index) have been used to show a relationship between climate and the distribution of natural vegetation. Through the use of these indicies, Mather and Yoshioka were able to differentiate the three major vegetation biochores (grassland, forest, and desert) in the coterminous United States (Mather and Yoshioka, 1968). Harman, by using meso-scale synoptic analysis, identified a relationship between the lake breeze front at the southern end of Lake Michigan and the compositional variability in the deciduous forest formation (Harman, 1970). His analysis indicates that climatic modification by Lake Michigan reduces fire frequency and leads to an increase in mesophytic tree species. In an analysis of the prairie-forest ecotone in south central Canada, Harman and Braud identified a relationship between flow direction at the 500 mb level and temperature and precipitation patterns at the surface (Harman and Braud, 1975). Northwesterly flow at the 500 mb level was shown to be related to patterns of maximum surface temperature and precipitation that suggested a gradient of decreased moisture stress northeastward across the ecotone.

The Research Hypothesis

This study deals with the nature of the climatic controls on vegetation distribution in the western Great Lakes region. Weather patterns at the earth's surface (including the movements of air masses) are physically associated with the persistent patterns of air flow in the mid-to-upper troposphere (Harman, 1971). Increased vertical motions produced by moving upper atmospheric disturbances (short-waves) are generally responsible for generating and guiding the storms and air masses that influence our day-to-day weather. The climate of a region is related to the frequency of different types of flow patterns aloft and the related variation in air masses and precipitation which affect it. Analysis of the mean 500 mb height contours (approximately 18,000 feet above mean sea level) for July shows that the upper Midwest is in an area of transition from anticyclonic curvature associated with a mean ridge over the western Great Plains to the cyclonic curvature associated with a mean trough in the eastern United States (Figure 4). Since surface weather disturbances are guided by the circulation aloft, the usual July movement of these systems is southeastward across this region and therefore parallels the orientation of the ecotones. Thus, the long-term pattern of surface weather generated by these disturbances also parallels the ecotones and suggests a clear relationship between the "steering" flow at the 500 mb level and the climatic stresses responsible for the present vegetation distribution. The problem of the ecological climatologist interested in explaining the distribution of natural vegetation, therefore, is to show a causal relationship between synoptic weather patterns and vegetation regions and their ecotones; this study will examine the nature of this relationship.

The hypothesis of this research is that modal (most frequent) patterns of upper atmospheric circulation are the controlling factors in determining the characteristics of surface environmental gradients that delimit the position of ecotones within the upper Midwest.

The specific aims of the study are:

1) to describe the presettlement vegetation transitions of the western Great Lakes region and show through an analysis of pertinent literature that similar patterns of vegetation exist today.

2) to summarize relevant plant physiological literature to demonstrate that various moisture stresses assume a primary role in contributing to the location of the transitions.

3) to identify the meteorological factors that induce these plant moisture stresses and examine their spatial distribution.

4) to identify the patterns of surface weather which relate to gradients

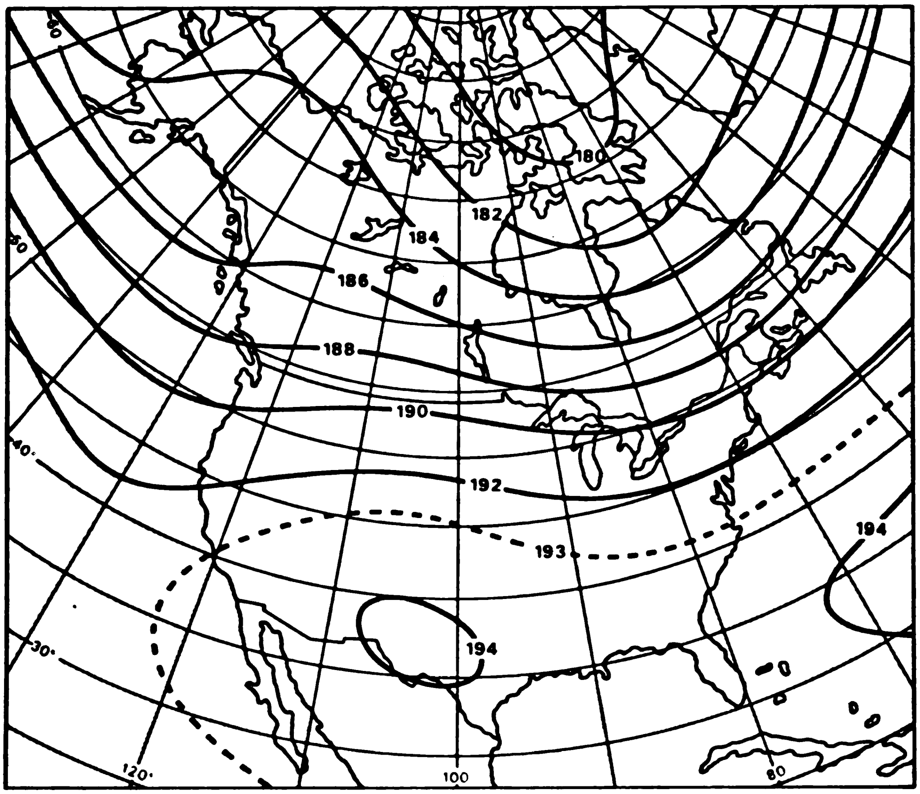

Figure 4. Mean Height of the 500 mb Surface for July (in 100's of feet). Source: Lahey et al., 1958.

of these meteorological factors.

5) to attempt to relate the surface weather patterns of ecotonal importance to the modal patterns of regional upper level atmospheric circulation.

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Chapter II

LITERATURE REVIEW

INTRODUCTION

Competition in biotic communities is influenced by the cumulative effect of environmental stresses associated with varying atmospheric conditions. Plant physiological research does not yet allow the specification of the critical environmental element(s) affecting every vegetation transition, and the degree of causation between climate and vegetation patterns is still imperfectly understood. Nevertheless, this research proceeds one step further to an examination of the synoptic weather patterns which may be responsible for atmospheric-induced stresses that generate or reinforce ecotones. Underlying this research is the assumption that the ecotones of the upper Middle West are climatically set and that eventually our knowledge of physiological ecology will permit us to identify the specific causative relationships. Certainly the general agreement between climatic patterns and plant distributions implies causation, and many research efforts have supported this implication. This research is presented as an example of how analysis of the relationship between daily weather and upper atmospheric flow (synoptic climatology) can help explain several phytogeographical patterns in North America and the following literature review builds the theoretical foundation on which this study is based.

The environment operates to help determine the distribution of woody species by affecting the rates of reproduction, mortality, and growth. In the western Great Lakes region, physiological damage that results in injury or death to seedlings and young saplings and therefore limits tree distribution is the result of a prolonged period of plant stress. A major cause of physiological stress in the upper Middle West is the inability of the plant to obtain sufficient moisture to carry on the necessary processes of photosynthesis and respiration. Plant moisture stress is directly related to several environmental variables, including low soil moisture content. In general, the longer soil moisture is deficient, the greater the effects of moisture insufficiency on plant activity. Soil drought is one way that plant moisture stress can be induced; deficits can also occur on any hot, dry afternoon when transpiration losses exceed the ability of the plant to extract moisture from the soil.

The general pattern of moisture availability and atmospheric-induced moisture flux (potential evapotranspiration) is a primary environmental factor determining the distribution of tree vegetation in the study area (Zimmermann and Brown, 1974). The amount of moisture available for plant growth can be evaluated using a water balance approach (Thornthwaite, 1948) in which the two major independent variables are precipitation receipts and evapotranspirative losses, both regulated by day-to-day changes in the patterns of surface weather. Daily evapotranspirative flux can be estimated from meteorological data using any one of several methods (McGuinness and Bordne, 1972). The following review of pertinent literature will support these introductory statements. Special attention will be given to the literature that deals specifically with the upper Middle West.

NATURAL VEGETATION PATTERNS AND CONTROLLING FACTORS IN THE WESTERN GREAT LAKES REGION

The Natural Vegetation Pattern

The natural vegetation of the upper Middle West consists of a series of transitions from the tall-grass prairie to the south and west through a central zone of oak-hickory and beech-maple or maple-basswood deciduous forests into the mixed coniferous and deciduous Hemlock-White Pine-Northern Hardwoods forest to the northeast (Figure 1). The ecotones of the western Great Lakes region exhibit a broadly curvilinear pattern such that the north-south trending ecotones of northwestern Minnesota arc gradually to the south and east, and become orientated east-west across Michigan, Indiana, and Ohio. In north-western Minnesota, the pattern of the vegetation transition is sharply defined; the west-east change from prairie through the deciduous forest zone to the mixed coniferous-deciduous forest occurs in less than 105 kilometers (McAndrews, 1967). Differences occur in the width and definition of the ecotones to the southeast. Local influences such as soil texture variability, drainage pattern, and slope aspect and angle result in a dispersed pattern in the Driftless Area of southwestern Wisconsin and northeastern Iowa; various attempts to map the northwest-southeast trending prairie-deciduous forest ecotone show positional variation of over 160 kilometers (Davis, 1977). Eastward from this area, the fragmented nature and curvilinear trend of the vegetation transitions continue. A mosaic of grasslands and oak-hickory forest extends across Illinois into northeastern Indiana; grassland outliers of the Prairie Peninsula occur as far east as southwestern Michigan and western Ohio. The ecotone from oak-hickory and beech-maple deciduous forests northward to the mixed coniferous-deciduous Great Lakes Hardwood forests follows a similar arcuate pattern. The north-south alignment of the transition zone in northwestern Minnesota changes gradually eastward to become an east-west trending zone that bisects the lower peninsula of Michigan. Increasing evidence suggests that the location of these ecotones and the distribution of natural vegetation is governed primarily by moisture availability. The following description of the vegetation associations in the upper Middle West will elaborate the role played by available moisture in determining the distribution of the natural vegetation.

The Prairie Grasslands

The dominant natural vegetation in the southwestern part of the study area is tall-grass prairie. The natural prairie is characterized in summer as a vast, monotonous area of tall, waving grasses with few trees and shrubs, except along the major stream courses (Weaver, 1954). Prairie grasses are subdivided into height classes (tall: 5 to 8 feet or more, medium: 2 to 4 feet, and short: .5 to 1.5 feet) that are also an expression of available water supply (Weaver, 1954). Prairie grasses normally reach their characteristic maximum heights by mid-summer. These warm-season, perennial grasses exhibit rapid rhizome development that results in the characteristic thick sod. Growth usually begins in mid-April with maximum height achieved by July and flowering reaching a maximum in August and September. Generally the grasses begin to lose their green color during the month of September, but this can occur earlier if the summer season is dry. The dominant species in the tall grass prairie on lower slopes or level land is big bluestem (Andropogon gerardii). Little bluestem (Andropogon scoparius) dominates on the more xeric upper slopes and hilltops, whereas wetter sites have a mixture of big bluestem and switchgrass (Panicum virgatum) (Weaver, 1958). This separation of the dominant herbaceous species by topographic position indicates the important role of available moisture in determining the specific composition of any given site within the region of grassland vegetation.

The Prairie-Forest Transition

Along the western margin of the eastern North American deciduous forests, tongues of riparian forest penetrate westward into the prairie region. These floodplain forests are of limited extent and confined to stream courses where micro-site conditions play an important role in moderating the environment for tree seedling survival. Major species include American elm (Ulmus americana), silver maple (Acer saccharinum), green ash (Fraxinus pennsylvanica var. subintegerrima), eastern cottonwood (Populus deltoides), and black willow (Salix nigra). Oaks (Quercus) usually are the most conspicuous tree of the upland areas in the western margin of the deciduous forest belt but hickories (Carya) are more or less abundant throughout the region (Weaver, 1954). Decreased available water to the south and west results in a replacement of the upland deciduous forests by prairie grassland (Walter, 1973).

An upland savanna vegetation of bur oak (Quercus macrocarpa) and prairie grasses was a widespread feature within this prairie-forest transition zone. Locally referred to as oak openings, these savannas were dominated by prairie grasses; bur oak was by far the most common local tree species but black oak (Quercus velutina) was also frequently found. Fire was necessary for the persistence of this vegetation type, and thick, fire-resistant bark enabled the larger bur oak trees to survive the frequent burnings (Cottam, 1949). A rapid rate of root growth during seedling development helps to explain the ability of this pioneer oak species to compete with prairie grasses for the limited available moisture (Holch, 1931). Westward expansion of agricultural settlement had a pronounced effect on the composition and structure of these oak openings, as fire supression accompanied agricultural occupation and the areas of fire-maintained oak savannas rapidly converted into oak forests within 25 to 30 years. Frequently, black oak was among the first arboreal species to proliferate in these developing oak forests. As a result of man's actions, "oak savanna, with its full compliment of original vegetation, is one of the rarest vegetation types in the United States today" (Curtis, 1956).

Deciduous Forests

The deciduous forest zone of the western Great Lakes region can be subdivided into major units based on species compositional differences. Throughout the deciduous forest zone, localized hardwood swamp communities have the greatest number of different species. Dominants of these bottomland, lake plain, or floodplain sites vary from American elm and white ash (*Fraxinus americana*) in the Black Swamp region of northwest Ohio (Gordon, 1969) through lowland forests in Wisconsin of silver maple, American elm, and green ash (Curtis, 1971) to the floodplain forests of Iowa, Minnesota, and the Dakotas, where eastern cottonwood and black willow join american elm as co-dominants (Kuchler, 1964). Oak forests with varying amounts of hickory occupy the more xeric sites within the region. Toward the north or on more mesic upland sites, sugar maple (*Acer saccharum*) co-dominates with American beech (*Fagus grandifolia*) from the western shore of Lake Michigan eastward or with american basswood (Tilia americana) from central Wisconsin westward. Because the distribution of all these upland and lowland deciduous forest associations is strongly related to variations of topography, drainage, and soils, a patchwork-like forest pattern results. Major geographic subdivisions of the upland deciduous forests based on dominant species include: 1) the mesic Maple-Basswood Forest region, 2) the mesic Beech-Maple Forest region, and 3) the xeric Oak-Hickory Forest region.

The dominants of the oak-hickory forests include black oak, white oak (Quercus alba), northern red oak (Quercus rubra), and shagbark hickory (Carya ovata). Hickories are prominent members in the oak forests of Ohio, Michigan, Indiana, and Illinois, but become of minor significance northwestward in Wisconsin and Minnesota (Curtis, 1971) and, in general, the number of species within the Oak-Hickory Forest region decreases to the west (Braun, 1950). Oak stands occupy the forest sites within the deciduous forest mosaic where moisture is most limiting. These areas, which are subject to late summer drought, include thin soils, hilltops, ridges, or slopes with south or west exposures (Curtis, 1971). Soil moisture availability is the major factor limiting the survival of oak seedlings (Ferrell, 1953). The ability of emergent oak seedlings to survive in this xeric habitat is dependent upon 1) their ability to use the carbohydrates stored in the acorn during periods of limited soil moisture and 2) the relatively fast root extension during the period immediately following germination in spring. Rapid root elongation allows soil moisture to be extracted from considerable depths. Disturbance plays an important role in determining local changes in species composition within the oak-hickory forests. Natural openings result primarily from fires, strong winds, or the oak wilt fungus (Charlara quercina). Temporary replacement of the oaks by opportunistic, shade-intolerant species (primarily black cherry (Prunus serotina) or bigtooth aspen (Populus grandidentata)) are the usual result of these forest openings. These interim local dominants represent a good example of the gap phase concept (Watt, 1947).

Sugar maple and beech are the dominant members of the more mesic Beech-Maple Forest region. Occurring in the eastern part of the upper Middle West, these forests occupy sites associated with "dissected till plains, lake plains, and much of the low lying glaciated plateau" (Gordon, 1969) in Ohio, Michigan, and Indiana. Composition is relatively uniform throughout the extent of these forests with beech the most important canopy tree and sugar maple seedlings and saplings dominating the understory. The western border of the Beech-Maple Forest association runs in an approximately north-south direction through central Indiana and eastern Wisconsin. Coinciding with the western limits of beech, this margin is thought to be climatically controlled through moisture effectiveness (Ward, 1956) and is "a sensitive indicator of a decline in mesophytism in habitat" (Potzger and Keller, 1952). Many inclusions of oak-hickory forest occur on areas of sandy soils within the Beech-Maple Forest region (Braun, 1950), but evidence suggests that beech-maple is not invading these xeric sites (Kenoyer, 1929). Differences exist in nutrient cycling between the oak-hickory and the more mesic deciduous forests. Oaks store nutrients in their trunks during the dormant season, whereas nutrients remain in the sugar maple leaves following the formation of the abscission layer and, as a result, fall to the ground and enrich the upper soil horizons. This annual cycle of nutrient transfer from the soil to the leaves and back to the soil again results in soils under sugar maple forests having a higher content of replaceable bases and higher cation exchange capacities due to the increase in humic soil colloids (Curtis, 1971). These differences in soil chemistry related to dissimilar forest associations suggest a reason in addition to moisture availability for the continued separation of these forest stands.

Mesic deciduous forests of sugar maple and basswood occur northwestward from the Driftless Area of southwestern Wisconsin and northeastern Iowa through the "Big Woods" of central Minnesota. The Maple-Basswood Forest region of southwestern Wisconsin is separated from the beech-maple forests to the east by a northward extension of oak and prairie (Braun, 1950). At times considered a western faciation of the Maple-Beech Forest association, the Maple-Basswood association is distinct because of its physical separation (Braun, 1950) and a distinctive post-glacial vegetational history. The boundaries of the Maple-Basswood Forest region are indefinite; stands occur in widely scattered "islands" where local conditions of topography and/or stream orientation have resulted in protection from fire. North and northeast-facing slopes provide the most favorable sites for this forest type because topographic breaks stop the progress of fires; basswood "appears to be quite sensitive to differences in micro-climate as influenced by topography, aspect, and the soil moisture regime" (Fowells, 1965).

Fire can be cited as an additional reason for the prevalence of this forest type on north-facing slopes. While basswood has the ability to sprout from the base after burning, sugar maple is fire sensitive and destructive cambial injury associated with ground fire occurs easily. While the greatest frequency of meteorological conditions that produce fire danger days occurs in the spring, autumn is the season with the most severe fire hazard in the deciduous forests because the litter is drier in the fall and the recently dropped leaves provide additional fuel (Curtis, 1971). Fire danger in the Lakes States region increases in the fall in association with a weakly meridional flow pattern at the 500 mb level (Schroeder et al., 1964). High autumnal fire frequencies occur in the upper Middle West in association with high pressure cells of Pacific origin (Schroeder et al., 1964). While October may be the month of greatest fire danger (Curtis, 1971), spring and early summer are the critical seasons for seedling survival.

The seedlings that survive in areas opened up by disturbance play an important role in determining the species succession and eventual composition of any site. Sugar maple seeds are shed in the fall at the same time as leaf drop and become incorporated into the litter. Seedlings emerge in the early spring and rooting may occur directly in the mineral soil or by passing around the ends of leaves. Seedlings with the latter rooting characteristic are likely to be killed during dry periods (Curtis, 1971). Early spring growth is related to stored carbohydrate, but later growth probably requires current-year photosynthetic production (Kozlowski and Ward, 1957). Thus a dry period in late spring or summer will severly reduce the number of surviving sugar maple seedlings. Diversity within the maple-basswood forests is created through the gap phase replacement process. Four phases of canopy replacement were identified for the "Big Woods" area northwest of Minneapolis, Minnesota (Bray, 1956).

The Hemlock-White Pine-Northern Hardwoods Forest

In the upper Middle West, the mixed coniferous and deciduous forests of the Hemlock-White Pine-Northern Hardwoods Forest region are primarily found to the north and east of an arcuate transition zone that stretches from northwestern Minnesota southeastward across central Wisconsin and then curves eastward to bisect the lower peninsula of Michigan. This Northern Mixed Forest region extends from the study area eastward to the Atlantic Ocean and is centered in the Great Lakes region (Nichols, 1935). The forests of this region have been characterized as forming an ecotone between the deciduous forests to the south and the coniferous boreal forest to the north (Shelford, 1963). A northward decrease in the deciduous component and an accompanying increase in circumpolar boreal species favors this interpretation (Braun, 1950). Despite this transition characteristic, the Hemlock-White Pine-Northern Hardwoods Forest region is regarded as a distinct forest region and three major reasons can be sited in support: 1) the mesophytic forest is a mixture of both deciduous and coniferous species, 2) the distributions of several of the dominant species, including white pine (Pinus strobus), hemlock (Tsuga canadensis), and yellow birch (Betula alleghaniesis), are centered within the region, and 3) red pine (Pinus resinosa), an important component of the forests on the drier sites associated with sandy soils, is endemic (Nichols, 1935). The Northern Mixed Forest region differs markedly today from the forest region to the south because most of this northern area is still forested, whereas many stands within the Deciduous Forest mosaic have been removed because of agricultural practices (Curtis, 1971).

Man's impact on these northern forests has been primarily to induce changes in the species composition (Stearns, 1949). A primary result of forest cutting in the late 1800's and the accompanying destructive slash fires was an increase in the prevalence of secondary communities in which bigtooth aspen, trembling aspen (Populus tremuloidies), balsam poplar (Populas balsamifera), and paper birch (Betula papyrifera) predominate (Braun, 1950). Within this Hemlock-White Pine-Northern Hardwoods Forest zone, water is the single most important ecological factor (Cowles, 1900) and compositional variability reflects this fact. Subdivisions within this forest region include bog or swamp forests on organic soils, the "pineries" on the relatively xeric, sandy soils, and the upland mesophytic forests consisting of a mixture of both coniferous and deciduous species on the finer textured soils.

Wetland forest communities occupy most flat, poorly drained areas including the beds of former glacial lakes, the borders of sluggish meandering streams, or the sites of small kettle or pothole lakes in areas of morainic topography. These lowland forests, which amount to less than ten percent of the region, can be subdivided along a moisture gradient into three distinct types based on species composition (Christensen, Clausen, and Curtis, 1959). The conifer swamps or bog forests are dominated by either black spruce (Picea mariana) or tamarack (Larix laricina) or both, whereas eastern white cedar (Thuja occidentalis), balsam fir (Abies balsamea), and black ash (Fraxinus nigra), are the dominants in the wet-mesic or cedar swamp communities (Clausen, 1957). The third type consists of hardwoods with yellow birch, sugar maple, and hemlock as dominants on the nearly mesic sites associated with former bogs or shallow upland depressions.

Black spruce and tamarack give the bog forests a distinctive physiognomic unity, despite the changes in the understory species throughout their range (Curtis, 1971). The outstanding structural feature of the conifer swamps is the uniform height of the tops of the trees; presumably, the trees with more vigorous apical growth are pruned back by "wind action akin to physiological tip-burning" (Curtis, 1971). Many bog forests are classical examples of the concept of primary plant succession with concentric rings of successional vegetation often found surrounding open water in the center of a depression. Tamarack usually inhabits the floating bog mat, whereas black spruce frequents the firmer, peaty substrate at the margin. Due to the anaerobic conditions and slow decay processes associated with the high water table and the highly acidic pH of the substrate, organic matter accumulates, and the forest encroaches upon and eventually fills in the open depression. In the southern part of this region, tamarack occupies both niches to the exclusion of black spruce (Curtis, 1971); black spruce generally increases in abundance northward (Braun, 1950).

Wet-mesic or cedar swamps comprise the second lowland forest type. White cedar dominates these bog sites or forested streamsides where ponds and flowages are frequently created by downed timber or beaver dams (Curtis, 1971). The majority of the cedar swamps exist in areas where water moves freely through the organic soils (Christensen, Clausen, and Curtis, 1959). The physiognomic character of level tree heights found in the conifer swamps is also exhibited in the dominant species of the wet-mesic forests; cedar thickets, dense clusters of vegetatively reproduced cedar trees, are a common feature of these swamp forests.

Black ash and balsam fir, the other important components, tend to be randomly distributed except where the cedar clumps exclude the establishment of these secondary species (Curtis, 1971). Both black ash and balsam fir obtain their highest level of importance within this forested wetland type (Christensen, Clausen, and Curtis, 1959).

Swamp hardwood forests are found on extensive peat deposits of former bogs, in shallow poorly drained upland depressions, or riverene swamps. These forests, which are rarely exposed to prolonged flooding, are similar in species composition to the mesophytic forests of the uplands. Sugar maple, hemlock, and yellow birch, normally not regarded as wet site species, are the most important trees of the northern swamp hardwood stands. Both hemlock and yellow birch obtain their best development in these relatively stable forests, where successional trends indicate an increased dominance of sugar maple (Christensen, Clausen and Curtis, 1959).

Conifers also dominate the xeric end of the environmental continuum in the Hemlock-White Pine-Northern Hardwoods Forest region. Edaphic factors play a prominant role in determining the sites for and the major subdivisions within the xeric portion of the compositional continuum. Dryness is relative within these northern forests with pines usually occupying the sandier soils with low water storage capacities and rapid internal drainage. Sandy glacial lake beds or outwash sands comprise the majority of the xeric sites where jack pine (Pinus banksiana), red pine (Pinus resinosa), and white pine (Pinus strobus), either separately or in combination, dominate the coniferous forests of the region. Wildfire plays a prominant role in the natural evolution of these forest communities. The structure, composition, and history of successional stages within these northern pine forests is largely determined by the effects of fire on the competitive nature of the species (Heinselman, 1973). Genetic adaptations of the pines include cone serotiny, seedling light requirements, and the need for an exposed mineral soil for germination (Mirov, 1967). Paleoecological evidence from the Boundary Waters Canoe Area of northeastern Minnesota indicates that over the last 1000 years, vegetational and fire history have been "relatively stable", with no evidence within the last few centuries of changes due to the presence of European man (Swain, 1973).

Successional changes within the upland forests of the Northern Mixed Forest region suggest that the xeric pioneer species are replaced by the more mesic shade-tolerant hardwoods. The theoretical sequence of successional changes is from jack pine through red pine, white pine, hemlock, and beech to sugar maple, but this order is rarely followed to completion and a pioneer species may be replaced by any of the more mesic species (Curtis, 1971). An uninterrupted transition along this successional trend is thought to require 800 to 1000 years, but natural disturbances such as windthrow and/or fire occur with much greater frequency (Curtis, 1971).

The Natural Fire Rotation, a term proposed to describe the "average number of years required in nature to burn-over and reproduce an area equal to the total area under consideration" (Heinselman, 1973), is an indication of the frequency of disturbance. In the Boundary Waters Canoe Area of northeast Minnesota, the Natural Fire Rotation varies depending on the plant community type, with jack pine stands burned at intervals as short as 50 years or less and red or white pine forests at 150 to 350 year intervals (Heinselman, 1973). A natural fire frequency of 22 yeras has been calculated for the Itasca State Park Location in northwestern Minnesota (Frissell, 1973). The park lies within the ecotonal area between the deciduous forests to the west and the mixed coniferous and deciduous forests and includes stands representative of both regions. It has been suggested that the frequency of burning in fire-dependent communities is non-random and related to the susceptibility of the vegetation to burning (Mutch, 1970). The relative dryness associated with the sandier soils and their lower available moisture during periods of drought contribute to a greater fire frequency on these sites. This high frequency of natural disturbances has the effect of keeping these sites at the pioneer end of the successional continuum.

The two major segments of the xeric end of the upland forest continuum are 1) the initial or dry segment on coarse sands where the pines (jack, red, and white) are the most important species and 2) the intermediate or dry mesic forests on sandy loams where white pine, red maple (Acer rubrum), and northern red oak frequently occur (Curtis, 1971). Within these conifer forests, the "pines may occur in nearly pure stands of a single species or in mixtures of two or all three" (Curtis, 1971). White pine, the tree that best exemplifies the mixed conifer-hardwood forests, has a distribution that is nearly co-extensive with this forest region (Nichols, 1935) and the species can be found in all segments of the moisture continuum (Curtis, 1971). Even-aged stands of nearly pure white pine date back to a major disturbance such as a forest fire, while the perpetuation of this opportunistic species in mixed stands is related to the random occurrence of small forest openings (Nichols, 1935). Red pine, which is endemic to this forest region, is able to germinate on drier sites than white pine, is not as shade-tolerant as many of its common associates, and becomes resistant to ground fires at maturity (Fowells, 1965). Jack pine is believed to have developed cone serotiny, a major adaptation to fire, in a lightning-fire environment of Late Tertiary or Early Pleistocene time (Heinselman, 1973). Both red pine and jack pine are found primarily in areas with sandy soils, due to their physiological adaptations to the dry conditions and higher fire frequencies associated with these sites. Within the Northern Mixed Forest region of the upper Middle West, pine forests become more extensive westward, whereas the occurrence of hardwood communities is more frequent in Wisconsin and Michigan (Braun, 1950).

The mesophytic upland forests of the Hemlock-White Pine-Northern Forest region are found primarily on the finer textured soils with better water-holding capacities. Sugar maple is the most universally distributed species within the region (Nichols, 1935). but there is considerable variation in species composition along an east-west transect across the study area. The composition of forest stands becomes simpler as one proceeds westward. The major dominants in these mesic forests include several species whose ranges terminate within the region. Beech, which is an important component of the forests in northern Lower Michigan, eastern Upper Michigan, and extreme northeastern Wisconsin may be limited in its westward extent by moisture effectiveness (Ward, 1956) at approximately 88^{o} W longitude, while others suggest that the species is still migrating westward in response to Holocene climatic changes (Davis, 1976). Hemlock, an important species in both Michigan and Wisconsin, has a range that extends only into the eastern counties of Minnesota (Fowells, 1965), and yellow birch, which reaches its greatest importance in northern Wisconsin (Curtis, 1971), rapidly declines to the west and is edaphically limited to moist soils in northwestern Minnesota (Braun, 1950). A result of the limited distribution of these major species is variation in the dominants of the mesophytic upland forests. In northern Lower Michigan, eastern Upper Michigan, and northeastern Wisconsin, sugar maple is generally the dominant species with variation in the proportion of the important co-dominants, (beech, hemlock, basswood, and yellow birch) dependent upon the amount of available moisture (Gleason, 1924). In northern Wisconsin west of the present range of beech, the mesophytic forests dominants include sugar maple, hemlock, and yellow birch (Stearns, 1949). The minor species of the mesophytic forests in the east become the dominants of the mixed forests to the west, since both beech and hemlock are non-existent and yellow birch is of minor significance. Basswood achieves its greatest importance (Curtis, 1971), several oak species become more abundant (Braun, 1950), and american elm becomes more extensive (Nichols, 1935) in the mixed coniferous-deciduous forests of Minnesota.

The existence of conifers within the mesophytic upland forests is a definitive characteristic of this forest region. White pine, the species that can be used to identify this forest region, is an opportunistic tree whose long life provides the ability for the species to reproduce itself in the occasional forest opening. White pine is a "normal, although minor" (Nichols, 1935) member of this forest type. In the eastern two-thirds of the study area, hemlock joins white pine as the coniferous component of the mesic forest. Shade-tolerant hemlock seedlings and saplings perpetuate the species through their ability to withstand low light-level supression. Westward from the limit of hemlock in eastern Minnesota, balsam fir, a circumboreal species, is a conspicuous coniferous element within the Northern Mixed Forest. A period of drought during either July or August is unfavorable for the survival of balsam fir seedlings (Curtis, 1971), and, as a result, these mixed forests of balsam fir, basswood, sugar maple, northern red oak and an occasional white spruce are generally found only on the relatively uncommon sites with heavy clay soils (Grant, 1934). Balsam fir, which obtains high densities of sapling size individuals but rarely becomes a prominent canopy member in Wisconsin (Curtis, 1971), is "more abundant and more generally distributed" in northern Minnesota (Braun, 1950).

Summary

The distribution of natural vegetation in the western Great Lakes region is influenced by many factors, but the broad pattern of grassland to the south and west, a central zone of deciduous forests, and forests with a mixture of coniferous and deciduous elements to the northeast is thought to be controlled by the regional transition in environmentally-induced plant stresses that affect reproduction, seedling and sapling survival, and subsequent growth. Locally, edaphic and topographic factors disrupt this regional pattern, but the amount of available soil moisture for plant growth and survival is the most important factor determining the species composition on a given site. The plant communities of the upper Middle West gradually change in structure and composition along a climatically controlled environmental gradient of moisture availability.

Contemporary Stability of the Vegetation Pattern

Considerable modification of the natural vegetation has occurred in association with western settlement in the last few centuries. The available meteorological data that were analyzed for this research are from the 14 year time period from 1961-1974, and it was assumed in this study that the climatic controls acting on the vegetation during this period are similar to the conditions that influenced the establishment of the presettlement regional phytogeographic pattern. Support for this assumption is based on the fact that vegetation distributions, particularly the location of the transition zones from one community to another, have not changed in the recent past. While it is recognized that floristic changes in response to the climatic fluctuation associated with Pleistocene glaciation are still occurring (Davis, 1976), the major vegetation formations of the western Great Lakes region have stabilized in their current location (Bernabo and Webb, 1977).

In the upper Middle West, the geographical distribution, or range, of any plant is a function of many interrelated factors including current climatic conditions, the rate of species migration into the region from its glacial refugium, and the vegetational history of the area. Floristic changes in the western Great Lakes region during the last several thousand years are primarily a function of species migration. Several important species of the mixed coniferous-deciduous forests are thought to be still migrating westward within the region. For example, white pine entered the eastern part of Minnesota approximately 7,000 years ago, remained there for the next 3,000 years and has been migrating slowly westward since then (Wright, 1968). Both red and jack pine retreated into northeast Minnesota during the mid-Holocene period of prairie expansion and have subsequently expanded to the west and south during the last 2.000 years (Wright, 1968). Maps of changes in pollen percentage for three time periods from 4,000 years ago to the present suggest that the significant period of pine migration was from 4,000 to 2,000 years before the present (Bernabo and Webb, 1977) (Figure 5). These maps support earlier research which concluded that white pine reached the Itasca region of Minnesota about 2,000 years ago and that red and jack pine arrived about 1,000 years ago (McAndrews, 1967).

In addition to the pines, several other species of the mesophytic upland forests are also thought to be still migrating within the Northern Mixed Forest region. Hemlock has been a dynamic species during the last four millenniums. Analysis of the migration of this shade-tolerant species suggests that the westward expansion of hemlock in the last 4,000 years is "in response to the more moist climatic conditions of the last few thousand years" (Davis, 1976). American beech has also been identified as a species that is currently migrating but some questions exist concerning the locational stability of the western-most limit of beech. One researcher has concluded that "beech has never been west of its present boundary and that it is in fact moving westward now" (Davis, 1976) whereas a study of the changes in composition in the beech forests of eastern Wisconsin based on a comparison of present stands with the original land survey data suggests that "the beech border is relatively stable in position and that, although less abundant now than in the past, beech will remain a part of the climax forests of the area (Ward, 1956).

While migration of important species is still occurring in the northern mixed forests, several researchers have concluded that recent

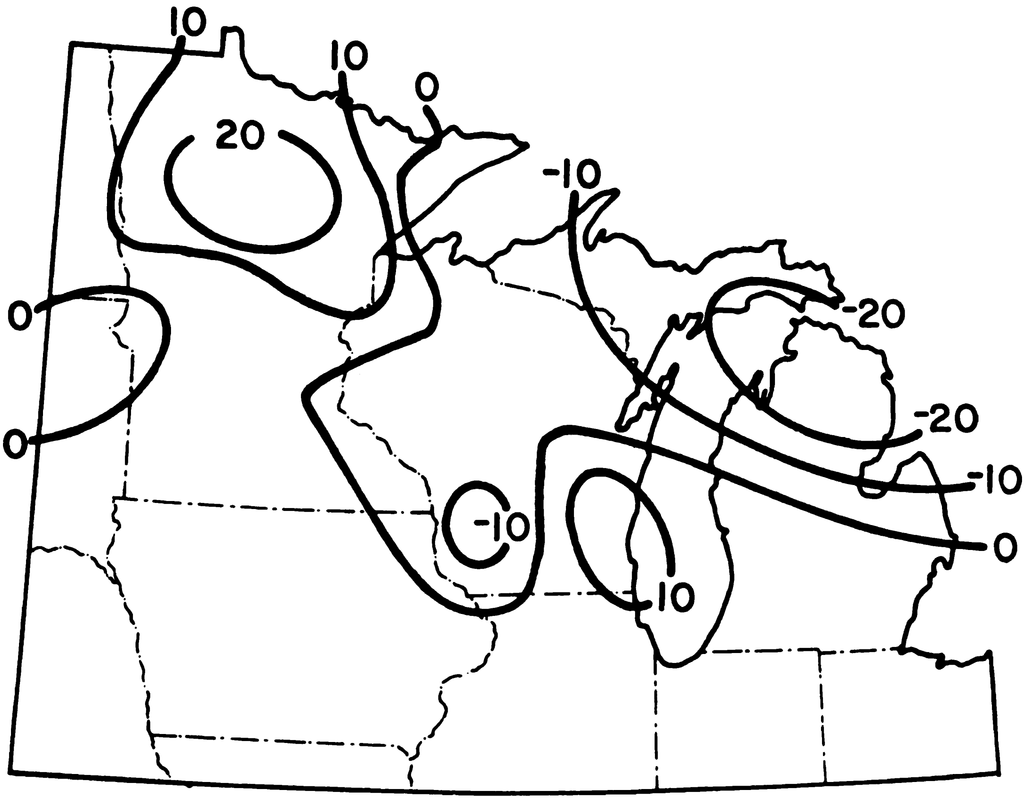

Figure 5a. Pine Pollen Differences 4000-2000 Years B.P.
Source: Bernabo and Webb, 1977.

