The Variation of Four Bioclimatic Indexes in Indiana

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Introduction

The concepts of biotemperature and potential evapotranspiration ratio were introduced by Holdridge (13, 14) to allow the relationship between plant communities and bioclimate to be studied. Although Holdridge's life zone classification was initially developed to give a more accurate picture than existing systems (15, 19, 20) of the relationship between climate and vegetation in the tropics, its use can also be extended into the temperate region. By combining mean annual biotemperature, potential evapotranspiration ratio, total annual precipitation, and latitudinal position, over 100 life zones as well as over 600 transitional zones between these life zones may be identified. Although each of the life zones appears to have been named after a specific plant association, the classification developed in the life zone chart is really based on climate and not forest composition. However, each life zone theoretically supports a physiognomically distinct vegetation type whose geographic boundaries are closely defined by the boundaries of the climatically defined life zone. In the absence of climatic data, the life zone could still be mapped using vegetational physiognomy. Because the life zones are not defined on the basis of species composition, similar life zones may occur and may be mapped on different continents.

The concepts of warmth (as measured by effective temperature) and temperateness (as measured by equability) were introduced by Bailey in 1960. Bailey (2, 3) was not interested in developing an extensive bioclimatic classification such as Holdridge's classification (13, 14). Bailey was concerned that conventional measurements of temperature (namely, mean annual temperature and mean annual range in temperature) were too approximate to adequately define the thermal requirements of living and, in particular, fossil plants. Therefore, he developed two new thermal measurements, warmth and temperateness. Warmth was defined as the temperature characteristic of the beginning and end of a warm period during which vegetational growth occurred. Temperateness measures the perennial and/or seasonal freedom of any locality from extremes of heat or cold. Initially, Bailey (2) felt that variation in warmth had a much greater influence on the vegetation than variation in temperateness. Subsequent observations that the mixed mesophytic forests of eastern North America, of the Sierra Madre Oriental in Mexico, and of southeastern Asia are confined to areas of temperate climate ($M > 50$) and that shifts in population within the United States are toward areas of increasing temperateness (California, Arizona, New Mexico, and Florida) led Bailey (3) to conclude that temperateness is also an important bioclimatic element influencing the distribution of plants and animals. These concepts have been used extensively by Axelrod (1), who believes that changes in warmth and temperateness are the basis of floral evolution in the western United States.

Materials and Methods

The maps discussed in this paper were produced by analyzing two data bases, TEMPDAT (TEMPerature DATa) and PRECDAT (PRECipitation DATa), using the microcomputer program, CLIMATE (10). CLIMATE will allow a researcher to analyze seven different climatic variables at 91 different weather stations in Indiana and the surrounding States of Ohio, Kentucky, Illinois, and Michigan. The climatic parameters include mean temperature, total precipitation, mean range in temperature, mean biotemperature, potential evapotranspiration ratio, effective temperature, and equability. Each of these parameters may be studied over the whole year or over only a portion of the year, such as the growing season. For the purposes of this study, the growing season was defined as those months of the year which are free from frost. Depending on the location, the growing season runs from either April (in southern Indiana) or May (in northern Indiana) to October. Two maps are presented for each of the seven climatic variables: the first map illustrates the variation in a specific climatic variable for the whole year, and the second map illustrates the variation in that climatic variable during the growing season.

The data bases used in this analysis contain monthly means for temperature and precipitation for the period from 1941 to 1970. The data were obtained from the National Climatic Center in Asheville, North Carolina (21-25). Temperature data were available from 65 weather stations and precipitation data were available from 84 weather stations in Indiana. Because calculation of the potential evapotranspiration ratio requires both temperature and precipitation data, the nineteen weather stations for which precipitation data but not temperature data were available were not included in the analysis. In addition to the 65 weather stations utilized in Indiana, an additional 26 weather stations from the surrounding states of Ohio, Kentucky, Illinois, and Michigan were analyzed.

Temperature, Range in Temperature, and Precipitation

In order to understand the variation in biotemperature, potential evapotranspiration ratio, effective temperature, and equability, the variation in the climatic parameters from which these bioclimatic indexes are calculated, namely, temperature (Figure 1a-b), precipitation (Figure 1c-d), and range in temperature (Figure 2a-b), must be understood. Data are available in the literature on the variation in temperature, range in temperature, and precipitation in Indiana, but the maps presented illustrate the variation of these climatic parameters in the English and not the metric system (4, 17, 26). The maps presented in this paper show the variation in temperature, range in temperature, and precipitation in the metric system. These maps compare quite favorably with those prepared by other authors (4, 17, 26).

The mean annual temperature (Figure 1a) increases from lows of less than 10 °C in northern Indiana to highs in excess of 13 °C in southern Indiana. The tendency is for temperature to increase in a slightly northeast to southwest direction. During the growing season (Figure 1b), the mean temperature increases from lows of less than 18 °C along southern Lake Michigan to highs of more than 20° in southern Indiana. In general, west-central and southern Indiana have a mean temperature during the growing season of more than 19 °C, whereas east-central and northern Indiana have a mean temperature during the growing season of less than 19 °C.

