Plant Geography

with special reference to North America

REXFORD DAUBENMIRE

PLANT
GEOGRAPHY

*with special reference
to North America*

PHYSIOLOGICAL ECOLOGY

A Series of Monographs, Texts, and Treatises

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INTRODUCTION

Plant geography (or phytogeography, or geobotany) is that branch of science concerned with describing and interpreting the uneven distribution of the earth's plant life. Clearly its origin had to await the birth of at least a primitive type of taxonomy, for only after plants came to have somewhat standardized names could information accumulate regarding the details of distribution, and thus expose patterns that challenge the mind for explanation. Even in the time of Theophrastus, however, there was enough known to elicit commentary on the restrictions of species to different geographic areas. During the Middle Ages nomenclatorial confusion was still a handicap to progress, as evident in comparing the herbals of that period. But when Linnaeus made his epic contribution to standardized nomenclature in the eighteenth century, taxonomic concepts were greatly improved and distribution patterns could be better defined. The stage was then set for serious inquiry into this fascinating field.

Interest at first centered simply upon description from a static point of view, but even as early as 1792, it became apparent to K. L. Willdenow, at least, that floras are not static, that they have attained their present composition and ranges by means of past evolution, dissemination efficiency, migration, and extinction. However, in those times, for fear of torture sponsored by entrenched religions, such a hypothesis had to be expressed cautiously by recognizing "centers of creation." Willdenow, for example, suggested that each major mountain system could have served as such a center, but Christian dogma would not admit the possibility of extinctions.

A century later, as Charles Darwin's dynamic concept of species permeated the fabric of the natural sciences, open assault was begun on the problems of origin, migration, and evolution in plants. If closely related species have evolved from a common ancestor, then a genus has to be older than its species, and in the same way the family still older. Also a species

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must have had a place of origin from which it spread until it encountered barriers, and if the features of the earth's surface are to be given dynamic interpretation, then old barriers could disappear and new discontinuities arise. Paleobotany, historical geology, and taxonomy began to be drawn closer together by these considerations, and in the present century cytogenetics too has made important contributions toward the solution of problems concerning the origin and spread of taxa.

A different approach was added to the field of plant geography during the nineteenth century when those botanists who became interested in plant communities began to study the distribution of these composite entities in relation to climate. Alexander von Humboldt stands out as the first to recognize physiognomic groups of plants, irrespective of their taxonomic relations, and show that these are geographic units relatable to climate. This shifting of emphasis away from taxonomy toward ecology attracted increasing numbers of workers so that by 1849 J. Thurman called attention to the fact that there had developed two major approaches to plant geography and defined their scope.

One of these is *floristic plant geography*, which is primarily a study of evolutionary divergence, migration, and decline of taxa, as influenced by past events of the earth's history. The basic data here consist of maps of plant ranges and geologic features, fossil floras, and chromosome counts. Differences or similarities in the composition of floras of different regions are determined and given historical interpretation. The relative abundance of species is of little concern, except that special attention is accorded rare species. Neither the physiognomy of plant life, nor the dynamic interrelations among species, is considered. In this endeavor the disciplines of geology, paleontology, morphology, and cytogenetics are employed more often in making explanations than is autecology.

The alternative approach to plant geography, which came to be known as *ecologic plant geography*, takes plant communities as units having ranges to be interpreted. Here the outlook is dominated by sociologic and physiologic, rather than phylogenetic and historic considerations. Explanations of the boundaries of vegetation units are sought on the basis of structural and functional adaptations to various environmental complexes, without laying particular stress on the geographic position of the region. The problem of how and when a group of ecologically related plants came to be where it is at present is usually considered of minor importance as compared with the problem of how this community is able to maintain its space relations in the present pattern of environments. Convergent evolution is the chief aspect of paleobotany of concern to the ecologic plant geographer, for he is acutely aware that under similar environments taxonomically diverse floras may produce communities having ecologic and physiognomic similarity through adaptive evolution. Also, plant succession leading to the closest possible fit of community composition to each combination of environmental factors is a

matter of prime importance to ecologic plant geography, whereas it is of no particular significance in floristic plant geography. Abundant and regularly present species that determine the distinctive character of each vegetation unit get more attention than the rare ones.