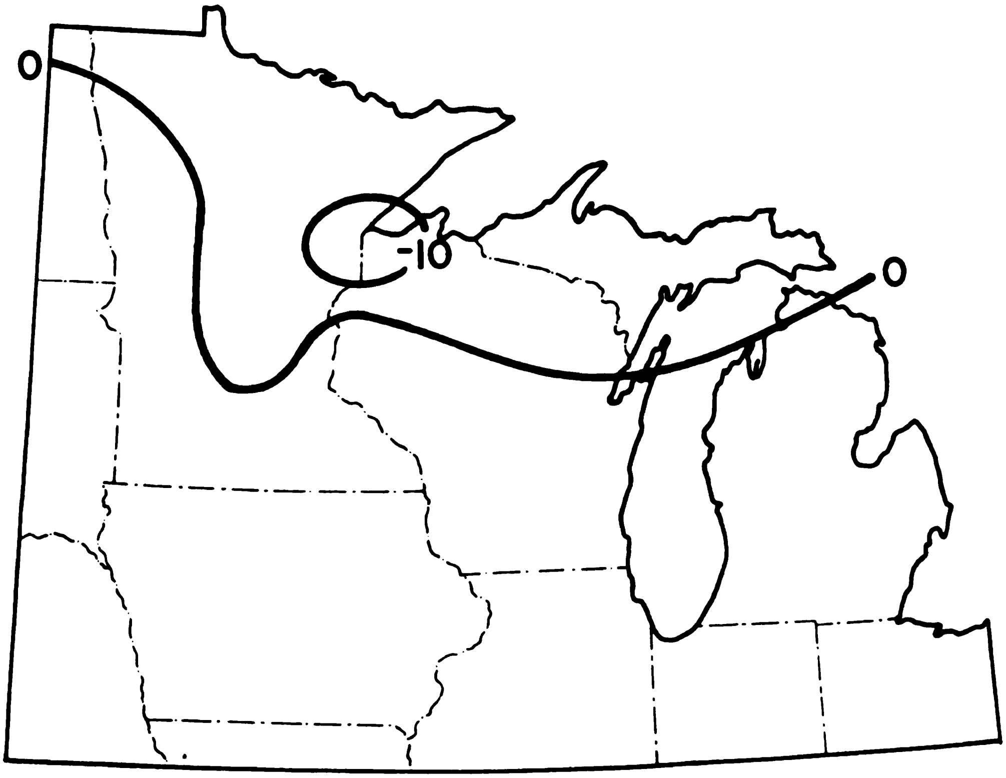

Figure 5b. Pine Pollen Differences 2000-500 Years B.P.
Source: Bernabo and Webb, 1977.

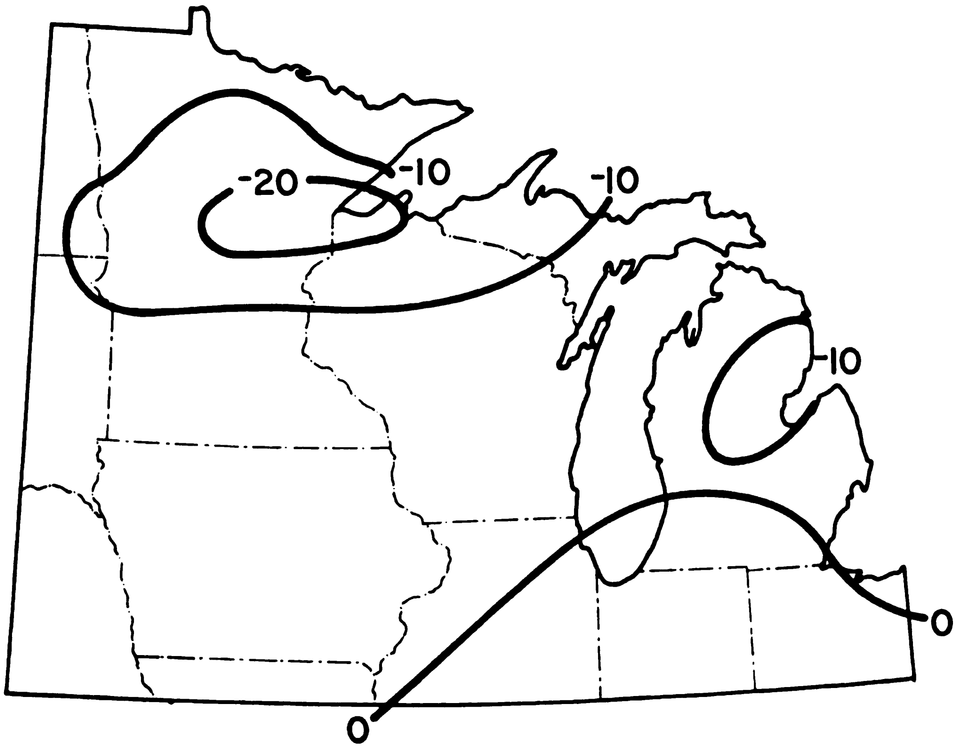

Figure 5c. Pine Pollen Differences 500 Years B.P. - Present.
Source: Bernabo and Webb, 1977.

successional tendencies confirm the relative stability of the forest mosaic within the deciduous forest zone. In Kalamazoo County, Michigan, the separation between beech-maple and oak-hickory forest stands is still pronounced today and no evidence can be found to support a successional change from oak-hickory to beech-maple (Kenoyer, 1929). Analysis of the forests in the ecotonal area separating beech-maple forests from oak-hickory forests near Valparaiso, Indiana, indicates that the contemporary forest distribution is similar to the presettlement phytogeographical pattern (Harman and Elton, 1971). The researchers conclude that there is "no indication of a successional trend away from the present composition...in any of the beech-maple woodlots" (Harman and Elton, 1971). In Kane County, Illinois, a historical study of the presettlement vegetation demonstrated that the boundaries between soil types and associated vegetation were nearly identical. This indicates that there is "no simple explanation for the distribution and co-existence of forest and prairie in this ecotonal area" (Kilburn, 1959) and that the vegetation formations have remained stable during the last century.

Paleoecological investigations within the upper Middle West indicate that the movements of the major vegetation associations that marked the first half of the Holocene have ceased. It has been suggested that the species that comprise the vegetation of the northern United States have "evolved during an epoch characterized by climatic and floristic instability" (Davis, 1976). While interglacial periods may have been too brief for the achievement of a climatic equilibrium by every species (Davis, 1976), the recent locational stability of the major vegetation transitions of the western Great Lakes region during the present interglacial implies a regional adjustment of the plant formations to the atmospheric-induced gradient of available moisture. The present location of the prairie-forest ecotone stabilized approximately 2,000 years ago and changes in ecotone configuration since then have been minor (Bernabo and Webb, 1977). The current position of the deciduous/conifer-hardwood forest ecotone was established approximately 4,000 years ago. Although significant compositional trends have been identified within these plant formations, these trends have not altered the character and location of the individual phytogeographic regions.

Phytogeographic Controls in the Western Great Lakes Region

I have described the natural vegetation of the upper Middle West with emphasis on the role that available moisture has on the growth and reproduction of the dominant species within each plant association. Additionally, I have described the dynamic character of the vegetation and the recent phytogeographic stability of the major vegetation types within the region. This third section of the literature review deals with the major factors that have been identified as phytogeographic controls within the study region. While several factors are important in delimiting the natural distribution of the vegetation in the upper Middle West, many of them operate on only a local scale, However, one factor, climate, acts to determine the regional pattern of the vegetation formations. Topography, anthropogenic or lightning fire, migration rates of important species, favorable sites for the survival of relic species, and soil factors have been related to the local or regional vegetation pattern, whereas moisture stress has been identified as the major climatic influence on the general distribution of plants in the western Great Lakes region. The following section treats each of these factors in detail.

Topography

Topography exerts its control on the microscale distribution of natural vegetation in at least three different ways. Variation in land configuration provides: 1) suitable habitats for the persistence of a relic species, 2) barriers to the spread of natural ground or anthropogenic fires, and 3) localized habitat variability where major differences in available soil moisture exist.

Within the upper Middle West, suitable microclimatic variability for the presistence of relic species exists primarily in the Driftless Area of southwestern Wisconsin, northeastern Iowa, and southeastern Minnesota. Relic pine stands are found occupying north-facing steeply-sloping sites overlying sandstone bedrock of Cambrian or Ordovician age (Curtis, 1971), while relic wetland communities are located in oxbows on floodplains of meandering rivers. Palynological evidence indicates that these stands have persisted since the final melting of the Wisconsinan Ice Sheet (Hansen, 1939) and there is no evidence that the stands are on the decline (Curtis, 1971). The persistence of these communities is thought to be related to their protection from crown fire. The presence of relic wetland communities of spruce and tamarack is also thought to be a function of wetland size and the related frequency of plant stresses associated with fire-induced changes in microenvironment (Davis, 1977).

The restriction of the isolated forest stands on the Great Plains to specific sites downwind from topographic breaks is believed to be related to the protection from fire provided by a scarp or watercourse. Escarpments or other abrupt breaks in topography are sites of woodlands throughout the Great Plains region, despite the prevalence of grassland on most other sites (Wells, 1965). Topography is considered to be a primary control of the natural vegetation pattern within the Central Plains because grasslands occupy the flat to gently sloping areas and non-riparian woodlands are limited to areas of rough, dissected land (Wells, 1970a). Within the prairie-forest transition zone in central and northern Illinois, the location of isolated forest groves indicates the effectiveness of ponds or streams to act as fire breaks (Gleason, 1913). Abrupt topographic breaks served the same purpose within the Great Plains (Wells, 1970b) and the upper Middle West.

Hillslope position also has an effect on the character of the vegetation mosaic. Variability in the amount of moisture available for plant growth and reproduction is related to topographic position. The general nature of this relationship between hillslope position and the depth of the water table is well known and the amount of moisture in the rooting zone follows a similar pattern. The presence within the upper Middle West of lowland forest communities which are richer in species composition than the upland forests underscores the relative importance of greater availability of moisture for plant growth and survival. Topographic differences in northeastern Illinois have been cited as the major reason for variation in the natural vegetation mosaic in the area (Kilburn, 1959).

Fire

Considerable debate concerning the nature of wildfire as an agent in the distribution of the regional vegetation has occurred within the past century. Major disagreement has been centered on the climax status of the regional vegetation and the cause(s) of the frequent burnings. The effects of fire on the vegetation are not a subject of disagreement and the importance of frequent burning in the maintenance of the structure and composition of grassland and savanna vegetation is well understood (Anderson, 1973). In general, the repeated burning of a site is less harmful to grasses than to woody vegetation and forest expansion into areas where fire prevention or suppression are practiced is well documented (Foster, 1917; Leopold, 1924; and Gartner and Thompson, 1973). Factors favoring the establishment and persistence of a grassland vegetation achieved by burning include a removal of the accumulated dry vegetative matter (Weaver, 1954), an increase in soil temperature, a related earlier initiation of growth in the spring (Kucera and Ehrenreich, 1962), an increase in organic matter and nitrogen within the soil (Anderson, 1972), and a resultant increase in the amount of dry matter produced (Kucera and Ehrenreich, 1962).

It is important to realize that moisture availability plays a major role in determining seedling and sapling survival and, therefore, helps determine the natural vegetation that occupies a frequently-burned site. Within the deciduous forest zone, natural grasslands existed only on certain edaphically or topographically controlled dry sites. On the other hand, forest stands dominated by oak are not eliminated by burning, but are reduced in stature to scrubby stands of brush with bur oak and hill's oak (Quercus ellipsoidallis) the most conspicuous species (Curtis, 1971). In the mixed-deciduous-coniferous forests, frequent burning also produces a scrub forest with red pine, jack pine, and hill's oak as the prominant woody species present (Kittredge and Chittenden, 1929). The existence of grasslands as a natural vegetation unit is linked not only to fire but also to the regional climate and the amount of moisture available for plant survival and growth. Naturally-occurring grassland vegetation "can exist on a large scale only within a particular climatic regime, and that is one characterized largely by an excess of potential evaporation over available rainfall. Within the area with this climate, soils and topography are of minor importance" (Curtis, 1971). Experimental tree plantings have demonstrated that trees can survive in the region where the natural vegetation was prairie grasslands, but fire is "a natural environmental factor favoring the grasses" (Walter, 1973).

Suggested causes of the frequent burnings of the grassland vegetation in the great Plains have included both anthropogenic and natural ignitions. Burning is thought to be a universal cultural pattern among the Indians of the United States (Stewart, 1953). Warm dry periods during autumn, referred to as Indian Summer, are commonly cited as the time of most frequent burning (Sauer, 1975). Researchers who state that man was the primary factor determining the distribution of grassland vegetation list a number of reasons for the native Indians to have set prairie fires. The use of fire as a hunting device to drive game is often cited (Sauer, 1944). The setting of fires for the purposes of communication has also been given as a possible reason for the frequent grassland fires (Moore, 1973). Grazing animals prefer the forage on areas that have been burned within the past year (Smith and Owensby, 1973) and it has been suggested that the Indians intentionally burned areas to create selected sites with good spring growth and as a result insure good hunting grounds (Sauer, 1975). The following list summarizes the reasons identified for anthropogenic burnings of the prairie (Table 1). Researchers favoring the anthropogenic orgin of the grassland fires rely repeatedly on the present day expansion of forest vegetation into areas that were grasslands (Stewart, 1953) to support their reasoning, while some have argued that a climate favoring recurrent droughts is not a satisfactory explanation for prairie vegetation (Sauer, 1944).

The composition of the grasslands of the Great Plains is fire-dependent in that fire selectively favors dominance by herbaceous plants at the expense of woody species. Repeated burning at frequent intervals prevents the accumulation of fuel for large conflagrations and light burning of the litter produced in one or two seasons kills young woody seedlings (Sauer, 1975). Researchers favoring anthropogenic causes for prairie fires discount the role played by natural lightning fires. In regards to the forests of the western United States where lightning fires are an important component of the natural environment, a researcher favoring the importance of anthropogenic burning has concluded that "lightning fires are not known to alter the ecology in any permanent direction" (Sauer, 1944). Recently published conclusions concerning fire ecology are in disagreement. Suppression of fires in mountainous areas of California has led to increases in forest density (Vankat, 1977), changes in species composition (Vale, 1977), and the build up of fuels to a level such that the natural ground fires have been replaced by severe crown fires (Vankat, 1977). Researchers who favor man as the cause of the prairie fires, and hence the prairie vegetation, have concluded that lightning-ignited ground fires rarely account for the existence of grasslands (Sauer, 1975). Any documentation of lightning set fires on the Great Plains was unknown to one researcher as recently as 1944 (Sauer, 1944).

Table 1. Reasons cited for anthropogenic burning of the natural vegetation

Hunting aid - to drive game

Pasture improvement

To improve visibility

For insect collection

To increase seed or berry yields

To increase the availability of other wild vegetable foods

Forest management - thin trees to keep down brush

Maintainence of valuable timber

Land clearance for planting purposes

Growth stimulation of wild tobacco

As an aid in warfare

To facilitate travel

For the production of a spectacle

To reduce danger from snakes or insects

Sheer carelessness

To signal the presence of enemies or strangers

For signaling the departure of expeditions

To indicate that a group was returning to its village

For locating friendly tribal bands

To indicate the location of game

To identify the beginning of a communal hunt

Source: List compiled by author from the writings of several cultural geographers who have written on the subject (Stewart, 1953; Sauer, 1944 and 1975; and Moore, 1973).

Nevertheless, support for lightning-generated natural wildfires in the grassland region can be found. The development of grassland vegetation in central North America during Tertiary time prior to the migration of man to the continent (Komareck, 1965) is cited as evidence that grasslands can occur naturally without the influence of anthropogenic fires. Natural fires in the forests of the western United States are generally small in areal extent (Taylor, 1971), and usually are extinguished in one to three days (Kilgore and Briggs, 1972). This burning serves many functions in fire dependent ecosystems. Ground fires are "more important ecologically than generally recognized" (Taylor, 1971) because they help create small openings within forest stands, help promote nutrient cycling, prepare seedbeds by exposing the mineral soil, and help maintain diversity, productivity, and stability within the ecosystem (Heinselman, 1973). Lightning is a natural component of the climate of central North America. Statistics presented for the North American prairies for 1965 show that an average of one lightning fire occurred per fifty square kilometers (one fire per twenty square miles) of grassland (Walter, 1973). Records for Superior National Forest indicate that 113 lightning fires occurred in the 15 year interval from 1956 through 1970. July and August are the months of greatest lightning fire frequency but rains that accompany the thunderstorms usually extinguish the fire. Occasionally, dry thunderstorms with little or no precipitation occur and a natural forest fire may result (Heinselman, 1973).

Lightning fires in the upper Middle West are warm seasonal phenomena with highest frequencies of critical fire weather occurring in the months from May to October (Komareck, 1965). Critical fire weather is related to specific synoptic weather patterns (Schroeder et al., 1964) and is both periodic and recurring. Researchers who suggest that lightning fires are a major factor in the existence and persistence of the North American grasslands support their conclusion by arguing that lightning fires are a component of the climate and therefore the fire dependent vegetation climax is also a climatic climax (Komareck, 1968). In the western Great Lakes region, the Natural Fire Rotation increases towards the southwest to a frequency such that annual burning is believed to be typical for areas at the edge of the grasslands (Louks, 1970).

While both schools of thought regarding the cause of grassland fires have their logical arguments and supporters, they agree that the vegetational composition of the North American grasslands is fire-dependent. But the history of atmospheric conditions determines whether or not the fuel is dry enough to burn and how rapidly the fire spreads or dies out. A major role played by fire in determining the distribution of vegetation is to affect seedling and sapling survival rates either through killing of young seedlings or by preparing a seedbed for germination. It is important to emphasize that fire may create the disturbance that allows a change in composition at a site, but the subsequent survival of an individual seedling on the disturbed site is governed by the amount of available moisture and the genetically determined growth habit of the species. Since the frequency of the fire is a function of climate, the source of the ignition plays a minor role in controlling the regional plant geography. Climatic differences across the region are responsible for both the increase in available moisture for plant growth along a transect toward the northeast (Borchert, 1950) and the gradient in the period between natural fires which increases from the suggested annual burning in the grasslands to an interval of 200 to 300 years for mesophytic forests within the White Pine-Hemlock-Northern Hardwoods Forest region.

Migration Patterns of Individual Species

Vegetation history influences the pattern of compositional variation within a forest association through changes in the availability of seed sources and the resultant changes in site occupance. It is recognized that the northward migration of the flora of the upper Middle West following the Wisconsinan glaciation did not occur in a simple expansion from one specific refugium (Gleason, 1923). Rather, the direction of migration and rate of movement varied with each species (Davis, 1976). Postglacial migration of spruce northward from the central United States was rapid; the distance between the northern margin of spruce forest and the southern margin of stagnating glacial ice decreased to the point where the forest may have advanced onto the ablating, drift-covered ice (Moran, 1973). Following the rapid emigration of the glacial spruce forest, pine became predominant in a belt stretching from Minnesota to the Atlantic coast (Bernabo and Webb, 1977). The diploxylon pine species (either jack or red pine, but most likely jack pine) arrived from the southeastern United States approximately 11,000 years ago (Wright, 1968). Immigration of a haploxylon species (white pine) along a more east-west transect into the upper Middle West occurred approximately 1000 years later. Palynological evidence suggests that "white pine may have grown at least part of the time on the exposed continental shelf" (Davis, 1976) off the mid-Atlantic coast during the period of Wisconsinan glaciation and Holocene movement was primarily westward from there. The northward migration of hemlock and beech, two shade-tolerant species, occurred at slower rates as these species penetrated closed forest stands (Davis, 1976). In response to the change in post-glacial climate, hickory spread slowly northeastward from the lower Mississippi Valley region and reached the southern part of the western Great Lakes region about 10,000 years ago, but its arrival in southern New England did not occur until about 5,000 years later (Davis, 1976).

The significance of these variable patterns and rates of migration is evident in the interpretation of the vegetational history of a region. Interpretations of changes in local pollen frequencies usually have attempted to invoke climatic change as an explanation. It now seems reasonable to conclude that many changes in the local pollen rain can be attributed to the immigration and establishment of a species. Compositional variability within the Northern Mixed forests is related to the distribution of several species that are thought to be still migrating within the region. Hence, the vegetational history is an additional factor controlling the distribution of vegetation in the upper Middle West. The attainment of an equilibrium location by the ecotones separating the major forest associations over 2,000 years ago suggests that the current role of vegetational history is localized in extent and only helps to explain the pattern of the vegetation mosaic within a forest association.

Edaphic Factors

Soil factors also play a role in controlling the local distribution of natural vegetation in the western Great Lakes region. Relationships between vegetation and soils are complex and interrelated. Within a forested region, compositional variations are associated with an environmental continuum that corresponds strongly with soil texture. Analysis of the relationship between soils and presettlement vegetation in Indiana, for example, indicates that beech-maple forest stands were limited primarily to areas of silt loam soil texture, whereas oak-hickory stands occupy sites with a generally lighter texture (Lindsey, Crankshaw, and Qadir, 1965). Studies on the vegetation pattern along the Valpariso Moraine in northwestern Indiana indicate that textural variation (and resultant difference in soil water budget) is the primary phytogeographic control (Harman and Elton, 1971). Dendrochronological analysis of mature white oak trees along the moraine complex has shown that greater stress occurs in areas of finer textured soils and therefore supports the hypothesis that soil texture is the major control of plant distribution in the area (Charton and Harman, 1973).

In northeastern Iowa, edaphic features which strongly affect the amount of water available for plant growth are correlated with both stand composition and the productive capacity of oak forest lands (Einspahr and McComb, 1951). The species which dominate forest stands in Wisconsin "vary according to a pattern commonly associated with a soil-moisture gradient" (Crutis, 1971). Compositional variation in northeastern Michigan is "strongly related to soil textural variations" (Harman and Nutter, 1973), with pines on the sandy soils and mesic hardwoods dominating on the loamy soils. Analysis of variability in eleven soil characteristics and the associated changes in the pre-settlement deciduous tree cover indicated that "depth of the soil hor-izons, percentage of nitrogen, and percentage of clay" (Crankshaw, Qadir, Lindsey, 1965) were the most important edaphic factors related to forest composition in Indiana. The same authors have concluded that "soil texture, drainage profile, and catena related attributes of substrates all exert a strong influence in determining forest types in Indiana" (Lindsey, Crankshaw, Qadir, 1965).

In the ecotonal area between the deciduous forests and the grasslands, soil differences have been suggested as a possible reason for the occurrence of both vegetation types within the same area (Norton and Smith, 1932). Several differences develop between the soils that form under a grassland cover as compared with forest cover because "prairies tend to persist on prairie soils and forest on forest soils, because each type of vegetation has produced a type of soil suited to itself" (Cowles, 1928). Environmental modifications associated with permanent settlement have led to an expansion of oak forests within the prairie-forest transition zone, but much of this recent "forest invasion" has occurred in areas that were originally oak savanna (McComb and Loomis, 1944). Forest expansion into areas where grass was the original vegetative cover has occurred following the suppression of natural wildfires primarily in areas where the original sod cover has been destroyed either by breaking the soil for agriculture or by accelerated erosion. A study of the soils and natural vegetation in LaSalle County, north-central Illinois, indicates that

> the original distribution of upland forest in this portion of Illinois, where the vegetation is predominantly grassland, is limited to a particular type of soil bordering the streams and somewhat below the prairie upland. Hence it seems fair to conclude that here, at least, the character of the soil is the limiting factor in controlling the area of tree growth. As this soil is uncovered by erosion its extent is being gradually increased, and this extension is leading to the well known gradual encroachment of forest upon the grassland now occurring in this transition area (Fuller, 1923).

This recognizable relationship concerning the distribution of vegetation in Illinois has led to the conclusion that "soil is the primary factor governing native vegetation in the state" (Norton and Smith, 1932).

Recognizable differences exist between grassland and forest soils. Analysis of the contrast in soil chemical properties indicates that prairie soils "are somewhat higher in total nitrogen, base exchange capacity, and replaceable bases, but lower in available potash and available phosphorus" (White, 1941). Since the nutrient deficiencies of grassland soils do not account for the poor growth of trees planted in prairie soil, the absence of mycorrhizal fungi in prairie soils was suggested as a possible reason for the exclusion of trees from certain grassland soil sites (White, 1941). High calcium content which retards tree growth and high nitrogen content which favors rapid resodding have also been suggested as reasons for the natural exclusion of tree growth from prairie soils (McComb and Loomis, 1944). It has been suggested for the western part of the study area that the change in vegetation from full-glacial spruce forest to Holocene prairie grassland was favored by the high lime content of the soils, flat topography, and poor soil aeration which "favored grass rather than oak during this increasingly xeric period" (McComb and Loomis, 1944).

In general, the role played by soil factors in the distribution of natural vegetation in the upper Middle West is localized in extent. Spatial variability in the dominants within a forest association are related to a number of factors and soil characteristics have been shown to play a significant role. In other areas, additional factors are necessary to explain the local vegetation mosaic. Forest composition in northeastern lower Michigan correlates with soil texture, but other factors are necessary to account for the compositional variability in northwestern lower Michigan (Harman and Nutter, 1973) and edaphic factors are apparently of minor importance in separating beech-maple from oak-hickory sites in Ohio (Transeau, 1935). A general conclusion concerning the role played by soils in the grassland region is that:

> climatic factors are of primary importance in determining the general boundaries of distribution of the prairie, while the ever changing topography and water content of the soil are important in determining where sloughs, prairies, or forests will develop within these boundaries. The effect of these soil factors is more prominent near the boundaries of the prairie region than near its center of distribution where we find prairies growing on the greatest range of soil conditions (Sampson, 1921).

A similar conclusion concerning the role played by soils in the forested portion of the upper Middle West is that "climatic factors are responsible in a large scale for the boundaries of distribution of forest species, while the soil determines more precisely the composition of the main forest stand" (Wilde, 1933).

Climate

On a global or regional scale, the predominant environmental factor determining the major vegetation formations present in any area is the synoptic climate. The two most important climatically-derived environmental elements are energy for plant growth and the availability of water (Walter, 1973). While favorable conditions can be provided locally by topography or soil conditions, regional climate generally regulates the thermic conditions and the plant-water relationships (Walter, 1973). A correlation has been shown for the coterminous United States between three of the four major biochores and climatic factors related to plant-water need and the energy for plant development (Mather and Yoshioka, 1968). Desert, grassland, and forest occur in discrete, non-overlapping regions that are distinguishable on the basis of annual potential evapotranspiration and the climatic moisture index (Mather and Yoshioka, 1968). Within the upper Middle West, a distinct transition from tall grass prairie to deciduous forest vegetation is not evident based on this analysis using mean monthly statistics; the mosaic pattern in the natural vegetation "is shown by the scatter of plotted points" (Mather and Yoshioka, 1968). Two possible reasons can be identified for the lack of a clear prairie-forest separation: 1) the use of mean monthly statistics tends to mask the effects of individual events that may be important in establishment of the ecotone and 2) an analysis based on a single transect rather than a random scattering of points might provide a sharp separation, since the analysis will be confined to a single spatial gradient.

The interrelatedness of plant energy requirements and moisture availability has been demonstrated through the use of potential evapotranspiration as a measure of energy for plant development. Actual evapotranspiration can be used as an index of plant growth and "those plants which make up the zonal vegetation seem to have a seasonal course of activity corresponding to the seasonal march in evapo-transpiration" (Major, 1963). As early as 1905, it was recognized that a ratio of precipitation and evaporation corresponded with the major centers of plant distributions (Transeau, 1905). While a number of moisture factors, including the amount and seasonal distribution of precipitation, the ratio of precipitation and evaporation, and the frequency and persistence of drought, affect the distribution of forest species (Braun, 1950), it can be generally concluded that "the availability of water is the chief determinant of the major plant formations" (Dansereau, 1957). Within the western Great Lakes region, a northeast-southwest moisture stress gradient "appears to be the major climatic constraint"

(Davis, 1977) on the location of the plant formations.

The Prairie Peninsula, an eastward extension of grassland vegetation across Iowa and into northern Illinois and Indiana, has been the subject of considerable debate concerning the prevailing climate and the climax status of the tall grass vegetation. It has been argued that the area is an edaphic climax, because tree vegetation will expand into areas where the prairie sod is broken (McComb and Loomis, 1944). Analysis of meteorological data for the region indicates that "present climate, especially the precipitation and evaporation, is perhaps sufficient to account for the Prairie Peninsula and the forest vegetation, east and south of it" (Transeau, 1935) and that "the prairie of the region from Iowa to Ohio seems to be just as 'climax' and just as 'true' as the other types of prairie farther west" (Transeau, 1935).

Several investigators have attempted to illustrate the nature of the regional climatic gradient through an examination of the meteorological factors that correlate with the vegetation transition. While most researchers conclude that growing season moisture availability is the key factor in the distribution of the natural vegetation in the western Great Lakes region, it is interesting to note the correspondence between the vegetation distribution and winter season climatic data. A significant change in the amount of snowfall occurs from the grasslands northeastward into the forests of eastern Canada (Figure 6a). This dramatic gradient in the amount of snow received also corresponds with gradients in the depth of snow at the end of any month and the persistence of snow cover into the spring (Borchert, 1950). A more recent map, which incorporates data from the lake-effect snow belt areas (Figure 6b), also indicates the trends described by Borchert but not as dramatically. Mean summer season (May-August) precipitation totals do not correspond

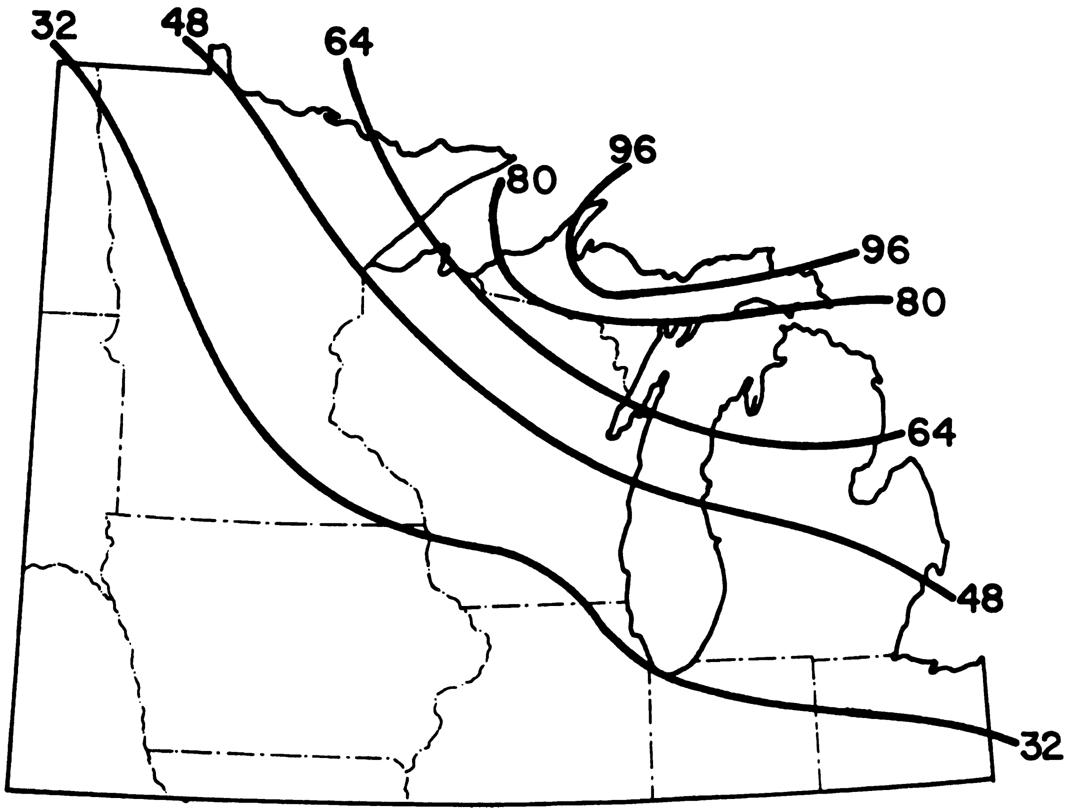

Figure 6a. Average Annual Snowfall in Inches.
Source: Borchert, 1950.

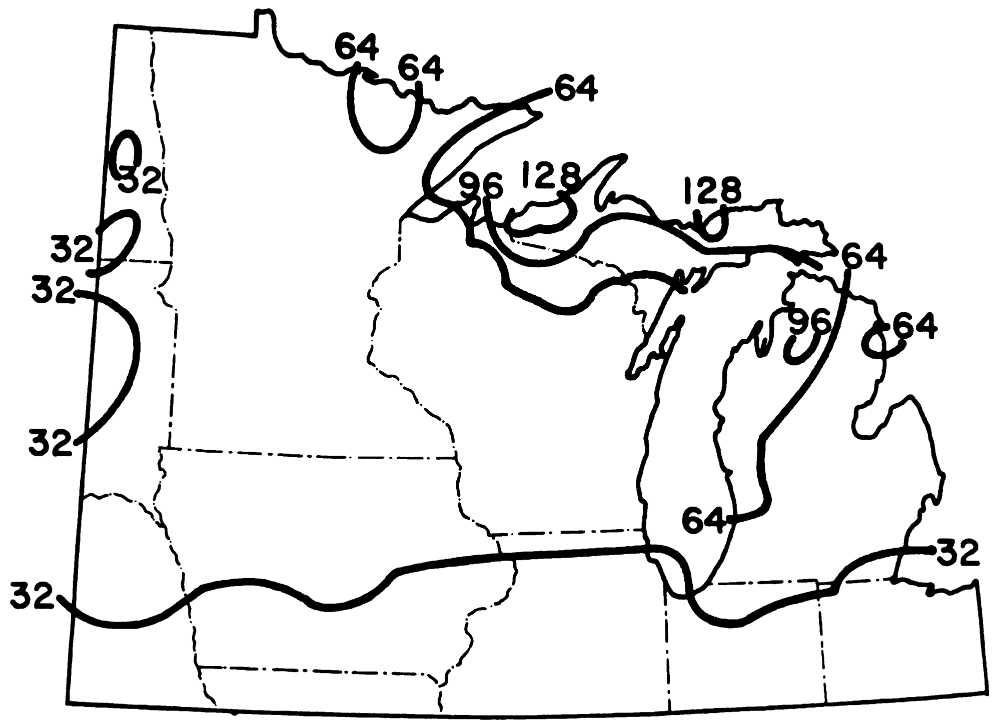

Figure 6b. Average Annual Snowfall in Inches.
Source: National Atlas, 1970.

with the vegetation distribution (Borchert, 1950), but there is a relationship with the number of days with measurable precipitation (Figure 7). A result of the logical combination of these two precipitation statistics is that there are longer periods of rainless conditions within the grassland portion of the upper Middle West and that the summer rains that do occur are of greater intensity which implies a higher percentage of runoff and, as a result, less moisture available for plant growth (Borchert, 1950). Additional evidence to support the concept of greater reliability of precipitation toward the northeast can be obtained from the mapped pattern of the coefficient of variation of annual precipitation (Figure 8). Both the balance between precipitation and evaporation (Figure 9) and average relative humidity in July (Figure 10) suggest that plant moisture stress increases toward the southwest where the average summer season cloud cover is lower (Borchert, 1950) and the average daily solar radiation receipts for the month of July (Figure 11) are higher in the prairies.

The weather in the Prairie Peninsula varies from one year to the next but in most years the climate is similar to that of the adjacent deciduous forest region to the east. During drought years, however, meteorological conditions are similar across the entire grassland region, including the Prairie Peninsula, and dry continental westerly air flow at the gradient level is causally related (Borchert, 1950). The climate of the Prairie Peninsula is distinct because, even though most years the climate is comparable with the bordering forest region, greater severity and frequency of droughts set it apart. Analysis of seasonal air mass frequencies also indicates the uniqueness of the climate of the Prairie Peninsula and has led to the conclusion that "there is, then, a distinctive 'cornbelt' climate"

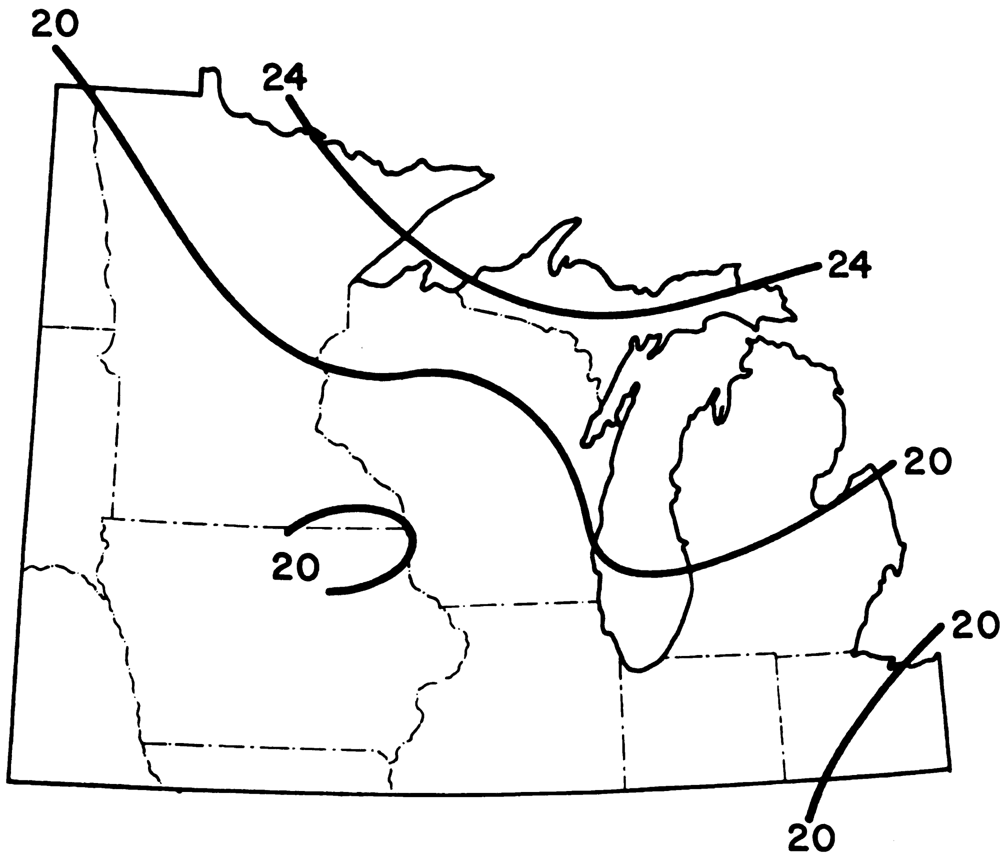

Figure 7. Average Number of Days with .01" or More of Rainfall During July and August. Source: Borchert, 1950.