Total annual precipitation also increases from north to south (Figure 1c). The total annual precipitation increases from lows of less than 90 cm/yr in northern Indiana to highs in excess of 110 cm/yr in southern Indiana. The gradual increase in precipitation from northern to southern Indiana is interrupted by a local high in north-central Indiana reflecting increased precipitation to the southeast of Lake Michigan. In this area, the total annual precipitation exceeds 95 cm/yr, and local highs can exceed 120 cm/yr. During the growing season (Figure 1d), the precipitation is lowest in northern and extreme eastern Indiana. In this region, the average summer precipitation is less than 55 cm. In central and southern Indiana, the precipitation during the growing season increases toward the southwest from lows of less than 55 cm to highs in excess of 65 cm. Locally, the precipitation during the growing season around southern Lake Michigan exceeds 60 cm.

The mean annual range in temperature decreases from the northwest to the southeast

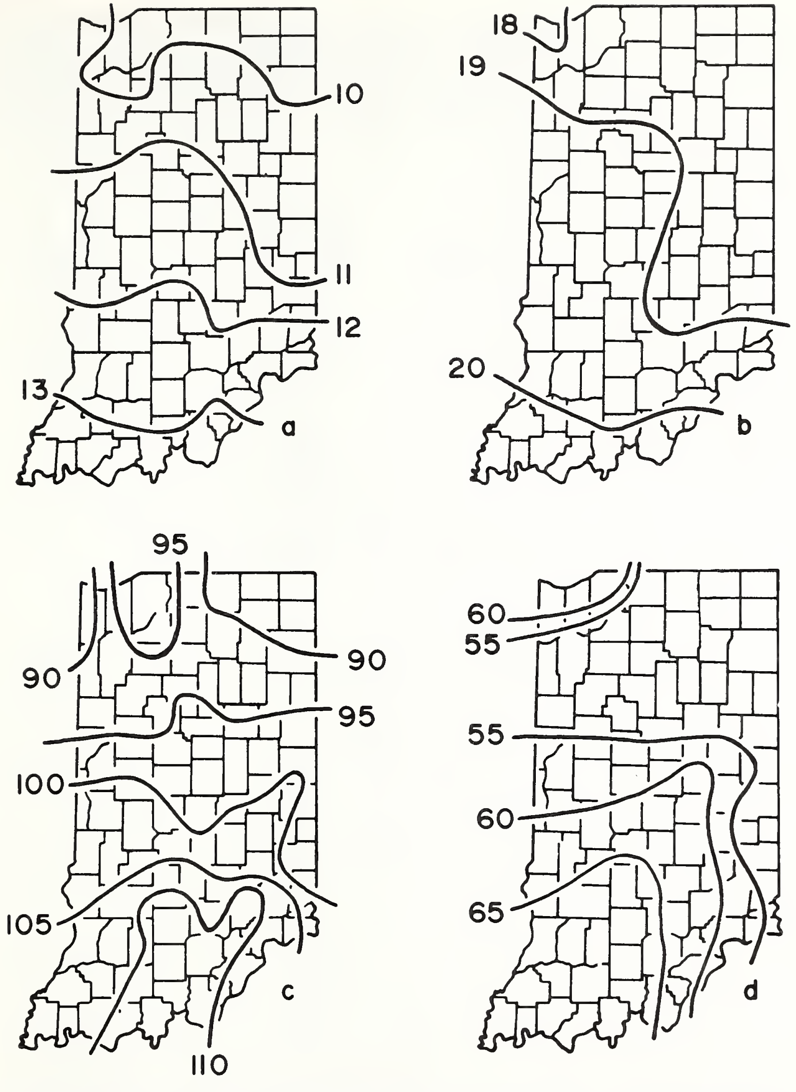

FIGURE 1. Variation in mean annual temperature (a), mean temperature during the growing season (b), total annual precipitation (c), and total precipitation during the growing season (d) in the counties of Indiana.

(Figure 2a) from differences of more than 27 °C in northwestern Indiana to differences of less than 25 °C in southeastern Indiana. The difference is also less than 27 °C in the immediate vicinity of Lake Michigan. In contrast, the mean range in temperature during the growing season (Figure 2b) is highest in south-central Indiana, where the difference exceeds 12 °C, and lowest in northern and southern Indiana, where the difference is less than 11 °C in northern Indiana and less than 12 °C in southern Indiana.

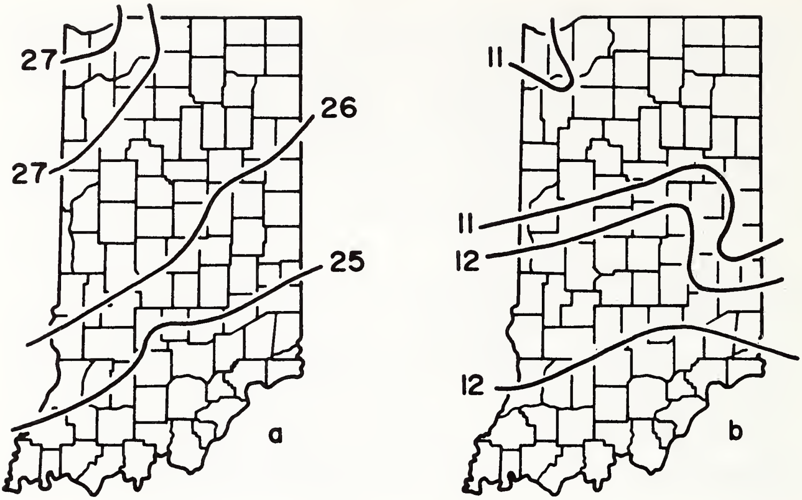

FIGURE 2. Variation in mean annual range in temperature (a) and mean range in temperature during the growing season (b) in the counties of Indiana.

