

LECTURE 2: Vegetation Patterns in Relation to Climate, Other Environmental Factors, and History

Purpose

Green Plants are the energetic foundation of almost all of the earth's ecosystems. If you understand the mechanisms that control the distribution of different types of plants, you will have achieved an excellent first step toward an understanding of ecosystem development and function. Animal distributions, and to a significant extent human uses of particular landscapes, are either controlled by plant distributions or respond to similar environmental controls. Of course, Ecosystems are governed by a complex set of interactions between their abiotic, plant, animal and human constituents; the distribution of plants does not alone determine everything else. Nevertheless, particularly in biogeography, it is convenient to start with plants.

The Biogeographic Hypotheses

Biogeographers have discovered that two general kinds of processes influence the distribution of plants and animals and the functional properties of ecosystems, namely, the physical environment and history. As you saw in the last lecture, there is a striking general resemblance between the present pattern of the earth's climate and the pattern of distribution of vegetation (Figure 1.1 and 1.2). Throughout the course we will develop the reasons for this resemblance in more detail. However, there are also quite significant differences between the biomes of similar climates.

Partly these differences can be explained by additional physical variables, such as bedrock types, but some of the differences are certainly historical. In addition to a functional classification of the earth into biome units, it can also be divided into biogeographical realms (Figures 2.1a, b, 2.2) that reflect the different evolutionary history of the continents. Accidents of history -- long lasting results of past environments, evolutionary accidents, and continental separation -- influence the differences between present day ecosystems. The influence of humans on a system's current condition is more "historical" and less "ecological" than the effects of plants and other animals, at least at the present time. Human activities have imposed major changes on natural ecosystems that reflect the history of human colonization and economic development more than they do environmental processes. In many cases, biogeographers are unsure just how much of ecosystem differences to attribute to biotic history, human history, and environmental differences.

Biogeographic Classification

There is a series of useful terms that biogeographers use to subdivide the earth's biosphere:

1. Realms - used both for the major physical subdivision of the biosphere (e.g. marine realm) and for the historical evolutionary subdivisions of the terrestrial fauna and flora as in Figures 2.1a, b (from slide in lecture) (e.g. neotropical realm).
2. Provinces - biotic units defined on the basis of similarity of species composition, as in Figure 2.2 (from slide in lecture). It reflects both biotic history and environmental effects.
3. Biomes - Units much like provinces, except that they are designed to group together environmentally and structurally similar ecosystems, even when biotic histories are quite distinct (e.g. tropical rainforest biome). This is the unit around which this course is organized.

4. **Communities and ecosystems** - The associations of plants and animals that actually interact with each other on a given site at a given time. Usually a biome is thought to be made up of a series of more or less distinct ecosystems or communities. The term "ecosystem" implies a preoccupation with the functional interaction of biotic and abiotic factors (as in nutrient budgets), while the use of "community" implies an interest in species composition. Otherwise, the terms are roughly synonymous. We will use the functional terminology of ecosystems from time to time. Refer to Figure 2.3 (from slide in lecture) for a guide to this terminology.
5. **Ecotones** - the boundaries between communities or biomes. These boundaries are not usually sharp. The term ecotone is then used for the intermediate transitional systems between the better defined ones.
6. **Guilds** - Groups of species that do similar things in a given ecosystem. For example, the numerous herbivorous large mammals that live in African savannahs compose a guild.
7. **Species-populations** - The basic units of both historical and functional biogeography: the group of interbreeding individuals that have a common gene pool.

You should be aware that the usage of taxonomic terms in ecology is quite idiosyncratic. Species are hard enough to define, and larger ecological units are harder yet, especially since the historical and functional aspects are partly cross-cutting. In reaction to an earlier excessive preoccupation with terminology, the present situation is anarchistic. Biogeographers and ecologists seem to have an unwritten rule never to argue about each others systems of classification, even if someone decides to use a conventional term in unusual ways. If you become confused about this terminology, it is probably an ecologist's fault, not yours.

Terrestrial Biomes

Our main unit, the biome, is characterized by the dominant vegetation, i.e. the most common plant communities covering large geographical areas. Most of the communities that make up a biome have many adaptations in common, even when they occur on different continents and have completely different species compositions. That is, convergent adaptations to similar environments predominate over historical differences. It is, then, possible to define biomes independent of continents. Needless to say, the details of community structure within any biome are complex, reflecting both environmental variations and history. In the next lecture we will consider the plant and animal adaptations that characterize each biome in more detail. Here we will briefly characterize the nine main terrestrial biomes of the earth. Ideally, according to the physical environment hypothesis, each biome is characterized by a similar climate, functionally similar plants and animals, and even similar soils. This ideal scheme is presented in Table 2.2 (also compare Figures 1.1, 1.2, and 2.4 (from slide in lecture)).