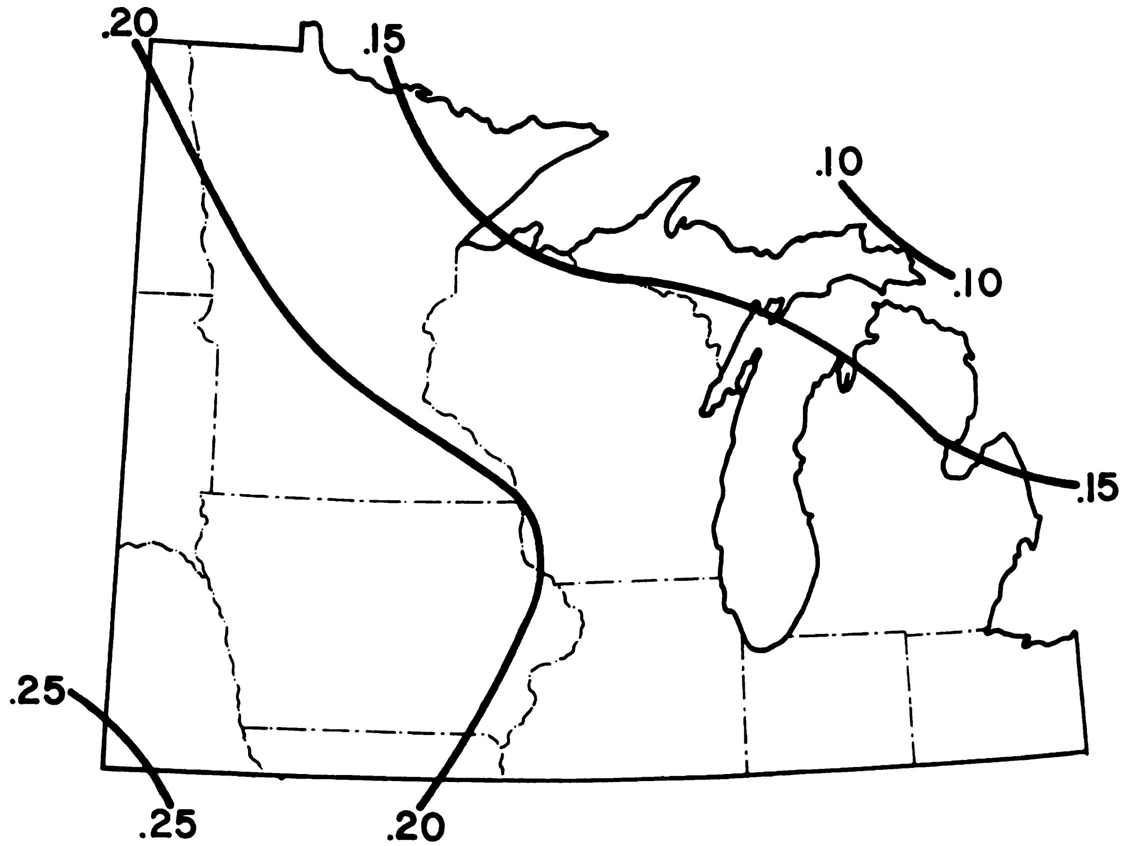

Figure 8. Coefficient of Variation of Annual Precipitation.
Source: Hershfield, 1962.

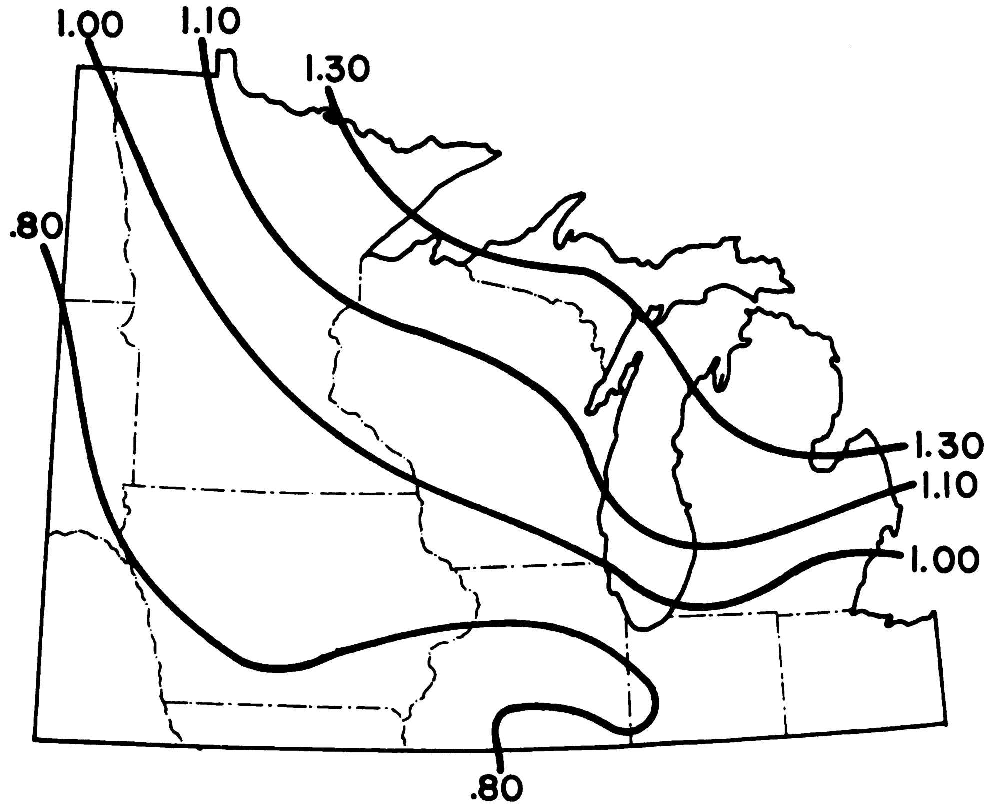

Figure 9. Precipitation - Evaporation Ratio.
Source: Transeau, 1905.

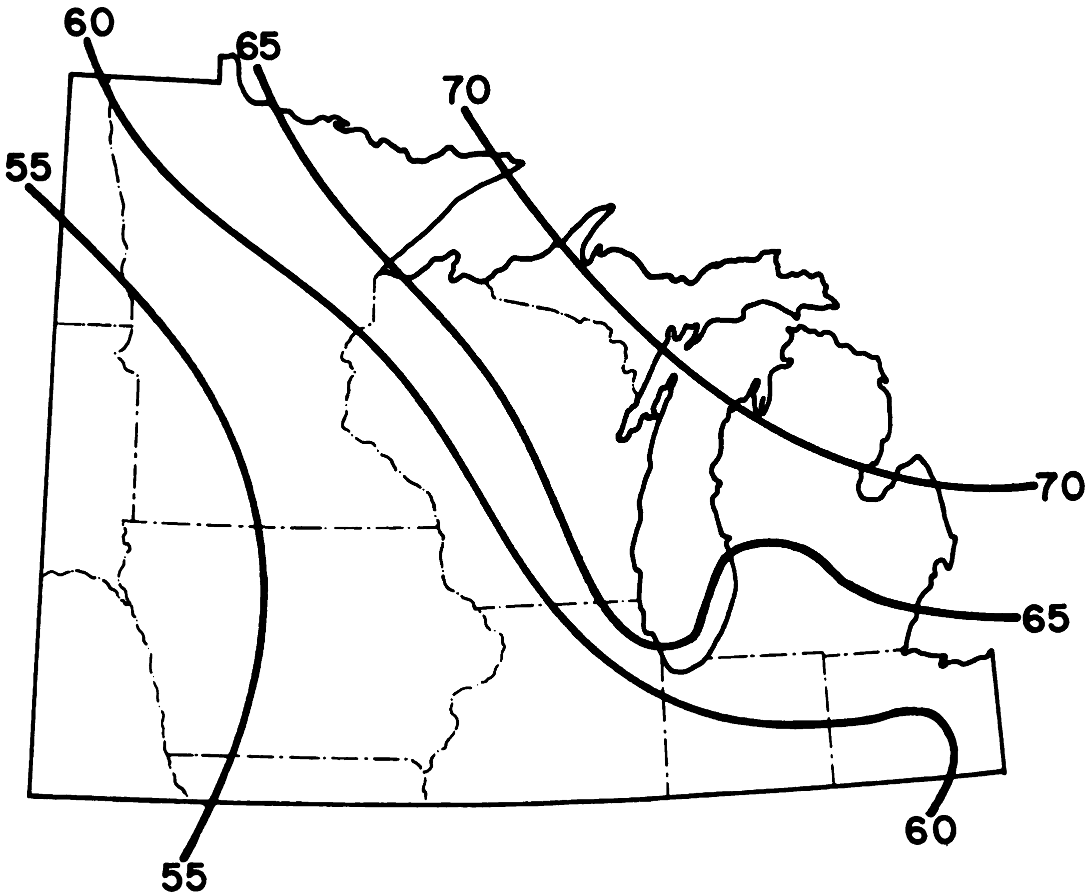

Figure 10. Average Relative Humidity in July.
Source: Transeau, 1935.

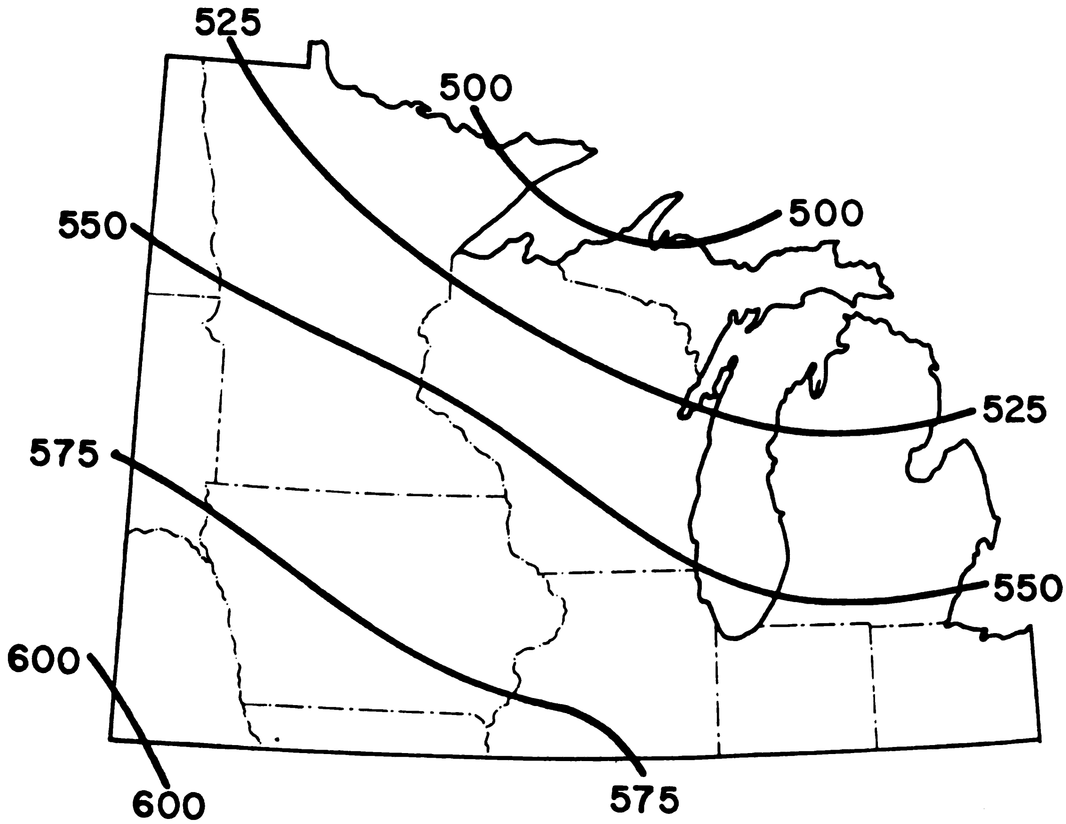

Figure 11. Average Daily Solar Radiation Receipts in Langleys (July). Source: Fritz and MacDonald, 1949.

(Bryson, 1966).

The primary factor controlling the distribution of natural vegetation in the upper Middle West is regional climate (Davis, 1977) and the associated gradient in surface environmental conditions. Natural prairie may require fire as an important ecosystem component in order to maintain its structure and composition, but the frequency of wildfire is a function of the climatic conditions that regulate fuel flamability. It is generally concluded that available water is the most important environmental factor that limits the growth and distribution of trees (Zimmermann and Brown, 1974) and one researcher has boldly stated that the grasslands "are clearly due to insufficient water for tree growth" (Cowles, 1928). While I believe that successful reproduction and subsequent seedling and sapling survival are of greater importance than growth in determining the phytogeographic distribution in the western Great Lakes region, it is clear that the primary environmental factor controlling all of these life processes is the supply of available water. An eco-physiological analysis of global vegetation has led to the conclusion that "the replacement of the forest zone by steppe in continental regions is governed by the supply of water" (Walter, 1973). It is clear that in the upper Middle West "climate is the ultimate ecological control" (Hare, 1951).

PLANT RESPONSES TO PHYSIOLOGICAL STRESS

Introduction

The preceeding review of much of the relevant ecological and biogeographic literature has indicated that plant moisture relationships are of paramount importance in controlling the distribution of natural vegetation in the western Great Lakes region. In other areas, such as the ecotonal area between the boreal forest and tundra vegetation formations, different environmental factors may be of considerable importance in limiting the distribution of arboreal vegetation. Many researchers have suggested that the location of the arctic tree line corresponds with growing season temperature conditions and "it has been shown that mid-summer temperature (late June, July) is highly correlated in northern conifers with both radial grwoth and lengthing" (Hare, 1954). An examination of ecoclimatological relationships in eastern Canada indicates that adequate supplies of precipitation are available to meet the needs of growth and that thermal efficiency as defined by Thornthwaite (Thornthwaite, 1948) is correlated with the zonal forest divisions (Hare, 1950).

Recent physiological analysis of the effects of cold summer temperatures on the native species in the forest-tundra transition zone suggests that "temperature is probably the most important factor limiting growth and development in northern regions" (Larsen, 1974). Several important temperature-dependent physiological processes are the rates of photosynthesis, translocation, and water absorption (Warren Wilson, 1957) and it can be concluded that an effect of the cold temperatures is a reduction in the amount of water available for photosynthetic production and a resultant decrease in net growth. In the upper Middle West, the moisture stresses that affect biogeographic distributions are not directly related to temperature-dependent conditions; water deficits occur primarily due to the inability of a plant to obtain enough water from the soil reservoir. It can be argued that a similar plant-water relationship exists in arctic environments, where cold temperatures restrict the uptake of the readily available moisture.

In general, the same climatically controlled factor, moisture availability, will govern the effectiveness of seedling survival, the production of viable seeds, and growth. Based on a review of relevant literature, I conclude that the climatic control of the distribution of plant species in the western Great Lakes region occurs primarily through the regulation of seedling and young sapling survival. The successful establishment of windbreaks on the Great Plains indicates that the regional climate is less limiting to growth than it is to either reproduction or seedling survival except during unusually droughty conditions (Albertson and Weaver, 1945). While successful reproduction is rare in the tree plantings on the Great Plains, those areas where reproduction does occur indicate that a proper microhabitat for seedling protection is essential (George, 1939). In arctic areas, the production of viable seeds (successful reproduction) may be a limiting factor (Elliott, 1979), but the growth and expansion of forest trees into areas that were formerly natural grasslands once the prairie sod has been broken is an indication that successful reproduction is not a limiting factor in the upper Middle West. I conclude that, in the western Great Lakes region, the significant factor governing the distribution of natural vegetation is seedling and sapling survival and the single most important variable "in determining the survival of tree seedlings is the relative abundancy of soil water" (Ferrell, 1953).

The precise physiological mechanism(s) regulating the important plant life processes are still relatively obscure (Zimmermann and Brown, 1974), but despite this inability to identify the exact mechanisms through which plant processes are affected due to moisture stress, enough measurements have been made to establish the nature of the impacts and to suggest that "reduced water uptake and dehydration can have deleterious effects on most physiological processes" (Slayter, 1973). In order to more fully summarize the importance of moisture in regulating physiological processes and in controlling both seedling survival and growth, the following literature review deals with the effects of moisture stress on plant processes. In addition, in order to demonstrate that atmospheric demands are an important regulator of moisture availability, this review examines the means by which plants extract water from the soil reservoir. These sections are included to support the author's view that moisture stress is a primary phytogeographic control in the western Great Lakes region through a summary of the known impacts of water deficits on the native vegetation.

Physiological Damage and Plant Moisture Stress

The inability of a plant to obtain sufficient moisture has a number of potentially harmful effects. In general, moderate stresses result in reduced growth and temporary physiologic adjustments, but permanent damage requires a lengthy period of adverse conditions (Albertson and Weaver, 1945). Growth form is an excellent indicator of environmental stress; trees growing in regions of periodic moisture stress exhibit an "unusual shrubby appearance due to reduced growth and early loss of apical control" (Zimmermann and Brown, 1974). "Both the initiation and differentiation of vegetation and reproductive primordia in the apical meristems...are very sensitive to water stress" (Slayter, 1973). During drought periods, older shoots of terminal and lateral branches dry off and the subsequent new shoots are established inward. This repeated dieback associated with periods of moisture stress results in a knarled and twisted appearance of the tree crown (Zimmermann and Brown, 1974). Grasses differ from tree vegetation in their adaptation to periodic moisture stress. Temporary domancy of roots and rhizomes in response to decreased available water provides a competitive advantage for many perennial grasses (Lane and McComb, 1948). In general, the drought-survival mechanisms in tree seedlings and saplings are not as effective.

Two symptoms of plant water stress have been identified for woody vegetation (Federer and Gee, 1976). Limited uptake of carbon dioxide and observed reductions in net photosynthesis are attributable to closure of the stomates (Slayter, 1973) whereas decreased water potential in leaves independent of the actions of the stomates results in biochemical stress (Hsiao, 1973). Vegetative adaptations to decreased moisture can be subdivided into two components: drought tolerance, the ability to withstand periods of moisture deficiency; and drought avoidance, the ability of the plant to postpone drought (Seidel, 1972). Differences in ability to survive drought vary considerably among the different vegetative life forms. Grasses avoid drought through dormancy whereas leaf stomatal closure is a common avoidance mechanism for mid-latitude deciduous trees (Tobiessen and Kawa, 1974). Other deciduous trees survive in areas of temporary water shortage through their ability to tolerate tissue desiccation and recover leaf turgidity when moisture becomes available again. These xerophytic species exhibit a tendency for higher values of water use efficiency due to their greater diffusion resistance (Wuenscher and Kozlowski, 1971). Studies dealing with the effects of soil drought on several species of oak seedlings indicate that species segregation is related to differential ability of the leaf tissues to withstand dehydration and that oaks with insufficient drought resistance were eliminated from xeric sites during their first dry summer (Bourdeau, 1954).

Climatic fluctuations toward increasing aridity have a pronounced impact on the regional vegetation. Changes in the local water balance associated with periods of drought can produce an unusually stressful environment for the regional vegetation. Conclusions based on the effects of the major drought in the Great Plains during the mid-1930's indicate that injury or death of woody plants was the result of an extended period of adverse conditions (Albertson and Weaver, 1945). Historical studies of the effects of this drought on grassland vegetation show that changes occurred in the dominant species within the herbaceous community and that there was an accompanying decrease in basal cover (Tomanek and Hulett, 1970).

The cumulative effects of internal moisture stress are inversely related to plant growth (Dickson and Broyer, 1972). Reduction in cell growth is usually the first sign of moisture stress and stunted growth is a common indication of periodic plant water deficits (Slayter, 1973). Genetic differences between genera, species, and even individual plants result in variability in plant responses to limited available water supplies. Decreases in growth, changes in the important life sustaining processes, and decreased seedling germination and survival rates are all associated with moisture deficits. Both root and shoot growth are reduced under high stress conditions, with shoot growth showing greater suppression (Larson and Palashev, 1973). Analysis of the effects of reduced soil moisture tension on tree ring formation indicates that tracheid radial diameters decrease and that the impact is greatest near the apical meristem (Glerum, 1970). Cell division, RNA content, DNA content, and protein levels are all affected by stress and the formation of new leaf primordia virtually ceases as soon as stress is initiated (Slayter, 1973). Apparently, the reduction in growth of periderm during periods of water deficit is not as great as the decline in the growth of xylem (Borger and Kozlowski, 1971). In general, almost all measures of net biomass production, including shoot and leaf growth (Quraishi and Kramer, 1970), seedling height and diameter, stem area and weight, and foliage weight (Heiligmann and Schneider, 1974), show the effects of decreased growth during periods of stress.

The important plant processes of photosynthesis, respiration, and transpiration are all affected during periods of declining soil water potential. Variability in the response of these vital functions differs from one species to another and helps to determine the drought resistance of an individual. In general, net photosynthesis declines rapidly as stress begins and production eventually levels off at the zero rate if moisture deficits intensify (Puritch, 1973). Decreases in carbon dioxide levels, resulting from stomatal closure, are primarily responsible for the initial reduction since the photosynthetic plant structures are "relatively unaffected until severe water stress exists" (Slayter, 1973). The effects of moisture stress on respiration are more difficult to identify because temperature changes are a complicating factor (Slayter, 1973). Dark respiration is thought to be relatively unaffected by moisture stress, but reduction is possible if the deficits exceed moderate stress levels (Slayter, 1973). Studies on four different fir (*Abies*) species suggest that respiration rates decline as stress increases and photosynthetic production drops (Puritch, 1973). Measurements of changes in the carbon dioxide compensation point indicate that "photorespiration increases even at moderate stress levels" (Slayter, 1973). Transpiration rates tend to decline as water deficits increase with stomatal closure occurring in response to the plant water losses (Lopushinsky and Klock, 1974). The plant water conducting system is "remarkably resistant to water stress" (Slayter, 1973) and permanent physiological damage to the translocation structures requires high levels of moisture deficit. At the stress level where stomatal closure first begins, recovery of photosynthetic ability is rapid when moisture is applied. If complete stomatal closure occurs in association with decreased soil water potential, physiological recovery may be incomplete or delayed depending on both the length and level of moisture stress (Larcher, 1975).

Environmental controls on seedling survival rates vary from species to species, but soil moisture availability is the primary factor (Ferrell, 1953). The period of greatest seedling mortality occurs just after germination during the early summer season (Ferrell, 1953). Water deficits during the germination period can effectively prohibit successful seedling development (Borger and Kozlowski, 1972). Seedlings that manage to germinate during periods of low water potential exhibit poor development in comparison with seedlings not subjected to a moisture deficit accompanying the germination period (Larson and Schubert, 1969). During an extended period of moisture deficit, a tree seedling will "become progressively desiccated until all parts die" (Lane and McComb, 1948). Competition between tree seedlings and grasses for available water is a critical survival factor because the roots of tree seedlings generally do not extend below the grass root system during the first season of growth (Lane and McComb, 1948). Differences among tree species in the amount of carbohydrates stored in their seeds determines the potential environmental dependence of an individual seedling. Larger seeds, such as oak acorns, provide more stored food which can be utilized in immediate root extension that eventually permits extraction of soil water from greater depths (Ferrell, 1953).

Plant Moisture Deficits and Soil Moisture

The movement of water from the soil column to the plant tissues is a complex process. Rates of water uptake depend on the root surface area and the difference in moisture potential between the roots and the soil solution (Larcher, 1975). The ascent of water from the base of a tree to the transpiring leaf surfaces is a passive process which involves dead tissues as a major transport corridor (Zimmermann and Brown, 1974). The generally accepted cohesion theory of sap ascent states that water is pulled upwards along a gradient of decreasing pressure that is related to transpirative losses from leaf cell walls (Zimmermann and Brown, 1974). Therefore, the internal water status of a plant is more closely related to the transpiration rate than to the soil water potential (Gardner, 1973). At low soil moisture tensions, leaf water deficits seem unrelated to soil moisture but, as water is extracted and soil moisture tensions increase, only small decreases in available soil water result in marked increases in leaf water deficits (Harms, 1969). The "intimate coupling between transpiration and photosynthesis through stomatal control of gaseous exchange" (Gardner, 1973) provides the linkage between soil moisture, plant-leaf water potential, and plant physiological processes.

Diurnal changes in atmospheric evaporative potential are closely correlated with variations in plant water stress and the accompanying changes in soil moisture (Haas and Dodd, 1972). Evapotranspiration within a given climatic region is independent of the specific plant cover and is primarily regulated by solar radiation recepits (Zahner, 1955). Local variability in the rate of moisture return to the atmosphere by the plant cover is related to the water holding capacity of the soil and the amount of moisture in the soil. These differences in soil moisture characteristics are a function of soil texture and structure. During periods of declining soil moisture, little difference exists in the rate of water loss for soils of differing texture, but the amount of available water that remains varies due to initial differences in water holding capacity (Zahner, 1955).

The influence of available soil moisture on natural vegetation communities is nicely illustrated in the prairie-forest ecotonal area of central Iowa. Here, available soil moisture is highest at all times in the maple-basswood forests, decreases in the oak-hickory forest stands, and is lowest in the prairie (Aikman and Smelser, 1938). These differences in available soil moisture corresponds with a physiognomic variation in plant rooting habit. Increasing dryness in the soil environment is accompanied by a greater percentage of shallow rooted plants (Aikman and Smelser, 1938) with the absence of sufficient moisture at greater soil depth suggested as a possible reason for the shallow rooting characteristic (George, 1939). An implication of this decrease in rooting depth with increasing aridity is that the vegetation in the prairies and prairie-forest transition must "rely largely on current moisture" (George, 1939) for survival and/or growth.

The environmental factors that regulate the availability of moisture and, hence, the rate of seedling survival are primarily a function of the current growing season supply of water and the short-term (day-to-day) changes in weather conditions. One method for determining the amount of soil water available is the water budget approach. This system of estimating the amount of water available for seedling and sapling survival or plant growth allows the calculation of daily values of water surplus or deficit based on precipitation inputs and evapotranspirative outflows.

SOIL MOISTURE AND THE WATER BALANCE

Since the concept was first promoted as an alternative means of climatic classification (Thornthwaite, 1948), water budget analysis has been of increasing importance in environmental monitoring (Mather, 1978). An accounting of precipitation inputs and the subsequent movement of water along the multitude of pathways that it can take within the earth's biosphere is a complex problem and a number of the factors involved have been measured only during experimental conditions (Mather, 1978). A water budget provides a reporting of moisture additions, subtractions, and storage changes at a particular site or over a given region, and if considered at the global scale the budget provides a statement of the earth's hydrologic cycle. Major factors incorporated into this accounting system are precipitation receipts, evapotranspirative losses, changes in soil moisture storage, runoff from the soil surface, and water movements from the rooting zone downward toward the local water table. Reserves of water in the plant rooting zone depend almost entirely on the balance between precipitation inputs and evapotranspirative losses. (Mather, 1978) and both of these principle factors are basic climatic elements. These final paragraphs of the literature review deal with the components of the water balance, the methods and equations for estimating potential evapotranspiration, and an evaluation of the applicability of these equations for this research effort. The last section will deal specifically with the Christiansen method of estimating potential evapotranspiration (Christiansen, 1966) and a justification will be presented for the selection of these equations for the data analysis.

Monitoring Soil Moisture - The Water Budget Approach

The importance of available soil moisture for plant survival and growth in the upper Middle West has been documented in the preceeding pages. Water budget analysis provides a means of relating vegetative stress associated with moisture deficits to the atmospheric conditions influencing the rates of photosynthesis and respiration. Utilization of energy by plants is a function of the water status of the vegetation (Shawcroft, Lemon, and Stewart, 1973) and phytogeographic distributions are a response to potential evapotranspiration, the atmospheric flux of moisture from the surface which is primarily a function of solar radiation receipts, and the replacement of that water through precipitation (Mather and Yoshioka, 1968). The intimate coupling of diurnal changes in plant physiological functions with the diurnal patterns of energy flux (Shawcroft, Lemon, and Stewart, 1973) helps demonstrate the importance of climatic controls on plant processes, and therefore, phytogeographic boundaries. Since changes in soil moisture are largely a function of day-to-day changes in weather conditions, obtaining quantitative estimates of soil moisture surpluses and deficits is possible through the monitoring of atmospheric properties. The water balance is a system that has been used successfully to monitor the important environmental changes that affect the amount of water in the plant rooting zone.

A number of atmospheric and edaphic factors are responsible for controlling the movement of water within the upper few feet of the soil, but it is possible to quantitatively monitor deficits in the amount of water necessary for plant survival or growth through an analysis of just two meteorological parameters, precipitation and potential evapotranspiration (Mather, 1978). The Thornthwaite method of computing the water budget and calculating potential evapotranspiration (Thornthwaite, 1948) has been widely used and most applications have involved the use of monthly mean climatic statistics (Mather, 1978). Problems exist in water budget studies of vegetation communities based on the use of monthly summary statistics, however, because changes in the plant rooting zone occur at time intervals much shorter than one month, "since precipitation is episodic while the evaporative demand is practically relentless, (and) a precipitation event might come too late (in the month) to save the plants" (Hillel, 1972). Other water balance approaches allow calculation of the daily changes in soil moisture surpluses or deficits that would not be evident using monthly statistics. Thornthwaite designed his equations for use with monthly climatic values, and, therefore, wind speed and humidity values were not taken into account because these parameters do not vary greatly from month-to-month in humid mid-latitude locations (Mather, 1978). "The Thornthwaite formula, which ignores humidity and wind, cannot be responsive to these significant daily changes and so computed daily potential evapotranspiration may deviate markedly from actual conditions" (Mather, 1978) and, therefore, other more complex equations may be necessary for water budget accounting on a daily basis.

Studies dealing with vegetation stress and its effects on either plant growth or reproduction and survival require water balance information for time periods much shorter than one month because short-term atmospheric iterations affect the supply of available moisture. Development of a water budget model for the state of Kentucky based on a two-layer soil moisture model has indicated that changes in available soil moisture relate to short-term fluctuations in precipitation and evapotranspiration and that weekly calculations of potential evapotranspiration provide a suitable index of plant water status (Hill, 1974). An earlier study that measured daily losses of water from the soil also implied an atmospheric control on the amount of soil moisture remaining for plant growth; this research indicated "that the rate of moisture extraction is not influenced by the amount of water present in the soil when the soil moisture is above the permanent wilting percentage" (Veihmeyer and Hendrickson, 1955) and, therefore, day-to-day changes in plant stresses are a response to short-term atmospheric variations. Calculations of correlation coefficients based on thirty three-day periods and relating accumulated moisture loss in the upper foot of soil with climatic factors at Vicksburg, Mississippi, indicate that both evaporation ($r=.79$) and solar radiation ($r=.76$) have a high correlation with water loss, whereas lower correlations exist with air temperature ($r=.60$), vapor pressure deficit ($r=.52$), relative humidity ($r=.21$), and wind ($r=.08$) (Stearns, 1958). These results suggest that a number of meteorological elements must be taken into account in order to accurately estimate the evapotranspirative flux induced by atmospheric conditions on a day-to-day basis, but the most important factor is the input of solar energy. One researcher has concluded that potential evapotranspiration can be thought of as a measure of the evaporative flux that results from radiation receipts (Barry, 1969).

Estimation of Potential Evapotranspiration

A number of different approaches have been successfully utilized in either experimental studies or in practical applications to estimate soil water losses. The majority of these equations were developed for use in irrigation scheduling in semi-arid or arid regions and it has been suggested that agricultural applications are one of the greatest potential uses of evapotranspiration technology (Jensen, Wright, and Pratt, 1971). Most of the models in practical application are designed to estimate daily values of soil moisture depletion based on the use of standard meteorological data; excessive costs, the necessary technical skills for the complex equipment, and data processing requirements prohibit the use of the more accurate energy balance or mass transfer methods for anything more than experimental studies (Jensen, 1972). Of the two principle components of the water budget, precipitation is normally measured at most Weather Service recording stations, whereas potential evapotranspiration must be estimated based on the meteorological elements that are monitored.

In order for evaporation to occur, two conditions must be satisfied: 1) a gradient in vapor pressure must exist away from the evaporating surface, and 2) a source of energy must be available to provide the heat of vaporization necessary for the phase change from liquid water to the vapor or gaseous state. The rate at which evaporation occurs depends on the strength of the vapor pressure gradient, the amount of energy available, the temperature of the evaporating surface, and the rate of vapor diffusion (a function of wind speed) away from the source location (Barry, 1969). Not all soil water losses occur directly through evaporation; transpiration, a passive process where water moves from the soil through the plant to the atmosphere in amounts generally exceeding the direct water needs of the plant, "takes place when the vapour pressure in the air is less than that in the leaf cells (Barry, 1969).

A number of different approaches have been developed to estimate the potential water loss from both the soil and plant cover based on measurable environmental parameters. As early as 1915, Meyer developed a formula based on wind velocity and vapor pressure deficit (Meyer, 1915). Blaney and Criddle developed their formula based primarily on temperature and radiation data during the 1940's (Blaney and Criddle, 1945) and their formula was widely used in irrigation scheduling. By 1953, it was suggested that weather data provide a real possibility for calculating irrigation water requirements and that solar radiation and pan evaporation tend to show the best results (Ashcroft and Taylor, 1953). At least seven different approaches (Table 2) have been presented for determining an estimate of the evaporative flux to the atmosphere (Tanner, 1968; Barry, 1969; Bordne and McGuinnes, 1973; and Mather, 1978). Essentially all of these approaches are designed to ascertain the precipitation-evapotranspiration relationships for a given location. Almost all assume that drainage downward from the rooting zone is negligible, but this is one potential source of error since in some cases it may not be reasonable to omit this factor (Tanner, 1968). Another possible source of error is the assumption that all precipitation that falls goes into soil storage until the reservoir is full, and then all remaining precipitation results in runoff until the soil reservoir is again depleted. As the potential sources of error indicate, at any given location there are a number of ways that water can be removed from the soil, but "evapotranspiration accounts for most of the depletion" (Jensen, Wright, and Pratt, 1971).

Table 2. A Grouping of Potential Evapotranspiration Estimation Methods

A. Direct Measurement

1) Eddy Correlation - measurement of the upward moisture flux in the atmosphere; this requires complex equipment and is subject to the limitations of the sensors.

2) Evaporation Measurement - devices that monitor the amount of water lost through evaporation from a moist surface. Atmometers, evaporation pans, and lysimeters are included in the group.

B. Modeling the Physics of the Evapotranspiration Process

3) Energy Budget - a micrometeorological partitioning of available net radiation and energy flows; the energy utilized in evaporation is computed as a residual from the equation.

4) Aerodynamic or Profile - a determination of the mass vapor flux based on the amount of turbulent diffusion that results from atmospheric instability and surface winds.

5) Mass Transport - expressions developed from Dalton's 1798 statement of the general principles of evaporation that relate evaporation to wind speed and the vapor pressure gradient.

6) Combination Methods - equations developed by combining the aerodynamic and energy budget approaches to eliminate unmeasured terms in the equation; Penman's method is one of the most widely utilized of the combination approaches.

C. Statistical Correlation

7) Empirical - a bookkeeping approach, usually based on only one or two climatic parameters (air temperature and solar radiation); these estimates of potential evapotranspiration are generally easy to evaluate since they rely on limited climatic data, but may not be of value outside the climatic region for which the empirical correlations were developed.

Examination of the different methods that have been proposed as a means of monitoring the transfer of moisture from the soil and plant cover back to the atmosphere (Table 2) indicates three major groupings of the approaches. The eddy correlation and evaporation measurement methods, both attempting to monitor and record the outward movement of soil water, either require the use of sophisticated equipment too technical to be widely utilized or as in the case of evaporation, are not among the data normally collected at first-order weather stations. The energy budget, aerodynamic, mass transport, and combination methods all attempt to model the physics of the evaporation process and quantify the important components. These methods require some data not normally measured by the United States Weather Bureau (e.g. solar radiation) and do not provide a means to estimate the missing parameters. Because direct measurements of evapotranspiration were not made by the U.S. Weather Bureau for the station network that was selected for this study and because the equations that treat the physics of the evaporation process could not be used, an empirical approach was selected for this research.

Empirical formulas attempt to correlate the known losses in soil water with pertinent climatic data based primarily on the results of regression analysis (Table 3).

Table 3. Empirical Potential Evapotranspiration Computation Methods

Temperature Only	Temperature and Solar Radiation	All Pertinent Data
Thornthwaite	Grassi	Christiansen
Blaney-Criddle	Turc	
Hamon	Makkink	
Papadakis	Jensen-Haise	
	Stephens-Stewart	

Most empirical equations were developed for a specific climatic area and new regression coefficients are usually calculated when the equation is applied in a different climatic realm. Several scientific investigators have proposed equations that require air temperature as the only measure of atmospheric conditions. The Thornthwaite and Blaney-Criddle methods are the best known and most widely used, whereas the Hamon and Papadakis approaches include a humidity term that is read from tabled values based on temperature (McGuinness and Bordne, 1972). A second group of researchers have utilized both air temperature and solar radiation as the climatic inputs into the regression equation. Examples of methods that use this approach are the equations by Grassi, Turc, Makkink, Jensen-Haise, and Stephens-Stewart (McGuinness and Bordne, 1972). One empirical formula (Christiansen, 1966) has been developed to include as many of the available meteorological parameters as possible. The Christiansen method also allows unmeasured variables to be estimated from the known data (e.g. percent possible sunshine can be estimated from sky cover in tenths) (Christiansen, 1966). While none of the empirical formulas are asthetically pleasing in a scientific sense, since they do not attempt to model the physics of the evaporation process, the Christiansen method alone incorporates a number of the meteorological parameters that effect the day-to-day changes in the evapotranspiration process.