Biotemperature and Potential Evapotranspiration Ratio

Unlike temperature, biotemperature measures only the heat which affects plant growth. The mean annual biotemperature (13, 14) is defined as the mean of all unit-period temperatures having an average temperature of more than 0 °C and less than 30 °C. If the mean temperature for a month is less than 0 °C or more than 30 °C, then the mean temperature for that month is not added to the total of mean monthly temperatures. Zero is added instead. Temperatures of less than 0 °C or more than 30 °C do not physiologically affect the vegetation. The vegetation merely remains dormant until more favorable conditions return. When temperatures are below 0 °C, the plants lose their leaves, and no growth takes place. At temperatures over 30 °C, the plants also become dormant to prevent respirational losses of photosynthate and to limit water stress.

Moving from the equator to the poles, Holdridge (13, 14) defined seven latitudinal regions based on mean annual biotemperature: tropical (> 24 °C), subtropical ($\sim$18 °C to 24 °C), warm temperate (12 °C to $\sim$18 °C), cool temperate (6 °C to 12 °C), boreal (3 °C to 6 °C), subpolar (3 °C to 1.5 °C), and polar (< 1.5 °C). In any single latitudinal region, up to six altitudinal belts may also be recognized based on mean annual biotemperature: premontane ($\sim$18 °C to 24 °C), lower montane (12 °C to $\sim$18 °C), montane (6 °C to 12 °C), subalpine (3 °C to 6 °C), alpine (1.5 °C to 3°C), and nival (< 1.5 °C). All six altitudinal belts are present in the tropical latitudinal region, but the number of altitudinal belts decreases in latitudinal regions closer to the poles, because the lower, warmer altitudinal belts are not represented.

The value of the mean annual biotemperature which separates the subtropical from the warm temperate latitudinal region and the premontane from the lower montane altitudinal belt is not fixed at 18 °C (see above). The actual value of the mean annual biotemperature separating these life zones can vary from 16 °C to 18 °C. The value is an approximation of the mean annual biotemperature at which temperature-sensitive tropical plants can no longer live within a forest.

The mean annual biotemperature increases from north to south in Indiana. The mean annual biotemperature increases from lows of less than 11 °C in northern Indiana to highs of more than 13 °C in southern Indiana (Figure 3a). In northern Indiana, the weather stations all record subfreezing temperatures for at least a portion of the winter. In southern Indiana, subfreezing temperatures may occur on some days of the year, but

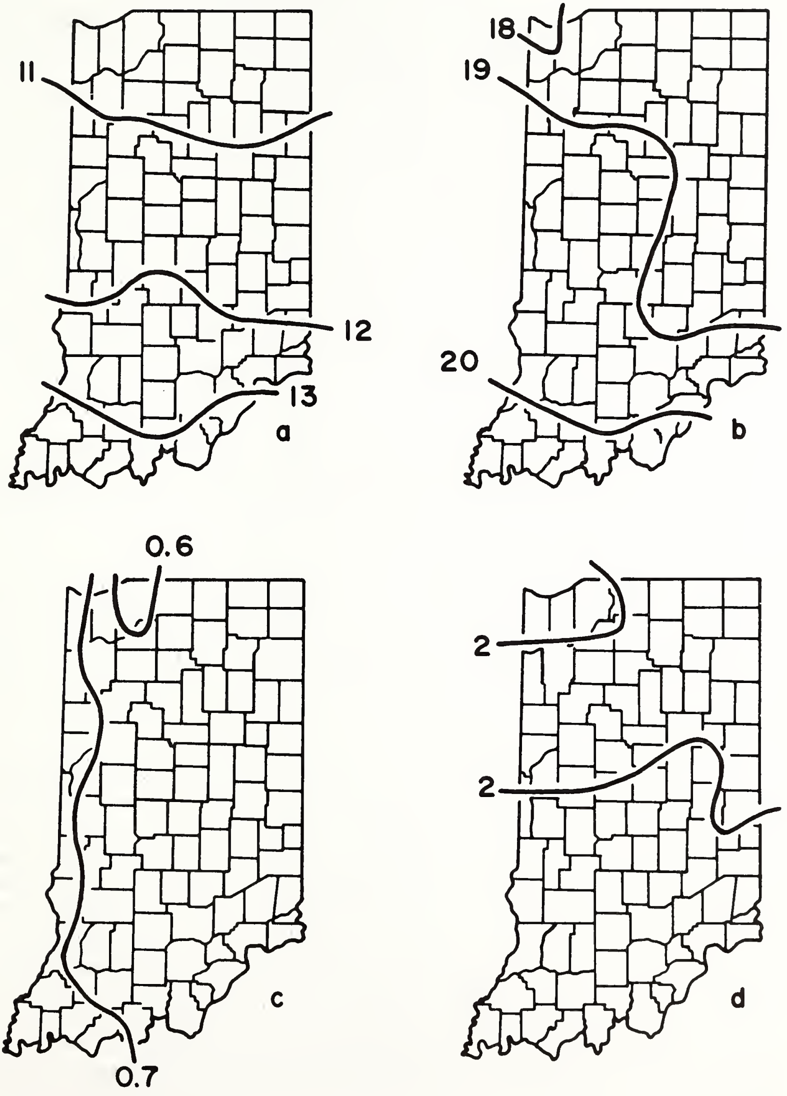

FIGURE 3. Variation in mean annual biotemperature (a), mean biotemperature during the growing season (b), potential evapotranspiration ratio (c), and potential evapotranspiration ratio during the growing season (d) in the counties of Indiana.

the monthly average temperatures rarely fall below freezing. In no county in Indiana does the monthly average temperature rise above 30 °C. As a result, the mean annual biotemperature in southern Indiana closely parallels the variation in mean annual temperature. Only in northern Indiana, where some months of the year average less than 0 °C, is there a significant variation in the maps for mean annual biotemperature and mean annual temperature. The mean annual biotemperature tends to be higher in northern Indiana, because the means of the months having subfreezing temperatures are not subtracted from the total of mean monthly temperatures. Values for mean annual biotemperature place northern and central Indiana in the cool temperate latitudinal region and southern Indiana in the warm temperate latitudinal region.

