Notes on the Construction of Leaf Size Distributions

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Introduction

In a recent review article, Dolph and Dilcher (11) synthesized the available literature on leaf size variation in the tropical latitudinal region of the western hemisphere. Based on the percentage of species having large leaves at 73 sample sites, the tropical latitudinal region was divided into four foliar belts. Each foliar belt had a characteristic average percentage of species having large leaves, but the variation either within or between the foliar belts was not continuous. An attempt was made to extend this analysis into the subtropical and warm temperate latitudinal regions of the western hemisphere, but a lack of pertinent data prevented any definitive conclusions from being reached.

Although variation in leaf size did occur, a close correlation between leaf size and climate in the western hemisphere could not be demonstrated (11) at the present time. This is due in part to the lack of data, particularly from non-tropical life zones, and in part to the way in which leaf size data were collected in the past. Seven problems complicated the attempt to correlate leaf size variation with climate: 1) only five sample sites have been studied outside of the tropical life zones; 2) the sample stands represent a mixture of climatic and non-climatic associations (*sensu* 16, 17); 3) sample populations differed depending on the investigator; 4) sampling techniques varied; 5) data from several sample stands were lumped together in many studies; 6) adequate climatic data were not given for the majority of the sample stands; and 7) leaf area was not estimated in a consistent fashion. In order to develop a hypothesis which successfully relates leaf size variation with climate, future field studies will have to be carried out in a consistent fashion.

Life Zones Sampled

Of the 78 sample stands studied (11), 73 (93.6%) were located in the tropical latitudinal region. Two (2.4%) sample stands were studied in the subtropical latitudinal region. Three (4.0%) were from the warm temperate latitudinal region. Sampling has been carried out in 9 tropical life zones. Twenty-eight life zones in the tropical latitudinal region have not been studied. In the subtropical latitudinal region, sampling has been carried out only in the moist forest life zone, leaving 28 additional life zones to be sampled. Outside of the tropical and subtropical latitudinal regions, only 2 life zones (the warm temperate moist and montane wet forest life zones) have been sampled, leaving data to be collected from an additional 48 life zones. Sampling outside of the tropical latitudinal region is particularly crucial because the decrease in leaf size predicted (21) does not occur based on the available data (11). Dolph and Dilcher (10, work in progress) are currently analyzing the flora of North and South Carolina, and Dolph (work in progress) is analyzing the flora of Indiana.

Nature of the Sample Stands

The analysis of the variation in leaf size with respect to climate (11) was based on Holdridge's (16, 17) life zone chart. Holdridge (16, 17) recognized 4 basic classes of associations (climatic, atmospheric, edaphic, and hydric), although various combinations of these classes are possible. A climatic association is one in which only the three major climatic factors (temperature, rainfall, and humidity) influence the plant community (16, 17). In comparison, atmospheric, edaphic, and hydric associations are referred to as non-climatic or non-zonal associations. In non-zonal associations, the physiognomy of the vegetation will indicate conditions that are drier or wetter than the climatic association normal for that life zone. The difference in physiognomy results from the action of the second order environmental factors such as soil type, drainage, or wind (16, 17). Successional associations are recognized in the colder regions of the world but not in the warmer where the successional stages are of shorter duration (16). According to Holdridge (16), if plant form is related to climate, there should be one characteristic physiognomy for the vegetation of the life zone, that of the climatic association. The non-zonal associations may occur in any life zone, but the plants found in these associations have physiognomies that are very divergent from those of the climatic association. Because of their divergent physiognomies, the non-zonal associations have received more attention than the zonal. Swamps (12, 25), gallery forests (6, 12, 25), vegetation on soils having excessive drainage (1, 19), transitional forests (12, 25), cloud forests (18), or secondary successional forests (12, 13, 28) should not be expected to support vegetation having the physiognomy characteristic of the climatic association. Theoretically, these associations should not be used when attempting to correlate leaf form with climate.

Nevertheless, in many cases, the use of data from non-climatic associations did not affect the outcome of the study (11). A good example was the use of secondary forest sites. Five sample stands representing successional semi-evergreen to evergreen seasonal forest on Trinidad (13) had an average percentage of species having large leaves of 87.8% (11). This percentage was only somewhat higher than the average percentage from the tropical basal belt (83.0%, 11) and only slightly different from the percentage reported by Beard (4) from the undisturbed seasonal evergreen forest of Trinidad (87.1%). Most ecological measurements require the use of undisturbed vegetation because they reflect the structure of the mature vegetation. Because the percentage of large leaves at individual sample stands was based on the species present and not the individuals present, the disturbed nature of secondary forests does not influence the outcome of the calculation. In other instances, such as with stream side and upland vegetation, significant differences in leaf size occurred within the same life zone. Additional studies should attempt to find a basis for these differences.

Sample Populations

The sample populations utilized when studying leaf form have not been constant. The chief differences occur in (1) the types of life forms studied and (2) the number of species recorded. By varying the types of plants included in a study, significantly different leaf size distributions may be produced. For example, studies in the tropics (4, 5, 6, 12, 14, 28) have emphasized trees and neglected shrubs and vines. Cain *et al.* (6) provided leaf size distributions for the entire plant community and the trees alone. The percentage of species having large leaves was greater for the trees (84.1%) than for the entire flora (79.5%). Ideally, the leaf size for all species of dicotyledonous trees, shrubs, and vines should be recorded (2, 3, 21). In studying the warm temperate moist forest life zone, Dolph (8, 9) utilized all the dicotyledonous trees, shrubs, and vines. Monocotyledons such as the palms (12), herbaceous angiosperms (6, 18), and ferns (6) should not be used, particularly if the data is to be used in estimating paleoclimate.