Evaluation of Potential Evapotranspiration Estimation Method Applicability in the Great Lakes Region

One reason for the large number of different potential evapotranspiration estimation methods is that many were developed for use in a specific climatic regime. For example, Thornthwaite developed his equations based on climatic data from mid-latitude locations (Mather, 1978); the Stephens-Stewart equation was developed specifically for the atmospheric conditions in Florida (Stephens and Stewart, 1963) and a number of other approaches (Jensen and Haise, 1963; Blaney and Criddle, 1962; and Christiansen, 1966) were designed for irrigation scheduling in arid or semi-arid areas. An equation that works in one climatic region might not be applicable in all other areas and, therefore, analysis of the usefulness of each method in the Great Lakes region was necessary. A study designed to determine the applicability of fourteen different methods to compute daily values of potential evapotranspiration in humid continental climatic regions was conducted at Coshocton, Ohio. Based on their analysis using lysimeter values to determine the day-to-day changes in potential evapotranspiration, the authors concluded that six of the approaches gave satisfactory results for planning the use of available water supplies (Bordne and McGuinness, 1973). Of the six acceptable methods, two were methods that attempted to model the physics of the evaporation process. These combination approaches devised by Penman (Penman, 1963) and van Bavel (van Bavel, 1966) were not used in this study due to the unavailability of data. The United States Weather Bureau pan evaporation estimation method also produced a good fit with the lysimeter derived data, but data limitations prohibit the use of this method also. The three remaining recommended techniques, Jensen-Haise, Blaney-Criddle, and Christiansen, all involve an empirical approach. It is interesting to note that the Thornthwaite method, which was developed using data from the humid continental climatic region, was not satisfactory for daily computations of potential evapotranspiration. Of the three acceptable empirical methods, the Christiansen equations were chosen for use in this study because the computations are based on the same types of data that are used in the combination equations that attempt to model the physics of the evaporation process.

The potential evaporation estimation method developed at Utah State University by Christiansen and his students was designed to compute estimated monthly values of potential evapotranspiration in northern Utah. The equations were developed to:

1) include more of the climatological factors that affect evapotranspiration,

2) use the data published by the United States Weather Bureau,

3) allow the use of tables for computed climatic coefficients, and

4) provide for meaningful results even if some of the data are missing (Christiansen, 1966).

A summary equation can be written

$$PET = K * RT * CT * CW * CH * CS * CE * CV$$

in which PET is potential evapotranspiration, K is a dimensionless constant, RT is the amount of solar radiation reaching the outer layers of the earth's atmosphere, CT is a coefficient of mean air temperature, CW is a windspeed coefficient, CH is a coefficient of average daily relative humidity, CS is a sunshine percentage coefficient, CE is an elevation coefficient, and CV is a vegetative coefficient. Each coefficient that is based on atmospheric data is determined using regression equations that involve the input of either standard meteorological data or data obtained from tables. The Christiansen method was modified to compute daily values and regression coefficients were determined to allow the testing at Coshocton, Ohio, based on the region's humid continental climate (Bordne and McGuinness, 1973). The equations and tabled values presented by McGuinness and Bordne (McGuinness and Bordne, 1972) were used to compute daily estimates of potential evapotranspiration for each of the fourteen first-order weather stations selected for this study.

Summary

Water budget analysis has been shown to provide an acceptable means of estimating the amount of moisture available for plant survival and growth. Most plant moisture stresses are directly related to the day-to-day changes in the atmospheric demand for water (potential evapotranspiration), the precipitation received, and the amount of water remaining in the rooting zone. A number of different equations have been developed to estimate potential evapotranspiration, but only the empirical equations can be utilized in most geographic studies since the data for many of the other equations that deal with the physics of the evaporation process are not normally collected by the United States Weather Bureau. An empirical method based on regression analysis and developed by Christiansen allows for the use of as many of the pertinent meteorological parameters as possible. The Christiansen equations have been modified for use in humid continental clmiate locations and, as a result, provide acceptable estimates of the daily evapotranspirative flux. In this research, a daily water balance is computed based on precipitation receipts minus the estimated potential evapotranspiration and the resultant computed value of daily soil water status is used as an indication of plant water stress.

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Chapter III

METHODS

Assumptions and General Research Aims

In the introductory chapter, I surveyed the progress that has been made in understanding the relationships between the distribution of natural vegetation and patterns of surface weather. Ecoclimatological studies have advanced to the point where atmospheric factors thought to be related to physiological factors that regulate plant growth and survival have been incorporated into the research design (Larsen, 1971; Harman and Braud, 1975; and Sorenson, 1977). Following a review of the pertinent eco-physiological literature (Chapter 2) which suggests to this author that moisture stress is a primary factor controlling the distribution of natural vegetation in the upper Middle West, this research proceeds another step further to an eco-climatic analysis of potential evapotranspiration, a measure of plant moisture stress, and the associated wind flow patterns in the middle troposphere. In order to examine the possibility of a causal relationship between upper atmospheric circulation and the distribution of natural vegetation, I developed a research design to identify both the surface meteorological conditions associated with days that exhibit a gradient in environmentally-induced plant stress across the study area and the corresponding wind flow patterns in the middle troposphere. The specific research hypothesis to be tested is that modal (most frequent) patterns of upper atmospheric wind flow are associated with the surface environmental gradients in plant moisture stress that appear to delimit the position of the major vegetation transitions in the western Great Lakes region.

The following sequence of generalized statements summarizes the nature of the postulated climatic control of vegetation in the western Great Lakes region. Day-to-day changes in the strength and direction of the wind flow pattern in the mid-to-upper troposphere result in variation in the amount of precipitation and evapotranspiration as storms and different air masses traverse the region. These patterns of surface weather regulate the amount of water available for seedling survival and subsequent plant growth. Northwesterly wind flow in the upper atmosphere, the most frequent pattern affecting the upper Middle West, produces weather conditions which reinforce the contemporary vegetation distribution whereas other circulations produce surface climatic patterns with isorithms that tend to intersect rather than parallel the ecotone. The balance between precipitation receipts and evapotranspirative losses governs the amount of water in the soil zone. Plant roots extract this necessary moisture from temporary storage in the soil and as the amount of water in the soil decreases between precipitation events, the ability of a plant to extract moisture also decreases because the remaining soil water is held with greater resistance by capillary and hygroscopic forces. In general, the availability of soil water increases in a northeasterly direction within the western Great Lakes region because precipitation events are more frequent, relative humidity values are higher, solar radiation receipts are lower, and cloud cover is greater toward the Northern Mixed Forest region. Since tissue damage that leads to a general weakening of the plants within a community and to a greater potential for premature death of an individual occurs with higher frequency as the duration of the moisture deficit-induced physiological stress lengthens, the physiological damage and possiblity of death that result when a seedling is unable to obtain enough water necessary for the growth and maintenance functions of photosynthesis and respiration are more likely toward the southwest.

Development of this research design is based on the assumption that the climatic conditions during the study period, 1961 through 1974, can be used to represent the climate of the last 2,000 to 4,000 years, a time period when paleoecological evidence concerning the locational stability of the major ecotones in the upper Middle West indicates that a balance between climate and the major vegetation formations has existed (Bernabo and Webb, 1977). Additionally, it is assumed that the broad-scale phytogeographic pattern of the western Great Lakes region is set by atmospherically-controlled environmental conditions. I realize that not every plant distribution is a function of solely autecological conditions and that biotic influences are predominant in certain situations. While modern flora are thought to have evolved under conditions of climatic instability and the distributions of individual species, such as hemlock, may not reach an equilibrium condition during any interglacial (Davis, 1976), the strong correlation between the global climatic zones of today and the earth's major vegetation formations suggests that conditions have approached the equilibrium situation. Floristic changes associated with retrogressive succession have been identified for the present and past interglacials as soils have become increasingly acidic during the course of each interglacial (Iverson, 1964), but it is assumed in this research that the past 2,000 to 4,000 years of locational stability of the major plant formations indicates that edaphic factors will not further affect the location of the vegetation transition zones under study here.

This examination of the role played by middle tropospheric wind flow patterns in influencing the plant physiological processes which convert atmospheric inputs into parameters that regulate the range of a species and hence the distribution of major plant formations involves several major steps for the completion of the research. Based on a review of pertinent literature which indicates that plant physiological adaptations to atmospherically-induced moisture stress are important in controlling the distribution of vegetation in the western Great Lakes region, these steps include:

1) the identification of a daily meteorological statistic derived from surface data that can be used as a measure of the strength of atmospherically-induced plant stress,

2) determining both the surface weather patterns and the associated middle tropospheric wind flow patterns which are associated with gradients of this meteorological statistic that correspond with the plan of the major ecotones in the upper Middle West, and

3) linking together all aspects of the research to demonstrate the impact of the general circulation of the atmosphere on the natural vegetation distribution in the western Great Lakes region.

Location of the Study Area

The study area is located in the north central portion of the United States and includes the states of Minnesota, Iowa, Wisconsin, Michigan, and parts of North Dakota, South Dakota, Nebraska, Missouri, Illinois, Indiana, and Ohio (Figure 12). Boundaries of the study area are defined by the 98^{o} West meridian of longitude on the west, the 82^{o} West meridian of longitude on the east, the 40^{o} North parallel of latitude on the south, and the political boundary between the United States and Canada on the north. This region, with its major biogeographic gradients, was selected as an area to test the relationship between upper atmospheric controls and the surface weather patterns that generate the environmental stresses that reinforce the location of an ecotone. These specific states were selected to include the ecotone between the natural grasslands and the deciduous forest formation as well as the transition zone from the deciduous forests to the mixed deciduous-coniferous, Hemlock-White Pine-Northern Hardwoods, forests. Within the study area, contours of the mean summer season 500 mb surface (Figure 4), an indication of modal upper atmospheric wind flow, correspond with the mapped pattern of the vegetation transitions.

The vegetation transition from grassland through deciduous forest to northern mixed forest occurs in a lengthy northwest-southeast trending zone that stretches from the province of Alberta, Canada, to Michigan (Figure 13). This study deals with that portion of the transition zone that exists within the United States. The western boundary of the study area was selected to include the first-order weather stations at Fargo, North Dakota; Sioux Falls, South Dakota;

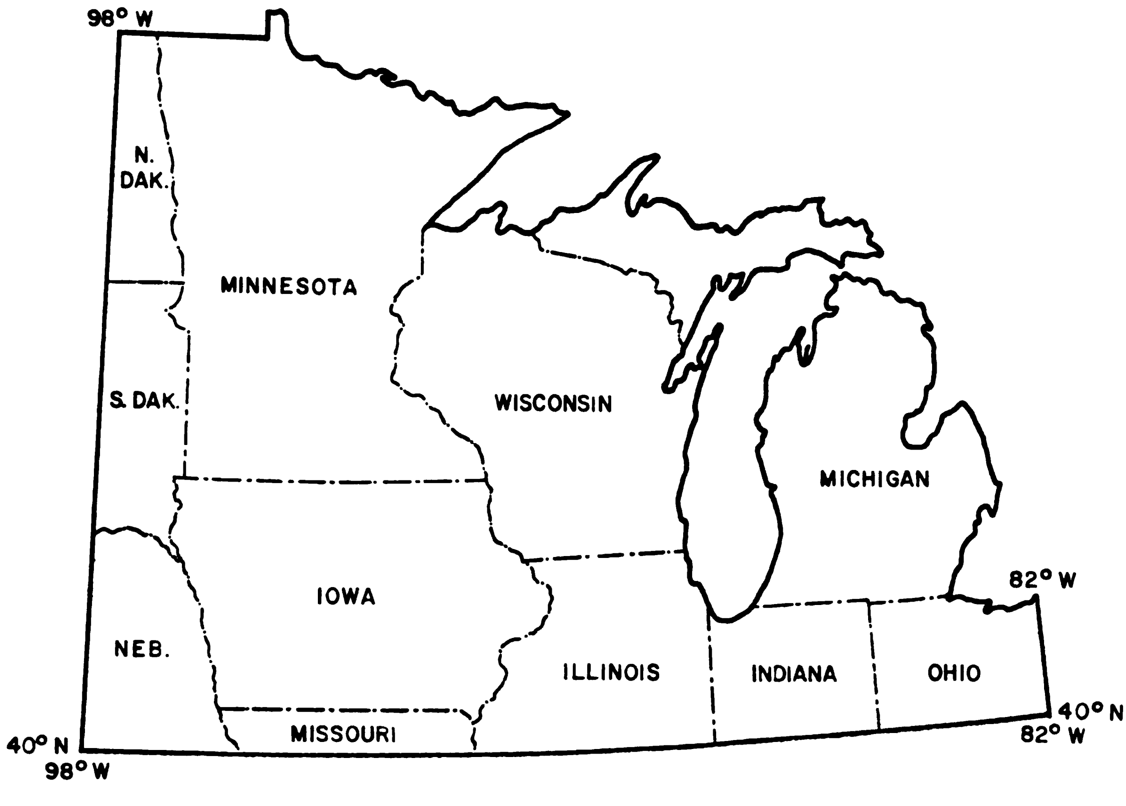

Figure 12. The Study Area.

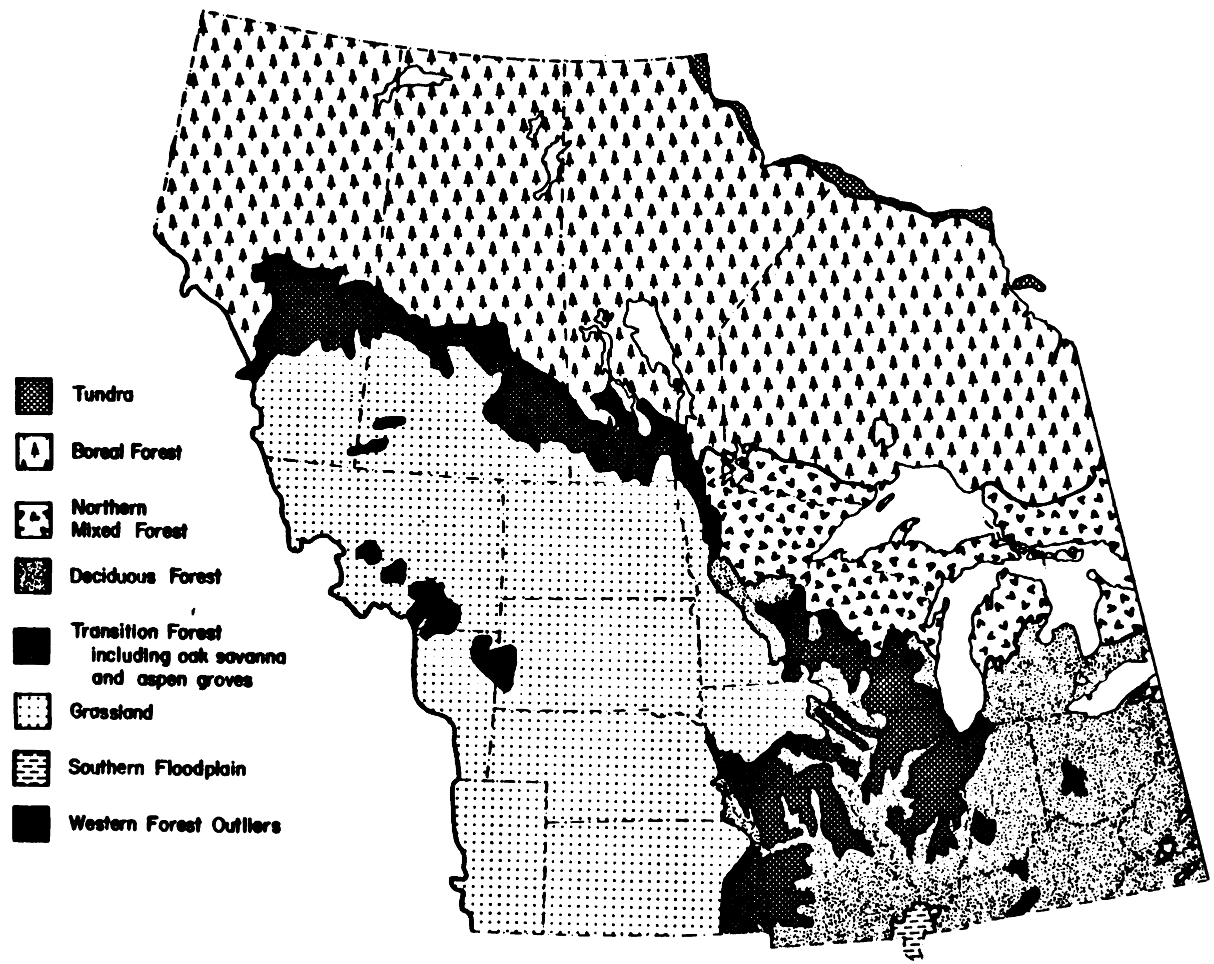

Figure 13. Generalized Vegetation Patterns in Central North America.
Source: Oxford Regional Economic Atlas, 1967.

and Lincoln, Nebraska, within the study area; these stations provide meteorological data from areas where the predominant natural vegetation was prairie grassland. In the eastern part of the study area, the boundary was selected at 82° West longitude to limit the eastward extent of the study region to the area with a pronounced southwest-northeast vegetation gradient. The southern boundary (Figure 14) was selected so as to essentially bisect the Prairie Peninsula, the eastward extension of natural grassland vegetation that extends across Illinois, Indiana, and into Ohio (Transeau, 1935). Different climatic gradients are thought to characterize the northern and southern margins of the Prairie Peninsula.

> "The northern margin of the region is characterized by (1) a relatively steep gradient of winter snowfall and snowcover and (2) a small but abrupt increase in frequency of days with rain in summer and an accompanying increase in cloud cover and relative humidity. The southeastern margin of the prairies is marked by a zone of steep winter rainfall gradient" (Borchert, 1950).

Thus, the southern boundary of the study area is defined at 40° North latitude to exclude the vegetation transitions of the southeast margin of the Prairie Peninsula and thereby reduce the complexity of vegetation change within the study area.

Research Procedures

The first step in this research effort was a review of much of the eco-physiological literature dealing with both the dominant plant species of the western Great Lakes region and the factors identified as possible controls of the distribution of natural vegetation within the area. Results of this review suggest to the author that moisture stress is the critical environmental element in controlling the

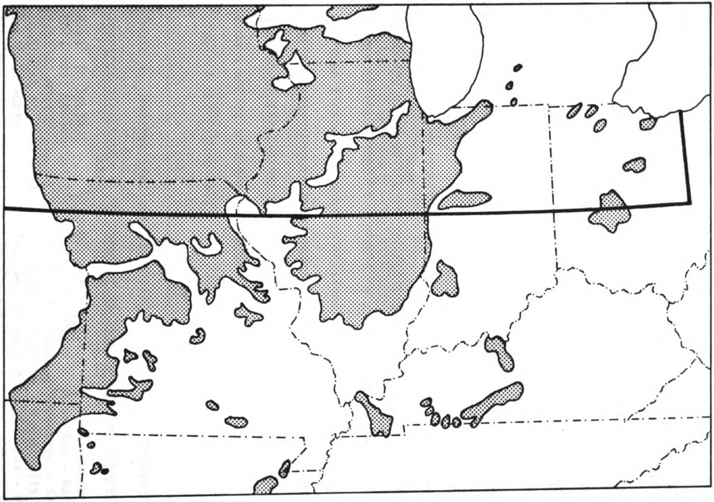

Figure 14. The Southern Boundary of the Study Area and its Relationship to the Prairie Peninsula. Source: Transeau, 1935.

phytogeographical distributions of the region and that potential evapotranspiration estimates combined with precipitation data could be used on a daily basis as a measure of the magnitude of this environmentally-induced plant physiological stress. Based on these conclusions, this climatological study was designed to examine the relationship between the general circulation of the atmosphere and the patterns of potential evapotranspirative flux across the upper Middle West.

Since plants are thought to respond to the changes in environmental conditions on a day-to-day basis, the research was designed to identify the geographic pattern of daily potential evapotranspirative flux. The Christiansen equations of estimating potential evapotranspiration, which are based on the use of all available meteorological data, were chosen as the method of determining a surogate measure of plant stress. Fourteen first-order weather stations were selected for the surface data analysis (Figure 15). These locations were chosen from the population of first-order weather stations within the study area to provide a series of eight transects across the western Great Lakes region (Table 4 and Figure 16).

Table 4. Weather stations comprising the study area transects

Transect direction	Weather stations along the transect
North to South	Marquette - Green Bay - Milwaukee - Peoria
Northeast to Southwest	Sault Ste. Marie - Green Bay - Waterloo - Lincoln
East to West	Flint - Milwaukee - Rochester - Sioux Falls
Southeast to Northwest	Ft. Wayne - Madison - Minneapolis - Fargo
South to North	Peoria - Milwaukee - Green Bay - Marquette
Southwest to Northeast	Lincoln - Waterloo - Green Bay - Sault Ste. Marie
West to East	Sioux Falls - Rochester - Milwaukee - Flint
Northwest to Southeast	Fargo - Minneapolis - Madison - Ft. Wayne

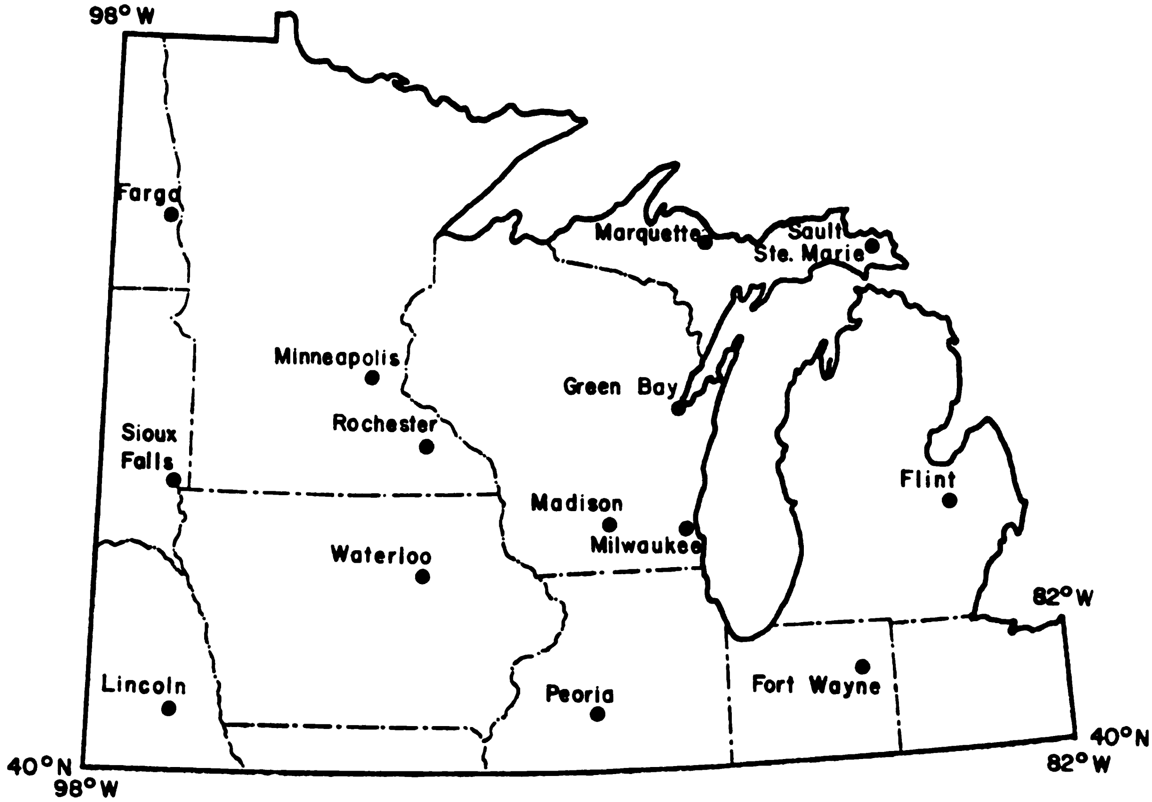

Figure 15. Location of Selected Weather Stations.

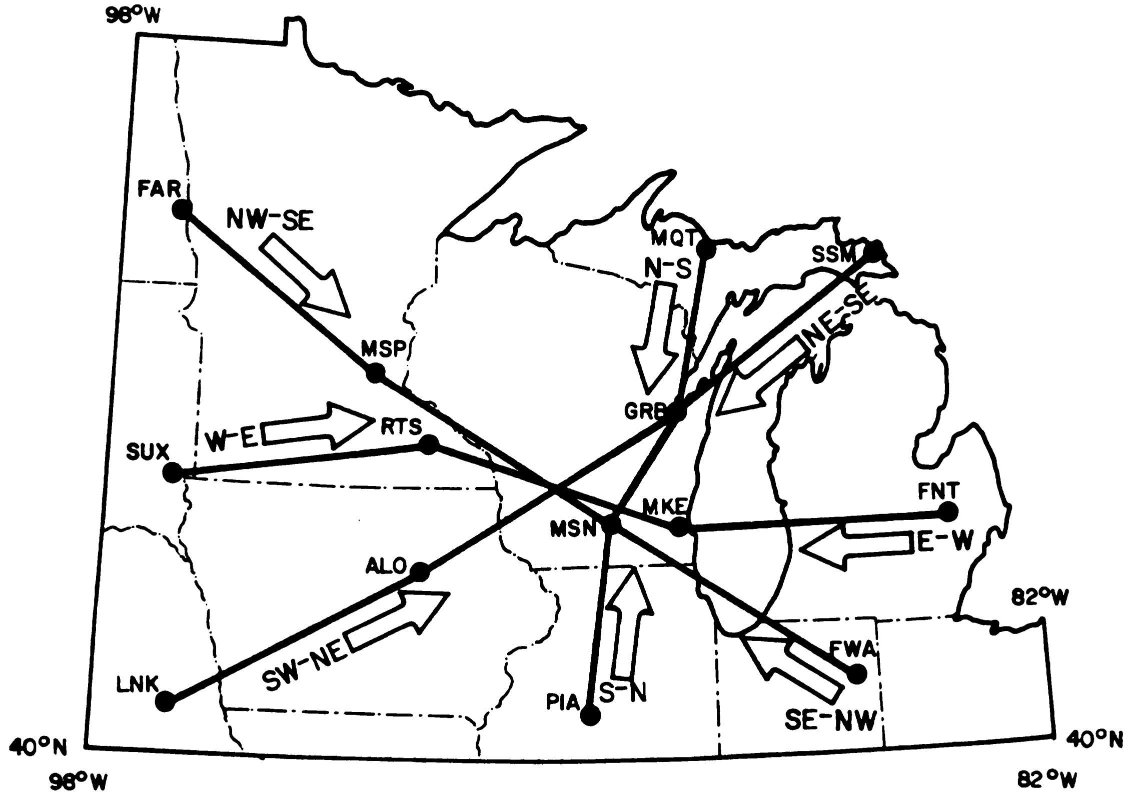

Figure 16. Study Area Transects.

Four months, May through August, were selected for the climatological analysis because these late spring and summer months comprise the critical season for seedling and sapling survival in the Great Lakes region and it was assumed that moisture-stress-related seedling survival rates are a primary phytogeographic control. The period from 1961 through 1974 was selected for analysis because of the availability of upper atmospheric data for that fourteen year time interval. Using a stratified random sampling procedure, I selected eight months from the fourteen year period for detailed surface and middle tropospheric climatological analysis (Table 5). The sampling procedure was designed to insure that each month (May through August) was equally represented. The selection of two years of data for each month was made to insure an adequate sample size while at the same time limiting the amount of data to be processed. For each date within a selected month, the meteorological data were analyzed to identify those study area transects that had a continuous decrease in plant moisture stress as indicated by the balance of precipitation and potential evapotranspiration estimates. Sample days thus were separated into eight different groups that were not mutually exclusive based on the direction(s) of the stress gradient(s) on the date in question. A day could be placed into more than one group if a continuous decrease in moisture stress

Table 5 Months selected for detailed analysis

May	June	July	August
1961	1965	1973	1968
1972	1970	1974	1970

occurred along two or more transects. Days that did not exhibit a continuous gradient in potential evapotranspiration-estimated plant stress values were excluded from further study. The frequency and intensity of the daily stress gradients along each transect were determined and composite maps showing the surface pressure distribution were prepared to depict the synoptic weather pattern(s) associated with each group.

Middle tropospheric wind flow conditions were also analyzed for each of the eight transect groups and monthly summaries of the fourteen years of data were tabulated for comparative purposes. Histograms showing the frequency of the direction of upper level wind flow were produced for each transect grouping and for the total population of fourteen years (May through August) of upper level winds for the study area; these mid-tropospheric climatological data were also used to produce mean 500 millibar height contour maps for each of the eight transect groupings.

The following sections of this chapter describe the types of climatological data that were obtained for this research effort, the data sources, and the data processing procedures that were utilized. The last section is a statement of the procedures used to test the hypothesis.

Data Sources

In this research effort, meteorological data from both the surface and upper levels were required. The surface data were used for computing daily values of potential evapotranspirative flux and in the production of composite maps showing the distribution of surface pressure (an indication of the synoptic weather pattern) for each of the eight transect groups. A primary source for surface meteorological data was the daily summary statistics available for each first order weather station in the publication Local Climatological Data. Copies of necessary Local Climatological Data publications were obtained from the National Climatic Center in Asheville, North Carolina, and from the Michigan Weather Service office in East Lansing, Michigan. Data extracted from the weather station summary statistics included the daily values of mean temperature, noon relative humidity, average wind speed, the percent of possible sunshine, and precipitation total. Some of the required data, not found in Local Climatological Data, were obtained by contacting the individual offices that compile the state weather records, e.g. wind data for Lincoln, Nebraska, were obtained by this method. Additional missing data were obtained through estimates based on related factors; for stations with no data concerning the percentage of possible sunshine or noon relative humidity, the sky cover (in tenths) from sunrise to sunset was used to obtain an estimate of percent possible sunshine (Table 6) and the daily temperature range was used to obtain an estimate of the noon relative humidity percentage through the use of a regression equation identified by Christiansen (noon relative humidity = 113 - (2.5) (the difference in degrees fahrenheit between the maximum and minimum temperatures)) (Christiansen, 1966). Values of noon relative humidity obtained from the regression equation were adjusted to fit within the known limits of the relative humidity values; most of the adjustments were made to lower the estimated value from the regression equation to 100% if the daily temperature range was small and the computed value exceeded

Table 6 Sky Cover Conversion to Percent of Possible Sunshine

Sky Cover (tenths)	% Possible Sunshine
0	100.0
1	97.6
2	93.4
3	87.6
4	80.2
5	71.0
6	60.2
7	47.6
8	33.4
9	17.6
10	0.0

100%. Infrequently, adjustments were made to change the estimated noon humidity value to the known minimum or maximum value for the date if the computed value exceeded the daily limits published in Local Climatological Data. As stated earlier, the surface weather observations and estimated values were used to compute estimates of the daily potential evapotranspiration for each of the fourteen weather stations for each day in the eight months selected for detailed analysis. The value of daily precipitation minus the potential evapotranspiration estimate was calculated to provide an indication of the daily water balance or the amount of plant moisture stress on any given date.

An additional source of surface weather data was the Daily Weather Maps, Weekly Series published by the National Weather Service. These maps depicting surface weather observations made at 1200Z GMT (7 am CDT) were the source of barometric pressure and frontal location data used in the construction of composite maps showing the average weather pattern associated with each transect grouping.

Fourteen years of upper atmospheric data were obtained from the National Center for Atmospheric Research in preparation for this study. These tropospheric meteorological data covering the United States, Canada, and Mexico include temperature, dew point depression, wind direction, wind speed, and height values for the 300, 500, and 700 millibar surfaces. The rawinsonde data for approximately 150 North American station locations cover the fourteen year period from January, 1961 through December, 1974.

Data Processing

A major portion of this scientific effort involved data processing and summarization in an effort to test the research hypothesis that upper level wind flow and the distribution of natural vegetation are interrelated. Meteorological data were used to compute daily estimates of potential evapotranspiration using the Christiansen method and these estimates were then combined with the daily precipitation values to produce the daily water balance, a surrogate for plant moisture stress. A transect analysis of the daily estimates of the gradient in moisture stress across the study area was then used to identify the pattern, frequency, and intensity of this important eco-physiological control. With the identification of specific dates with known plant moisture stress patterns, it became possible to correlate the wind flow direction at the 500 millibar level with those patterns and deduce a relationship between upper-air circulation and plant stress. Height contour maps of the 500 millibar surface were produced for each transect grouping to assist further in the explanation of the relationship between the upper level wind flow pattern and the distribution of natural vegetation. Additional support for the climatological explanation was gained through the production and interpretation of composite maps of the surface weather conditions for each transect group. The following paragraphs detail more fully the steps taken in this analysis.

Computation of potential evapotranspiration estimates based on the Christiansen method (Christiansen, 1966) was accomplished through the use of interactive computer software, Program PEVAP (see appendix 1), written by the author for use on Michigan State University's CDC 6500 computer. The required input data included: the station name, date, daily mean temperature, daily mean wind speed, relative humidity at noon (LST), percent possible sunshine, and the daily precipitation total. The Christiansen formula:

$$PET = (.473)\ (RT)\ (CT)\ (CW)\ (CH)\ (CS)\ (CE)\ (CV)$$

involves the multiplication of a numerical constant and several empirically derived coefficients that represent the meteorological factors that influence potential evapotranspiration. The value of RT, a measure of solar radiation at the top of the atmosphere, is read from meteorological tables. The CT term in the equation is an expression of air temperature where

$$CT = -.0673 + .0132\ (TA) + .0000367\ (TA)^2$$

and TA is the mean daily air temperature. Wind data are also incorporated into the equation through the CW coefficient where

$$CW = .708 + .00546\ (W) - .00001\ (W)^2$$

and W is the wind speed in miles per day at two feet above the surface. Converting the National Weather Service wind speed measured in miles per hour at the standard height of twenty feet to miles per day at two feet above the surface is accomplished with the formula:

$$W_2 = (.215)\ (W_{20}) + (.00154)\ (W_{20})^2$$

if the average wind speed in miles per hour is less than 7.9 and where W_2 = the wind speed in miles per day at two feet above the surface and W_{20} = the wind speed in miles per day at the standard height (wind speed in miles per day is obtained by multiplying the wind speed in miles per hour by a factor of 24). The formula:

$$W_2 = (.817)\ (W_{20}) - 58.4$$

is used if the wind speed in miles per hour is greater than 7.9 (Christiansen, 1966). An additional factor included in the formula is CH, a humidity term, where

$$CH = 1.25 - (.0087)\ (RH) + (.000075)\ (RH)^2 - (.0000000085)\ (RH)^4$$

and where RH is the relative humidity percentage at noon (LST). The sunshine coefficient, CS, is computed from

$$CS = .542 + .008\ (S) - .000078\ (S)^2 + .00000062\ (S)^3$$

where S is the percentage of possible sunshine. The station elevation is entered into the computations through the CE term,

$$CE = .97 + (.03)\ (E)$$

where E is the site elevation above mean sea level in thousands of feet. The final term, CV, is a vegetative coefficient that is read from tabled values. In this study the vegetative coefficients used were the daily values extrapolated from monthly data for Indiana presented by Christiansen (McGuinness and Bordne, 1972). The multiplication of all the terms in the equation results in an estimate of the value of potential evapotranspiration in inches of water per day.

The output from program PEVAP includes both the daily estimate of potential evapotranspiration and the daily precipitation total. These statistics were the required input for additional interactive computer software, program PESLOPE (see appendix 2), which was designed to determine the spatial changes in the values of both the potential evapotranspiration estimates and a new variable, stress, determined by subtracting the daily precipitation total from the potential evapotranspiration. The program determines the change in both the potential evapotranspiration and the stress values between each station along each of the eight study area transects and identifies those transects which exhibit a continuous decrease in the values. The output identifies, for each day during the month, the magnitude of the change along any transect which had a continuous decrease.

The specific dates identified through the surface analysis of the balance between precipitation and potential evapotranspiration were then used to form eight different data subsets, each of which corresponded with a gradient of decreasing values of plant moisture stress along a study area transect. Daily rawinsonde data for the 500 millibar surface were extracted from the National Center for Atmospheric Research data tapes for those dates and grouped together to form eight subsets corresponding with the individual stress gradients. These data for the recording stations within the study area (Table 7) were used to produce histograms of the combined frequency of wind flow direction for the seven stations for each of the eight transect groups; summary statistics for all dates during the fourteen years of analysis were also obtained for comparison purposes. In addition, pressure height data were used to construct mean maps of the 500 millibar surface for each subset of stress gradient days. Height data for each date identified within a transect subset were averaged for each station location and these mean height statistics were used as input into the Surface II mapping program (Sampson, 1977).

Table 7. Rawinsonde Data Stations Used to Produce The Summary Histograms For Each Transect Group

Flint, Michigan
Green Bay, Wisconsin
International Falls, Minnesota
Omaha, Nebraska
Peoria, Illinois
St. Cloud, Minnesota
Sault Ste Marie, Michigan

The Surface II software produces labeled contour maps with a wide variety of options available through user specifications.

Additional data processing included the production of composite surface pressure maps for the eight stress gradient day groupings. Composite maps are prepared by averaging statistics describing the characteristics of the pressure distribution rather than averaging the pressure values recorded for individual station locations. The descriptive statistics used to produce the composite maps included: the central pressure value and pressure difference between the center and the outermost closed isobar surrounding each pressure cell, the size of the pressure cells in both a north-south and an east-west direction, and the geographic location of the center of each pressure cell. Also included is a descriptive statement of the shape of the pressure pattern and an indication of both the type(s) of front(s) and the frontal location(s). Based on the resultant mean descriptive statistics, composite maps are drawn using the averaged values as a guide in the map construction.