A comparison of Figure 1b with Figure 3b indicates that the variation in temperature and biotemperature during the growing season is identical. The maps are identical because monthly mean temperatures below 0 °C and above 30 °C do not occur during the growing season in Indiana. Therefore, the calculated means for both variables are the same at all weather stations. During the growing season, the mean biotemperature in Indiana is as high as the mean annual biotemperature in the subtropical latitudinal region.

The potential evapotranspiration ratio is a comparison between the amount of water lost in a life zone by the processes of evaporation and transpiration (the potential evapotranspiration) and the amount of water gained in a life zone as measured by the total precipitation. Potential evapotranspiration is calculated by multiplying the mean biotemperature by 58.93. The potential evapotranspiration ratio (PER) is calculated using the following equation (13, 14):

$$PER = (58.93 \times T^{BIO})/P,$$

where the potential evapotranspiration ratio is a dimensionless number, T^{BIO} is the average biotemperature in °C over the time period under study, and P is the average precipitation in mm over the same time period. Ideally, total annual precipitation should balance potential evapotranspiration, resulting in a potential evapotranspiration ratio of 1.0 or unity. If potential evapotranspiration is greater than the total annual precipitation, the potential evapotranspiration ratio is greater than unity, the total annual precipitation is less than is needed to balance the water lost through evaporation and transpiration, and the climate becomes more arid. If potential evapotranspiration is less than the total annual precipitation, the potential evapotranspiration ratio is less than unity, the total annual precipitation is more than is needed to balance the water lost through evaporation and transpiration, and the climate becomes more humid.

The life zones which have similar humidity conditions, as measured by the potential evapotranspiration ratio, can be grouped into the same humidity province. Holdridge (13, 14) recognized twelve humidity provinces based on the potential evapotranspiration ratio: semiparched (64.0 to 32.0), superarid (32.0 to 16.0), perarid (16.0 to 8.0), arid (8.0 to 4.0), semiarid (4.0 to 2.0), subhumid (2.0 to 1.0), humid (1.0 to 0.5), perhumid (0.5 to 0.25), superhumid (0.25 to 0.125), semisaturated (0.125 to 0.0625), subsaturated (0.0625 to 0.03125), and saturated ($<$ 0.03125). The most favorable humidity provinces for plant growth and animal activity cluster around a potential evapotranspiration ration of 1.0 and include the subhumid (1.0 to 2.0) and humid (0.5 to 1.0) humidity provinces. With respect to human activity, the choice of life zone tends toward the drier life zones of the subhumid humidity province as temperature increases.

The potential evapotranspiration ratio decreases from highs in excess of 0.7 in western Indiana and to lows of less than 0.7 in eastern and central Indiana (Figure 3c). Because the area southwest of Lake Michigan receives an unusually high amount of precipitation (Figure 1c), this area also has an unusually low potential evapotranspiration ratio. More precipitation falls in Indiana during the year than is needed to balance potential evapotranspiration, and the potential evapotranspiration ratio is less than unity. Indiana is located in the humid (PER between 0.5 and 1.0) humidity province. The humid humidity province is one of the two most favorable provinces for plant growth, accounting at least in part for Indiana's impressive agricultural output.

During the growing season (Figure 3d), the potential evapotranspiration ratio is highest in northern Indiana with highs in excess of 2.0 and lowest around Lake Michigan and in central and southern Indiana with lows of less than 2.0. Less precipitation falls in Indiana during the growing season than during the remainder of the year. The precipitation is less than is required to balance the water lost through evaporation and transpiration, and the potential evapotranspiration ratio is higher during the growing season than during the whole year. During the growing season, the values of the potential evapotranspiration ratio in Indiana are as high as the annual values in the semiarid (PER > 2.0) to subhumid (PER between 1.0 and 2.0) humidity provinces.

Warmth and Temperateness

Bailey (2, 3) did not feel that mean annual temperature and mean annual range in temperature effectively described the thermal regimes under which plants and animals exist. Therefore, he defined two new indexes to quantify the warmth and temperateness of any locality. These indexes are effective temperature and equability. Effective temperature is a measure of warmth. Equability is a measure of temperateness. Graphically, effective temperature is represented as a series of rays and equability as a series of concentric circles superimposed on a normal Cartesian coordinate system having mean annual temperature as the abscissa and mean annual range in temperature as the ordinate (a nomogram, Figure 5b).