In addition to sampling different life forms, different sampling intensities have been used in different studies. A lower sampling intensity than desirable was a characteristic of the majority of the sample stands studied in the tropics. In the tropical latitudinal region, the number of species recorded ranged from a low of 7 (12) to a maximum of 218 (6). The number of species sampled at the 73 localities (11) was very different. Sampling was rarely complete. For example, Gentry (12) recorded 7 tree species from a ridge top south of Osa Station in the tropical wet forest life zone. In comparison, 97 tree species were recorded west of Rincon and a minimum of 82 tree species south of Rincon in ridge top forests on the Osa Pennisula by Holdridge *et al.* (17). The calculation of leaf area for only the more common or dominant species in a sample stand was proposed by Richards *et al.* (22). Because the correlation of leaf form with climate can vary depending on the sampling intensity, more complete samples are desirable.

Improper Sampling Technique

A low species diversity in the sample could also result from improper sampling of the vegetation. In a number of studies, a sufficiently large sampling area was used to record either all the tree species (4, 6), all the phanerophytes (1, 19), or all the woody dicotyledons (8, 9). At many sample stands (12, 16, 17, 23, 24, 27), the sampling area was inadequate for complete analysis of the vegetation. In sampling the tropical dry and wet forest life zones, Gentry (12) analyzed between approximately 60 to 90 sq m at each locality by the line transect method. This sampling area is less than the 200-500 sq m suggested for use in temperate forests (20) and is insufficient for sampling more diverse tropical woodlands. In contrast, Dolph (8, 9) sampled 1,000 sq m when studying the warm temperate moist forest of Indiana. For some sample sites (18, 28), sampling area was not discussed. Grubb *et al.* (14) did not feel that sampling area had a great influence on the analysis of leaf size distribution. Because the number of species recorded is dependent on the intensity of sampling, this conclusion is in error. The determination of leaf size distribution at any locality must be based on an adequate sample.

Generalized Vegetation Descriptions

Some investigators (4, 25, 26) did not record leaf size distribution by locality but gave synthesized data for an entire vegetation type. For example, Stehlé (25, 26) normally did not record leaf size distributions for specific forests on the Caribbean Islands. Instead, the common species in the different associations studies throughout the Caribbean and the range in leaf size of each were listed. Depending on how the data are used, very divergent results can be obtained. Using the data for the mesophytic forest at St. Luce, Martinque (25), the percentage of species having large leaves was 30.5%, if the smallest sizes in the range of each species were applied; and 80%, if the largest were used. Generalized leaf size distributions should not be used because they fail to account for the local effect of climate on vegetation. Leaf size distributions should be given on a stand by stand basis.

Lack of Climatic Data

Considerable difficulty was encountered in estimating the precise climate at each of the sample sites, particularly in the tropical life zones. This problem is a direct result of the lack of weather stations in the tropics (17). In the initial survey (11), the mean annual biotemperature of 19 of the original 78 sample sites had to be estimated from nearby weather stations. Additional climatic data might shift the position of the data points slightly on the life zone chart, particularly along the axis indicating mean annual biotemperature. This problem did not affect the initial study of leaf size distributions (11) because the relative and not the absolute position of the sample stands was most important. If larger amounts of data or a different method of analysis (e.g., Wisconsin polar ordination) are used, more exact climatic data will be necessary.

Estimation of Leaf Area

Finally, a better method of estimating leaf area must be used. In the majority of studies (4, 5, 6, 12, 18, 28), leaf area was estimated as two-thirds of the product of leaf length and width. A recent study (9) has indicated that as many as 30% of the species studied at a single locality can be placed in the wrong size class by using this equation. The best approach (9) is to use a dot planimeter (15) to estimate leaf area. Sophisticated electronic equipment is available to carry out these estimates, but it can only be transported back and forth to the sample site with great difficulty.

Conclusions

The theories relating leaf form with climate (2, 3, 21) were all proposed over forty years ago. Analysis of the available data on leaf size has indicated that theoretical predictions and field observations do not always agree (11). If the theories are to be revised, more data must be collected using a uniform procedure. The need for a uniform method of data analysis was first noted in 1940 (22) but was disregarded. If followed, the proposals presented in this paper should increase the accuracy of studies on the variation in leaf morphology and make data from different areas of the world more directly comparable.

The need for accuracy in the determination of leaf size distributions is particularly important for the estimation of paleoclimates. Currently, there are two methods available for estimating paleoclimate. One method is based on estimating the climate under which a fossil species lived by the climate under which its nearest living relative currently exists. If the fossil species is misidentified, paleoclimatic estimates based on its nearest living relative will be inaccurate. The second method involves using the correlation between modern climates and leaf morphology to estimate paleoclimates. As the study of local variation in leaf form with climate has revealed (11), this approach, although promising, will yield useful results only after more data has been collected using a standardized system of analysis.

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