Environmental Factors

According to the physical environment hypothesis, the climate of a region is the primary determinant of biome structure. Climate itself has two components of overwhelming importance, temperature and precipitation. The climate diagram is designed to summarize and display these climate data and their seemed relationships. We will use Walter's diagram system: Figure 2.5a provides a key to these very useful diagrams. In addition to mean and seasonality of temperature and precipitation, important features that can be read from these diagrams include the length and severity of any drought season, and the length of the frost free growing season. These diagrams also make it easy to recognize at a glance homoclimates, similar climates found in different places. We will make frequent use of these diagrams, so please familiarize yourself with their structure and meaning. Typical climate diagrams for each biome are presented in Figure 2.5b. Incidentally, systems similar to Walter's are frequently used for practical purposes in agriculture, gardening, building design, etc.

Topographic relief is a special class of environmental effects which have an influence on vegetation by modifying climate effects and soil development. For example, north-facing slopes (in the Northern Hemisphere) with lower incident solar radiation have communities resembling those of cooler, wetter regions than south-facing slopes, because the lower radiation results in lower temperatures and evaporation. Higher mountains create strong rainfall and temperature gradients, which create a series of biomes up their slopes (see Figure 2.6 [from slide in lecture]). This altitudinal transition of vegetation resembles a portion of equator-pole latitudinal transition of vegetation starting from the low elevation biome. However, the analogy is imperfect because the seasonality of light and precipitation and the relationship between temperature and evaporation differ for altitudinal and latitudinal gradients. Tropical mountains, for example, never lose aseasonal patterns of light and temperature, and evaporation is much higher than for an equivalent temperature at lower elevations. Thus the mountain biomes of each climate region exhibit vegetation patterns of their own (see the subsequent lecture on mountains).

Soils

Soil quality is very important to the vegetation. Soils themselves are complex mixtures of organisms, the remains of organisms, and minerals. They are ecosystems in their own right and have a complex evolutionary dynamic.

The basic properties of soils include their texture, pH, and nutrient holding capacity. Soil textures are described as stony, sandy, silty, loamy, and clayey, depending on the predominant particle sizes of the soil. (These terms can be mixed, e.g. stony loam.) Loams are approximately equal mixtures of sand, silt, and clay. Soils tending to the sandy side are described as light; those dominated by clay, as heavy. Light soils are soft, easy for roots to penetrate, and easy to plow, but have little water or nutrient holding capacity. Heavy soils are very hard when dry, and sticky when wet. Oxygen can be exhausted in the pore spaces when they are wet, and they are easily compacted and hard to plow. However, they hold much water and nutrients compared to lighter soils, and thus tend to be more fertile. Soil pH refers to its acidity. Desert soils sometimes contain calcium sulfate or sodium carbonate and can be very basic. Slightly basic to neutral soils have lots of calcium carbonate and other basic ions, such as potassium. Since plants require calcium and potassium to grow, base rich soils are generally fertile. In acid soils the bases are replaced by hydrogen ion. Such soils are quite infertile, especially as the acid condition becomes extreme.

Clays and organic matter are responsible for the nutrient holding capacity of soils. Figure 2.7 shows the basic structure of two typical clay minerals, kaolinite and montmorillonite. Clays are layered minerals composed of sheets of silicate and aluminum oxides. The particle size of clays is very small (less than 2 microns), and many of them permit the entry of water and cations (positively charged ions like calcium and hydrogen) into the spaces between the sheets. The alumino-silicate clays have vast surface areas because of their small size and internal spaces. They also tend to have negative charges on their surfaces, so that cations stick to them, including the all important nutrients, calcium, potassium, and ammonia. These charged ions also attract water, so each tiny clay particle becomes a wet, nutrient-soaked colloidal blob. The charges are mainly due to imperfections in the crystal structure, such as the substitution of magnesium ions with a 2+ charge for an aluminum with 3+, leaving the associated oxygen to generate a net one unit of negative charge, which attract the positively charged cations.

Organic matter, especially the long-lived humic substances resulting from the breakdown of woody tissue, incorporate a large pool of nitrogen that is slowly released to support plant growth. Also, humic substances tend to bind clays into loose aggregates that make soil structure loamier. In sandy soils, organic matter can compensate to some extent for the lack of clay in water and nutrient retention.

Classically, soils are said to develop as a function of (a) parent material (the rock, alluvium, volcanic ash, windblown sand, etc., from which the soil develops), (b) climate, (c) organisms, (d) relief (flat, steep, well-drained, waterlogged), and (e) time. "Raw" solid parent materials, such as dune sand or recently deposited alluvium, gives rise to azonal soils. These types tend to be found in

all biomes. As soils develop and age under a given climate and its associated vegetation, they tend to converge on a general soil type that is characteristic of the biome. These are called zonal soils. We will meet podsoils in cool, humid climates, chernozems in the semiarid steppe, and latosols in the tropics.