The temperature characteristic of the beginning and end of a warm period during which vegetational growth prospers is a measure of the warmth of that locality. This time period will be largely free from frost. One measure of warmth is effective temperature (1, 2):

$$ET = (8T + 14A)/(8 + A),$$

where ET is the effective temperature in °C, T is the mean temperature in °C for the time period under study, and A is the range in temperature in °C for the same time period. The change from polar to tropical climates is indicated by increasing values of effective temperature from 0 °C in polar climates to 30 °C in tropical climates. Standard temperature designations, such as cold and warm temperate, subtropical, and tropical, cannot be applied to values of effective temperature. Instead, Bailey (2) recognized three major climatic zones based on relative warmth: low latitude climates (ET > 18.0 °C), midlatitude climates (ET between 10.0 °C and 18.0 °C), and high latitude and altitude climates (ET < 10.0 °C). Each of these major climatic zones was further subdivided into a number of minor climatic categories. The low latitude climates were subdivided into torrid (ET > 24.1 °C), hot (ET between 20.8 °C and 24.1 °C), and very warm (ET between 18.0 °C and 20.8 °C) climates; the midlatitude climates were subdivided into warm (ET between 15.5 °C and 18.0 °C), mild (ET between 13.4 °C and 15.5 °C), cool (ET between 11.6 °C and 13.4 °C), and very cool (ET between 10.0 °C and 11.6 °C) climates; and the high latitude and altitude climates were subdivided into cold (ET between 8.6 °C and 10.0 °C), very cold (ET between 7.5 °C and 8.6 °C), and glacial (ET < 7.5 °C) climates. Drought and continentality do not affect the calculation of effective temperature, although altitude will modify the results. Therefore, isotherms for effective temperature tend to extend from coast to coast except where lower effective temperatures are deflected toward the equator by high mountains.

The variation in mean annual effective temperature in Indiana (Figure 4a) has a total magnitude of less than one degree. The mean annual effective temperature increases from lows of less than 13.4 °C in northern and central Indiana to highs of slightly more

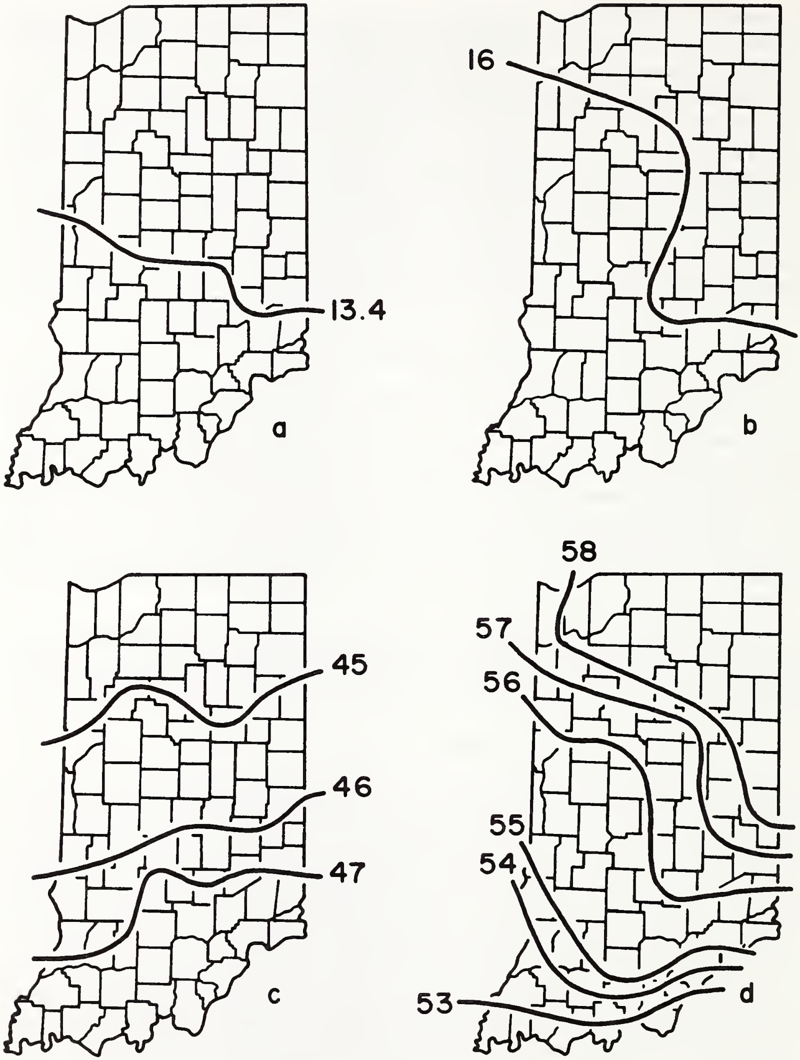

FIGURE 4. Variation in effective temperature (a), effective temperature during the growing season (b), equability (c), and equability during the growing season (d) in the counties of Indiana.

than 13.4°C in southern Indiana. An isotherm of 13.4°C was mapped, because this isotherm represents the dividing line between cool midlatitude climates (ET < 13.4°C) and mild midlatitude climates (ET > 13.4°C). Northern Indiana has a cool midlatitude climate, and southern Indiana has a mild midlatitude climate. Bailey (2) also divided the climate of Indiana into a northern, cool and a southern, mild midlatitude climate, although he could not place the boundary with precision due to the small scale of his map.

During the growing season in Indiana (Figure 4b), the effective temperature decreases from northeast to southwest from lows of less than 16 °C in northern and east-central Indiana to highs of more than 16 °C in southern and west-central Indiana. During the growing season, a warm midlatitude climate (ET between 15.5 °C and 18.0 °C) exists in Indiana. The values for effective temperature do not fall below 15.5 °C during the growing season, and, therefore, this major isothermal boundary cannot be mapped.