Detailed quantitative studies of existing vegetation and measurements of present environmental conditions can be subjected to endless tests, therefore all problems of ecologic plant geography are theoretically capable of solution. The great handicaps here are the complexity of vegetation, and the complexity of environment, including problems created by man's activities in the recent past.

Floristic plant geography is not burdened with these complexities, but it usually necessitates tenuous hypotheses concerning the remote past, many of which cannot be proven. For each problem in this field there are several to many plausible explanations, and such can only be rated as to their probable correctness, as best man can judge. Taxonomic concepts are vital, and these are subject to frequent revision. Accurate distribution maps are essential, but most maps are only crude approximations. There is no way of determining accurately the age of a taxon, the absolute limits of its effective dissemination, or whether it is now expanding or contracting its range. These problems lie at the core of floristic plant geography.

Diverse as these two viewpoints seem and as diversely as they have been treated, especially in North America, they are really mutually supporting aspects of the broader field of plant geography. No segment of the earth's green mantle can be well understood without recourse to both types of inquiry. Although books on plant geography vary greatly as to their content, most of them have been largely, if not exclusively, devoted to floristic plant geography, with little or no attention given to a vegetation hierarchy related to climate, soil, and disturbance, i.e., to ecologic plant geography. Both aspects of the subject are considered in the treatment that follows, although not with equal emphasis. Only a concise summary is given of some of the main concepts of floristic plant geography, with most of the space devoted to ecologic plant geography, and in both parts interest is centered on the northern half of the Western Hemisphere. In addition to this special combination and direction of emphasis, more than usual consideration has been given to the probable geologic history of each vegetation unit, as well as this can be surmised from the present stock of paleontologic and geologic information.

Only international names have been used for plants as a means of saving space and avoiding confusion. Most persons would like to imagine that each species has but one colloquial name, but many have none (e.g., in *Carex*, *Panicum*, *Quercus*, *Rubus*, *Salix*.) and most have several. Even in western North America, where it is endemic, *Purshia tridentata* is called "antelope brush" in places, and "bitterbrush" elsewhere. The "beargrass" of the hot Texas plains is in a different genus than the "beargrass" of cold ridgetops in

the Cascade Mountains, or the "beargrass" of Florida sands, and none is a grass. "Ironwood" refers to trees in different families in Arizona, Indiana, and Florida, etc. Since Mexico is considered to the extent which the status of vegetation research there permits, would English-speaking readers take kindly to colloquial Spanish names and vice versa, despite the equal validity of the English and Spanish names?

Infraspecific taxa are commonly indicated as trinomials, and in places I have used trinomials (even names considered out of date) instead of widely accepted binomials, simply to point up significant taxonomic relationships otherwise unrecognizable. Unless species names are alphabetized in listing, there is a connotation of their characteristic order of relative abundance or ubiquity. A genus name used alone usually implies more than one species.

Nearly every term that could possibly be used in describing and interpreting vegetation has been used in different senses, usually with little or no attempt to clarify the special meaning attached to it by each author. It seems futile to try to cast aside terms owing to multiple definitions, so I have selected those that appear to be most meaningful in the English language, and appended a glossary to indicate the particular meaning attached here.

The rod that appears for scale in many of my photographs is 1 m in length, marked off in tenths.

Part I

FLORISTIC PLANT GEOGRAPHY

Floristic plant geography becomes a valid field of inquiry only if one accepts the thesis that the ranges of plants have changed through time. To appraise the validity of this widely held thesis, we shall consider the supporting evidence, but first some basic terms and concepts need clarification.

RELATION BETWEEN DISSEMINATION AND MIGRATION

Within the margin of a species' range,* the scattering of reproductive structures away from each parent plant serves three functions. (1) It minimizes intraspecific competition. (2) It allows new genes to spread through all habitats where the resulting characters are compatible. (3) It tends to extend the range of a species over all the area in which completion of its life cycle is possible.