The zonal soils result from a characteristic pattern of physical and chemical weathering that depends on the temperature and moisture regime. In cool, humid regions, layered podsoils are the result of soil formation. Figure 2.8 shows a cross section of a classic podsol. As water leaches through the parent material, clays are degraded and moved downward into B horizons. Iron oxides may also be deposited in the B horizons. What is left in the "topsoil" is a bleached white sand overlain by a layer of decaying humus. Conifers especially produce quite acid humus, which accelerates the weathering of clays and replaces the nutrient cations like calcium with hydrogen ion. Clays weather by the loss of their more soluble impurities like magnesium, and by the deposition of an extra layer of alumina between layers of silica, converting clays such as montmorillonite into ones like kaolinite. The more weathered clays have less of the water and nutrient retaining properties than the less weathered ones. In hot, wet climates, weathering is more rapid and complete. The silica is weathered entirely out of the soil and layered clays disappear, leaving soils acid mixtures of simple iron and aluminum oxides. Figure 2.9 illustrates the sequence schematically. These are the latosols of the tropics. Hot climates also favor the rapid oxidation of soil organic matter, so tropical soils usually do not retain this important material either. In the semi-arid temperate grasslands, chemical weathering is relatively slow, and organic matter accumulation is favored. Chernozems are the result, soils with an abundance of clays, basic cations, and ample organic matter to considerable depths (turn ahead to Figure 11.3). These are the highly desirable agricultural soils of the World's temperate grain belts (Iowa, Ukraine).

Note that youthful soils are generally most productive. The weathering process results in degraded clays and poor, acid soils. Recognizable layering (horizons) can develop in podsoils in a few hundred years. The complete weathering to produce a latosol might take a few tens of thousands of years, not long at all in geological terms. Large areas of good soils are produced only when geological processes that make young soils are active. Many temperate grain belt soils are on loess, the windblown silt from the glaciers of the last ice age, last deposited about 15,000 years ago. Our rich Central Valley soils are a product of the rapid weathering of the steep, rapidly rising Sierras and Coast Ranges. In the tropics, good soils are often associated with alluvial soils from steep mountains like the Andes or the Himalayan complex, or volcanic regions, where recent ash deposits make excellent soils. Geologically stable areas have poor soils. The Amazon Basin away from the influence of Andean rivers is an example. Another is Australia. It has few steep mountains, violent rivers, or volcanoes, but few really good soils either. Dust storms, floods, earthquakes, volcanic eruptions, or bad soils. Take your pick! Soil color is a good rough index of soil age and productivity. Old, poor soils tend to be red due to the oxidation of iron to rust. Young, good soils tend to be gray or brown in color.

Fires and the activities of animals sometimes have important effects on vegetation, particularly in concert. The boundaries between steppes, shrublands, deserts, and forests is often regulated by a combination of fire and grazing. Human activities are a special case of animal effects of the utmost importance in the contemporary world. Large portions of many of the world's biomes have been completely transformed by clearing for agriculture, overgrazing, burning and sometimes pollution.