Temperateness, as recorded by equability, measures the freedom of a specific locality from extremes of heat and cold regardless of whether these extremes are seasonal (measured by mean annual range in temperature) or perennial (measured by mean annual temperature) in occurrence. The equability at a specific weather station is calculated as follows (1, 3):

$$M = 109.0 - 30 \log((T - 14)^2 + (1.46 + 0.366A)^2),$$

where M is the equability, a dimensionless index ranging from 0 to 100, T is the average temperature in °C for a specific time period, and A is the range in temperature in °C for the same time period. A climate which is totally free from extremes of heat and cold has an equability of 100 and a mean annual temperature of 14.0 °C. The greater the seasonal fluctuation in temperature, as measured by the mean annual range in temperature, and/or the greater the departure of the mean annual temperature at a site from the ideal mean of 14.0° C, the lower the calculated equability becomes.

Bailey (3) defined two different climatic orders based on temperateness: temperate climates ($M > 50$) and intemperate climates ($M < 50$). Each of these climatic orders was subdivided into three climatic classes. The temperate climatic order was subdivided into the supertemperate ($M > 80$), very temperate (M between 80 and 65), and temperate (M between 65 and 50) climatic classes; and the intemperate climatic order was subdivided into the subtemperate (M between 50 and 35), intemperate (M between 35 and 20), and extreme ($M < 20$) climatic classes. A two-layered classification was adopted to allow plotting of temperateness on maps of different scales. This classification (3) completely revised an earlier classification of temperate climates (2) by introducing the temperate and intemperate climatic orders, by changing the name of the most temperate class from constant to supertemperate, by reducing the lower limit of each temperateness class by M 5, and by modifying the original equations used to calculate equability.

Annual equability increases from north to south from lows of less than M 45 in northern Indiana to highs of more than M 47 in southern Indiana (Figure 4c). The mean annual temperature is approaching 14.0 °C in southern Indiana (Figure 1a), and the mean annual range in temperature is lowest in southern Indiana (Figure 2a). Changes which cause the mean annual temperature to become closer to the ideal value of 14.0 °C and which reduce the mean annual range in temperature will also cause the climate to become more temperate (the value of M increases). Therefore, southern Indiana has a more equable climate (a higher value of M) than northern Indiana. Based on equability, Indiana has a subtemperate (M between 50 and 35) climate. These results substantiate Bailey's claim (3) that the northeastern United States, including Indiana, have an intemperate ($M < 50$) and not a temperate climate. Equability measures extremes of heat and/or cold. The bioclimate of Indiana is rated as intemperate, because of the extreme cold waves that cross the State during winter.

The equability during the growing season in Indiana decreases from highs in excess of M 58 in northeastern Indiana to lows of less than M 53 in southwestern Indiana (Figure 4d). No other temperature index decreases toward the south in Indiana. The mean temperature during the growing season in southern Indiana is becoming increasingly greater than the ideal mean of 14.0 °C (Figure 1b), and the mean range in temperature during the growing season is greater in south-central Indiana than in northern Indiana (Figure 2b). Changes which cause the mean temperature to depart more radically from the ideal mean of 14.0 °C and which increase the mean range in temperature will cause the climate to become less temperate (the value of M decreases). Therefore, southern Indiana has a less temperate climate during the growing season (a lower value of M) than northern Indiana. During the growing season, Indiana does have a temperate (M between 50 and 65) climate.

Conclusions

Based on the life zone classification system of Holdridge (13, 14), northern and central Indiana are in the cool temperate moist forest life zone and southern Indiana is in the warm temperate moist forest life zone (Figure 5a). The intervening area is a

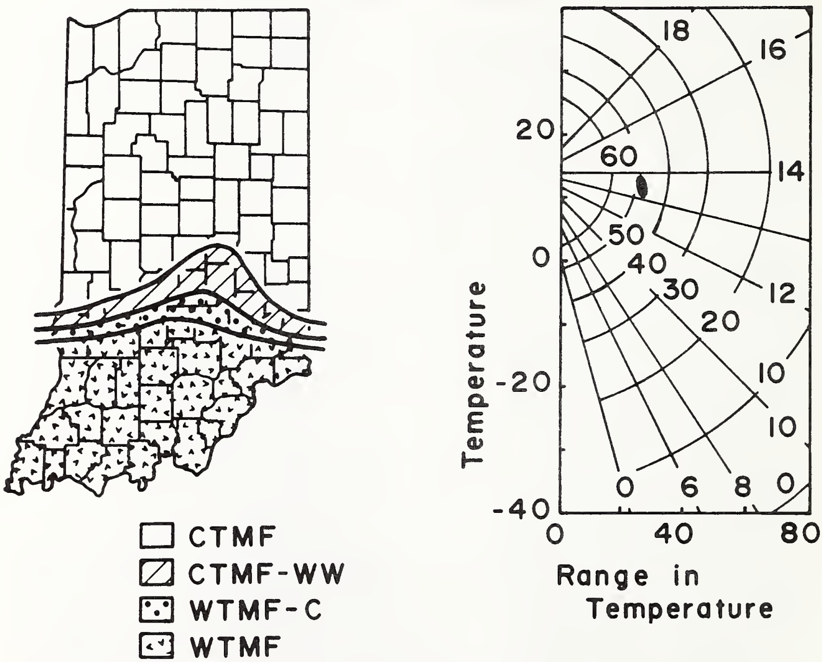

FIGURE 5. The bioclimatic formations of Indiana derived by application of Holdridge's system (a, on the left), and the nomogram of thermal data for Indiana derived by the application of Bailey's system (b, on the right).

zone of climatic transition. The cool temperate moist forest life zone terminates as the warm-wet transition of the cool temperate moist forest life zone; and the warm temperate moist forest life zone starts as the cool transition of the warm temperate moist forest life zone. These conclusions are similar to those reached by Sawyer and Lindsey (16) in their general study of the bioclimatic formations east of the 102 W meridian in the United States, except that the area representing warm temperate montane moist forest in their paper is considered a transitional climatic zone between the cool temperate and warm temperate moist forests in this paper.