At the margin of a range, dissemination in all directions from parent plants inevitably puts some disseminules into previously unoccupied territory, as for example, forest tree seeds falling in the margin of contiguous steppe. If the new area permits germination and the subsequent completion of the life cycle, then the process may be repeated with migration extending the range still farther.

Ignoring for the moment such spread as is accomplished by rhizome or runner extension, dissemination is necessary for migration, but by no means does it usually result in migration. Millions of forest tree seeds perish in the margin of contiguous steppe each year.

*See glossary for special terms, or common words used in a special sense.

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A species' range may remain under essentially continuous environmental control during migration, as when climate changes slowly enough for migration to keep in step. But range limits may be unrelated to environmental control if the plant represents a new mutation, or if it is an alien plant introduced well within the boundaries of suitable environment and it has not yet had time to exploit all the habitat to which it is adapted, or if the environment has changed rapidly.

Migration is a matter of *range expansion* when more territory is added to the previous range. It is a matter of *range displacement* if part or all of the original range becomes uninhabitable.

Migration may be expected to continue until some environmental factor becomes limiting. This factor is called a barrier. Should there be another tract of favorable territory beyond the barrier, the latter must form a continuous belt wider than the distance which any disseminule of the plant can cross if it is to impede migration indefinitely. Thus only a wide river can be a barrier to a plant with heavy disseminules which do not float. The narrow Isthmus of Panama has kept the mangrove tree *Pelliciera rhizophorae* restricted to the Pacific coast.

Since environmental gradients are numerous and often independent, the limiting factors along different segments of the periphery of a stabilized range are usually different. If inadequate heat limits the poleward distribution of an organism, some other factor must certainly set the equatorward limits, and between these borders oceans, or differences in the amount of seasonal distribution of precipitation, may set the east–west margins of its range.

EVIDENCES OF THE DYNAMIC CHARACTER OF RANGES

Since the remodeling of the earth's surface is a never-ending process, environments are continually changing. Old barriers to migration slowly change positions or disappear, and new ones come into being. Ranges tend to keep in adjustment with barriers, but the migration of plants, especially of vascular perennials, is very slow. Each step in migration requires the maturation of a new generation within the dissemination range of individuals which served as the preceding step. Then on the other hand, retractions are slow since once established, most perennials can live out their life span even if conditions that temporarily allowed their establishment cease to exist. Thus, there is often a considerable lag between environmental change and range adjustment. Range extensions and contractions are probably taking place in most parts of the earth at all times, but the rates of migration are so slow and rendered so uncertain by short-term superimposed climatic fluctuations, that man seldom has opportunity to observe significant migrations directly, and much of our knowledge of past migrations must be based on indirect evidence. The dynamic character of plant ranges is indicated by the follow-

ing types of evidence, with other types of evidence of less conclusive character to be brought out later.

Direct Observation

Accidentally or intentionally, man has often transported disseminules across ocean barriers and then has been able to observe, frequently with regret, the rapidity with which a plant may extend its range. *Salsola kali*, for example, was accidentally introduced into central North America from Eurasia in 1886, and within half a century it had radiated from its point of introduction to become one of the most common weeds on the continent. Although direct observation of plant migration has almost entirely concerned weeds or disease organisms (such as *Cronartium ribicola*, a rust parasite of *Haploxylon* pines), through geologic time new introductions with subsequent spread have occurred naturally from time to time.

Fossil Stratigraphy

Pollen preserved in successive layers of a peat deposit show the kinds of plants that have grown in that vicinity from the time peat began to accumulate up to the present day. In the Ohio Valley many of these profiles show that *Picea glauca*, *Abies balsamea*, and *Larix laricina* were abundant in that area soon after Pleistocene (Table 1) ice melted away and peat started accumulating in ponds. Pollens of most of the deciduous angiosperm trees now abundant in the same area are represented sparingly, if at all, in the bottom layers but coming up through the strata fossils of coniferous trees dwindle while those of angiosperms increase, showing clearly that the conifers emigrated as the angiosperms immigrated.

Fossils in older sedimentary rocks reveal similar mass migrations of floras throughout the earth's history, although in less detail than in the younger strata.