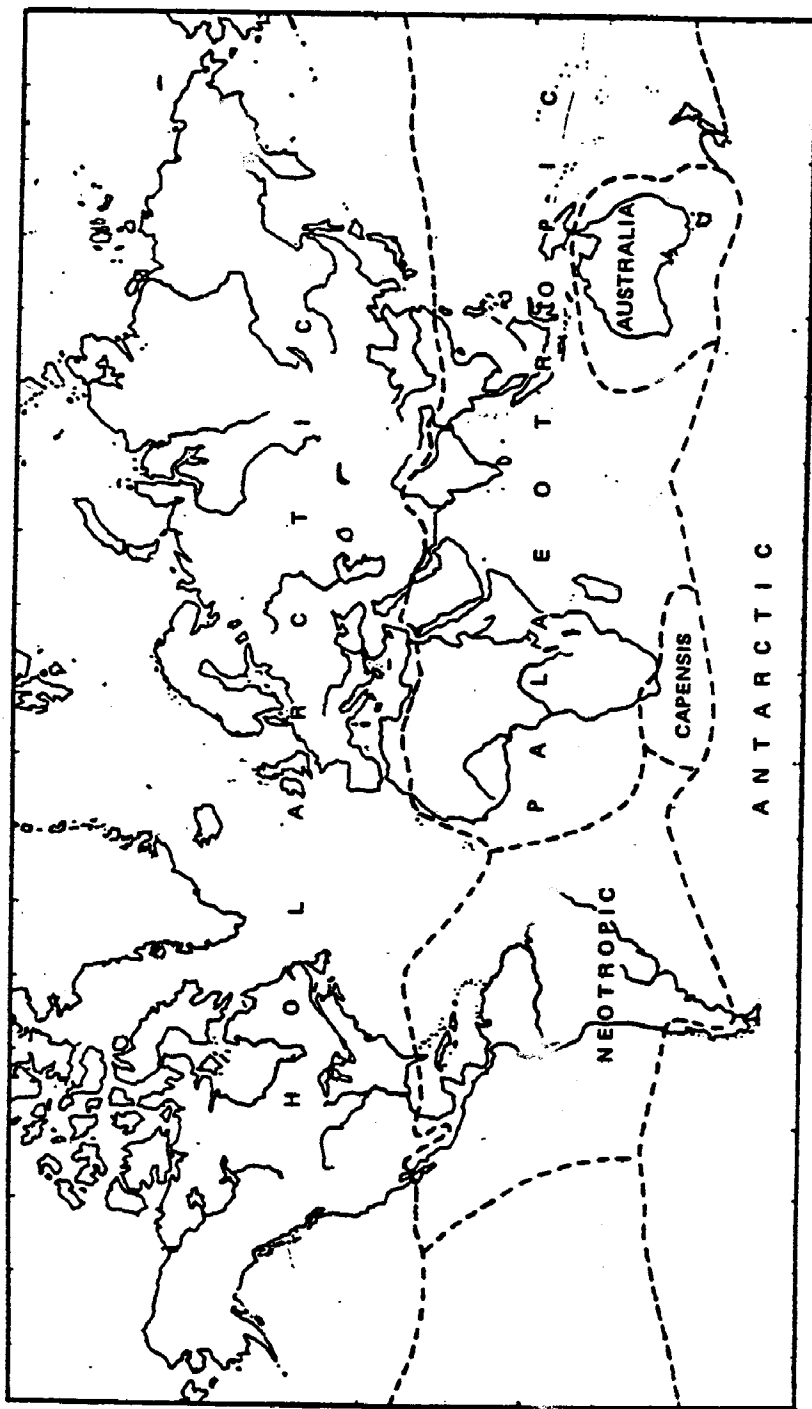


Figure 2.1a: The floristic realms of the Earth (Diels and Good, modified from Walter/Straka 1969). In New Zealand and Tasmania antarctic, as well as palaeotropical and australian elements occur. (Walter 1973)