An examination of the surface weather pattern on each day during the eight months selected for this study was used to produce a set of generalized synoptic descriptions for summer season surface weather patterns affecting the western Great Lakes area. Based on this preliminary examination, six simplified synoptic pressure distributions were arbitrarily choosen to encompass all the variability found on the maps (Table 8). These pressure cell distributions provided a simple scheme for classifying the individual days within a transect grouping. For each grouping of days with similar stress gradient orientations, the daily surface weather features were matched with one

Table 8. Synoptic Descriptions used in the Classification of Surface Pressure Distributions

1. Anticyclone dominating the western Great Lakes region.
2. Cyclone dominating the area.
3. Anticyclone to the west over the Great Plains, cyclone to the east.
4. Cyclone to the west, anticyclone over the eastern United States.
5. Anticyclone north of the study area in central Canada, cyclone to the south.
6. Cyclone north of the area, anticyclone over the southern Mississippi Valley.

of the six general synoptic patterns. Frequencies for each of the six generalized synoptic patterns were totaled for every transect group and, in the course of the study, it was determined that each of the transect groupings had at least one weather pattern that could be used to typify those stress gradient days. Composite maps were produced for the synoptic descriptions that accounted for at least 25% of the days within a transect grouping. This procedure, which combines descriptive statistics for days with the same synoptic pattern, produces a final map product which retains an appearance similar to a daily pressure distribution.

Hypothesis Testing Procedure

In order to test the hypothesis concerning the influence of modal atmospheric circulation on the distribution of natural vegetation, the following steps were taken. From an analysis of the 500 millibar wind flow data, the most frequent flow direction was determined for all growing season days (May through August) during the fourteen year period and for all days within the transect subgroup that represents days when the stress gradient corresponds with the alignment of the vegetation transition. In order for the hypothesis to be accepted, two conditions must be met. First, the mode of the subset of the population that represents the days in the category associated with ecotonal alignment should be similar to the mode of the population of all growing season days. Second, the subset must not be a random sample from the population, but a statistically significant grouping of the most frequent flow direction as demonstrated by a chi-square test on the frequencies of the various flow directions. If the hypothesis is to be accepted, the results will show that modal patterns of atmospheric circulation at the 500 mb level are associated with distributions of moisture stresses at the surface that conform to the plan of the ecotones, suggesting that Midwestern phytogeographic boundaries have adjusted not to rare, extreme events, but to the long term patterns of accumulated stresses.

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Chapter IV

RESULTS

The Ecoclimatological Hypothesis

As stated in the introductory chapter, a pronounced gradient exists within the natural vegetation of the western Great Lakes region. Middle tropospheric wind circulation is suggested to be an important factor in controlling the location of this marked transition, which separates the grasslands in the southwest from a deciduous forest belt and then the mixed coniferous and deciduous forest region to the northeast. The mean summer season long wave pattern over the mid-continent region of North America suggests that surface weather events are frequently steered along a path which parallels the ecotonal locations of the upper Middle West. In general, environmental conditions associated with a migrating surface cyclone vary spatially and greater precipitation effectiveness can be expected north of the low's track. Since the vegetation adjusts through competition to the spatial pattern of environmental stresses created in part by the day-to-day changes in atmospheric conditions, it is the purpose of this study to examine mid-tropospheric wind circulation on days when a gradient in evapotranspirative stress across the western Great Lakes region suggests a causative relationship with the position of the ecotones. The hypothesis of this study is that the frequency of circulations which are causally associated with the natural vegetation distribution has the same mode as the population of all summertime flow patterns and that these circulation days which are related to surface conditions reinforcing the ecotonal locations are not a random sample of the population.

In review, this examination of the nature of the relationship between phytogeographical distributions and climatic patterns used meteorological data from fourteen growing seasons and a subset of eight randomly selected summer season months which provided the data base for detailed analysis of weather conditions at both the surface and at the 500 millibar level in the middle troposphere. Specific days with a gradient in potential evapotranspiration across the western Great Lakes region were identified and these days were then used to examine the associated patterns of surface weather and upper atmospheric circulation. The following sections of this chapter present the results of: 1) the transect analysis of the surface data, 2) an analysis of the typical surface weather conditions that were identified for each stress days group, and 3) the examination of 500 millibar wind flow patterns for each transect grouping. Interpretation of the implications of the research findings will be presented in Chapter 5 (Discussion); the primary purpose here is to describe the results of the data analysis.

Analysis of the Surface Water Balance Data

Computations of a surrogate measure of plant moisture stress (estimated potential evapotranspiration minus the total precipitation) were made for every day in eight randomly selected months for each of fourteen surface data stations. Analysis involving eight transects across the western Great Lakes was then used to group together those days with similar stress patterns. The estimated values of plant stress computed using this water balance approach were compared for adjacent stations along a transect in the following manner. The value calculated for the second station was subtracted from the value for the first station and the result was checked to see if it was positive and greater than zero, which would indicate higher plant stress values at the beginning of the transect. Gradients of continuously decreasing stress in one or more transect directions across the study area were identified on 52% or 128 of the 246 days studied (Table 9). It can be noted that the frequency of days with one or more stress gradients increased from an average of only 44.3% for the months of May and June to 59.7% for the months of July and August.

The stress gradient analysis was done for each of the eight transects and days with a continuous change in stress values along one or more transect(s) were selected for further analysis. A decreasing gradient in plant moisture stress occurred most frequently along the transect from the southwest to the northeast (SW-NE)* (Table 10). The lowest frequency occurred in the opposite transect direction where only six cases were identified with high stress values in the forests of the northeast and a change to lower values as one proceeds toward the grasslands to the southwest. The net impact of the spatial variation in plant moisture stress can be illustrated by combining the frequency statistics for the transect groupings that are in opposite directions (Table 11). Based on the random sample used for this study, the cumulative effect of the occurrence of all stress gradients

*Transect abreviations (e.g. NW-SE) refer to the area with high stress values (NW) and the direction in which values continuously decrease (SE).

Table 9. Frequency and percentage of days of continuous stress gradient per month.

Month	Number of days with no stress gradient		Number of days with one or more stress gradients	
May, 1961	18	(58.1%)	13	(41.9%)
May, 1972	15	(48.4%)	16	(51.6%)
May totals	33	(53.2%)	29	(46.8%)
June, 1965	19	(63.3%)	11	(36.7%)
June, 1970	16	(53.3%)	14	(46.7%)
June totals	35	(58.3%)	25	(41.7%)
July, 1973	14	(45.2%)	17	(54.8%)
July, 1974	9	(29.0%)	22	(71.0%)
July totals	23	(37.1%)	39	(62.9%)
August, 1968	14	(45.2%)	17	(54.8%)
August, 1970	13	(41.9%)	18	(58.1%)
August totals	27	(43.5%)	35	(56.5%)
Grand total	118	(48.0%)	128	(52.0%)

Table 10. Frequency of occurrence and gradient descriptive statistics for each transect group.

Transect Direction	Number of Occurrences	Mean Gradient	Median Gradient	Gradient Range Highest	Gradient Range Lowest	Sum of Individual Occurrences
NW-SE	15	.218	.179	.477	.031	3.276
N-S	12	.167	.178	.270	.065	2.009
NE-SW	6	.265	.292	.345	.121	1.590
E-W	21	.202	.176	.422	.055	4.239
SE-NW	17	.226	.182	.551	.046	3.841
S-N	29	.207	.202	.429	.064	6.012
SW-NE	39	.261	.240	.552	.076	10.162
W-E	31	.258	.239	.482	.077	7.996

Table 11. Net frequency of continuous gradients along study area transects.

(SW-NE)	-	(NE-SW)	=	39	-	6	=	33
(S-N)	-	(N-W)	=	29	-	12	=	17
(W-E)	-	(E-W)	=	31	-	21	=	10
(SE-NW)	-	(NW-SE)	=	17	-	15	=	2

Table 12. Net stress differences along study area transects.

(SW-NE)	-	(NE-SW)	=	10.162	-	1.590	=	8.572
(S-N)	-	(N-S)	=	6.012	-	2.009	=	4.003
(W-E)	-	(E-W)	=	7.996	-	4.239	=	3.757
(SE-NW)	-	(NW-SE)	=	3.841	-	3.276	=	0.565

Table 13. Frequency of stress events longer than one day

Transect	Number of stress days followed by at least one additional stress day	Number of stress days followed by at least two additional stress days
NW-SE	3 (20.0%)	2 (13.3%)
N-S	4 (33.3%)	1 (8.3%)
NE-SW	1 (16.7%)	0 (0.0%)
E-W	6 (28.6%)	2 (9.5%)
SE-NW	2 (8.5%)	0 (0.0%)
S-N	5 (17.2%)	3 (10.3%)
SW-NE	12 (30.8%)	5 (12.8%)
W-E	8 (25.8%)	2 (6.5%)

is one of more frequent stress in the southwest with a continuous decrease toward the northeast. A net S-N gradient occurred only about half as frequently and a net W-E gradient was less than one-third as frequent.

The magnitude of the change in stress values along a transect is probably as important in plant geography as the frequency of a stress gradient. By summing the individual daily values of stress change along the transect for each group within the sample, an additional indication of the spatial dynamics of plant moisture stress in the western Great Lakes region is provided (Table 12). Again, the net impact is for the SW-NE transect to have the greatest slope or end-to-end contrast associated with it. The gradients along the S-N and W-E transects are very similar in magnitude with both less than half the change along the SW-NE transect. The two transects that parallel the plan of the ecotones, SE-NW and vice versa, show little difference in either frequency or magnitude and the net impact is near zero.

Another important aspect of the data analysis concerned the persistence from one day to the next of a stress event along any transect (Table 13). Again, the SW-NE transect had the greatest frequency values and high percentages of this persistence measure.

Analysis of the monthly summary statistics for both the magnitude of the stress values and the frequency of days falling within each transect group shows interesting seasonal changes. The values of the mean slope for each transect and for all eight groups combined indicate that in general July is the month with the steepest gradients (Table 14). Weakest gradients of plant stress along the study area transects occur most frequently in May and June whereas the summer

Table 14. Transect Mean Stress Values by Month.

Month	NW-SE	N-S	NE-SW	E-W	SE-NW	S-N	SW-NE	W-E	Total
May	.169	.093	.250	.236	.190	.129	.187	.197	.189
June	----	.148	.307	.236	.236	.225	.222	.237	.219
July	.261	.223	----	.173	.221	.243	.297	.280	.258
August	.262	.157	.227	.159	.286	.198	.293	.256	.241
Totals	.218	.167	.265	.202	.226	.207	.261	.258	.229

Table 15. Monthly variability in stress transect frequency and percentage

Transect	May		June		July		August	
NW-SE	7	(46.7)	0	(0.0)	3	(20.0)	5	(33.3)
N-S	2	(16.7)	1	(8.3)	4	(33.3)	5	(41.7)
NE-SW	3	(50.0)	2	(33.2)	0	(0.0)	1	(16.7)
E-W	8	(38.1)	6	(28.6)	4	(19.0)	3	(14.3)
SE-NW	5	(29.4)	3	(16.7)	6	(35.3)	3	(17.6)
S-N	4	(13.8)	12	(41.4)	5	(17.2)	8	(27.6)
SW-NE	7	(17.9)	8	(20.5)	11	(28.2)	13	(33.3)
W-E	4	(12.9)	3	(9.7)	15	(48.4)	9	(29.0)
Total	40	(23.5)	35	(20.6)	48	(28.2)	47	(27.6)

months of July and August are characterized by stronger contrasts across the region. These differences between late spring and summer months are also apparent in the statistics that show the frequency and percentage of stress days by month for each transect group (Table 15). For example, the transects with high values of stress in the northwest, northeast, and east obtain their greatest frequency and percentage of occurrence in May. In June, the NE-SW and E-W transect groups maintain relatively high values while the S-N trajectory reaches its greatest frequency. Different transect groupings have greater relative importance during the summer months. In July and August, the highest frequencies are obtained by the transects with high stress values in the southwest and west, with lesser maxima for the N-S and SE-NW trajectories.

In summary, considerable variability exists in the timing, occurrence frequency, and gradient magnitudes for the eight transect groups of the surface water balance data. This diversity can be seen in a comparison of transect statistics for both the frequency and magnitude of stress days, where the highest values occur in association with the southwest to northeast trajectory. Additional differences occur as the growing season progresses, with more variable stress gradient patterns characteristic primarily of the late spring months, while the moisture stress gradients that tend to reinforce the distribution of natural vegetation are more frequent during the summer months of July and August.

Surface Synoptic Patterns Associated with each Transect Group

Variation in the distribution of surface high and low pressure centers and the location of frontal positions play a prominent role in determining the exact meteorological conditions at any given site or along one of the study area transects. The importance of vertical motions in the atmosphere and the relationship between surface weather features and wind circulation in the middle troposphere have already been discussed in Chapter One and mean 500 millibar wind flow patterns for each of the eight stress day groupings are presented later in this chapter. This section presents the results of an analysis of the surface weather patterns associated with each transect group.

The NW-SE Transect

Higher values of potential evapotranspiration in the northwestern part of the upper Middle West with a continuous decrease toward the southeast are associated with a rapidly changing surface weather pattern. Seven of the fifteen days within this transect group were characterized by an anticyclone migrating into the northern Great Plains and a low pressure cell moving east from the study area into southern Canada (Figure 17). An additional feature that usually accompanies this pattern is a cold front trailing from the low center back to the southwest and cutting across the southeastern part of the study area. Clouds and precipitation probably occur in the area ahead of and immediately adjacent to the frontal position, whereas clear to partly cloudy skies are more likely in association with the subsident conditions and rising surface pressure values to the northwest.

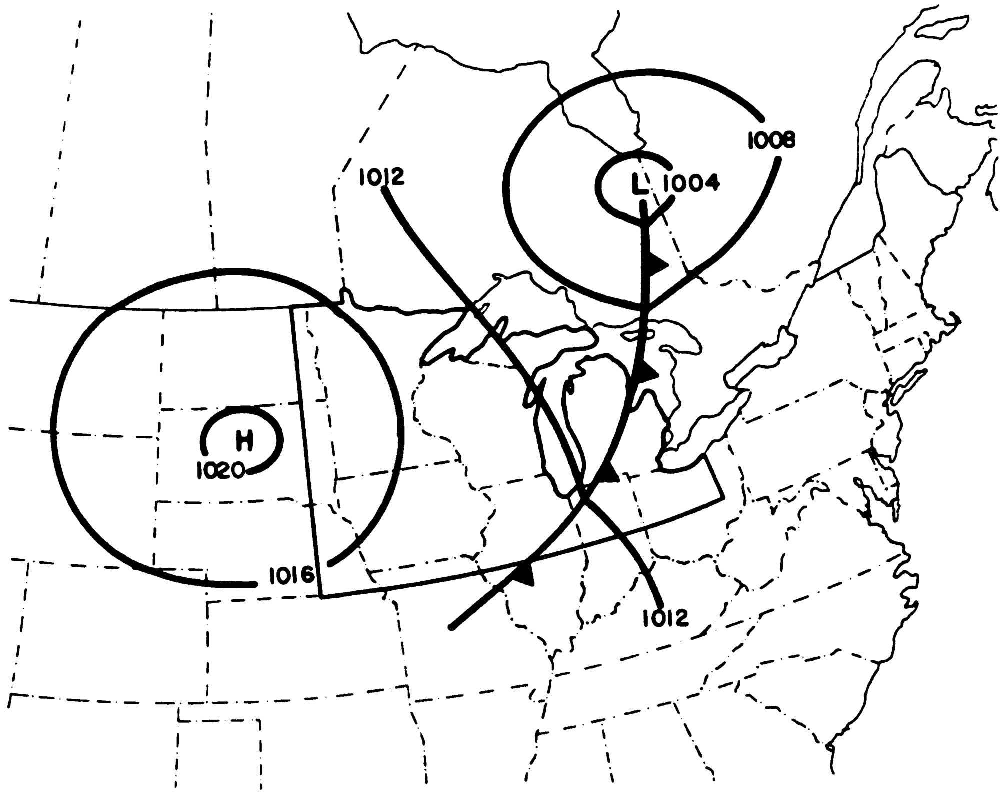

Figure 17. Composite Surface Pressure Map ... NW-SE Transect.

The N-S Transect

Weather conditions on a majority of days within the N-S transect group could produce cloud cover and the possibility of precipitation across the southern part of the western Great Lakes region. The primary features on the synoptic map for this group are an anticyclone centered over the New England states, a low in the northern Great Plains, and a stationary front which might be associated with overcast skies across Iowa and northern Illinois (Figure 18). Temperature changes along the north-south transect are minor on the days that fit in this group and a probable reason for the differences in the surrogate plant stress values is the distribution of cloud cover.

The NE-SW Transect

Five of the six days identified with higher stress values towards the northeastern part of the study area had a similar surface synoptic pattern. Major map features for this transect group include a surface cyclone in the eastern Great Plains and a relatively large high pressure cell over eastern Canada (Figure 19). The influence of the subsident conditions associated with the anticyclone extends back into the northeastern portion of Great Lakes region while the southwestern part of the study area may be receiving some precipitation.

The E-W Transect

A similar synoptic pattern, with a surface low in the eastern Great Plains and a high pressure cell centered to the east of the study area, exists on the majority of days within the E-W transect group (Figure 20). Comparison with the mapped pattern for the NE-SW

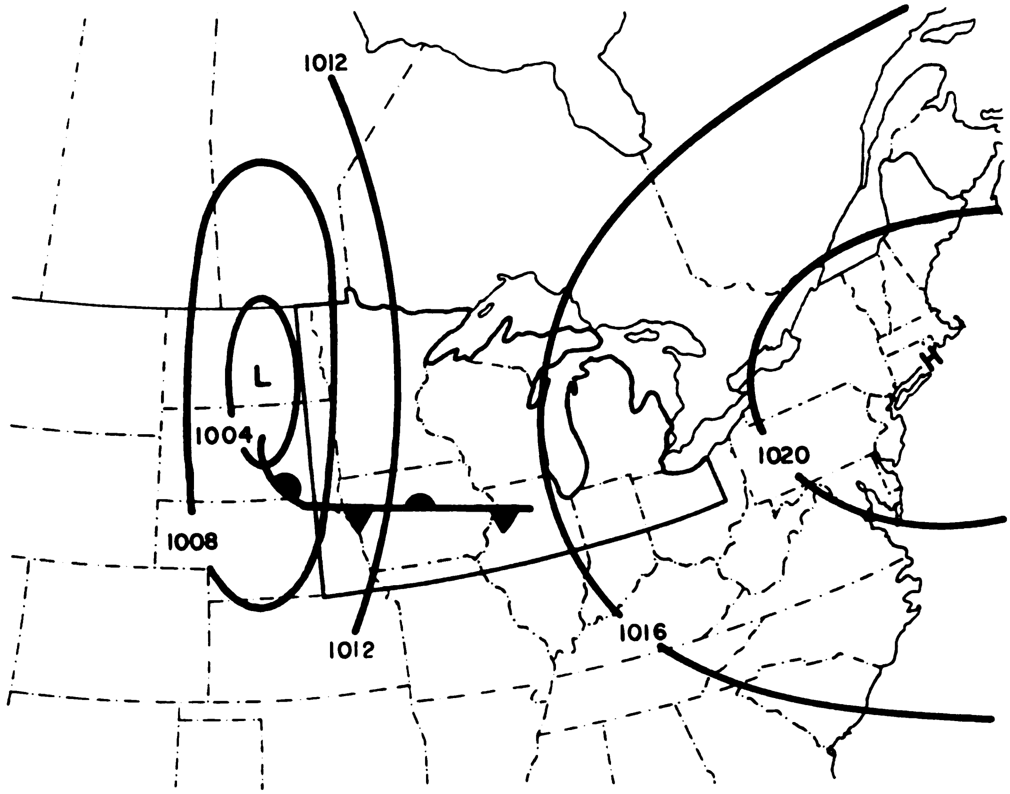

Figure 18. Composite Surface Pressure Map ... N-S Transect.

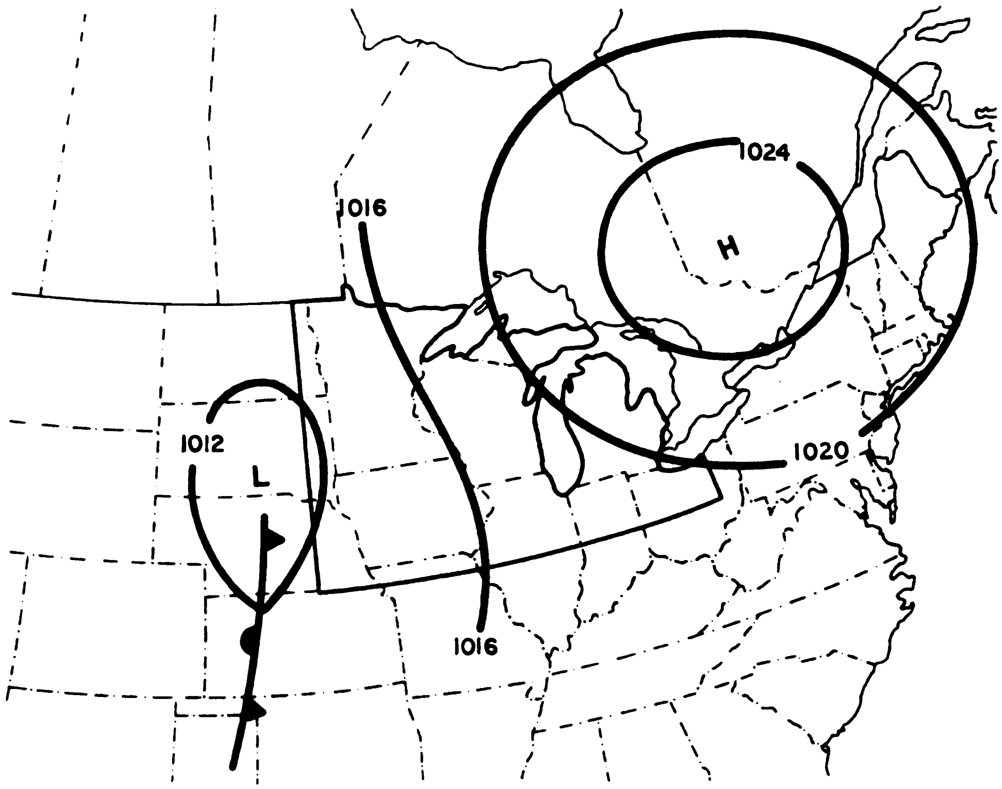

Figure 19. Composite Surface Pressure Map ... NE-SW Transect.

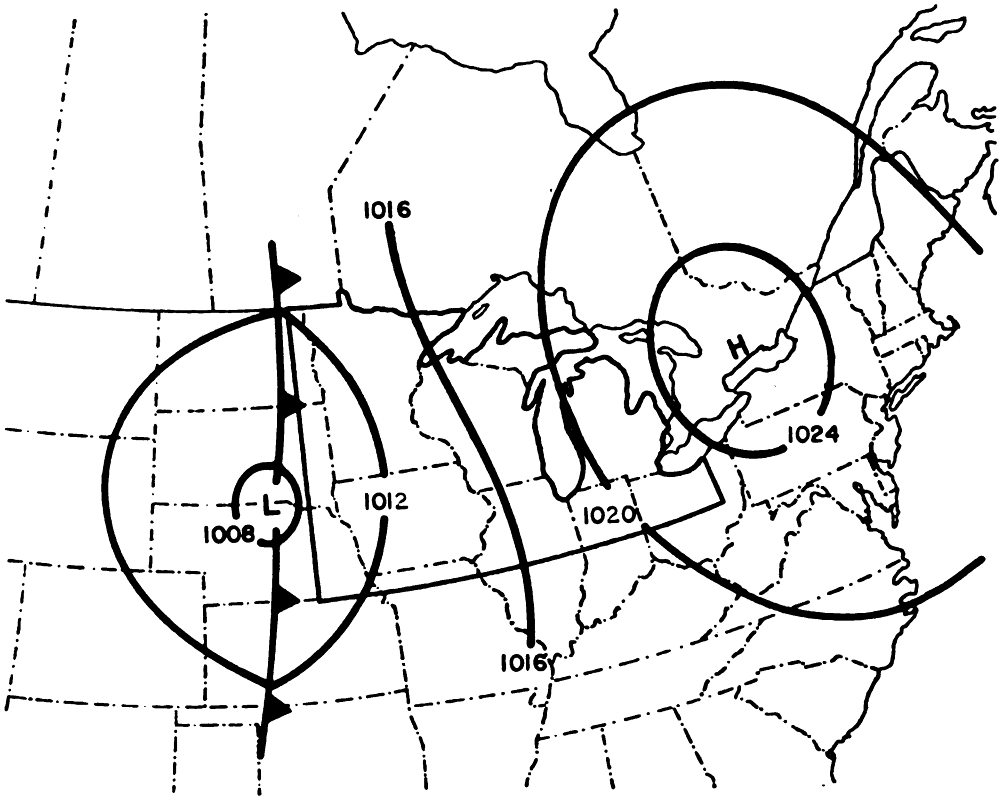

Figure 20. Composite Surface Pressure Map ... E-W Transect.

transect indicates that E-W stress gradient days are associated with a stronger low pressure center to the west and an anticyclone centered more directly to the east over southern Ontario and western New York state. Return flow on the backside of the high pressure cell will generally produce clear skies and warmer conditions over the eastern part of the study area, while an upper level trough in the western United States and the related surface low pressure in Kansas, Nebraska, and the Dakotas could be expected to yield both an increased cloud cover and higher precipitation probabilities.

The SE-NW Transect

Twelve of the seventeen days that had a gradient from higher values of stress in the southeast to lower values in the northwest had a synoptic weather pattern with a low to the west and high in the east. The composite map for this transect group differs from the seemingly similar patterns previously discussed in that the surface cyclone is farther to the north and the anticyclone is displaced southward over the Middle Atlantic states (Figure 21). The persistence data (Table 13) suggest that this is a progressive pattern with both the low pressure center and accompanying cold front moving east-southeastward in association with the steering flow aloft. Cloud cover and precipitation are highly probable in the northwestern part of the study area whereas clear to partly cloudy skies would tend to dominate under the subsident conditions in Ohio, Indiana and southern Michigan.

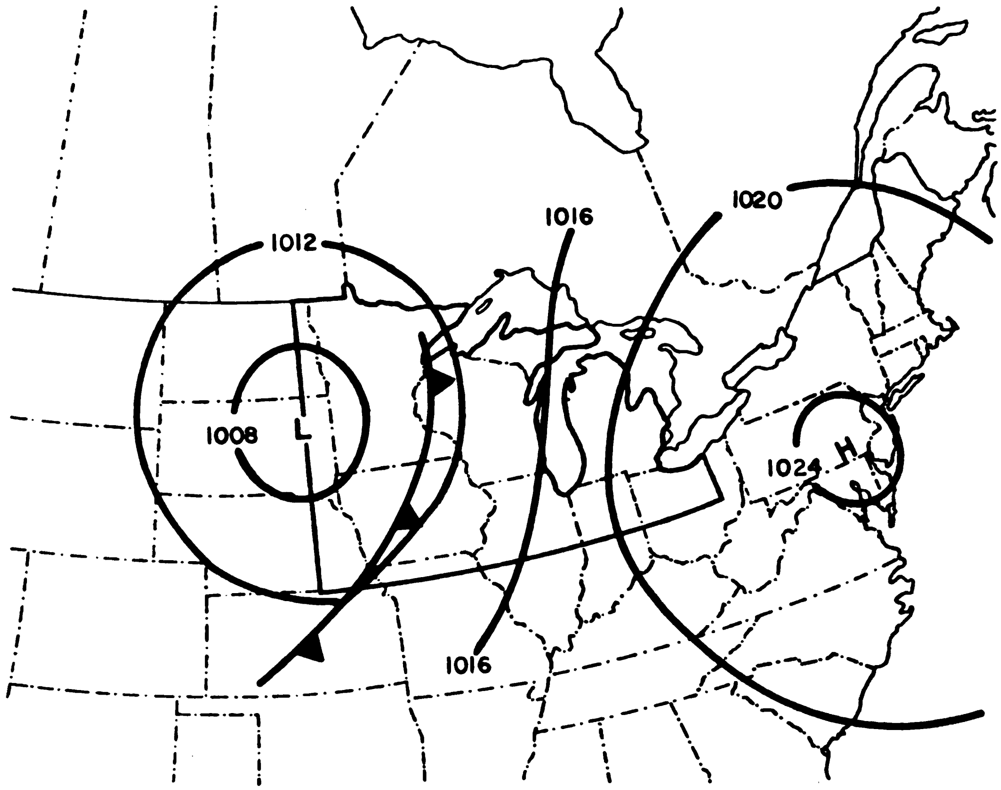

Figure 21. Composite Surface Pressure Map ... SE-NW Transect.

The S-N Transect

Two distinctly different synoptic patterns are identifiable with the S-N transect group. Thirteen of the twenty-nine days were classified as having a low to the west and a high to the east (the Eastern Anticyclone subgroup) whereas eight days had the relative location of the pressure cells reversed (the Advancing Canadian High subgroup). The composite map for the Eastern Anticyclone subgroup has a surface low over the Dakotas and a cold front stretching southward across the Great Plains; dominating most of the upper Middle West is a large high pressure cell centered over the eastern Great Lakes (Figure 22). This synoptic pattern suggests that the higher stress in the southern part of the study area would result from both subsidence and the advection of warmer air into the region from the south and southeast.

Different reasoning is necessary to explain the distribution of potential evapotranspiration values along the S-N transect associated with the Advancing Canadian High subgroup. Major features on the composite map are a low pressure cell over eastern Canada with a cold front trailing back into the eastern part of the study area and a high pressure center moving into the northwestern part of Minnesota (Figure 23). In this case, the surface wind flow would be primarily out of the northerly compass directions over most of the western Great Lakes region and, as a result, cooler air would be advected into the northern part of the study area.

The SW-NE Transect

The generalized synoptic weather type that had the greatest frequency of the days within this transect gradient group displays a low pressure cell to the west and an anticyclone to the east.

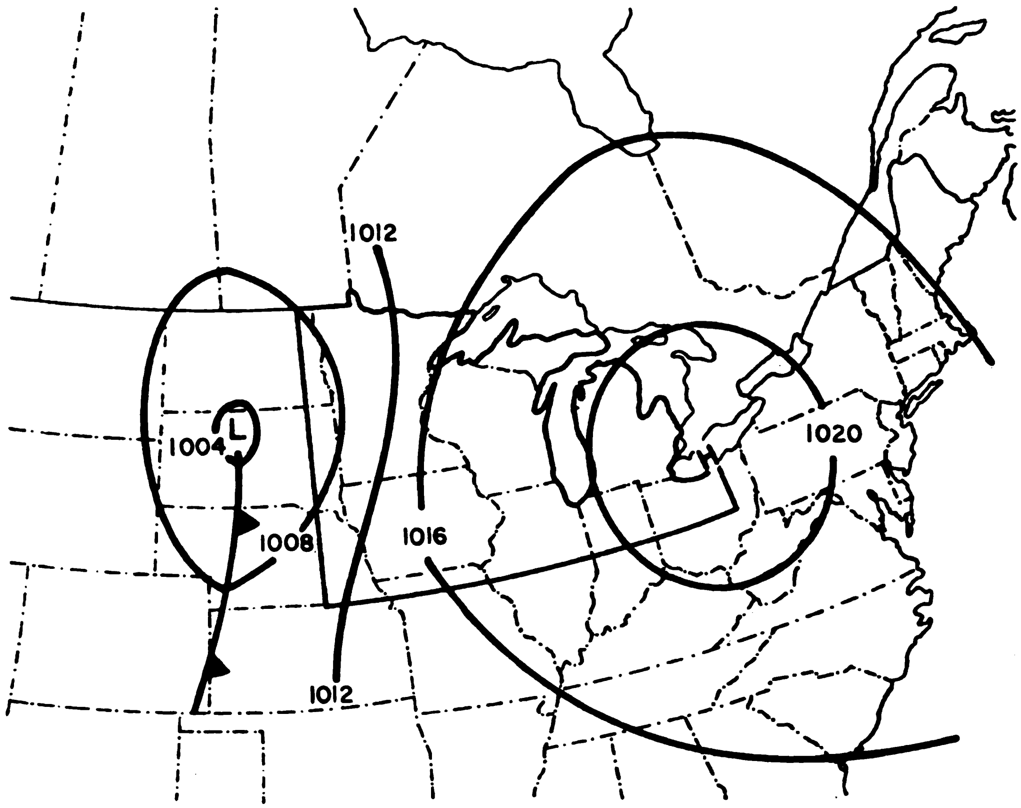

Figure 22. Composite Surface Pressure Map ... S-N Transect. Eastern Anticyclone Subgroup.

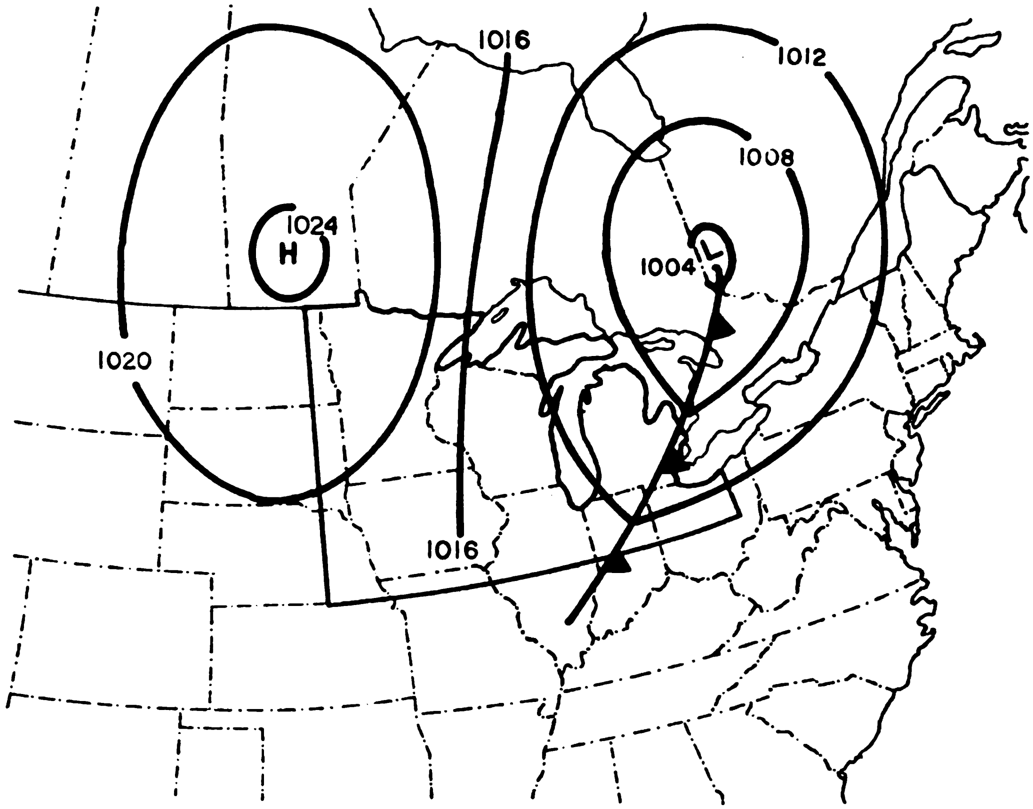

Figure 23. Composite Surface Pressure Map ..., S-N Transect. Advancing Canadian High Subgroup.

Composite map locations of these pressure cells produced using the data from twenty-five of the thirty-nine days within the SW-NE group indicate the advection of warmer and drier air into the southwestern part of the study area (Figure 24). The weather patterns on the days that comprise this subset have a tendency to remain nearly stationary for forty-eight to seventy-two hours or more during the months of July and August and, as a result, the cold front trailing south from the low pressure center, and marked on both the surface maps produced by the National Weather Service and the composite map, may be misleading because of the front's tendency to remain in the same location for an extended period. The surface anticyclone covering much of the eastern United States dominates the southeastern two-thirds of the study area, with south to southwesterly surface winds and drier air subsiding into the region.

The W-E Transect

Higher values of potential evapotranspiration in the western part of the study area and lower stress totals toward the east are associated with a composite weather map pattern that is very similar to the conditions for the SW-NE transect. Data from twenty-one of the thirty-one days in the W-E group were combined to produce a weather map which typifies the surface pressure distribution on the majority of the days with this stress gradient (Figure 25). The major difference between this map pattern and the chart for the SW-NE transect is the location of the surface cyclone; positioned on the border between Saskatchewan and North Dakota, the mean location of the low pressure cell is approximately 2^{o} longitude farther to the west. As was the case with the SW-NE transect, the dominant feature affecting

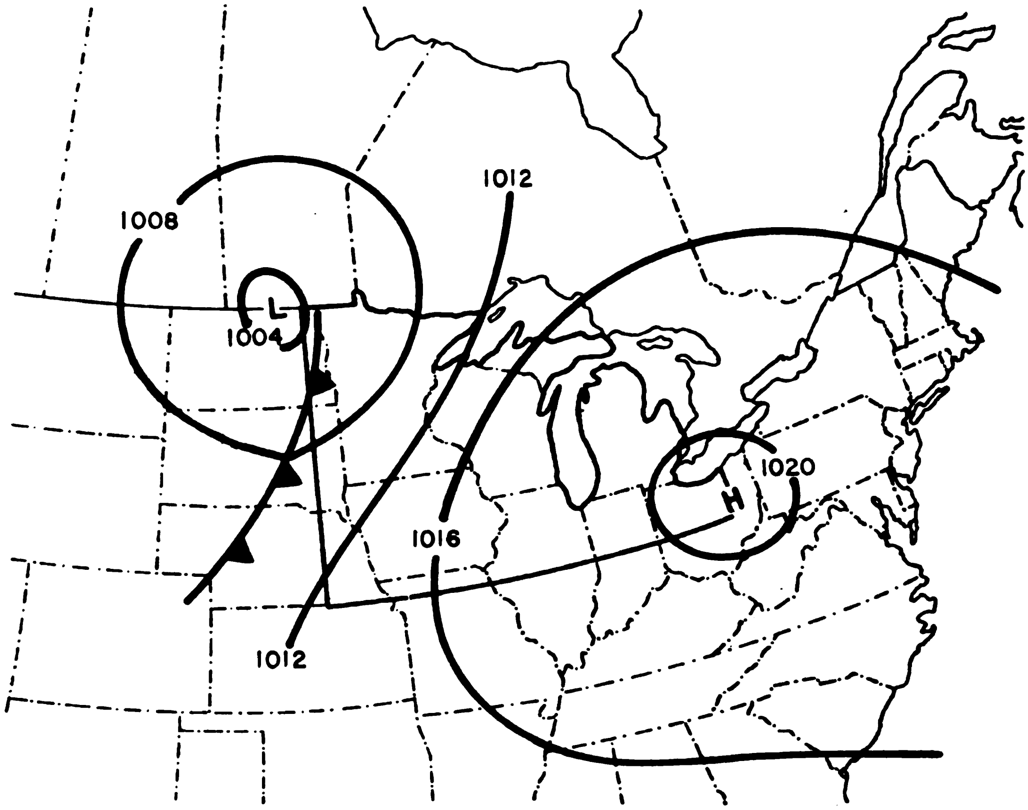

Figure 24. Composite Surface Pressure Map ... SW-NE Transect.