Holdridge (14) makes two important points about transition zones and the two life zones adjacent to them. First, the transition zone should be very narrow. The transition zone is very narrow in Indiana, and it is confined to the south-central portion of the State. Second, the plant associations in the life zones on either side of the transition zone should have distinctly different physiognomies. Although a large number of floristic and synecological studies have been published dealing with the vegetation of Indiana, few physiognomic analyses have been carried out.

The only large-scale physiognomic study that has been carried out in Indiana attempted to relate the variation in leaf margin type of the woody, dicotyledonous plant species with bioclimate (9, 11). Initially, the variation in the percentage of woody, dicotyledonous plant species having leaves with entire margins seemed more closely related to edaphic conditions influencing the distribution of the woody, dicotyledonous shrub and vine species than to the influence of any major climatic parameter, such as temperature or precipitation (9). In the counties of northern Indiana, the percentage of woody, dicotyledonous plant species having leaves with entire margins is as high (> 20%) as the percentage in southern Indiana. Edaphic conditions certainly exert a controlling influence on species distribution and indirectly on foliar physiognomy in northern Indiana. One of the chief physiographic features that distinguishes northern from central and southern Indiana is the large number of lakes and bogs covering the area (18). A number of tree (e.g., *Betula lutea*, *Quercus ellipsoidalis*, or *Salix amygdaloides*), shrub (e.g., *Betula pumila*, *Cornus rugosa*, or *Sambucus pubens*), and vine (e.g., *Parthenocissus vitacea*) species extend into northern Indiana from Michigan and western Ohio only because the appropriate edaphic conditions are available. The southernmost distributional boundary of these species is not the transition zone between the cool temperate and warm temperate moist forest life zones. Their distributional boundary is the southern limit of the Northern Moraine and Lake Region. However, the high percentage of woody dicotyledonous plant species having leaves with entire margins in northern Indiana does not indicate that the cool temperate and warm temperate moist forest life zones do not have distinct physiognomies. The flora of northern Indiana represents an edaphic association and not the climatic or zonal association characteristic of the cool temperate moist forest life zone.

The percentage of woody, dicotyledonous plant species having leaves with entire margins in the counties corresponding to the warm temperate moist forest life zone is greater (> 20%) than the percentage of woody, dicotyledonous plant species having leaves with entire margins (< 15%) in the adjacent counties found in the cool temperate moist forest life zone. The change in foliar physiognomy occurs within the transition zone. The transition zone between the cool temperate and warm temperate moist forest life zones does accurately delimit the northernmost boundary to which many southern species extend. The trees, shrubs, and vines reaching the northern limit of their distribution in southern Indiana include *Aesculus octandra*, *Oxydendrum arboreum*, *Tilia heterophylla*, *Forestiera acuminata*, *Rubus odoratus*, *Viburnum molle*, *Anisostichus capreolata*, and *Calycocarpum Lyoni*.

The simplest explanation for these patterns is that the foliar physiognomy of northern Indiana is edaphically controlled while the foliar physiognomy of southern Indiana is climatically controlled. However, a number of shrub (e.g., *Gaylussacia baccata* and *Vaccinium vacillans*) and vine (e.g., *Lonicera dioica* and *L. prolifera*) species, whose distributions are edaphically controlled, occur in both northern and southern Indiana. Because these species have leaves with entire margins, they also exert a significant influence on the foliar physiognomy of northern and southern Indiana. The physiognomic difference between the cool temperate and warm temperate moist forest life zones does reflect a climatically controlled floristic difference, but the final percentage is modified somewhat by the presence of species whose distribution in both northern and southern Indiana is edaphically and not climatologically controlled.

Application of the concepts of warmth and temperateness developed by Bailey (2,

3) to the climate of Indiana (Figures 4a-d and 5b) substantiate the conclusions reached using the Holdridge system of life zone classification. The 13.4°C isotherm for effective temperature divides Indiana into two parts: a northern and central portion having a cool midlatitude climate and a southern portion having a mild midlatitude climate. The 13.4°C isotherm for effective temperature falls in approximately the same position as the transition zone identified using Holdridge's life zone classification (Figure 5a). The shift from a warm midlatitude climate to a cool midlatitude climate at an effective temperature of 13.4°C effectively delimits the northernmost distributional boundary of the woody, dicotyledonous plants which enter Indiana from the south as well as a major change in foliar physiognomy (see above).

Although a correlation between foliar physiognomy and the variation in warmth and equability has been intimated (1), no detailed analysis of the relationship between these variables has been carried out. Studies of the percentage of species having large leaves (> 20.25 sq cm *sensu* 5) in the tropical lowlands of the Western Hemisphere and in Indiana indicate that the two areas have a similar foliar physiognomy with respect to leaf size. The average percentage of species having large leaves is 83.7% in Indiana (6, 8, 27) and 83.0% in the tropical lowlands of the Western Hemisphere (7). The similarity can be explained by examining the variation in warmth and equability in Indiana.