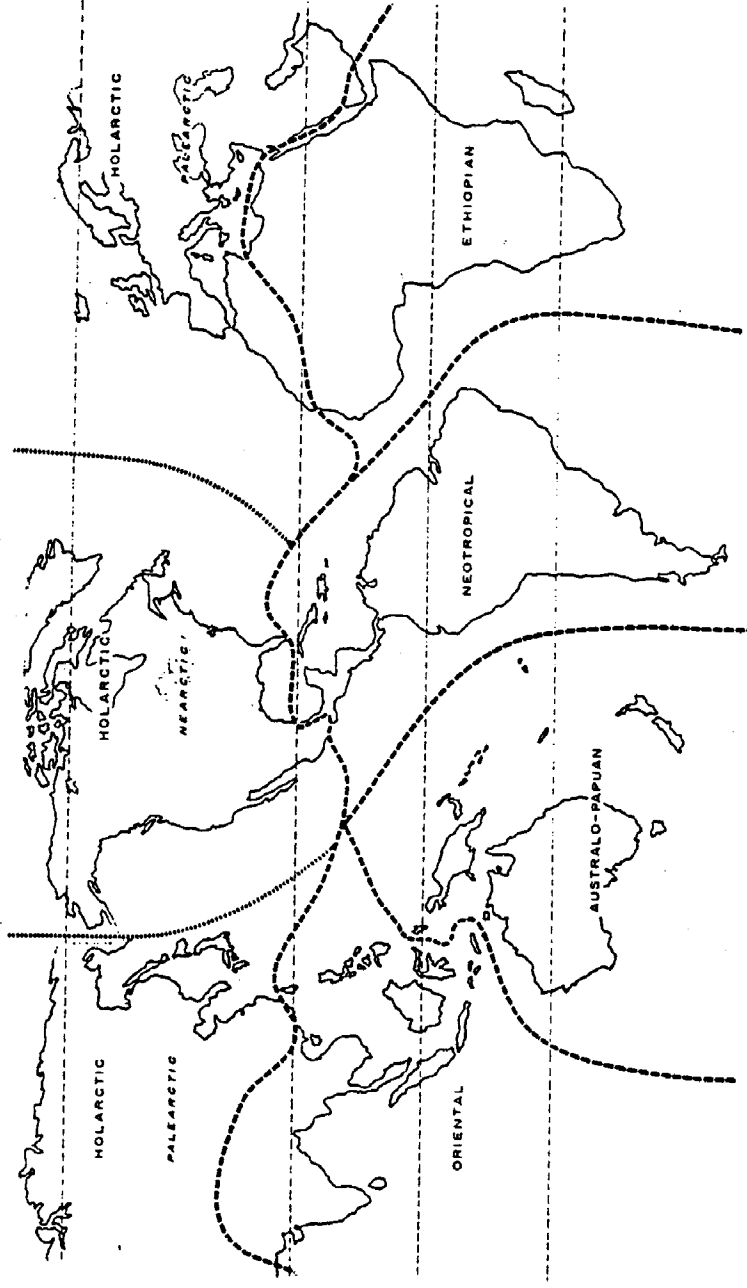


Figure 2.1b: Zoological regions of the world (adapted from Map No. 201 HA, Goode Base Map Series; copyright by the University of Chicago). (Kendeigh)

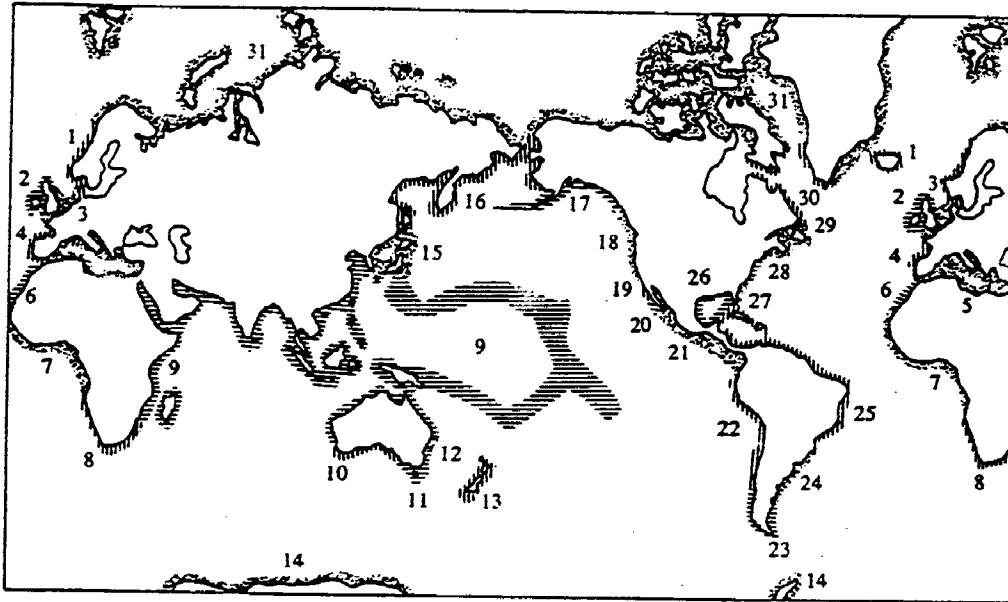


Fig. 8-7 Marine molluscan provinces of the world's shelves. (1) Norwegian. (2) Caledonian. (3) Celtic. (4) Lusitanian. (5) Mediterranean. (6) Mauritanian. (7) Guinean. (8) South African. (9) Indo-Pacific. (10) South Australian. (11) Maugean. (12) Peronian. (13) Zealandian. (14) Antarctic. (15) Japonic. (16) Bering. (17) Aleutian. (18) Oregonian. (19) Californian. (20) Surian. (21) Panamanian. (22) Peruvian. (23) Magellanic. (24) Patagonian. (25) Caribbean. (26) Gulf. (27) Carolinian. (28) Virginian. (29) Nova Scotian. (30) Labradorian. (31) Arctic.

(Valentini 1973)