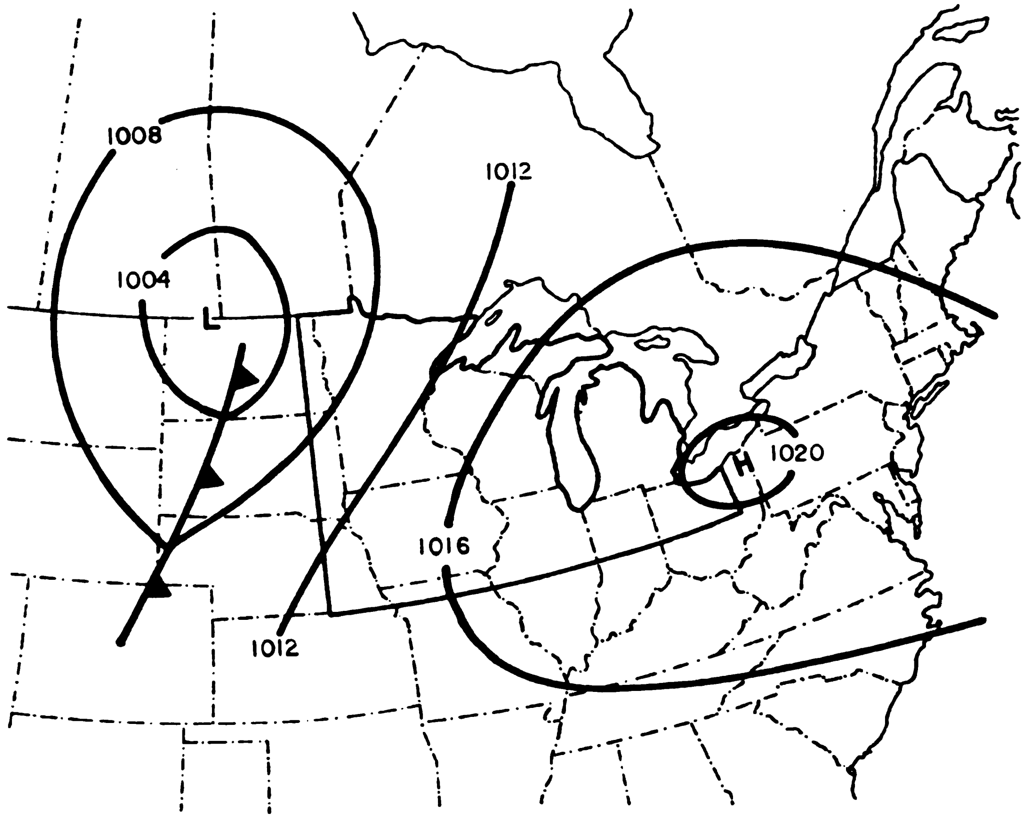

Figure 25. Composite Surface Pressure Map ... W-E Transect.

the weather in the western Great Lakes region is the large high pressure center over the eastern states. Again, subsidence and the advection of warmer air from the southwest helps explain the gradient in environmental conditions across the study area.

Summary

Composite maps of the surface pressure distribution on selected days within each transect group demonstrate weather conditions that can produce a gradient in potential evapotranspiration across the upper Middle West. It is interesting to note that synoptic patterns with low pressure centers over the Great Plains and anticyclones to the east of the study area are associated with the majority of days within all but the NW-SE transect group. Significant changes in the positioning of the pressure cells for each of the transect groups account for the differences in the direction of the stress gradient. In general, the location of the low pressure cell to the west tends to increase in latitude as the direction of the stress gradient shifts around from the northeast through the south and to the west; the center of the anticyclone to the east makes an accompanying shift to lower latitudes. As was stated earlier, these composite maps help to illustrate a typical situation in which the identified environmental gradient can occur, but specific micro- or meso-scale meteorological features may disrupt the environmental conditions on some days that fit these generalized composite patterns.

Upper Atmospheric Wind Flow Associated with each Transect Group

The dates and transect groupings identified in the surface data analysis were used to examine the associated characteristics of the wind flow patterns in the middle troposphere. For each of the eight groups which represent different stress gradient patterns, daily values of wind flow direction at the 500 millibar level were extracted from the National Center for Atmospheric Research data tapes for the seven rawinsonde data stations within the study area (Table 7). Additionally, the height values of the 500 millibar surface for all stations in North America were compiled from the tapes for the production of mean height contour maps for each transect group to demonstrate the associated wind flow patterns. Histograms depicting the combined frequency distribution of wind flow directions for the seven rawinsonde stations from the study area were produced for each of the eight groups of stress gradient days. In addition, a similar bar graph was produced for these same stations that shows the distribution of all flow directions for all summer season days (May-August) for the fourteen year study period (Figure 26).

Dramatic changes in the earth's atmospheric circulation result in the shift from winter to summer in extratropical latitudes. As the northern hemisphere warms during the first half of the year, the circumpolar westerly wind current decreases in its geographical extent and magnitude with the most pronounced changes occurring during the spring. In general, these circulation shifts that accompany the on-set of summer season climatic conditions are evident by mid-June (Bryson and Hare, 1974). Normal conditions during the months of July and August have the circumpolar wind flow dominated by a single westerly wind maximum that bisects the North American continent at approximately the political boundary between the United States and Canada. The strength of these summer season wind currents (the jet stream) is usually the weakest of any time during the year and total

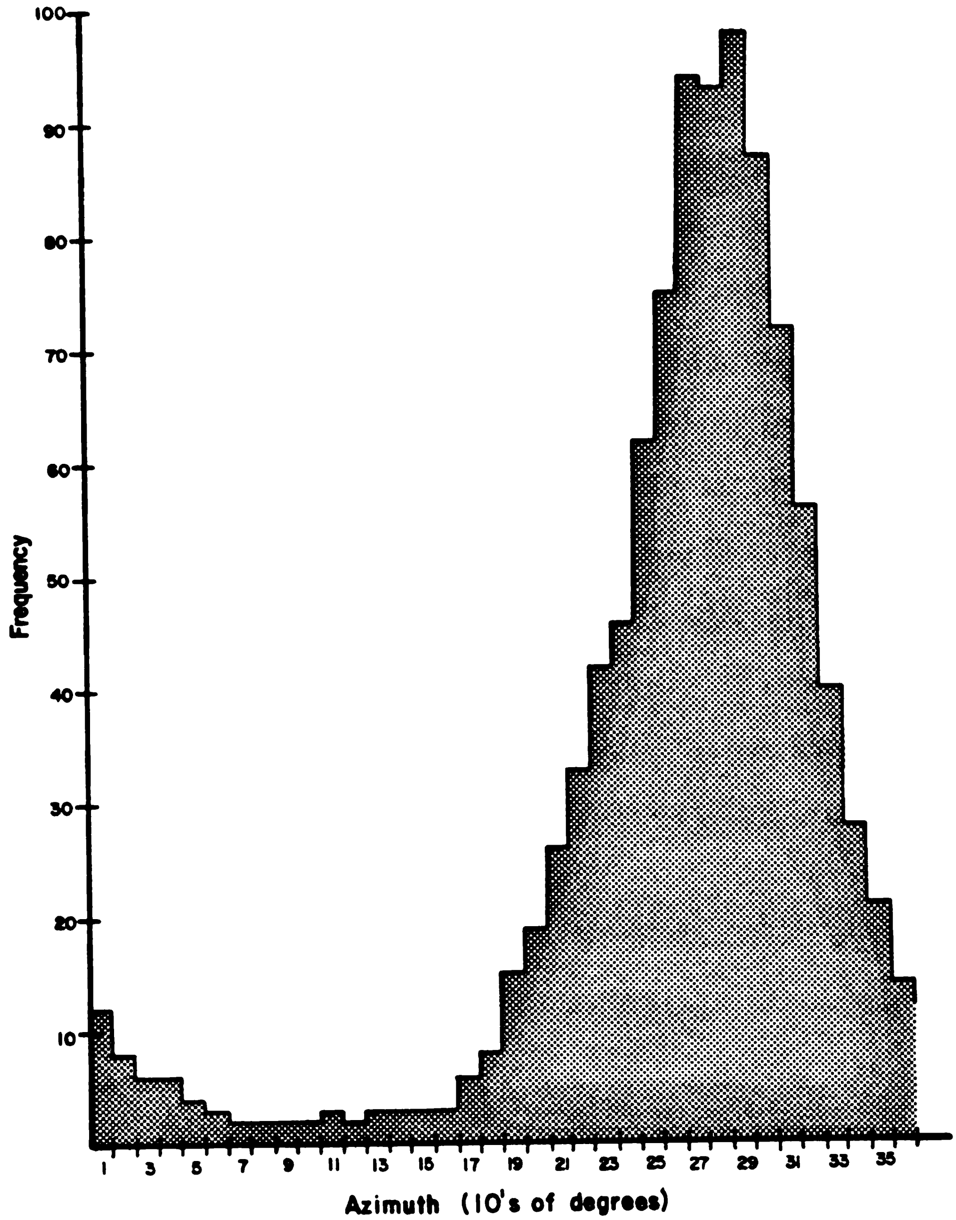

Figure 26. Frequency Distribution of 500 mb Flow Directions, Total Population.

kinetic energy is only about one-third the magnitude of mean winter circulation conditions (Bryson and Hare, 1974).

The mean (and modal) pattern of 500 millibar wind circulation over North America during the summer season (Figure 4) shows the impact of the western cordillera as well as strong heating of the continental interior. A semi-permanent ridge is associated throughout the year with this mountain barrier and during the summer season the axis of highest pressure heights shifts eastward over the western Great Plains as the atmospheric column expands in this area due to a positive radiation balance. The net result of these factors produces a pattern over North America with a ridge over the continental interior and lower pressure heights (troughs) off the west coast and over the eastern part of the continent. The resultant modal wind flow over the study area is not straight from west to east but is displaced slightly to the northwest from an aximuth of 290^{o} (Figure 26).

Upper atmospheric data were statistically tested to determine if the distributions of wind flow directions associated with each transect grouping of stress gradient days were random samples of the population of all wind flow directions for the months of May through August during the 1961-1974 period. Data grouped by compass direction are nominal in character and, as a result, the Chi-square non-parametric technique was utilized to determine if a significant difference existed between the frequency distribution that would be expected in a random sample and the actual data for the transect group. A requirement of the Chi-square technique is that expected frequencies in any cell (for any compass direction) must not be too small (Lewis and Burke, 1969) and the test should be used only when no cell has an expected frequency less than one and at least 80% of the cells have expected frequencies greater than or equal to five (Siegel, 1956). In order to satisfy these limitations, several flow directions were aggregated to insure that most cells had expected values larger than five. A loss of detail resulted from this cell aggregation, but grouping observations together was an essential step in testing the significance of each transect data set. The following paragraphs describe the flow direction data and the significance of statistical tests for each transect group; maps and histograms are presented to graphically depict these patterns.

The NW-SE Transect

The mean wind flow pattern for the fifteen days with stress values decreasing along a transect from the northwest part of the study area toward the southeast shows pronounced ridge development over the Canadian Rockies and west-northwesterly flow into the western Great Lakes region (Figure 27). Pressure heights at the 500 millibar level are approximately 50 to 75 meters lower than average summer season conditions across most of North America indicating a relative expansion of the circumpolar vortex. Additional analysis of the long wave pattern associated with this transect group shows greater wave amplitude than mean summer season conditions while the wave length and positioning of ridge and trough axes are similar to the average conditions.

Analysis of the frequency and direction of wind flow at the 500 millibar level for the seven rawinsonde data stations within the study area shows that westerly and slightly west-northwesterly winds are most frequent (Table 16). A statistical comparison of the wind flow directions for this transect group with the population of the fourteen years of growing season wind flow directions for these same seven stations indicates that the sample is significantly different from the population at the .05 confidence level. The histogram of the sample distribution differs from the predicted pattern with higher than expected wind frequencies out of the west to west-northwest, whereas most other wind flow directions had frequencies lower than the expected value (Figure 28).

The N-S Transect

Very little difference exists between the mean flow pattern for the twelve days within the N-S transect group and mean conditions during the growing season (Figure 29). The long wave pattern for the N-S transect group, with a trough off the west coast, ridge in the western Great Plains, and a second trough in eastern North America, is similar in wave positions, wave amplitude, and pressure heights to the seasonal mean conditions. Statistical analysis of the frequency and direction of wind flows associated with this transect group indicates that the transect sample distribution is significantly different from that of the overall population at the .001 confidence level (Table 17). The frequency distribution shows that higher than expected values were observed from the west to northwest directions whereas lower than expected frequencies occurred from the other wind flow trajectory groupings (Figure 30).

Table 16. Frequency of 500mb Wind Flow by Compass Direction - NW-SE Transect

Compass Direction By Azimuth	Frequency	Expected Value	Difference^2 / Expected Value
360 - 180	5	5.61	.07
190 - 220	1	5.67	3.85
230, 240	6	5.37	.07
250, 260	6	8.36	.67
270	11	5.73	4.85
280	10	5.63	3.39
290	6	5.98	.00
300	7	5.31	.54
310, 320	5	7.81	1.01
330 - 350	4	5.43	.38
			14.83

Degrees of freedom = 7

Significant at the .05 confidence level

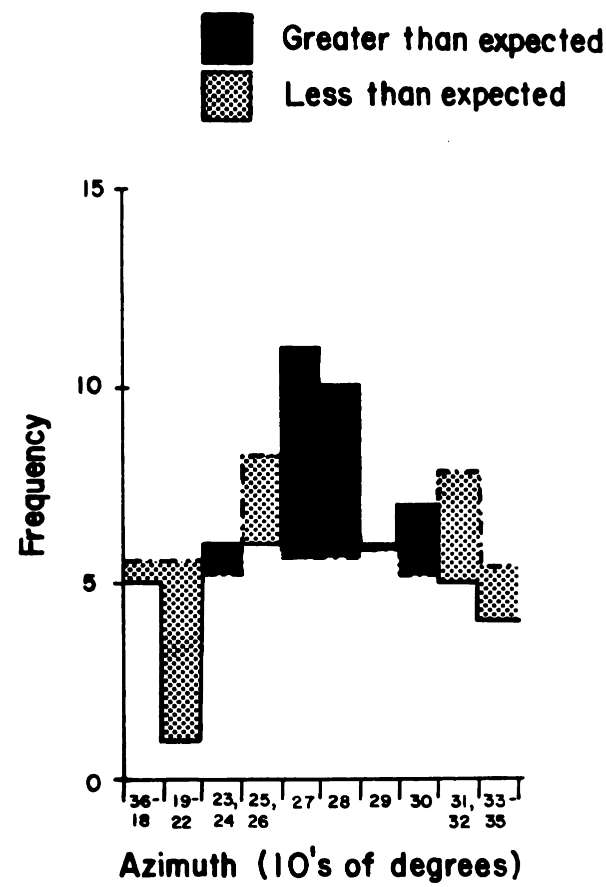

Figure 28. Deviation of Wind Flow Direction from the Expected ... NW-SE Transect.

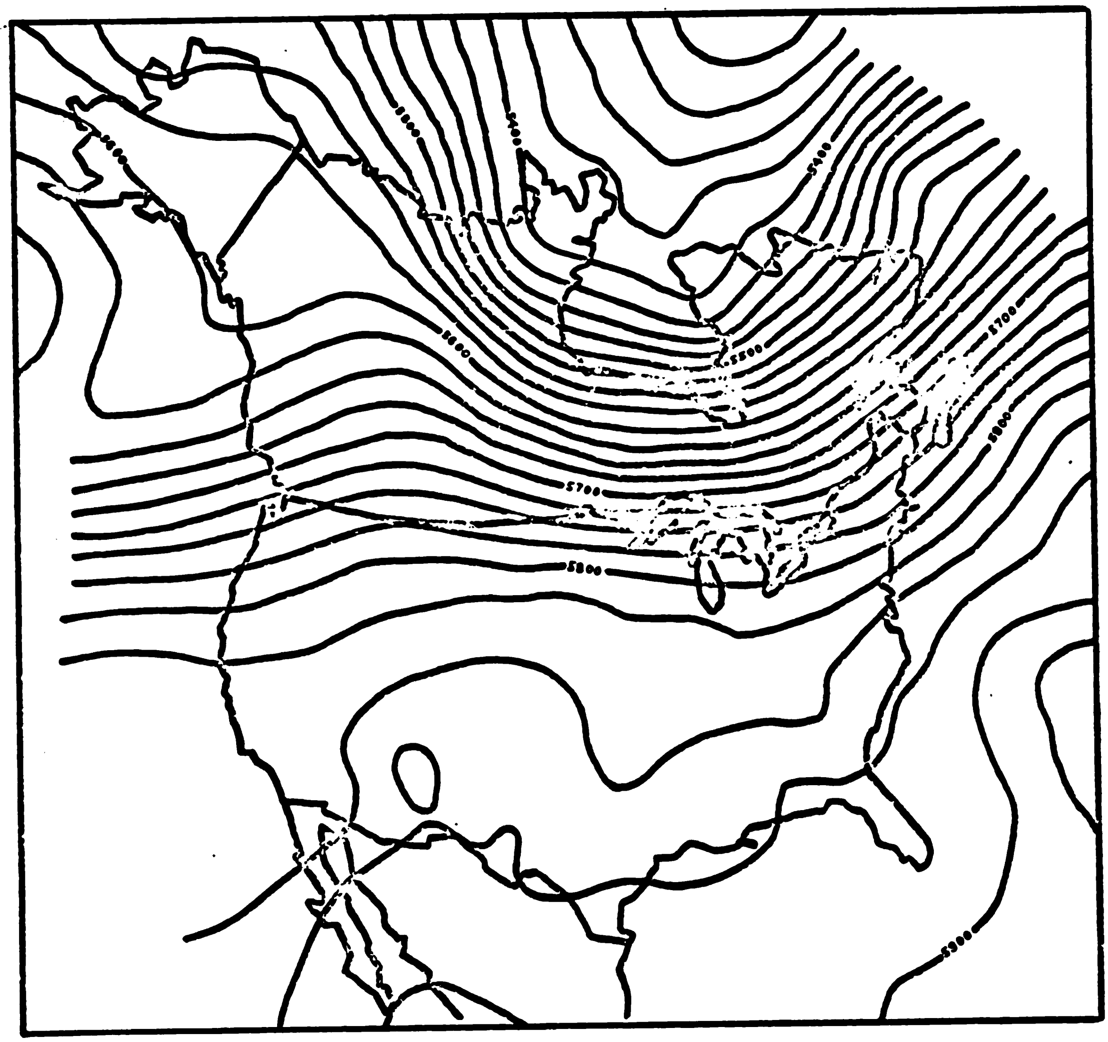

Figure 29. Mean 500 mb Heights ... N-S Transect.

Table 17. Frequency of 500mb Wind Flow by Compass Direction - N-S Transect

Compass Direction By Azimuth	Frequency	Expected Value	$Difference^2$ / Expected Value
350 - 200	0	6.03	6.03
210 - 240	2	6.03	2.69
250, 260	5	5.62	.07
270, 280	11	7.67	1.45
290	6	4.02	.98
300, 310	14	6.52	8.58
320 - 340	3	5.08	..85
			20.65

Degrees of freedom - 4

Significant at the .001 confidence level

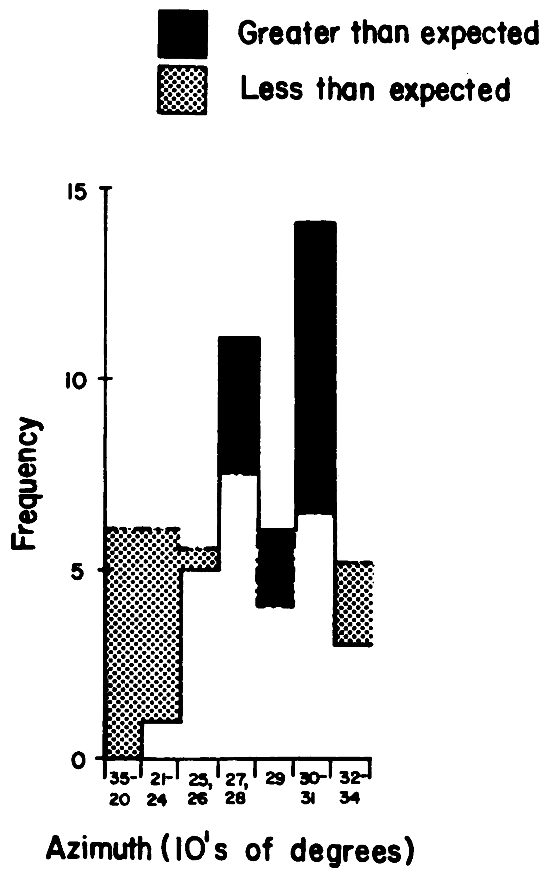

Figure 30. Deviation of Wind Flow Direction from the Expected ... N-S Transect.

The NE-SW Transect

A near zonal mean 500 millibar wind flow pattern with a short-wave trough in the western Great Plains and a weak ridge over the western Great Lakes region is associated with the six days that had higher values of stress in the northeastern part of the study area and a continuous decrease toward the southwest (Figure 31). Due to the small size of this transect group, Chi-square testing of the significance of the associated wind flow direction distribution was not of much value; the data had to be combined into just two groups to insure that the expected frequency in either cell was high enough and, as a result, the actual distribution was not significantly different from that expected based on a random sampling of the population (Table 18).

The E-W Transect

The long wave pattern associated with the E-W transect group exhibits a deep trough in the western United States and a ridge axis stretching northward from the Mississippi River Valley into central Canada (Figure 32). Environmental stress patterns associated with this transect are most frequent in the late spring months (Table 15) and the associated upper atmospheric flow pattern with a trough over the interior of the western United States also occurs frequently during these months. Examination of the distribution of wind flow directions for the twenty-one days in this transect group produced interesting results (Table 19). A consistent and explainable pattern is difficult to distinguish due to the character of the data, because adjacent trajectory groupings have either a greater or less than expected total; however, wind flows for the grouping that combines northeasterly through easterly to southeasterly directions were more frequent than

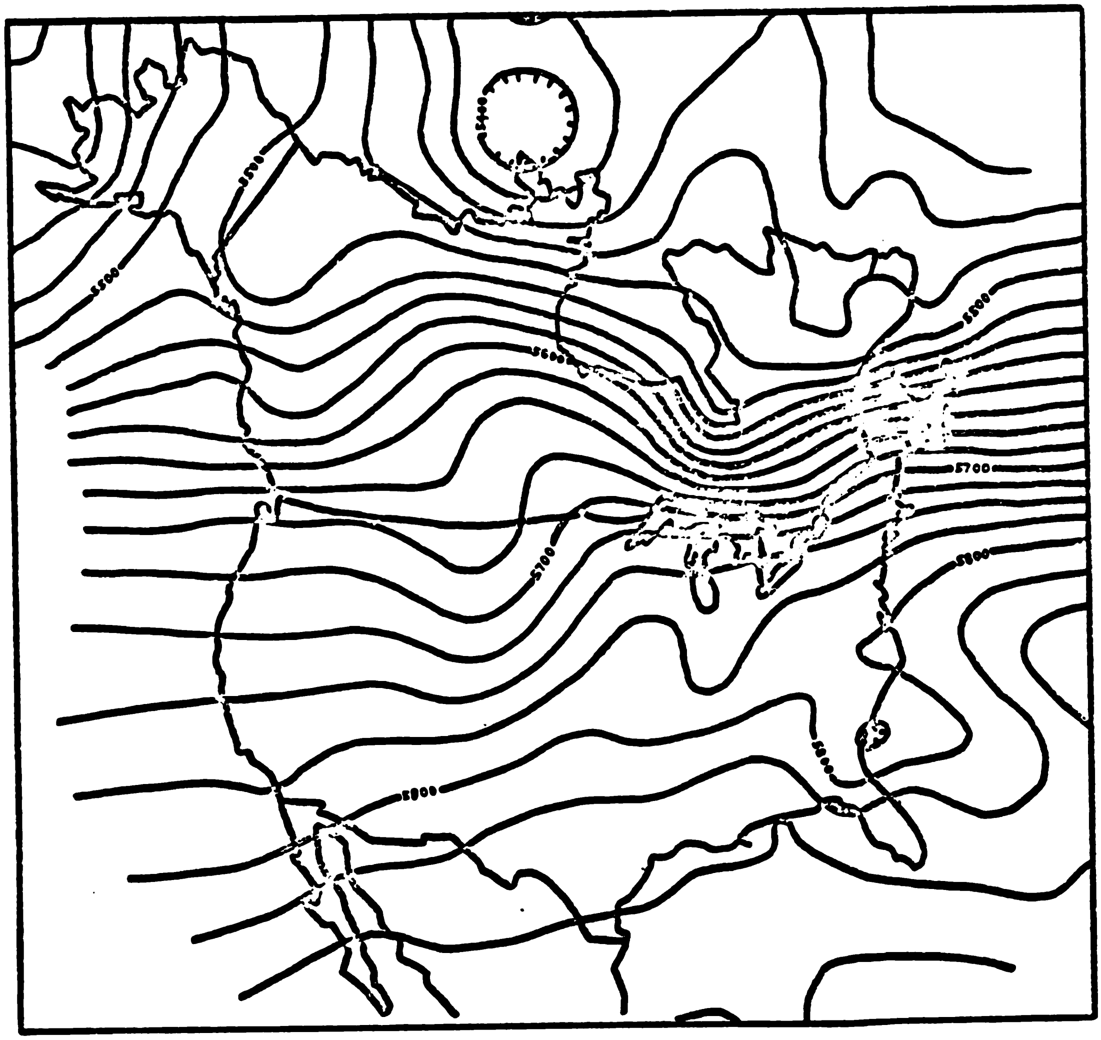

Figure 31. Mean 500 mb Pressure Heights ... NE-SW Transect.

Table 18. Frequency of 500mb Wind Flow by Compass Direction - NE-SW Transect

Compass Direction By Azimuth	Frequency	Expected Value	Difference^2 / Expected Value
320 - 260	6	7.22	.20
270 - 310	7	5.77	.26
			.46

Degrees of freedom = 1

Not significant

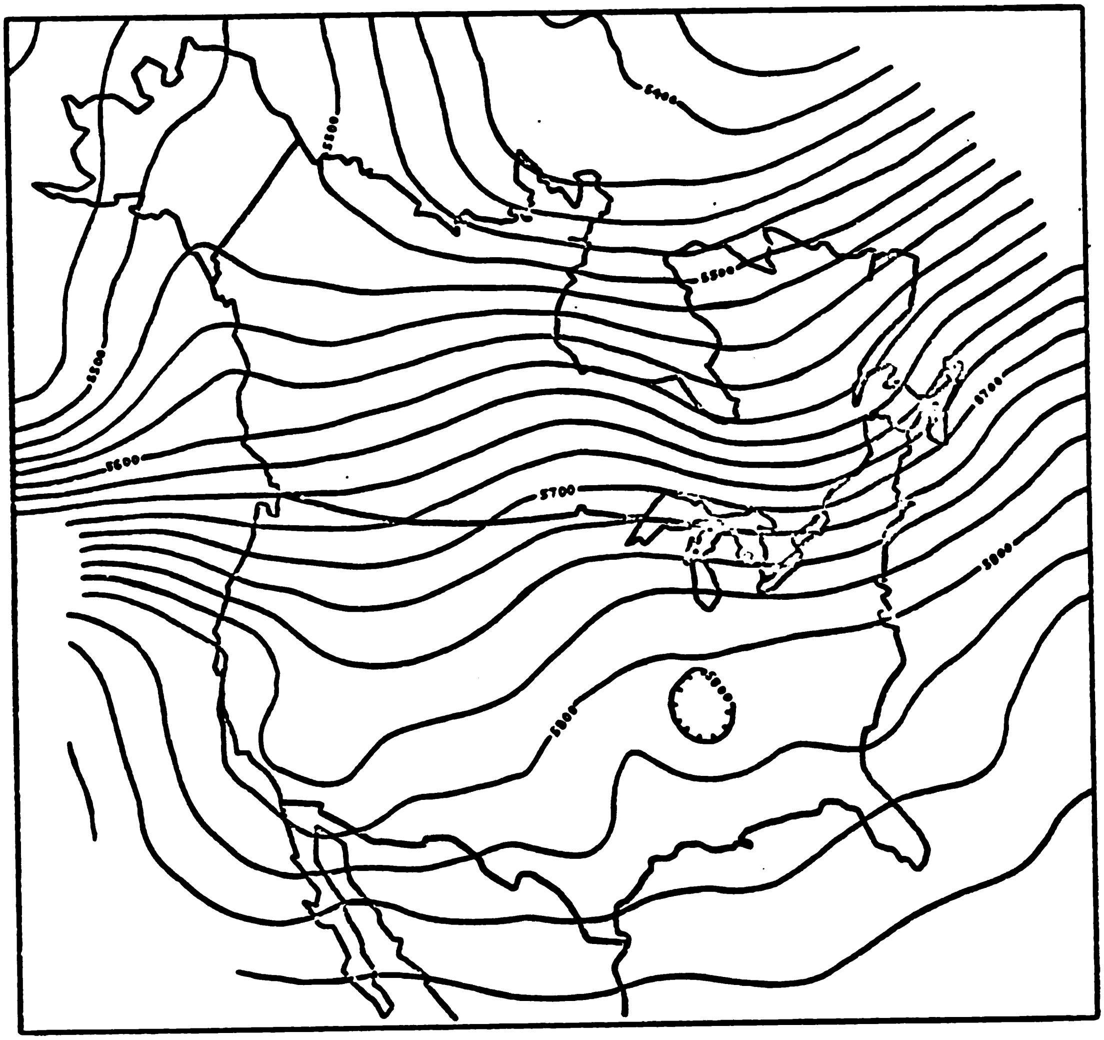

Figure 32. Mean 500 mb Pressure Heights ... E-W Transect.

Table 19. Frequency of 500mb Wind Flow by Compass Direction - E-W Transect

Compass Direction By Aximuth	Frequency	Expected Value	Difference^2 / Expected Value
30 - 160	16	4.53	29.04
170 - 200	5	4.94	.00
210, 220	2	6.08	2.74
230, 240	10	9.06	.10
250	0	6.39	6.39
260	6	7.73	.39
270	8	9.68	.29
280	15	9.58	3.07
290	5	10.09	2.57
300	11	8.96	.46
310	6	7.42	.27
320	6	5.77	.01
330, 340	6	7.00	.14
350 - 20	7	5.67	.31
			45.78

Degrees of freedom = 11

Significant at the .001 confidence level

expected (Figure 33). This could be the result of a greater frequency of cut-off or closed lows associated with this pattern but the data collected did not allow the testing of this hypothesis. Chi-square analysis of the frequency distribution indicates that the transect sample is significantly different from the pattern expected based on the overall population at the .001 confidence level.

The SE-NW Transect

The mean tropospheric wave pattern associated with the seventeen days in the SE-NW transect group is similar in characteristics to the E-W stress days 500 millibar contour height map with a trough in the western United States and a ridge over the Mississippi River Valley (Figure 34). The amplitude of the long wave pattern associated with the SE-NW group is not as great, but the wave length, ridge and trough axis locations, and, in general, the distribution of pressure height values are quite similar to the conditions for the E-W transect group. Environmental conditions with high values of stress in the southeast and an accompanying decrease toward the northwest did not show a pronounced seasonal concentration; these transect gradients were a minor but consistent feature each month, with the SE-NW group accounting for about 5 to 15% of the stress transects identified per month.

Analysis of the frequency distribution of wind flow directions for the SE-NW transect group indicates that this sample is significantly different at the .05 confidence level from the expected distribution based on the total population of all flow directions (Table 20). Highest frequency occurs from the west-northwest (290^{o} azimuth), but an overall analysis (Figure 35) shows lower than expected wind

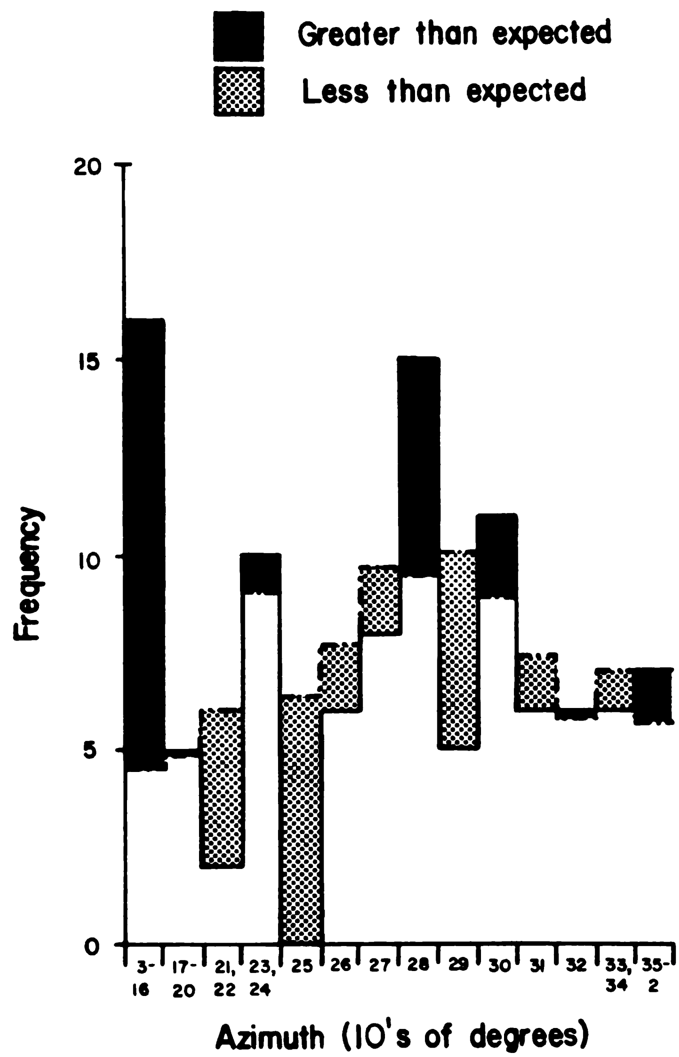

Figure 33. Deviation of Wind Flow Direction from the Expected ... E-W Transect.

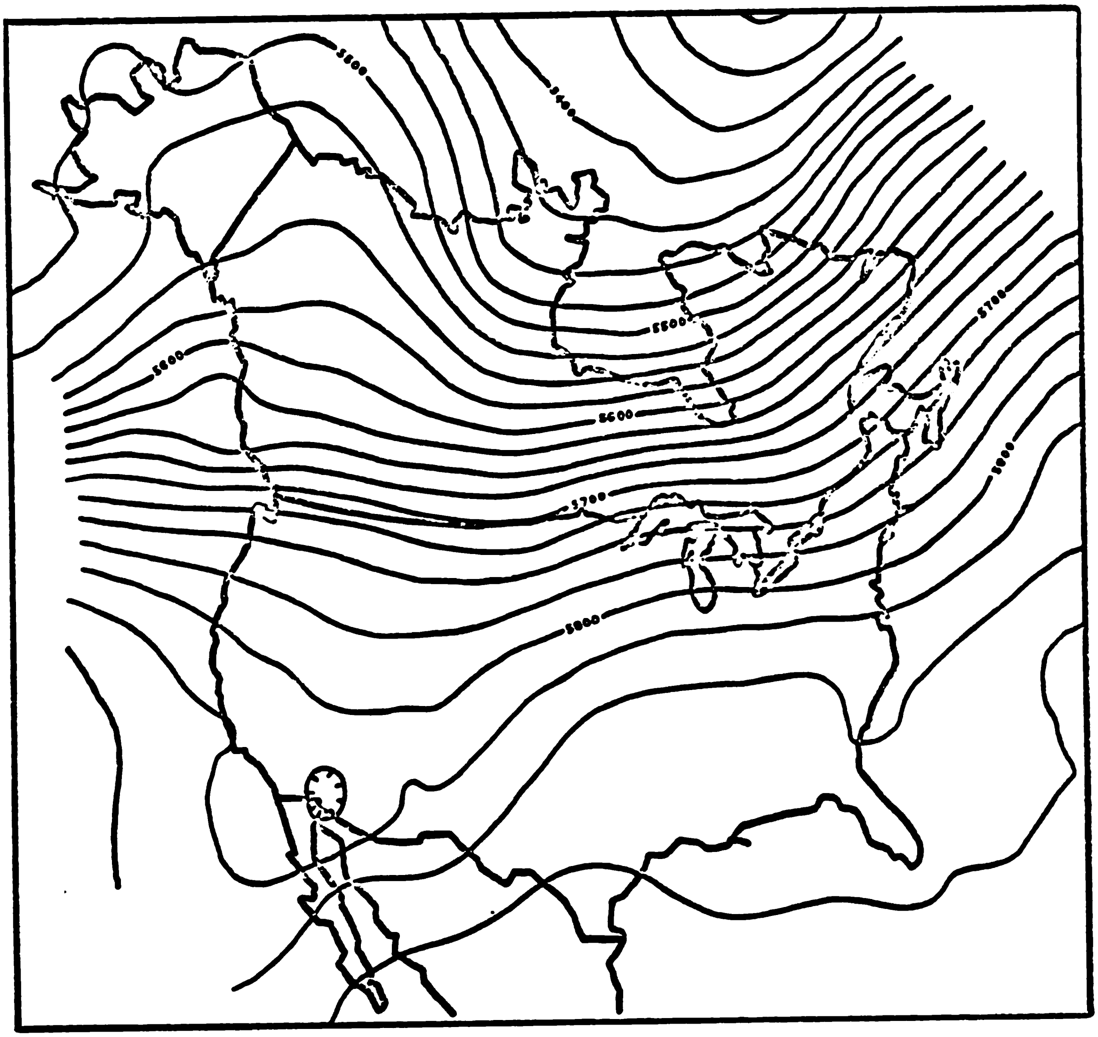

Figure 34. Mean 500 mb Pressure Heights ... SE-NW Transect.