The effective temperature in Indiana averages 13.4°C/yr. During the growing season, the effective temperature increases to 16.1°C. The increase in effective temperature is equivalent to a change from a cool to mild midlatitude climate to a warm midlatitude climate during the growing season. Based on equability (Figure 4c), the annual climate of Indiana is intemperate ($M < 50$), but only marginally so. During the growing season, the climate of Indiana becomes distinctly temperate ($M > 50$, Figure 4d). During the growing season, the position of Indiana on the nomogram shifts upwards towards greater warmth and to the left towards greater equability. In other words, the climate becomes more tropical and less temperate in nature. Givnish (12) predicted that average leaf size in warm temperate and tropical forests should be approximately equal. Because the plants are only photosynthetically active during the growing season in Indiana, the plants respond to the higher than average warmth and greater equability of the climate by producing leaves which are as large on the average as those in the tropics. Winter has no influence on leaf size, because no leaves are present in the winter.

Acknowledgments

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Literature Cited

1. Axelrod, D.I. and H.P. Bailey. 1969. Paleotemperature analysis of Tertiary floras. Palaeogeogr., Palaeoclim., Palaeoecol. 6: 163-195.
2. Bailey, H.P. 1960. A method of determining warmth and temperateness of climate. Geograf. Ann. 42: 1-16.
3. ____. 1964. Toward a unified concept of temperate climate. Geograph. Rev. 54: 516-545.
4. Clark, G.D. and D. Larrison. 1980. The Indiana water resource: Availability, uses, and needs. Indiana Department of Natural Resources, Indianapolis, Indiana, 508 pp.
5. Dilcher, D.L. 1973. The Eocene floras of southeastern North America. In: A. Graham (Ed.), *Vegetation and Vegetational History of Northern Latin America*, pp. 39-59, Elsevier, New York, 393 pp.
6. Dolph, G.E. 1971. A comparison of local and regional leaf characteristics in Indiana. Proc. Indiana Acad. Sci. 80: 99-103.

7. ____. 1978. Variation in leaf size and margin type with respect to climate. Cour. Forsch.-Inst. Senckenberg 30: 153-158.
8. ____. 1979. Leaf size variation at Cook's woods. Proc. Indiana Acad. Sci. 88: 77-82.
9. ____. 1984. Leaf form of the woody plants of Indiana as related to environment. In: N.S. Margaris, M. Arianoustou-Farragitaki, and W.C. Oechel (Eds.), *Being Alive on Land*, pp. 51-61, Tasks for Vegetation Science, Dr. W. Junk Publishers, The Hague, 322 pp.
10. ____. 1985. CLIMATE: A microcomputer program allowing student preparation of climatic maps for Indiana. Proc. Indiana Acad. Sci. 94: 489-498.
11. ____. 1986 LEAF MARGIN, A computer simulation of leaf margin variation in Indiana. Proc. Indiana Acad. Sci. 95: 469-477.
12. Givnish, T.J. 1976. Leaf form in relation to environment: A theoretical study. Ph.D. Thesis, Princeton Univ., 467 pp.
13. Holdridge, L.R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica, 206 pp.
14. ____, W.C. Grenke, W.H. Hatheway, T. Liang, and J.A. Tosi, Jr. 1971. Forest environments in tropical life zones: A pilot study. Pergamon, New York, 747 pp.
15. Köppen, W. and R. Geiger. Handbuch der Climatologie. Teil I D, Borntraeger, Berlin.
16. Sawyer, J.O., Jr. and A.A. Lindsey. 1964. The Holdridge bioclimatic formations of the eastern and central United States. Proc. Indiana Acad. Sci. 73: 105-112.
17. Schaal, L.A. 1966. Climate. In: A.A. Lindsey (Ed.), *Natural Features of Indiana*, pp. 156-170, Indiana Academy of Science, Indianapolis, Indiana, 597 pp.
18. Schneider, A.F. 1966. Physiography. In: A.A. Lindsey (Ed.), *Natural Features of Indiana*, pp. 40-56, Indiana Academy of Science, Indianapolis, Indiana, 597 pp.
19. Thornthwaite, C.W. 1931. The climates of North America according to a new classification. Geograph. Rev. 21(4): 633-655.
20. ____. 1948. An approach to a rational classification of climate. Geograph. Rev. 38(1): 55-94.
21. U.S. Department of Commerce Environmental Data Service. 1973a. Climatology of the United States, No. 81 (Illinois). Monthly normals of temperature, precipitation, and heating and cooling degree days 1941-1970. Asheville, North Carolina.
22. ____. 1973b. Climatology of the United States, No. 81 (Indiana). Monthly normals of temperature, precipitation, and heating and cooling degree days 1941-1970. Asheville, North Carolina.
23. ____. 1973c. Climatology of the United States, No. 81 (Kentucky). Monthly normals of temperature, precipitation, and heating and cooling degree days 1941-1970. Asheville, North Carolina.
24. ____. 1973d. Climatology of the United States, No. 81 (Michigan). Monthly normals of temperature, precipitation, and heating and cooling degree days 1941-1970. Asheville, North Carolina.
25. ____. 1973e. Climatology of the United States, No. 81 (Ohio). Monthly normals of temperature, precipitation, and heating and cooling degree days 1941-1970. Asheville, North Carolina.
26. Visher, S.S. 1944. Climate of Indiana. Indiana University, Bloomington, 511 pp.
27. Withrow, A.P. 1932. Life forms and leaf size classes of certain plant communities of the Cincinnati region. Ecology 13: 12-35.