Figure 2.2

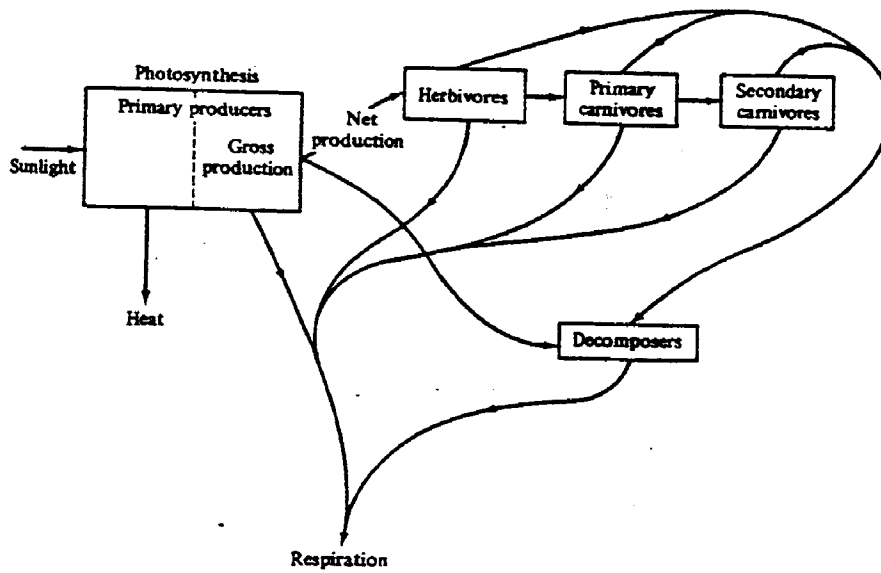


FIGURE 17-1
 A diagrammatic representation of the flow of energy through an ecosystem divided into a series of components. (Poole)

Figure 2.3

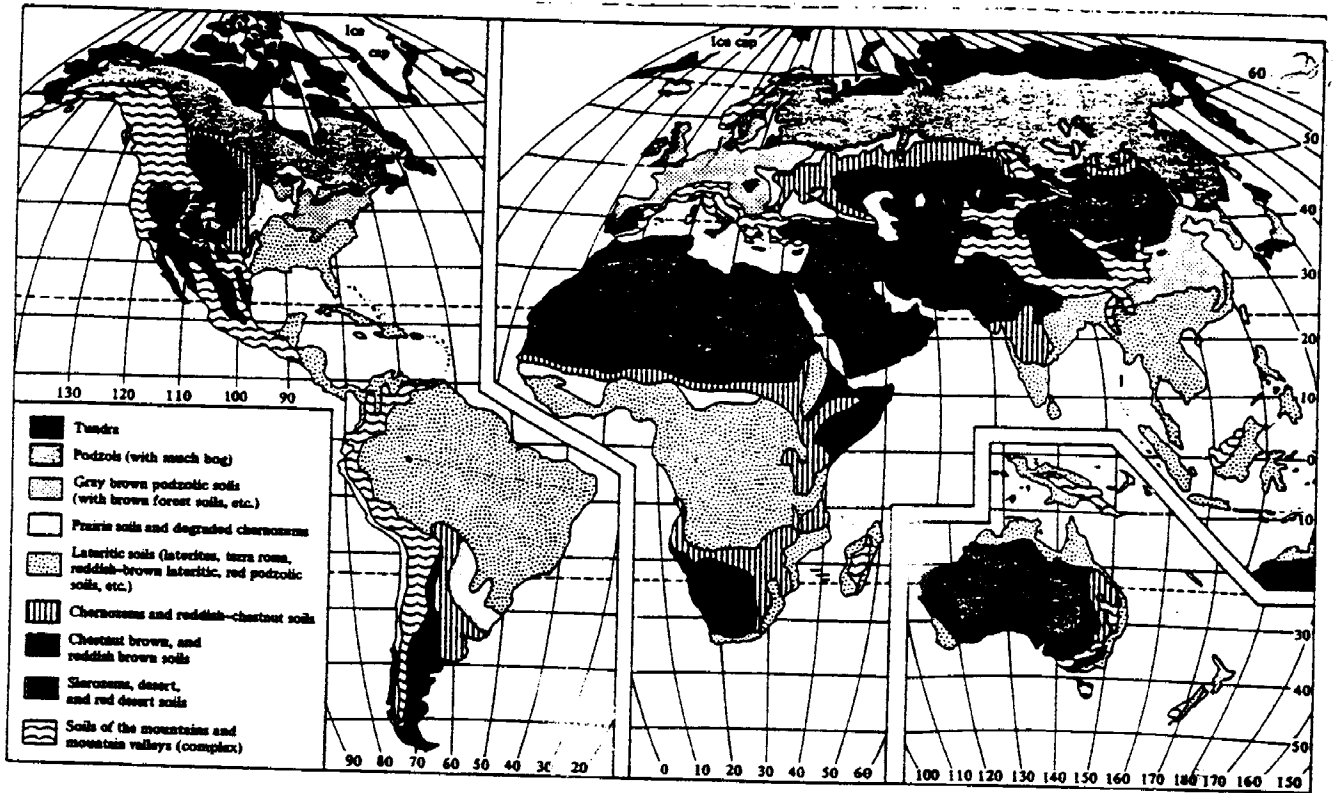


Figure 3.16 Geographic distribution of the primary soil types. Compare with Figure 3.1. [After Blumenstock and Thornthwaite (1941).]
(PIANKA 1974)

Supplimental figure : annual range of temperature.

