Climatic Patterns and the Distribution of $C_4$ Grasses in North America

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Summary. A stepwise multiple regression analysis was used in an attempt to correlate statistically the geographic patterns in the abundance of $C_4$ grasses with patterns in climatic variables. The percent of grasses having the $C_4$ pathway was computed for the total grass flora in twenty-seven widely spaced regions of North America. From long-term climatic records seasonal and annual values for solar irradiance, water supply, heat availability, and combinations of these variables were assigned to each of the twenty-seven regions. The results of the analysis suggest that high minimum temperatures during the growing season have the strongest correlation with the relative abundance of $C_4$ grass species in a regional flora. It appears that the deleterious effects of low temperatures during growth negate the advantages of possessing the $C_4$ pathway in cooler habitats.

Introduction

The purpose of this investigation is to determine which environmental parameters are most influential in determining the distributional patterns of the North American Gramineae species possessing the $C_4$ photosynthetic pathway. The large scale patterns of distribution of these $C_4$ grasses were statistically analyzed in an attempt to correlate these distributional patterns with geographic patterns in climatic variables. Recently there has been increasing speculation concerning the ecological and evolutionary relationships of the plant taxa which possess the $C_4$ pathway of photosynthesis. Many of the presently known $C_4$ species belong to genera and families that appear to have either their origins or major parts of their range in tropical and subtropical regions. The present understanding of the environmental relationships of $C_4$ plants is based primarily on extrapolation of observational and experimental information from a few $C_4$ taxa that represent only a small proportion of the total floristic and geographic composition of the world $C_4$ flora. While certain habitats have been found to contain a high percentage of $C_4$ species among their total angiosperm flora (e.g., the
summer-active flora of Death Valley, California (Pearcy et al., 1971); and temperate saltmarshes), the total number of species in these habitats is a very small percent of the several hundred known C4 taxa. Recent surveys of the presence of C4 angiosperms in the Colorado Desert (Philpott and Troughton, 1974) and arid coastal regions of California and Chile (Mooney et al., 1974) have demonstrated that in these arid regions, the number of species having the C4 pathway is relatively small. High levels of photosynthetically active irradiance (PAR), high temperatures, restricted water availability, soil salinity, and various combinations of these parameters are among the variables that have been proposed as primary environmental determinants of the relative success of C4 plants in particular habitats (Bjorkman, 1971; Black, 1973; Laetsch, 1974). The present analysis will attempt to correlate macroscale patterns in climate with broad geographic patterns in abundance of a large number of C4 species.

The analysis was restricted to the Gramineae because this group contains nearly half (Downton, 1975) of the known C4 angiosperm species, it has a broad geographic distribution, and the taxonomic distribution of the C4 and C3 pathways is well understood, which minimizes the error in our floristic data. The Crassulacean Acid Metabolism (CAM) pathway of photosynthesis is not known to occur in this group. Furthermore, although there exist large differences in morphology and physiology among grasses, we felt that the graminoid life form offered at least a partial control on morphological variations that could potentially alter the microenvironment of the individual plant.

Methods

Complete species lists for the Gramineae were obtained from local floras for 32 locations in North America. Species were placed in subfamilies, genera and subgenera according to the treatment of Gould (1968). Any species of doubtful identity, as well as species growing only in cultivation, were excluded from the tabulations. The distribution of the C4 or C3 photosynthetic pathways among the subfamilies, tribes and genera within the Gramineae appears to closely follow taxonomic categories (Smith and Brown, 1973; Downton, 1975). The genus Panicum contains both C3 and C4 species. However, of the major subgenera of Panicum, the subgenus Dicanthelium appears to be completely C3 and the subgenus Eupanicum nearly all C4 (data of Downton, 1975). In our analysis, all members of the subfamilies Festucoideae, Bambusoideae, Arundinoideae and Oryzoideae; and the Dicanthelium subgenus of Panicum, were assumed to possess the C3 photosynthetic pathway. All members of the subfamilies Eragrostoideae and Panicoideae (except Panicum), and the subgenera Paurochaetium and Eupanicum of the genus Panicum were assumed to possess the C4 photosynthetic pathway. Based on the above taxonomic distribution of photosynthetic pathways we calculated the percent of the total number of grass species that possessed the C4 pathway for each local flora (Fig. 1). In addition to the locations cited in Table 2, the additional locations in Figure 1 are: the arctic slope of Alaska (Wiggins and Thomas, 1962), Truelove Lowland, Devon Island, NWT (Barrett and Teeri, 1973), Northern Manitoba (Ritchie, 1962), Alberta (Moss, 1959), and the Gaspé Peninsula (Scoggan, 1950).

The environmental variables that we included (Table 1) were limited to those for which statistically comparable data could be obtained over the range of habitats. The variables include measures of irradiance, heat availability, potential length of the growth period, and water supply. Field observations and laboratory experiments have previously suggested that these climatic factors may

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Fig. 1. The percent C4 species in the grass floras of 32 regions in North America