Table 20. Frequency of 500mb Wind Flow by Compass Direction - SE-NW Transect

Compass Direction By Azimuth	Frequency	Expected Value	Difference^2 / Expected Value
20 - 170	9	6.96	.60
180 - 200	9	5.04	3.11
210, 220	11	7.08	2.17
230	8	5.04	1.74
240	6	5.52	.04
250	9	7.44	.33
260	8	9.00	.11
270	7	11.28	1.62
280	11	11.16	.00
290	15	11.76	.89
300	3	10.44	5.30
310	3	8.64	3.68
320	6	6.72	.08
330, 340	11	8.16	.99
350 - 10	4	5.64	.48
			21.14

Degrees of freedom - 12

Significant at the .05 confidence level

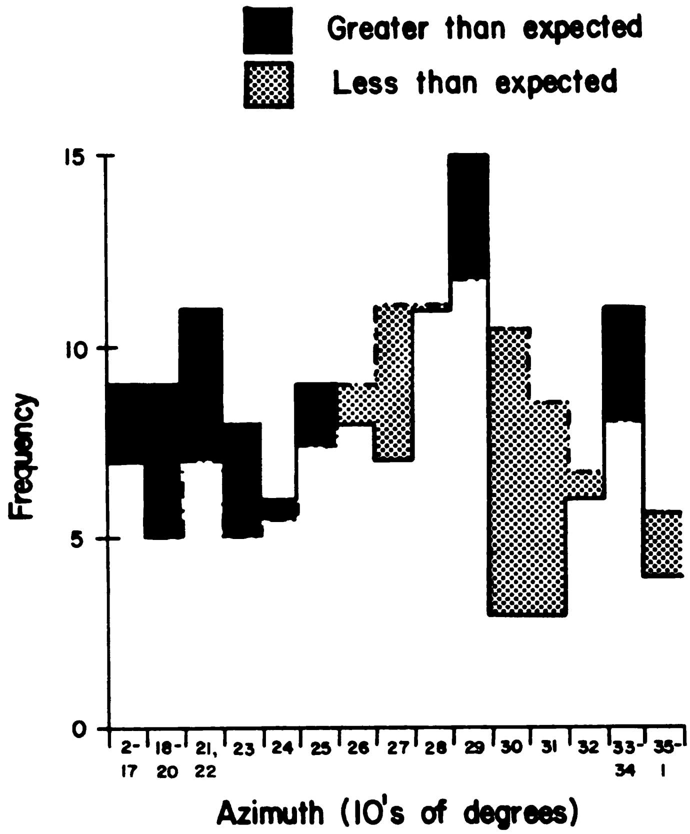

Figure 35. Deviation of Wind Flow Direction from the Expected ... SE-NW Transect.

direction totals for most azimuths from 260° through 360°. Higher than expected frequencies predominate for the directions from 20° through 250°; these statistical data are in agreement with the mapped pattern of 500 millibar heights and the resultant wind flow associated with the transect grouping.

The S-N Transect

Mapping the mean 500 millibar height contours for the S-N transect group produces a pattern which has both shorter and more amplified waves than average summer season conditions. The upper tropospheric wind flow associated with the twenty-nine days identified in the transect sample shows a trough over the southwestern United States with a downstream ridge over the northern Great Plains and a second trough over eastern Canada and the Great Lakes region (Figure 36). Statistical analysis of the frequency distribution indicates that the sample associated with the S-N transect is significantly different from the population at the .001 confidence level (Table 21). Higher than expected frequencies are observed from northwesterly, northerly, easterly, and southeasterly directions while southwesterly and westerly flows are less frequent than the overall population would suggest (Figure 37). More specifically, the S-N transect sample has its greatest frequency from the 320° azimuth and the 330° and 340° azimuths are well above the expected, whereas the 260° azimuth shows a markedly lower than expected total.

The SW-NE Transect

Thirty-nine days were identified by the sampling procedure as having a SW-NE transect stress gradient. Pressure height contours at the 500 millibar level associated with this most frequently occurring

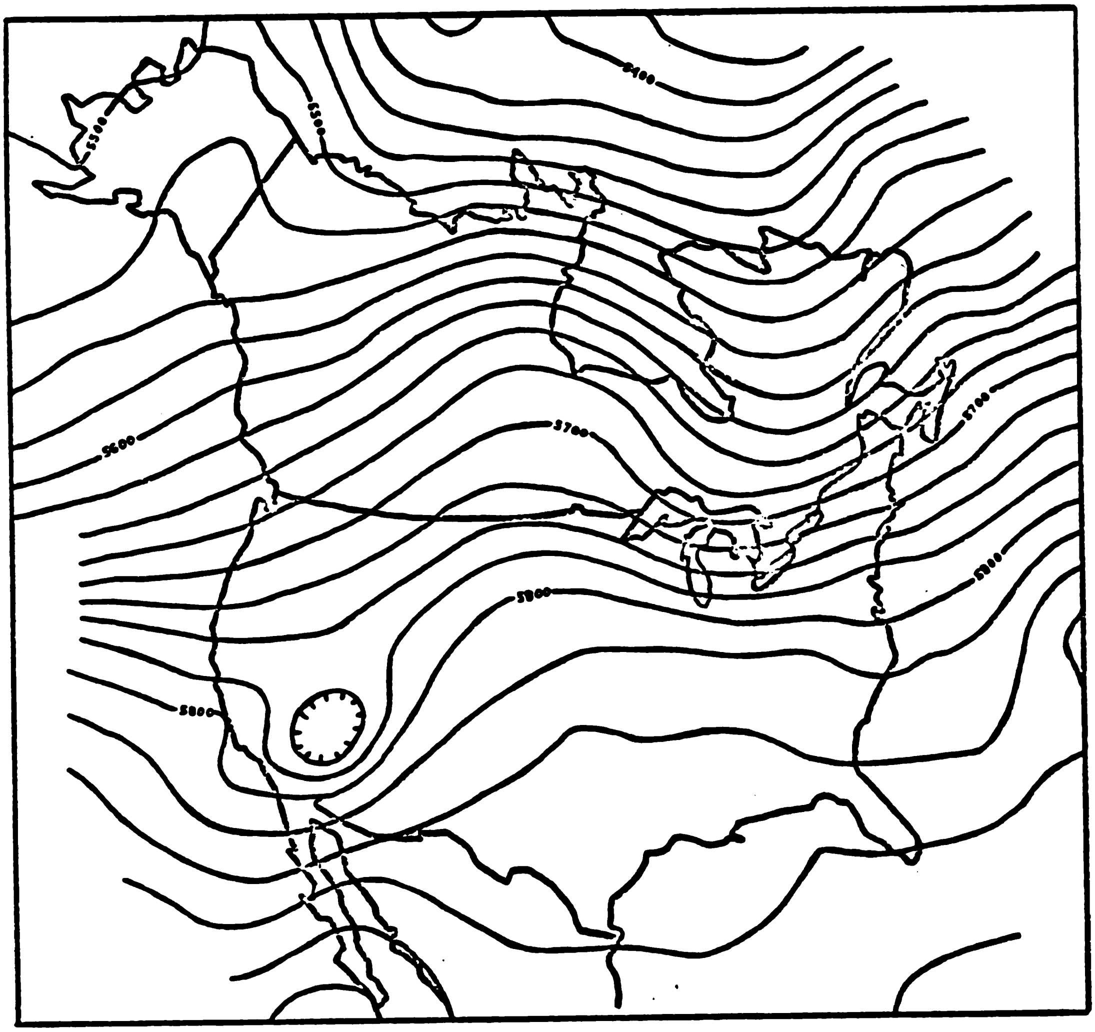

Figure 36. Mean 500 mb Pressure Heights ... S-N Transect.

Table 21. Frequency of 500mb Wind Flow by Compass Direction - S-N Transect

Compass Direction By Azimuth	Frequency	Expected Value	Difference^2 / Expected Value
10 - 40	11	5.47	5.59
50 - 150	12	4.96	9.99
160 - 190	7	5.47	.43
200, 210	6	7.70	.38
220	1	5.64	3.82
230	3	7.18	2.43
240	6	7.87	.44
250	6	10.60	2.00
260	4	12.83	6.08
270	12	16.07	1.03
280	11	15.90	1.51
290	15	16.76	.18
300	12	14.88	.56
310	9	12.31	.89
320	22	9.58	16.10
330	15	6.84	9.73
340	11	4.79	8.05
350, 360	8	5.99	.67
			69.88

Degrees of freedom = 15

Significant at the .001 confidence level

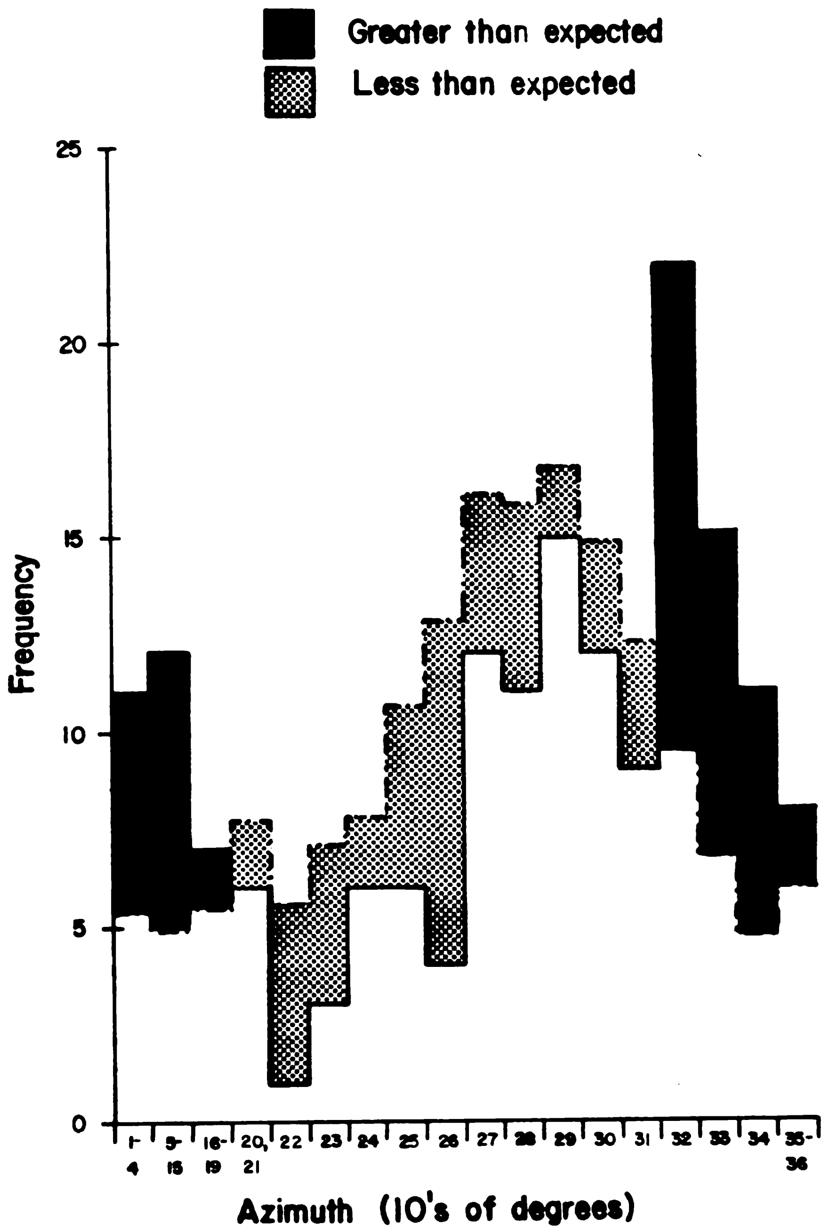

Figure 37. Deviation of Wind Flow Direction from the Expected ... S-N Transect.

surface stress pattern exhibit a configuration very similar to mean summer conditions with a trough-ridge-trough pattern across North America. The wind movement out of the west coast trough arches northeastward over the prairies of central Canada and then dips slightly southeastward across the study area into a trough over the eastern Great Lakes and St. Lawrence valley region (Figure 38). Closer examination of the pattern in comparison with summer season normals reveals a near normal amplitude and position of the west coast trough but a slightly longer than average wave length which results in an eastward displacement of the next downstream ridge and trough axes.

Chi-square analysis of the frequency statistics for wind flow direction associated with this transect group indicates that the distribution is significantly different from the population at the .02 confidence level (Table 22). The modal class of the sample, a 290^{o} azimuth, is the same as the modal class for the overall population (Figure 26), but significant differences occur in the frequency statistics for other flow directions. Lower than expected values associated with the transect sample occur primarily from the 250^{o} through 280^{o} azimuths (Figure 39); these low totals out of westerly and west-southwesterly directions are offset by higher than expected frequencies from the northwest (290^{o} through 340^{o} azimuths), the northeast and east (10^{o} through 130^{o} azimuths), and from the southwest (220^{o} through 240^{o} azimuths).

The W-E Transect

Upper tropospheric wind flow patterns associated with the W-E transect group are quite similar to the average summer season conditions as well as the patterns associated with the N-S and SW-NE transect groups (Figure 40). The usually recurring trough-ridge-trough pattern is again evident in the tropospheric wind flow and

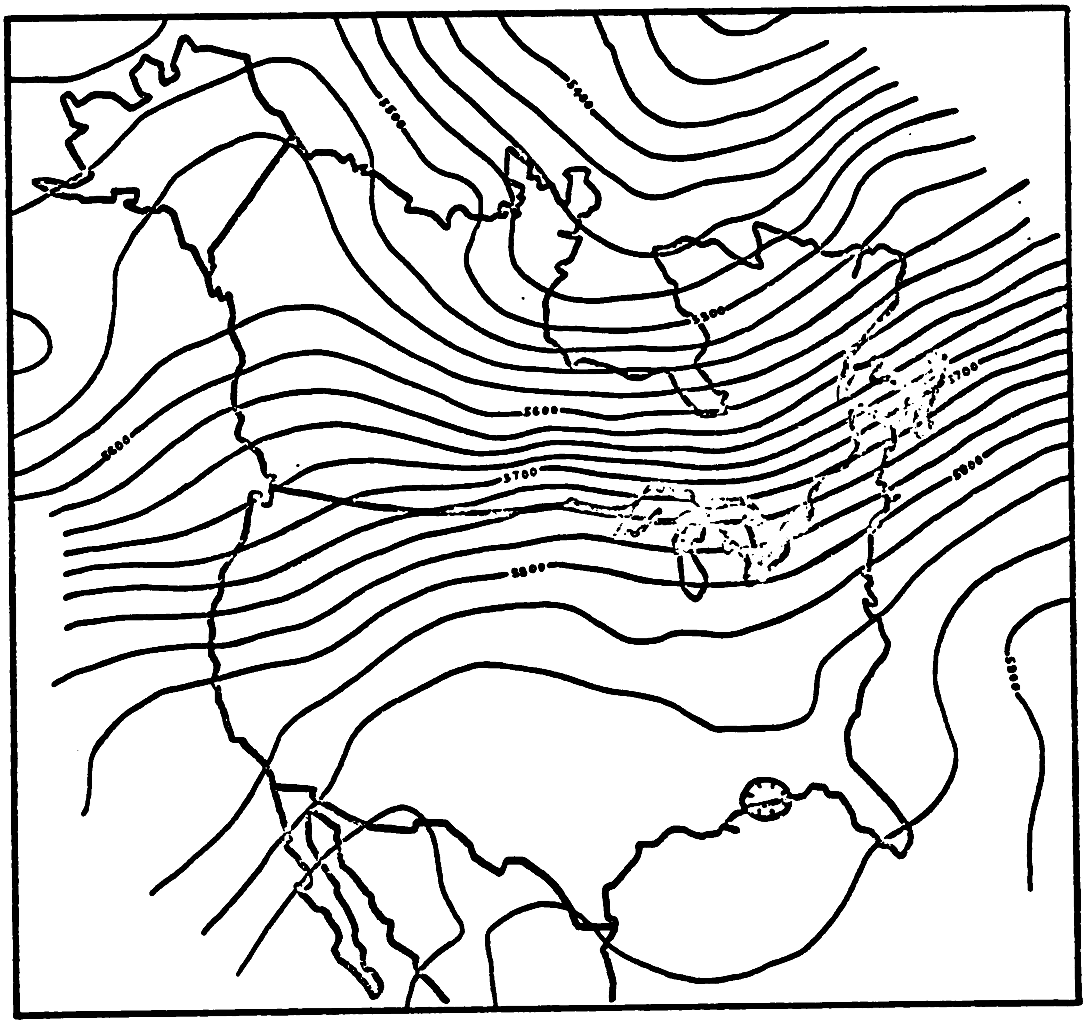

Figure 38. Mean 500 mb Pressure Heights ... SW-NE Transect.

Table 22. Frequency of 500 mb Wind Flow by Compass Direction - SW-NE Transect

Compass Direction By Azimuth	Frequency	Expected Value	$Difference^2$ / Expected Value
10 - 30	13	5.09	12.29
40 - 130	9	6.58	.89
140 - 180	4	5.22	.29
190, 200	10	7.49	.84
210	5	5.90	.14
220	8	7.49	.03
230	14	9.53	2.10
240	12	10.44	.23
250	8	14.07	2.62
260	16	17.03	.06
270	17	21.34	.88
280	10	21.11	5.85
290	29	22.25	2.05
300	21	19.75	.08
310	16	16.34	.01
320	13	12.71	..01
330	11	9.08	.41
340	7	6.36	.06
350, 360	4	7.95	1.96
			30.80

Degrees of freedom = 16

Significant at the .02 confidence level

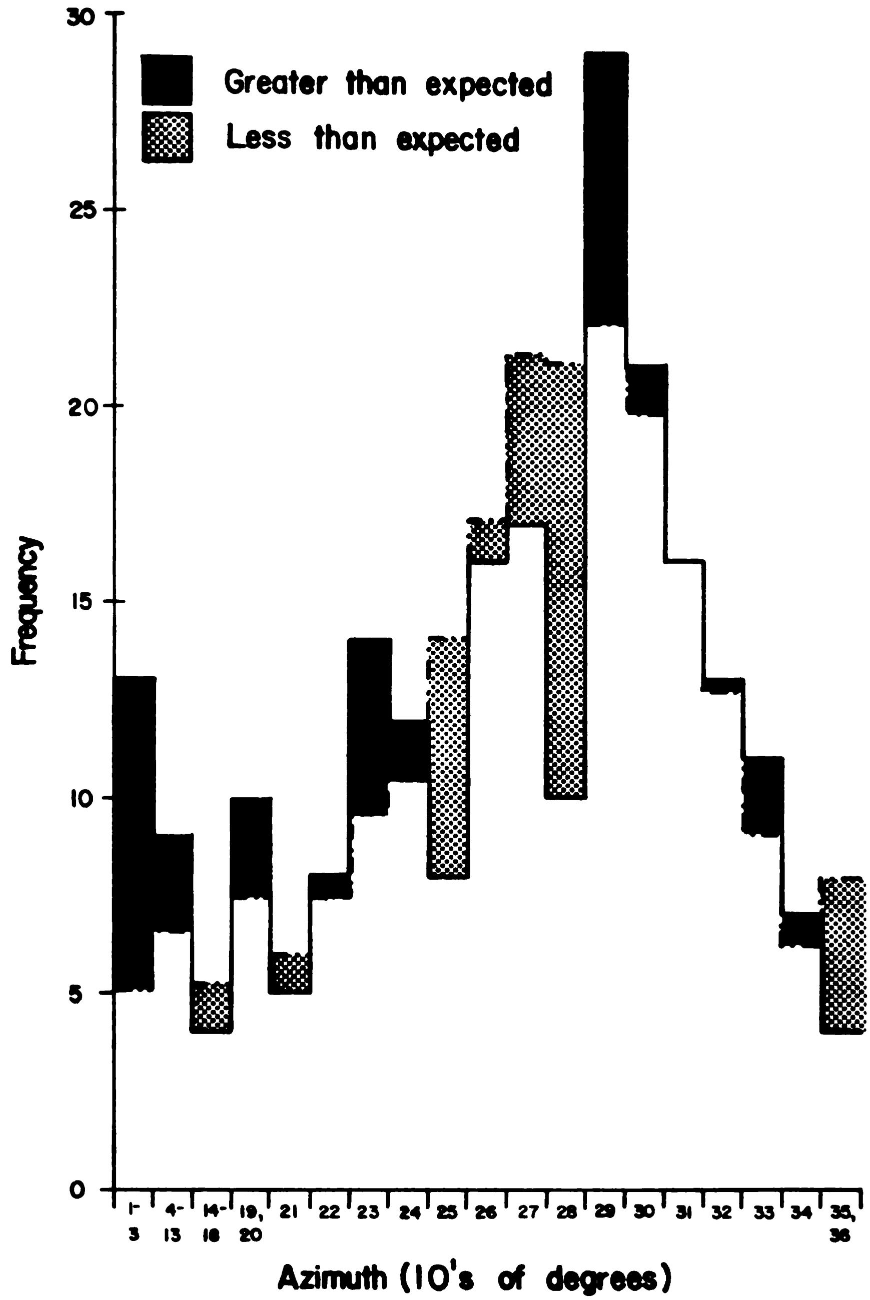

Figure 39. Deviation of Wind Flow Direction from the Expected ... SW-NE Transect.

the ridge axis is again displaced slightly eastward over the eastern Great Plains, as with the SW-NE group. Non-parametric testing of the nominal wind flow direction data indicates that the W-E transect sample is significantly different from the overall population at the .001 confidence level (Table 23). Again the modal class of the sample is the same (290^{o} azimuth) as the overall population, while identifiable trends are observable in a comparison of the transect distribution and the expected values (Figure 41). Lower than anticipated values are evident from the southeasterly, southerly, southwesterly, and westerly directions (130^{o} through 280^{o} azimuths), whereas, northwesterly, northerly, and northeasterly flows (290^{o} through 60^{o}) have generally greater totals than the population data would suggest.

Summary

The transect groupings identified in the analysis of the surface data produced at least two distinct 500 millibar circulation patterns in the middle troposphere and, in addition, statistical analysis of the wind frequency by direction indicates that the results are significant. An atypical summer season long wave pattern with low height values over the interior of the western United States was found to be associated with NE-SW, E-W, and SE-NW transect stress gradients, whereas a more normal pattern with a ridge to the west of the study area and trough to the east was identifiable for the other transect groups. All of the transect groupings except the NE-SW had a different and statistically significant wind flow distribution in a comparison with the overall population; a low frequency of occurrence (only six cases) and nominal data limited the capabilities of testing the NE-SW group. In most cases, the 500 millibar wind flow distribution

Table 23. Frequency of 500mb Wind Flow by Compass Direction - W-E Transect

Compass Direction By Azimuth	Frequency	Expected Value	Difference^2 / Expected Value
20 - 60	19	6.63	23.08
70 - 120	3	3.32	.03
130 - 180	3	6.89	2.20
190 - 200	4	8.42	2.32
210	5	6.63	.40
220	2	8.42	4.90
230	10	10.71	.05
240	6	11.73	2.80
250	4	15.81	8.82
260	18	19.13	.07
270	21	23.97	.37
280	21	23.72	.31
290	40	24.99	9.02
300	19	22.19	.46
310	34	18.36	13.32
320	17	14.28	.52
330	11	10.20	.06
340	7	7.14	.00
350	6	5.36	.08
360, 10	5	6.63	.40
			69.21

Degrees of freedom = 17

Significant at the .001 confidence level

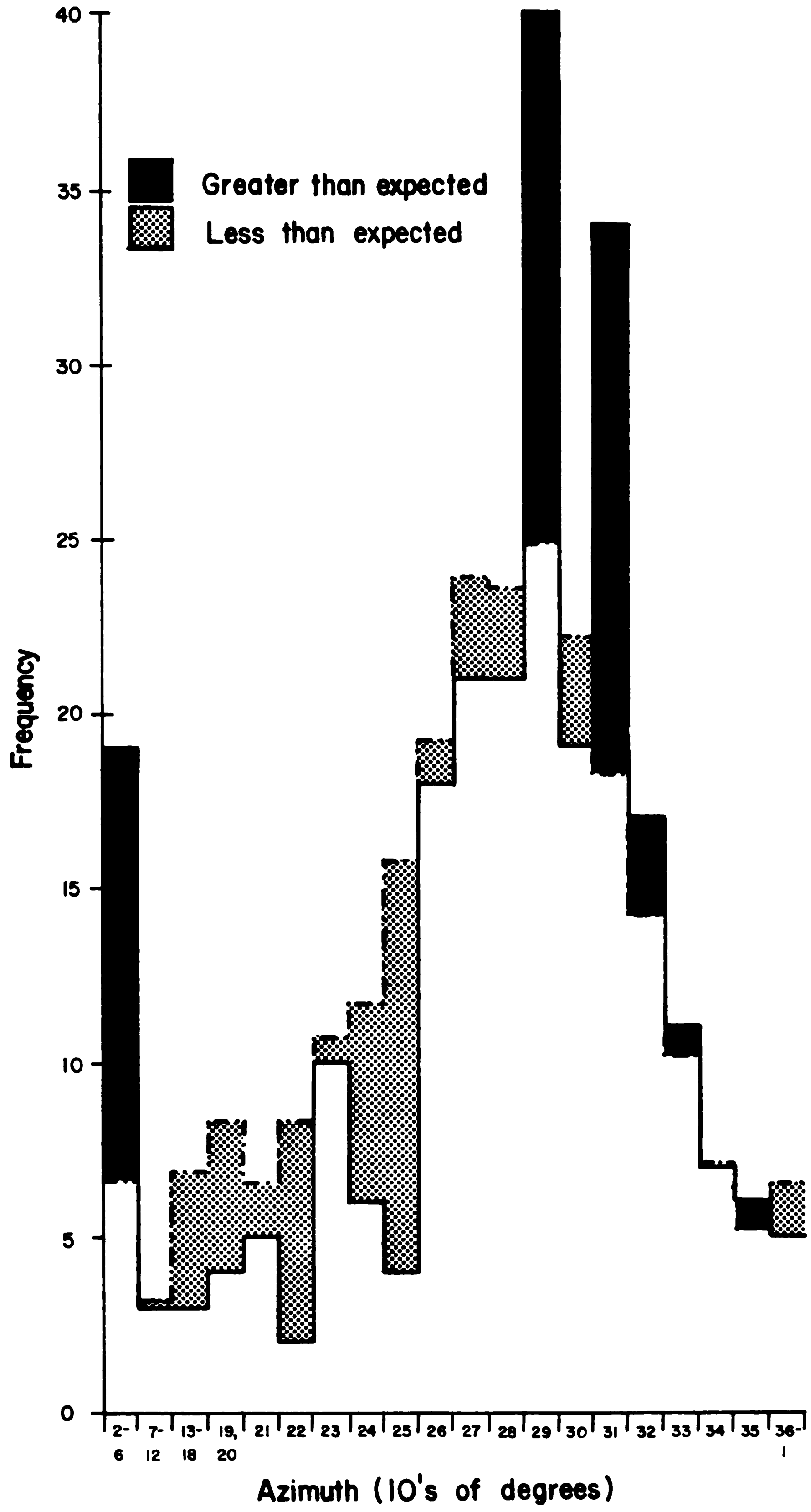

Figure 41. Deviation of Wind Flow Direction from the Expected ... W-E Transect.

associated with the various stress gradients across the study area exhibited a lower than expected frequency of winds out of a southwesterly direction, whereas higher than anticipated frequencies occurred out of the northwest. The only major exception to this generalization was the SE-NW transect group where the opposite conditions prevailed. Finally, the SW-NE and W-E transect groups both had a modal class (a 290° azimuth) that was equivalent to the modal class of the overall population.

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Chapter V

DISCUSSION

This research was concerned with the hypothesis that the patterns of atmospheric circulation associated with surface meteorological conditions which reinforce the position of the major vegetation transitions in the upper Middle West are both modal and non-random. This theoretical concept is accepted because the following patterns are evident in the data: 1) Modality: the most frequently occurring 500 millibar wind flow direction (a 290^{o} azimuth) for all days characterized by a stress gradient orientation coincident with the ecotones within the western Great Lakes region (SW-NE) is the same as the modal wind flow direction for all study season (May-August) upper atmospheric winds; 2) Non-randomness: in addition, the frequency distribution of wind flow directions associated with this stress gradient group (SW-NE) is significantly different from the distribution of the total population of 500 millibar late-spring and summer season wind flows based on statistical analysis using the Chi-square non-parametric test; 3) Dominance of the (SW-NE) Stress Gradients: analysis of the magnitude and frequency of the eight transects across the upper Middle West indicates that stress gradient days which are thought to be positively correlated with the position of the ecotone (the SW-NE transect) are more frequent and produce the greatest cross-transect differences in stress values; 4) Composite Maps: the composite surface pressure map associated with the SW-NE transect group exhibits a weather pattern which corroborates the concept of higher values of plant stress in the areas of natural grassland in the southwestern part of the study area and lower values of stress in the forests to the northeast; 5) 500 Millibar Height Contour Maps: mean wind flow patterns in the upper troposphere produced from the 500 millibar height contour data for the SW-NE stress gradient days are congruous with the above mentioned surface weather patterns and also do not differ markedly from "normal" summer season 500 millibar flow patterns; and 6) Circulation Adjustments: the frequency of SW-NE stress gradient days varies through time as the upper atmospheric circulation patterns adapt to a changing surface temperature (energy) distribution associated with seasonal adjustments in earth-sun relationships.

In addition, acceptance of these research findings is based on the soundness of the assumptions that were made in order to proceed with the analysis. During the course of this study, several important operational considerations were made to advance the research to the point where it could be accomplished. These include the assumptions that: 1) the period selected for analysis is representative of the climatic conditions which could have established and are maintaining the present phytogeographical pattern in the upper Middle West, 2) seedling and sapling survival rates, which vary primarily as a function of each species' response to periods of moisture stress, are the primary factor controlling the distribution of woody vegetation in the study area, 3) a daily water balance approach to environmental analysis is a suitable technique for estimating meteorologically induced plant stress, and 4) the study area selected is a representative segment of the major vegetation transition zone which separates the grasslands of the Great Plains from the Boreal Forest region.

These next sections examine each of the above mentioned data characteristics and assumptions in detail and, in some cases, suggestions are offered to indicate ways in which this type of study could be improved. In addition, the final paragraphs of the chapter will identify the original and significant findings of this research and discuss the possible applicability of the research design to other geographic areas.

Modality

The results presented in Chapter IV indicate that the 500 millibar wind flow azimuth data for the transect grouping whose surface meteorological conditions are thought to reinforce the ecotonal locations of the western Great Lakes region, the SW-NE stress gradient days, has the same mode as the overall population. An azimuth of 290° is associated with this most frequently occurring wind flow direction. Pressure height contours of the mean summer 500 millibar surface (Figure 4) indicate that normal conditions are quite similar with a west-northwesterly wind flow into the study region; this suggests that mean upper atmospheric wind flow patterns may also represent the modal (or most frequent) conditions.

It is also interesting to note that two additional stress gradient day groupings (SE-NW and W-E) have the same mode as the overall population. However, the distributions of wind flow directions associated with these two transect groups indicate that significant differences exist. Stresses along the SE-NW transect occur in conjunction with a mid-tropospheric trough over the western United States; accordingly, the frequency distribution of wind flows by compass direction (Figure 35) indicates a correspondingly higher than normal percentage of southerly and southwesterly winds at the 500 millibar level. In contrast, both the W-E and SW-NE stress gradient days are associated with a higher percentage of northwesterly and northerly wind circulations than are typical of the overall population, possibly due to a northward deflection of the wind flow around the central North American ridge during those stress days. Similarity between the SW-NE and W-E groups is also evident in their descriptive statistics (Table 10), the seasonal variability in the average slope of the stress gradients (Table 14), and in their frequency of occurrence (Table 15). This author's speculation concerning the phytogeographical implications of persistent modal flow conditions with an associated high frequency of both SW-NE and W-E stress days follows the next section which discusses the statistical significance of the transect groupings identified in the analysis.

Non-randomness

In order to accept the hypothesis that the SW-NE, or any other, transect grouping is a statistically significant climatic feature, the identified transect subset must not be a random sample of the total population. Application of the Chi-square non-parametric statistical test to the wind direction frequency data for each transect grouping indicated that the sample distributions were significantly different from the population of all summer season wind flow directions with the exception of the NE-SW grouping. This means that the SW-NE stress gradient days are pronounced and recurring phenomena associated with the summer season climate and atmospheric circulation of the upper Middle West; the associated surface meteorological characteristics are also distinct climatic features with specific properties which could be used to delimit climatic regions or their transition zones. In this case, a SW-NE decrease in plant moisture stress induced by potential evapotranspiration is an important environmental condition associated with this climatic feature.

An important conclusion drawn from the modal and non-random properties of the SW-NE stress gradient days is that the regional photogeographic boundaries of the upper Middle West are controlled by a distinct weather pattern which recurs at periodic and non-random intervals. The frequent occurrence of west-northwesterly wind flow in the upper atmosphere during the summer season is associated with strong physical controls which reinforce a trough-ridge-trough pattern over North America. This circulation pattern is partly the result of a baroclinic zone along the west coast of North America which reinforces the trough in that area; thermal contrasts between the cooler ocean waters and the land surface induce this baroclinic zone. The mean ridge over the continental interior is also supported by physical controls as a positive radiation balance associated with relatively long days and generally clear skies results in strong surface heating and a subsequent warming of the tropospheric portion of the atmospheric column. This leads to an eastward shift of the mean North American Ridge to a position over the western Great Plains during the summer season. In addition, a decreased hemispheric thermal gradient and the associated weaker wind speeds aloft imply a shorter wavelength for the mean 500 millibar flow; this seasonal adjustment in the distance from one wave axis to the next corresponds with the positions of the west coast trough and the ridge slightly to the west of the mid continent. Hence, the normal trough -ridge-trough is a highly stable configuration during the summer season that produces the modal west-northwesterly wind flows across the western Great Lakes region (a 290^{0} azimuth). This middle tropospheric wind pattern, associated with both the SW-NE and W-E stress gradient day, is climatologically prefered, conservative in character, and can result in the maintenance or repetition of phytogeographically important surface weather conditions.

It is recognized, however, that the identified phytogeographically important climatic feature, days with increasingly stressful meteorologic conditions toward the southwest, could occur only infrequently during some seasons or may dominate the weather conditions for an extended period during another summer because the controlling middle tropospheric wind flow patterns make periodic readjustments in spite of the influence of these forcing phenomena. A number of other input factors may contribute to these large-scale aperiodic alterations in the flow pattern, and day-to-day variability in the Rossby wind flow in the upper atmosphere is auto-correlated and circulation patterns have a tendency to persist for intervals that vary in length from less than one week to periods of several months. As a result, one pattern may dominate during one year's growing season whereas a totally different effect can be produced by a dissimilar combination of circulations during the following year (Harman and Harrington, 1978). Changes in the regional 500 millibar wind flow pattern are induced by a number of factors which include: 1) seasonal variation in poleward energy transport (Hare, 1960), 2) changing patterns of heat sources and sinks at the earth's surface (for example, an anomalous pool of warm or cold ocean surface waters (Namias, 1978) or an area of unusually extensive snow cover), 3) upstream changes in the wind circulation pattern and resultant teleconnection (Harman and Matley, 1976), and 4) factors related to solar activity (Wilcox, 1976; and Harlin, 1979). A result of this multitude of variables which influence the upper tropospheric circulation is that one year's summer season wind pattern is somewhat different from the next. Therefore, the SW-NE stress gradient days, which are generally associated with west-northwesterly wind flows, may be non-existent or rare during some summers or can dominate the climatic conditions for an extended period during one season or several summers in succession.

In the case of the major phytogeographical boundaries of the western Great Lakes region, the climatic patterns which are thought to have established and now reinforce the vegetation transition zones are a common occurrence (modal) and not rare events. It has been generally argued that climatic extremes and, hence, rare events, set the limits of most phytogeographic distributions (Good, 1974). In the upper Middle West, the evidence presented here suggests otherwise; the location of the ecotones in the western Great Lakes region could be a function of the frequency of recurrence interval of a common event. The vegetation transition zones of the upper Middle West are located primarily in response to the spatial pattern of meteorologically-induced summer season moisture stress. In the southwestern part of the study area, drought stress generally occurs more frequently (Klugman, 1978), and has the potential to last for a longer time interval. The natural vegetation of this part of the study area is prairie grassland.

Proceeding toward the northeast, the drought recurrence frequency declines and there is an associated change in the natural vegetation. It could be argued that the moisture stresses needed to establish and now reinforce the ecotone location may occur only once in about twenty to fourty years and, therefore, the "law of extremes" is supported by this research because we are again dealing with a rare event. But, in this case, the climatic situation of low probability is produced by the repeated occurrence of individual events that have a relatively high probability.