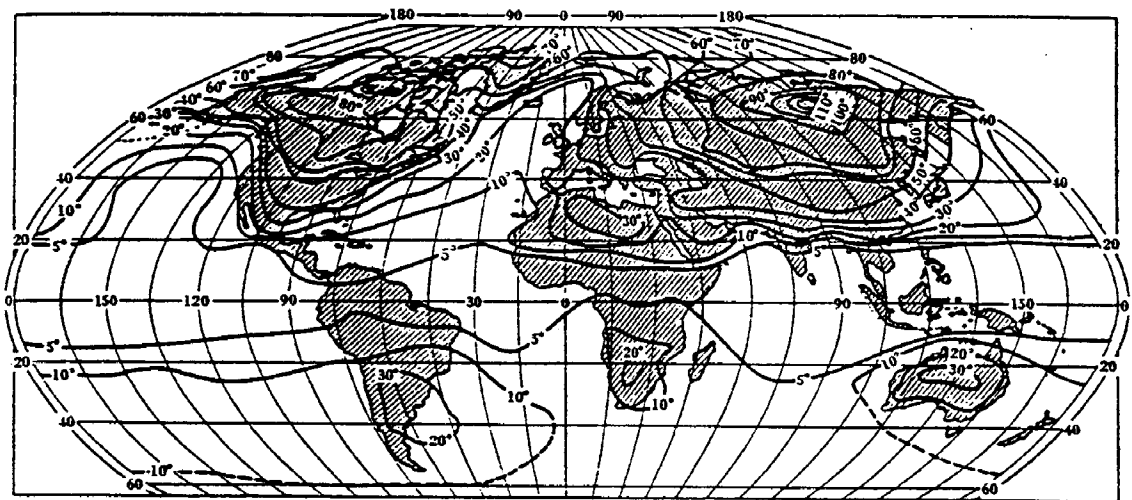


Figure 6.3. Average annual ranges of temperature ($^{\circ}\text{F}$) for the earth. The annual range is defined as the difference between the average temperatures of the warmest and coldest months. Temperature ranges are smallest in the low latitudes and over oceans, and largest over continents. (After Trewartha 1954, p. 37.)
(Krebs)