Distribution Patterns

Centers of Origin

For the most part each taxon has originated at one place, which may be designated as its center of origin. The center may represent a single point where a rare mutation or hybridization started a new line of descent, or it may be a sizable area in which evolution changed an entire population through a period of time. Among mammalian orders, the location of the earliest fossils in the geologic record has provided substantial evidence of the location of centers of origin of certain groups, but vascular plants are much older and their remains are less easily interpreted than are teeth and bones.

TABLE 1

Major Divisions[a] of Geologic Time, and Some Salient Features of the Earth's History Starting with the Period
in Which Angiosperms Achieved Dominance

Eras	Periods	Epochs	Millions[b] of years since start	Climate	Nature of North American land area
Cenozoic	Quaternary	{ Holocene	0.012		{ Elevated and
		} Pleistocene	2.5		enlarged
		(Pliocene	13.	(Progressive	(Cascades and Sierras form,
		{ Miocene	26.	{ cooling and }	} general uplife continues,
	Tertiary	{ Oligocene	40.	(local drying)	(Rocky Mountains rise
		Eocene	60.	Warmest	Low and restricted
		(Paleocene	75.	Cool	Elevated and enlarged
Mesozoic	Cretaceous		144.	Warm	Low and restricted
	Jurassic		180.	(Last period of fern–cycad–conifer dominance)	
	Triassic		225.		
Paleozoic	Permian		270.	(Cycads join ferns and conifers)	
	Carboniferous		350.	(Conifers start to share dominance with ferns)	
	Devonian		400.		
	Silurian		440.	(Ferns, the first land plants, appear)	
	Ordovician		500.		
	Cambrian		600.		
	Pre-Cambrian		4600.		

[a] Other names sometimes used in designating spans of geologic time are:
Paleogene = Paleocene + Eocene + Oligocene.
Neogene = Miocene + Pliocene.
Holocene = Recent + post-Pleistocene.
[b] Estimates, subject to revision.

Reliable fossil evidence indicating the centers of origin of angiosperm families is as yet unavailable. For genera and species many possible criteria for locating centers of origin have been suggested, but most are too uncertain to be useful. A few of these are as follows.

Centers of taxonomic diversity. If the ranges of species in a genus overlap, and the group is not very widespread, the region of overlap might be suspected as approximating their centers of origin (Fig. 1). Presumably these taxa could have been derived from a common ancestral stock through mutations that have (1) established reproductive incompatibility at once, (2) altered the season of reproduction, or (3) required invasions of new habitats in the environmental mosaic.

On the other hand, if applied to a widespread genus, there is a possibility that after the genus reached a remote area it underwent a burst of evolutionary differentiation. For example, both *Arceuthobium*[182] and *Pinus* are believed to have originated in Asia, but most species by far are in North America.

Another difficulty in applying this concept to widely distributed groups is that the taxonomic work may not be uniform, so that an apparent concentra-
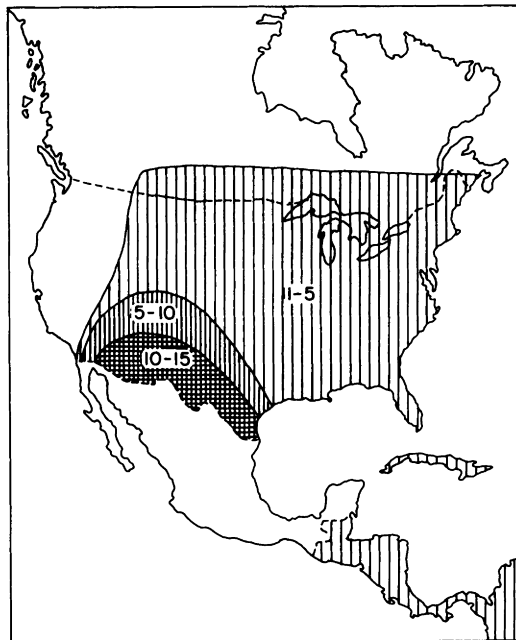

Fig. 1. Approximate concentration of species in the American genus *Bouteloua*. Only a few species continue southward into South America, so there is an indication of a center of maximum species diversity, and probable center of origin, in the arid belt astride the Mexico–United States border.