I suggest that the arguments presented here are not in direct conflict with established ecological theory which holds that climatic extremes set the limits of plant distributions; in fact, the range of individual species may reflect very closely the meteorological patterns produced by rare or extreme events. This research has indicated that boundaries between major vegetation associations are related to the modal wind flow patterns of the general circulation of the atmosphere. Drawing upon this relationship, two corollaries to the "Theory of Tolerance" (Good, 1974) are here postulated:

1) Climatic conditions which produce plant streses and, hence, delimit phytogeographical distributions can be the result of either a rare event (an extreme) or the gradual accumulation of physiological stress associated with a frequent (modal) pattern, and

2) Extreme climatic conditions which are responsible for demarking the limits of a given species or an entire association may be the result of the accumulation of a number of frequent events rather than the rare occurrence of a specific unique meteorological pattern.

The preceding sections have indicated that the original hypothesis has been accepted and have suggested several phytogeographical implications of this research. The following paragraphs discuss additional characteristics of the data analyzed in this study that lend strength to both the hypothesis and the identified biogeographic implications.

Dominance of the SW-NE Stress Gradients

Detailed analysis of the eight months randomly sampled from the fourteen years selected for this study indicates that SW-NE stress gradient days have the highest frequency of occurrence; 39 out of the 246 days examined (15.9%) had this pattern (Table 10). In addition, summing the individual daily stress gradients to identify the magnitude of these patterns shows that this grouping also has the greatest cross-transect difference in atmospheric demand for water; the meterological conditions on the SW-NE transect days account for a difference of more than ten inches of water in the balance between precipitation inputs and evapotranspirative demand for moisture during the eight randomly selected months used in this study (Table 10). The second highest frequency of occurrence (31 of 246 days of 12.6%) and summary difference in plant water availability from one end of the transect to the other (approximately eight inches) are associated with W-E stress gradients days (Table 10). Dominance of the SW-NE and W-E transects is in contrast to the global pattern of south to north changes in plant formations and meteorological conditions that in general coincide with the parallels of latitude; this south to north alignment is not demonstrated in either the phytogeographical pattern or the meteorological conditions of the western Great Lakes region. The dominance of the SW-NE and W-E transects lends support to the author's contention that the summer season regional patterns of atmospheric circulation are of greater phytogeographical importance in the western Great Lakes region than the general south-to-north decline in available energy that is partly responsible for the gross patterns of global plant distributions.

In addition to raw frequency statistics for the individual stress gradient groupings, net transect differences (e.g. SW-NE minus NE-SW) are also an indication of the impact of stress gradient days on the regional plant geography. Net frequency statistics (Table 11) and net transect differences in estimated potential evapotranspiration (Table 12) also illustrate the strength and importance of the southwest to northeast transition in plant water stress. The cumulative impact of stresses induced by potential evapotranspiration along all study area transects suggests that atmospheric demand for water is greatest in the southwestern part of the area and relatively high in the west and south; the transects that essentially parallel the ecotone have little net end-to-end differences.

Several phytogeographical implications can be drawn from these frequency statistics. One is the suggestion that the prairie-forest border in northwest Minnesota and the tip of the prairie peninsula in northwestern Indiana are similar in their frequency of summer season plant moisture stress, even though the southeast part of the study area receives a measurably different overall climate with both a greater mean annual precipitation and more growing degree days (Eichenlaub, 1979). Investigation concerning the timing of these stress periods was not attempted in this study; however, the data collected suggest that the southeastern part of the study area is more likely to receive early summer dry periods whereas the northwest has a tendency for more frequent mid-to-late summer moisture stress periods.

In addition, these descriptive statistics dealing with net frequency enhance this author's arguments concerning the phytogeographical importance of SW-NE stress gradient days and again point out the influence of the W-E transect. Analysis of the cumulative net frequency statistics (Table 12), shows that the W-E and S-N transects have similar gradients across the study area. Based on the generalized global pattern of energy sources and sinks and the earth's rotation on its axis, an extratropical middle tropospheric westerly wind flow is established; it would be reasonable to assume that the surface expression of this upper atmospheric circulation would result in global patterns with the S-N gradients having the steepest slopes. But, as stated earlier, the influence of the North American ridge, a predominant anchor in the middle tropospheric westerlies associated with the Rocky Mountain Cordillera, affects this regional pattern of atmospheric circulation in the upper Middle West so that the modal summer season 500 millibar wind flow is west-northwesterly; the air stream sweeps southeastward from the North American ridge and flows into a trough over the eastern Great Lakes-St. Lawrence Valley region. The resultant increase in the frequency of west-northwesterly middle tropospheric wind flows is related to a higher occurrence of both W-E and SW-NE stress gradient days (Figures 39 and 41). Impacts of this regional atmospheric circulation include a near equalization of the net W-E and S-N cumulative stress statistics and the predominance of the SW-NE transect. This relationship between surface gradients in plant moisture stress and the regional atmospheric circulation is also supported by the mapped pattern of surface pressure for both the SW-NE and W-E groups.

Composite Maps

The weather patterns demonstrated by the composite surface pressure distribution for both the SW-NE (Figure 24) and W-E (Figure 25) stress gradient days lend additional support to the phytogeographical implications of this research. As described in Chapter IV, the surface conditions are dominated by a high pressure cell in the southeastern United States; this atmospheric circulation suggests that the western Great Lakes region is affected by warmer and drier air moving in from the south and southwest as adiabatic warming and drying occurs through the subsident and clockwise circulation on the backside of the anticyclone. The southwesterly component of this subsident air flow at the surface results in advection of warm and usually dry air from the southern and western Great Plains into the southwestern part of the study area which is enhanced further by the existence of a weak low pressure center to the northwest of the study area over the northern Great Plains.

Evidence suggests that this circulation can persist for several days (Table 13) thereby increasing the potential for plant moisture stress induced physiological changes and possible damage to plant tissues as stresses accumulate; previous studies have indicated that persistent plant moisture deficits can lead to a significant alteration in plant dynamics (Albertson and Weaver, 1945). With this weather pattern associated with the SW-NE transect group, relatively warmer and drier air of continental tropical (cT) origin is brought northeastward into the study area. As a result, the greatest moisture stresses occur in the southwestern and western parts of the study area, whereas the demand for water is significantly lower to the northeast; the phytogeographical distributions reflect this pattern. The weather conditions that create and maintain this environmental gradient are produced by a wind circulation in the middle troposphere which corroborates the surface situation.

500 Millibar Height Contour Maps

A relative weak and contracted circumpolar wind flow characteristic of the northern hemisphere summer season is still strong enough to play a major role in the generation and movement of surface weather features across most of the United States. As noted earlier, climatological normals indicate an eastward shift of the North American ridge away from the Rocky Mountain Cordillera to a position over the western Great Plains during July and August and contour maps of the mean 500 millibar pressure height surface reveal a summer season trough-ridge-trough pattern over North America with troughs near both coasts and with the ridge axis over the continental interior.

Pressure height maps of the mean 500 millibar surface for the days in either the SW-NE or W-E transect groupings demonstrate a close correspondence between these days of surface stress gradients and the most frequently occurring flow pattern in the middle troposphere. Mean height contour maps for these two transect groups (Figures 38 and 40) demonstrate the "normal" trough-ridge-trough pattern with the North American ridge displaced eastward to its summer season position over the western Great Plains. Even though interrelationships between the surface weather patterns and the upper atmospheric circulation are generally weakest in the summer season, strong support exists for this link between the wind flow aloft and the surface pressure distribution. The weak surface low that is evident on the composite maps for both the SW-NE and W-E stress gradient days is a lee depression that forms partly due to adiabatic warming of the downslope winds to the east of the mountain barrier (McClain, 1960). An area of higher cyclogenesis exists in the northern Great Plains during the summer season (Klein, 1957; and Reitan, 1974) which corresponds with these lows that diminish in intensity with height. Moving weather systems (with the potential to enhance and displace these lee depressions which are normally located slightly west and north of the study area) are either steered northeastward into central Canada by the wind flow out of the trough over the west coast of North America or disrupted and significantly weakened by passage over the mountain barrier. In order to strengthen these weak lows, an area of positive vorticity advection and upper level divergence associated with a moving short wave trough is necessary (Hage, 1961). A readjustment of the wind flow into a more zonal or westerly circulation would allow the necessary enhancement of the surface features and their subsequent eastward movement. Due to the contracted nature of the circumpolar vortex during the summer season, the region affected by a zonal flow pattern is usually restricted to areas north of the United States. As a result, the movement of cyclonic cells through the study area generally decreases during July and August as lows tend to follow the Alberta storm track across southern Canada rather than through the study area.

The normal west-northwesterly wind circulation at the 500 millibar level also helps explain the existence and positioning of a surface high pressure cell in the eastern part of the United States. Maps depicting the areas of high anticyclone frequency, genesis, lysis, and the movements of these synoptic scale circulation systems indicate that their occurrence in the eastern United States generally marks the end of their life cycle (Zishka and Smith, 1980). These high pressure cells usually develop over the United States - Canadian border between Alberta and Montana and move southeastward in association with the flow aloft to reside over the Middle Atlantic states (Pennsylvania, Maryland, and Virginia) where they establish a semi-permanent position as they slowly weaken through time. The recurrent migration of these anticyclonic cells from their region of origin in the northern Great Plains to the eastern United States is guided by the modal flow in the upper atmosphere. The frequency of high pressure systems decreases to a minimal level during the summer season and, as a result, there are fewer anticyclones moving through the area. Because the frequency of high pressure cells is low, the circulation associated with any one decaying surface anticyclone may affect the study area for a period lasting from several days to over a week.

This research has shown that extended periods with higher plant moisture stress in the southwestern and western parts of the study area can be generated by modal upper atmospheric circulation; previous research dealing with the climatic record for the entire Great Plains suggests that the persistence of a circulation type, rather than a specific wind flow pattern, is associated with the severe droughts of historical record (Borchert, 1971). His analysis of dry periods affecting the grassland region of the central United States indicates that the major droughts can be separated into two distinct types: 1) the 1890's and the 1930's type droughts which affected the entire

Great Plains region with dry conditions extending eastward in the prairie peninsula area, whereas 2) the impact of the 1910's and 1950's type droughts is felt primarily in the southern Plains with an accompanying dry area in the southeastern United States (Borchert, 1971). Dissimilar circulation patterns are associated with these distinctly different distributions of drought; the wind flow pattern associated with the 1890's and 1930's dry periods produces below normal precipitation totals within the western Great Lakes region whereas the 1950's pattern resulted in near normal rainfall totals across the upper Middle West. Because only one of the two drought types identified by Borchert affects the upper Middle West (the 1930's type), I conclude that dry conditions which produce plant stresses that reinforce the ecotonal boundaries within the western Great Lakes region are associated with the establishment and persistence of a specific circulation type. The 1950's type drought conditions have their greatest impact in other parts of the grassland region.

An additional implication of these research findings is that modal 500 millibar flow can produce a gradient in potential fuel flamability across the study area such that the grassland areas will have a higher probability of fire. The same environmental conditions that produce high levels of moisture stress on germinating seedlings or young saplings will also tend to dry out the leaf litter and other possible fuels for either an anthropogenic or natural conflagration. Hence, the persistence of the modal pattern will also tend to regulate fire frequencies in the western Great Lakes region; in general, a gradient of decreasing likelihood of a damaging fire will exist along the transect across the major ecotones from southwest to northeast. These comments lend further support to the previous contention that fire is only one aspect of the "ecological complex" of the prairie-forest transition zone which is largely controlled by climate (Borchert, 1950).

Circulation Adjustments

Changes in the size and positioning of the circumpolar vortex exhibit an annual pattern with maximum southward extension during the winter months. As hemispheric temperature gradients (equator to pole) decrease during the spring and early summer, the westerlies contract in their areal extent. These changes in the upper atmospheric circulation follow an annual cycle which is generally similar from one year to the next; reorganization of the flow to form the normal summer season single westerly wind maximum in the mid-latitudes (approximately 45^{o} - 50^{o}N) generally occurs sometime in late June. As a result, the months of May and June are viewed as transitional with the specific date of reorganization varying from year to year (Bryson and Hare, 1974), while the months of July and August are associated with a "summer" circulation regime.

The impact of these recognizable circulation shifts is evident in the data presented on monthly variability in the frequency of stress gradients along any of the eight transects (Table 15). Combining this information with the data presented on the persistence of the stress gradient events (Table 13) yields an indication of not only the season when an individual transect stress day is most likely but also suggests when meteorological situations of potential phytogeographical importance (extended stress periods) may occur. In May, a heterogeneous mixture of transect groups exists as no stress gradient direction dominates the frequency statistics; the data indicate that every transect type occurred during the two sample months and that no one transect direction accounts for more than 20 percent of the total number of stress gradient events. A decrease in the probability of the transects which have highest stress values in the NW, N, and NE as well as a high frequency of S-N stress gradient days (34% of all events) are major features in the data for June. Accompanying the shift to a summertime circulation regime, a marked difference is evident in the data for July and August which indicates a dominance of SW-NE and W-E stress gradient days. These two transects account for over 54 percent of all stress gradient events in July and for over 47 percent in August. The phytogeographical significance of these mid to late summer events is demonstrated by both the steep gradients associated with these two groups (Table 14) and tendency for these events to persist for an additional day or more (Table 15). In summary, a progression in the occurrence of the various stress gradient types develops as the atmospheric circulation adjusts into its summer season pattern. These wind flow changes result in the months of July and August being dominated by transect groupings that are thought to have established and now reinforce the ecotonal positions in the western Great Lakes region.

Assumptions

The ability to proceed with any research effort is dependent upon a number of operational definitions which are often based on logical and supportable assumptions. In this study, methods designed to examine the nature of the relationship between upper atmospheric circulation and broadscale phytogeographical distributions within the upper Middle West were based on the assumptions that: 1) the period of study, 1961-1974, is representative of climatic conditions which established and now maintain the present vegetation pattern, 2) summer season moisture deficits regulating seedling survival rates are the primary factor controling phytogeographical distributions in the western Great Lakes region, 3) daily calculation of the water balance is a reasonable means for estimating atmospheric induced plant moisture stress, and 4) the study area selected is a representative segment of the transition zone which separates the grasslands of central North America from the forests to the north and east. These next paragraphs will consider, in retrospect, the validity of the reasoning behind these assumptions and identify research areas which future studies should address.

Meteorological data concerning the nature of wind flow in the upper atmosphere are available for climatic analysis since about the end of World War II. For this study, however, the analysis period is limited to 1961 through 1974 because the author had access to these data and because it was thought that sufficient variability exists within this time period to incorporate not only the common daily circulation patterns but also the low probability events. Certainly, the concept of climate implies natural fluctuation and numerous evidence, such as ocean cores or pollen profiles, demonstrates this variation (Skaggs, 1980). These natural shifts or oscillations tend to be irregular when analyzed on a time scale of a decade or less, however, periodicities have been found in analysis of longer time intervals (Landsberg, 1975). The identification of distinctly different meteorological conditions at specific times during the priod of instrument record suggests that these natural fluctuations in climate are produced by changes in the frequency of occurrence of various weather patterns. For example, the change from drought to excessively wet conditions in California during 1977 and 1978 (Namias, 1979), the cooler temperatures in the northern hemisphere mid-latitudes since 1950 (Kalnicky, 1974), the different patterns of drought in the Great Plains (Borchert, 1971), and the unusually cold winters in eastern North America of the late 1970's (Diaz and Quayle, 1980) have been related to shifts in the atmospheric circulation such that contrasting patterns tended to dominate in differing time periods.

These descriptions of the circulation for a given era and the natural variability at the time scale of a decade or more incorporate daily iterations which become smoothed into a general statement for a given time period. Fluctuations analyzed on a daily or weekly basis are generally more pronounced and also tend to incorporate individual days which mirror the long term patterns. Hence, a daily examination of the circulation should indicate both the short-term patterns of significance as well as suggest the conditions which are either very rare or quite frequent over a long time interval. Therefore, selection of the 1961 through 1974 period for analysis is justified because significant natural iteration exists during these fourteen years. It is recognized that the frequency distribution of various wind flow directions may shift during certain time periods such that the modal direction may differ from the 290^{o} azimuth found in this study; however, the physical controls which reinforce a trough-ridge-trough pattern over North America during the summer season support the long-term dominance of west-northwesterly wind flow in the western Great Lakes region.

Arguments in support of the second (summer season moisture stress) and third (water budget) assumptions were presented in detail in Chapter II. A retrospective view of these operational considerations based on the results suggests that additional questions could be addressed with only minor modifications in the research design. I do not mean to suggest that these assumptions were not well founded or that the results were contradictory; in general, the statistics calculated were in agreement with the expected outcomes of the study. One question identified by this research that future studies may address is the difference, if any, between the impact of a gradual accumulation of minor plant stresses associated with the normal (and variable) climatic regime versus the less frequent, but extended periods of stress that occur during major droughts. What role does either of these climatic situations play in delimiting phytogeographical boundaries; is one predominant?

The water balance approach for the identification of individual days of atmospheric-induced plant moisture stress also seems justified in my estimation because the surface weather conditions on the individual days identified exhibit patterns which would suggest a transect in stress values across the study area; however, the arguments presented in the ecophysiological literature indicate that extended periods of stress accumulation are important in affecting plant life processes. Additional studies dealing with the synoptic climatology of plant stress events might examine the role played by persistence of a specific weather pattern and, therefore, employ a research design which incorporates a cummulative water budget approach. Since the intent of this research was to identify specific days with meteorological conditions that reinforce the ecotonal locations, an autoregressive approach was not utilized in this study.

Finally, it was an intent of this investigation to demonstrate applicability of both the results and the research design to other areas with either similar transitions in vegetation or to zones where physiological factors other than moisture stress play the primary role. To meet this goal, the western Great Lakes region was chosen as the study area with an underlying assumption that it is a representative segment of the lengthy transition zone which separates the grassland areas of central North America from the wide band of coniferous forests which extend across the continent to the north. If conditions in the western Great Lakes region are similar to the rest of this transition zone which extends northwestward across the prairie provinces of Canada, the identified factors which control the vegetation distribution and the Holocene vegetational history should be similar in all areas. This appears to be the case. These vegetation transition zones have maintained a general northwest-southeast orientation during their cliseral migrations in the Holocene. Post-glacial movements of the major ecotones indicate an overall shift northeastward followed by a subsequent retreat to stabilize in their current location approximately 2500 BR (Ritchie, 1976). In addition, both fire and climate have been identified as major factors regulating these phytogeographical transitions with some debate concerning the importance of natural versus human-induced burnings. It is reasonable to conclude that climate is the primary control across Canada (Ritchie, 1976), as in the western Great Lakes region, since the transition zone is an area with a high frequency of natural fires (Kourtz, 1967) and because the climatic patterns have a general WNW-ESE trend (Rithcie, 1976). Modal northwesterly flow at the 500 millibar level establishes these summer season patterns with higher temperatures and lower precipitation frequencies to the southwest of the ecotonal area (Harman and Braud, 1975). These authors suggest that "existing gross phytogeographical patterns on the Canadian prairies are an adjustment to modal flow in the mid and upper troposphere" based on an examination of climatic patterns associated with selected flow directions (Harman and Braud, 1975).

Hence, the selected study area does not seem markedly different from the remainder of the prairie-forest ecotone in central North America. Use of the ecophysiological approach applied in this study would add significantly to understanding the phytogeographical controls of the dominant vegetation in other ecotonal environments. What climatic patterns regulate the production of viable seed in areas along the boreal forest-tundra transition zone in central Canada? Is there a climatic reason for the dispersed nature of the ecotone in eastern Canada? Additionally, the possibility of similar ecoclimatic effects in Eurasia could be examined with this type of approach. Are the generally west-east vegetative transitions in northern Eurasia associated with the modal atmospheric circulation?

Original and Significant Findings

The major contribution of this research is a demonstration of a linkage between surface weather patterns that may regulate plant life processes and the regional atmospheric circulation. A number of studies have demonstrated a correlation between vegetation and climatic patterns; this examination lends further strength to the arguments presented by these researchers who have implied a climatic control on vegetation boundaries. Ecological climatology has developed considerably since 1951 when it was stated that "climate is the ultimate ecological control" (Hare, 1951) and this study based on plant physiological responses to climatic elements adds a powerful analysis tool to the techniques available to the ecoclimatological researcher.

Significant findings of this research are the identification of the causal relationship between modal flow and phytogeographically important climatic parameters and the identification of moisture stress patterns that coincide with the distribution of woody vegetation in the western Great Lakes region. These results also suggest that phytogeographic theory needs clarification with respect to the role played by the persistence of relatively high probability events. The boundaries between major vegetation associations may not always be set by rare events. The accumulation of frequently occurring meteorological conditions may also set the limits.

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Chapter VI

SUMMARY AND CONCLUSIONS

Upper atmospheric circulation has been shown to be a major factor controlling surface environmental gradients of plant moisture stress in the western Great Lakes region where tall-grass prairie in the south and west gives way to deciduous forest and then to mixed deciduous and coniferous cover along a transect toward the northeast. The combination of an ecophysiological analysis of these natural vegetation transitions with a synoptic climatological study of atmospheric conditions has indicated a relationship between modal wind flow patterns in the middle troposphere and the plant moisture stresses that are thought to have created and now reinforce the contemporary vegetation distribution. This examination incorporates a research design that leads the way for more comprehensive analysis in future ecoclimatological studies because the research identifies a specific environmental parameter that is thought to be limiting (summer season moisture stress) and then proceeds with a climatic analysis of both the surface and upper atmospheric circulation patterns that are associated with gradients in this limiting factor across the upper Middle West. As a result, strong support is given to previous studies which have shown a correlation between areas of climatic transition and ecotonal location but have failed to identify the climatic property, feature, etc. that may exert control over plant life processes and thereby influence distributions.

Examination of ecological and plant physiological literature dealing with the western Great Lakes region suggested to the author that a primary control on the vegetation distribution of the study area is the survival rate of seedlings and saplings during periods of plant moisture deficit. In general, atmospheric conditions regulate the amount of water available to the vegetation through the processes of precipitation and evapotranspiration; a water budget analysis was used to estimate daily atmospheric-induced plant moisture stress for fourteen first-order weather stations in the western Great Lakes region. Transects developed from these stations and oriented with the eight cardinal compass points (N to S, NE to SW, E to W, etc.) were then used to examine the direction and strength of any continuously decreasing gradients across the study area for each day during the eight summer months that were randomly selected for the study. This procedure resulted in the identification of eight different directions along which daily stress developed within the study area. All days typical of one of the eight different patterns were grouped together and each group was subjected to a synoptic climatological analysis based on the pressure and wind flow patterns at both the surface and 500 millibar levels.

The results of this examination,completed through a surface map analysis and through the production of mean 500 millibar pressure height contour maps, demonstrate a strong linkage between the varying patterns of wind flow in the upper atmosphere and the distribution of surface weather. In addition, summary statistics concerning the frequence of occurrence and strength of the stress gradients, the persistence of the moisture stress patterns, and their seasonal variability were generated for each transect group. These data provided the information used in determining the relative importance and timing of the eight gradients in plant moisture stress across the western Great Lakes region.

Meteorological conditions that produce highest values of potential evapotranspiration in the southwestern (prairie) part of the study area with an accompanying decrease toward the northeast were found to be most frequent, non-random, and associated with modal (northwesterly) wind flow in the upper atmosphere. These SW-NE stress gradient days are thought to have produced the stresses which created and now reinforce the ecotonal orientation and positioning in the western Great Lakes region because they produce an atmospheric moisture demand pattern that is congruous with the vegetation transitions, i.e. highest over prairie and lowest over forest areas. Hence, the hypothesis of this research is accepted and the importance of regional atmospheric circulation in controlling phytogeographical patterns is demonstrated.

Additionally, the implication that plant association boundaries are delimited by the modal wind flow in the middle troposphere enhances understanding concerning the nature of climatic controls on vegetative patterns. Current phytogeographic theory holds that climatic extremes define the limits that regulate the distribution of plants (Good, 1974). The arguments presented here suggest that either a slow accumulation of physiologic stress associated with frequent recurrence of a common weather pattern or an extreme stress situation produced not by a rare event but by the persistence of a common circulation (Modal wind flow) could regulate the gross phytogeographical distributions in the upper Middle West.

Ecoclimatological studies have advanced considerably since the earliest researchers compared isorithms of mean annual climatic data with plant distributions. This research continues that growth with a demonstration of a strong relationship between modal wind flow patterns and the surface conditions that influence plant physiological processes. Subsequent ecoclimatic research might consider the systems theory and modelling approach that has shown potential in analysis of several dynamic geomorphic processes and their associated land forms (Strahler, 1980), proven useful for describing energy movements and partioning within ecosystems (Odum, 1972), and has been suggested as the research approach of the future for geographers interested in climatological studies (Terjung, 1976).

An important question that this research has identified but was not designed to answer is the exact way in which moisture deficits accumulate in developing seedlings and young saplings such that the physiological stresses influence the location of vegetation transitions. Additional research along these lines could address which of the multitude of ways that soil moisture deficits and subsequent plant stresses can be produced and are limiting to seedling survival and then examine the frequency and spatial patterns of the meteorological conditions responsible. An examination of this type might determine if an extreme event produced by a persistent upper atmospheric flow (a major drought) is more important in delimiting plant distributions than the "normal" summer season accumulation of stresses associated with the frequent recurrence of the modal pattern.

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Appendix I

```
      PROGRAM PEVAP(INPUT,OUTPUT,TAPE1,TAPE2)
      III=0
      PRINT 1
1     FORMAT (* THIS PROGRAM COMPUTES POTENTIAL EVAPOTRANSPIRATION*/
     +* USING THE CHRISTIANSEN METHOD.  THE STATION NAME, DATE, MEAN*/
     +* TEMPERATURE, WIND SPEED, RELATIVE HUMIDITY, PERCENT POSSIBLE*/
     +* SUNSHINE, PRECIP, AND THE PE VALUE WILL BE WRITTEN ON TAPE2.*/
     +* FOR PUNCHED CARD OUTPUT, DISPOSE,TAPE2,PU.*)
50    III=III+1
      IF(III.GT.1)GO TO 30
      PRINT 2
2     FORMAT (* WHAT IS THE STATION NAME(A3)?*)
      READ 100,STA
100   FORMAT(A3)
      PRINT 3
3     FORMAT (* WHAT IS THE DATE (YEAR,MONTH - 2(I2))?*)
      READ 101,LYR,LMO
101   FORMAT(2(I2))
30    LMD=LMO*100+III
      IF(LMD.GE.501.AND.LMD.LE.531)CALL MAY(LMD,RT)
      IF(LMD.GE.601.AND.LMD.LE.630)CALL JUNE(LMD,RT)
      IF(LMD.GE.701.AND.LMD.LE.731)CALL JULY(LMD,RT)
      IF(LMD.GE.801.AND.LMD.LE.831)CALL AUGUST(LMD,RT)
102   FORMAT(F7.3)
      READ(1,105) TA,DP,W,S,PRECIP
105   FORMAT(F2.0,1X,F3.0,1X,F4.1,1X,F3.0,1X,F6.3)
      IF(EOF(1))99,98
98    IF(TA.EQ.-9.)GO TO 61
      CT=0.0673+(.0132*TA)+.0000367*(TA**2.)
      GO TO 70
61    CT=1.
70    IF(DP.EQ.-9.)GO TO 81
      IF(III.GT.1)GO TO 75
18    PRINT 16
16    FORMAT(* TYPE...M.. FOR MEAN DAILY DEW POINT TEMP,*/
     +* TYPE...N.. FOR NOON HUMIDITY VALUE ...*)
      READ 104,ANSA
104   FORMAT(A1)
75    IF(ANSA.EQ.1HN)GO TO 14
      GO TO 19
14    RH=DP
      DP-0.0
      RHA=RH
```

```
19      IF(ANSA.EQ.1HN)GO TO 17
        IF(ANSA.NE.1HM)GO TO 18
        CALL RELHUM(TA,DP,RH)
        H=3.67+.233*RH+.00667*(RH**2.)
        RHA=H
17      CH=1.25-.0087*RHA+.000075*(RHA**2.)-.0000000085*(RHA**4.)
        GO TO 60
81      CH=1.
60      IF(W.EQ.-9.)GO TO 71
        WIND=W*24.
        IF(W.LE.7.9)WA=.215*WIND+.00154*(WIND**2.)
        IF(W.GT.7.9)WA=.817*WIND-58.4
        CW=.708+.00546*WA-.00001*(WA**2.)
        GO TO 80
71      CW=1.
80      IF(III.GT.1)GO TO 76
        PRINT 8
8       FORMAT(* TYPE...P.. FOR PERCENT POSSIBLE SUNSHINE OR NO DATA*/
       +* TYPE...S.. FOR SKY COVER  ...*)
        READ 104,ANSB
76      IF(ANSB.EQ.1HP)GO TO 20
        IF(ANSB.EQ.1HS)GO TO 21
20      IF(S.EQ.-9.)GO TO 91
        GO TO 23
21      SKY=100.-1.6*S-.84*(S**2.)
        S=SKY
        GO TO 23
23      CS=.542+.008*S-.000078*(S**2.)-.00000062*(S**3.)
        GO TO 90
91      CS=1.
90      IF(III.GT.1)GO TO 40
        PRINT 9
9       FORMAT(* WHAT IS THE STATION ELEVATION IN FEET (F5.0)?*)
        READ 103,EL
103     FORMAT(F5.0)
        E=EL/1000.
        CE=.97+(.03*E)
40      CONTINUE
        IF(LMD.LE.501)CM=.89
        IF(LMD.GT.501.AND.LMD.LE.524)CM=.88
        IF(LMD.GT.524.AND.LMD.LE.703)CM=.87
        IF(LMD.GE.703)CM=.88
        IF(LMD.GE.726)CM=.89
        IF(LMD.GE.807)CM=.90
        IF(LMD.GE.814)CM=.91
        IF(LMD.GE.818)CM=.92
        IF(LMD.GE.823)CM=.93
        IF(LMD.GE.826)CM=.94
        IF(LMD.GE.831)CM=.95
        PET=.473*RT*CT*CW*CH*CS*CE*CM
        WRITE(2,200)STA,LYR,LMO,III,TA,DP,RH,W,S,PRECIP,PET
200     FORMAT(A3,8X,3(I2),5(1X,F5.1),2(1X,F5.3))
        GO TO 50
99      PRINT 13
```

```
13     FORMAT(* YOUR INPUT DATA AND PE VALUES ARE ON THE FILE TAPE2*/
      +* REWIND TAPE2 BEFORE YOU DISPOSE IT*)
       PRINT 972
972    FORMAT(1H1*     GOOD BYE*)
       STOP
       END
       SUBROUTINE RELHUM(TA,DP,RH)
       DIMENSION SVP(80)
       DATA SVP/.110,.114,.119,.123,.130,.135,.141,.147,
      +.153,.160,.166,.173,.180,.188,.195,.203,.212,.220,.229,.238,.248,
      +.257,.268,.278,.289,.300,.312,.324,.336,.349,.362,.376,.390,.405,
      +.420,.436,.452,.468,.485,.503,.522,.540,.560,.580,.601,.622,.644,
      +.667,.690,.714,.739,.765,.791,.818,.846,.875,.905,.935,.967,.999,
      +1.032,1.067,1.103,1.138,1.175,1.214,1.253,1.294,1.335,1.378,
      +1.422,1.467,1.514,1.561,1.610,1.661,1.712,1.766,1.820,1.876/
       TA=INT(TA)
       IDP=INT(DP)
       JTA=ITA-20
       JDP=IDP-20
       RH=SVP(JDP)*100./SVP(JTA)
       RETURN
       END
       SUBROUTINE MAY(LMD,RT)
       DIMENSION ETR(31)
       DATA ETR/.585,.588,.591,.594,.597,.600,.603,.606,.609,.613,
      +.615,.618,.620,.622,.625,.627,.629,.631,.633,.635,
      +.637,.639,.641,.643,.645,.646,.647,.649,.651,.653,.654/
       KDATE=LMD-500
       RT=ETR(KDATE)
       RETURN
       END
       SUBROUTINE JUNE(LMD,RT)
       DIMENSION ETR(30)
       DATA ETR/.656,.658,.660,.661,.663,.664,.664,.665,.665,.666,
      +.667,.668,.669,.670,.670,.671,.671,.672,.672,.672,.672,
      +.672,.672,.672,.671,.670,.669,.667,.666,.665/
       KDATE=LMD-600
       RT=ETR(KDATE)
       RETURN
       END
       SUBROUTINE JULY(LMD,RT)
       DIMENSION ETR(31)
       DATA ETR/.663,.661,.659,.658,.657,.656,.655,.653,.652,.651,
      +.650,.649,.648,.646,.645,.643,.641,.639,.637,.636,.634,.632,
      +.630,.628,.626,.624,.622,.620,.618,.617,.614/
       KDATE=LMD-700
       RT=ETR(KDATE)
       RETURN
       END
       SUBROUTINE AUGUST (LMD,RT)
       DIMENSION ETR(31)
       DATA ETR/.613,.610,.607,.604,.602,.599,.596,.593,.591,.589,
      +.586,.584,.583,.582,.580,.578,.576,.574,.572,.570,
      +.568,.565,.563,.560,.557,.554,.551,.548,.545,.542,.539/
```

```
KDATE=LMD-800
RT=ETR(KDATE)
RETURN
END
```

Appendix 2

```
      PROGRAM PESLOPE(INPUT,OUTPUT,TAPE1,TAPE2)
      COMMON PE(14,31),STRESS(14,31)
      DIMENSION NWSE(31,2),NS(31,2),NESW(31,2),EW(31,2)
      DIMENSION SENW(31,2),SN(31,2),SWNE(31,2),WE(31,2)
      DIMENSION IDATE(2),PRECIP(14,31)
      DIMENSION INWSE(2),INS(2),INESW(2),IEW(2),ISENW(2),ISN(2),ISWNE(2)
      DIMENSION IWE(2)
      DATA INWSE,INS,INESW,IEW,ISENW,ISN,ISWNE,IWE/16*0/
      READ(1,101) (IDATE(L),L-1,2),IDAYS
101   FORMAT(R10,R2,1X,I2)
      DO 10 I=1,14
      DO 20 J=1,IDAYS
      READ(1,102) PRECIP(I,J),PE(I,J)
102   FORMAT(48X,F5.3,1X,F5.3)
      STRESS(I,J)=PE(I,J)-PRECIP(I,J)
      IF(PRECIP(I,J).EQ.0.001)STRESS(I,J)=PE(I,J)
      IF(STRESS(I,J).LT.0.0)STRESS(I,J)=0.0
20    CONTINUE
10    CONTINUE
      DO 30 I=1,IDAYS
      CALL SLOPE(INWSE,I,1,2,3,4,NWSE(I,1),NWSE(I,2))
      CALL SLOPE(ISWNE,I,5,6,7,8,SWNE(I,1),SWNE(I,2))
      CALL SLOPE(IWE,I,9,10,11,12,WE(I,1),WE(I,2))
      CALL SLOPE(INS,I,14,7,3,13,NW(I,1),NS(I,2))
      CALL SLOPE(ISENW,I,4,3,2,1,SENW(I,1),SENW(I,2))
      CALL SLOPE(INESW,I,8,7,6,5,NESW(I,1),NESW(I,2))
      CALL SLOPE(IEW,I,12,11,10,9,EW(I,1),EW(I,2))
      CALL SLOPE(ISN,I,13,3,7,14,SN(I,1),SN(I,2))
30    CONTINUE
      WRITE(2,201) (IDATE(L),L=1,2)
201   FORMAT(1H ,(PE GRADIENT ANALYSIS FOR *,R10,R2,//)
      WRITE(2,202)
202   FORMAT(1H ,*DAY    NW-SE  N-S  NE-SW  E-W  SE-NW  S-N*
     +*  SW-NE  W-E*)
      DO 40 I=1,IDAYS
      WRITE(2,203) I,NWSE(I,1),NS(I,1),NESW(I,1),EW(I,1),SENW(I,1)
     + ,SN(I,1),SWNE(I,1),WE(I,1)
203   FORMAT(2X,I2,3X,8(1X,F5.3))
40    CONTINUE
      WRITE(2,206) INWSE(1),INS(1),INESW(1),IEW(1),ISENW(1),ISN(1),
     + ISWNE(1),IWE(1)
206   FORMAT(1H ,/,*TOTAL*,3X,8(I2,4X),//)
      WRITE(2,204) (IDATE(L),L=1,2)
```

```
204    FORMAT(1H ,*PE - PRECIP GRADIENT ANALYSIS FOR *,R10,R2,//)
       WRITE(2,202)
       DO 50 I=1,IDAYS
       WRITE(2,203) I,NWSE(I,2),NS(I,2),NESW(I,2),EW(I,2),SENW(I,2)
      + ,SN(I,2),SWNE(I,2),WE(I,2)
50     CONTINUE
       WRITE(2,206) INWSE(2),INS(2),INESW(2),IEW(2),ISENW(2),ISN(2),
      + ISWNE(2),IWE(2)
       STOP
       END
       SUBROUTINE SLOPE(IX,I,II,IJ,IK,IL,X,Y)
       DIMENSION IX(2)
       COMMON PE(14,31),STRESS(14,31)
       A=PE(II,I)-PE(IJ,I)
       IF(A.LE.0.)GO TO 99
       B=PE(IJ,I)-PE(IK,I)
       IF(B.LE.0.)GO TO 99
       C=PE(IK,I)-PE(IL,I)
       IF(C.LE.0.)GO TO 99
       X=A+B+C
       IX(1)=IX(1)+1
       GO TO 98
99     X=999.
98     AA=STRESS(II,I)-STRESS(IJ,I)
       IF(AA.LE.0.)GO TO 97
       BB=STRESS(IJ,I)-STRESS(IK,I)
       IF(BB.LE.0.)GO TO (&
       CC=STRESS(IK,I)-STRESS(IL,I)
       IF(CC.LE.0.)GO TO 97
       Y=AA+BB+CC
       IX(2)=IX(2)+1
       GO TO 96
97     Y=999.
96     RETURN
       END
```

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