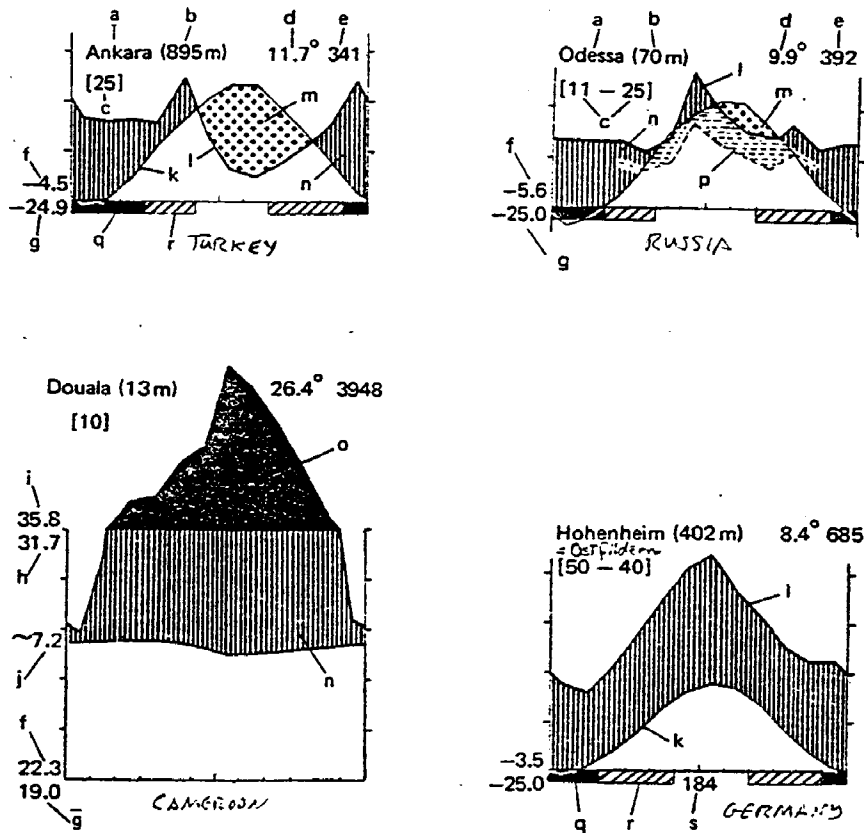


Fig. 7. Key to the climatic diagrams. Abscissa: Months (N. Hemisphere January—December, S. Hemisphere Juli—June); Ordinate: one division = 10° C or 20 mm rain. a = station, b = height above sealevel, c = duration of observations in years (of two figures the first indicatea temperature, the second precipitation), d = mean annual temperature in ° C, e = mean annual precipitation in mm, f = mean daily minimum of the coldest month, g = lowest temperature recorded, h = mean daily maximum of the warmest month, i = highest temperature recorded, j = mean daily temperature variations, k = curve of mean monthly temperature, l = curve of mean monthly precipitation, m = relative period of drought (dotted), n = relative humid season (vertical shading), o = mean monthly rain > 100 mm (black scale reduced to 1/10), p = reduced supplementary precipitation curve (10° C = 30 mm) and above it (dashes) dry period, q = months with mean daily minimum below 0° C (black) = cold season, r = months with absolute minimum below 0° C (diagonal shading) = late or early frosts occur, s = mean duration of frost-free period in days. Some values are missing, where no data are available for the stations concerned (h—j are only given for diurnal types of climate).

Figure 2.5a

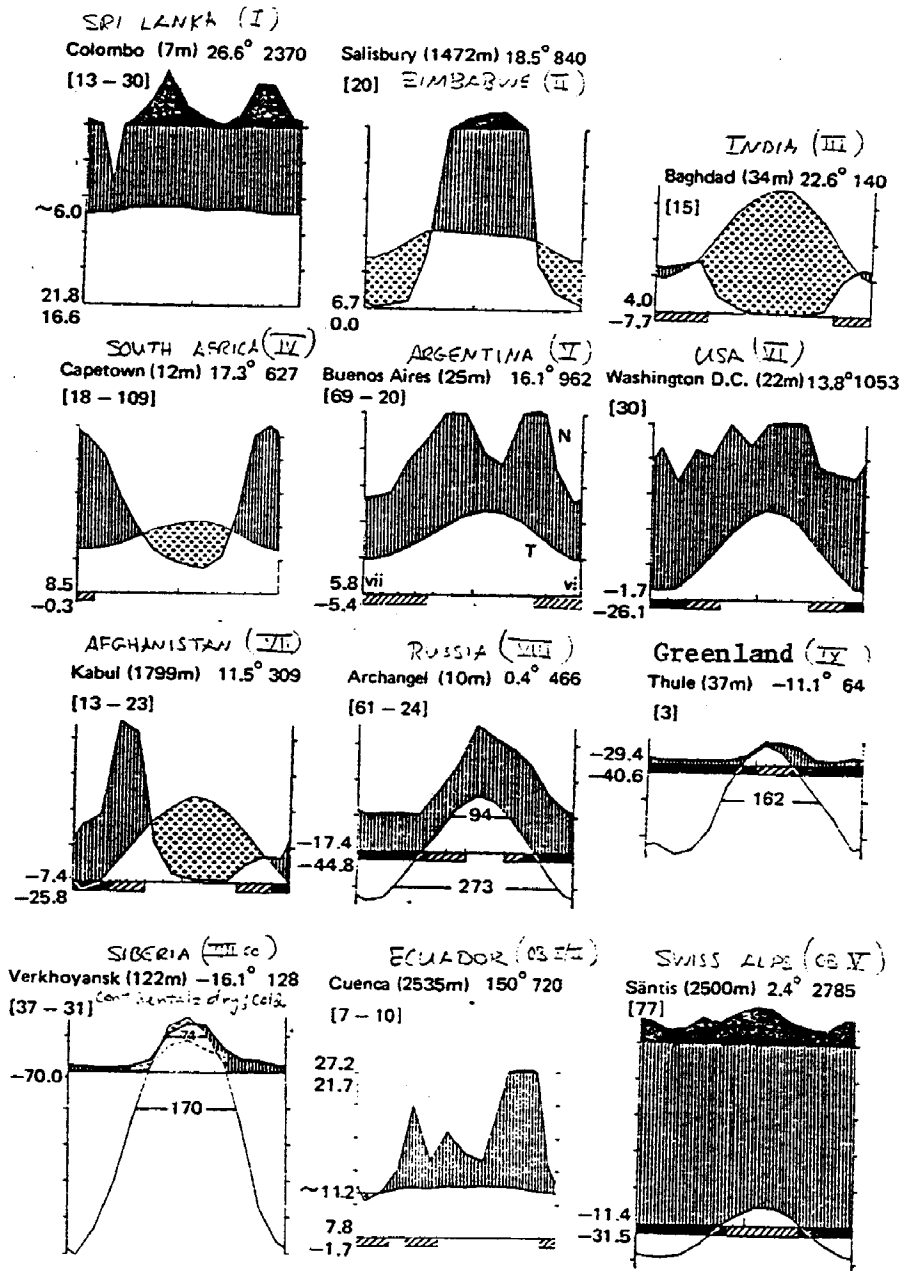


Fig. 8. Typical climatic diagrams for the climatic zones I-IX.

(Walter 1923)

Figure 2.5b

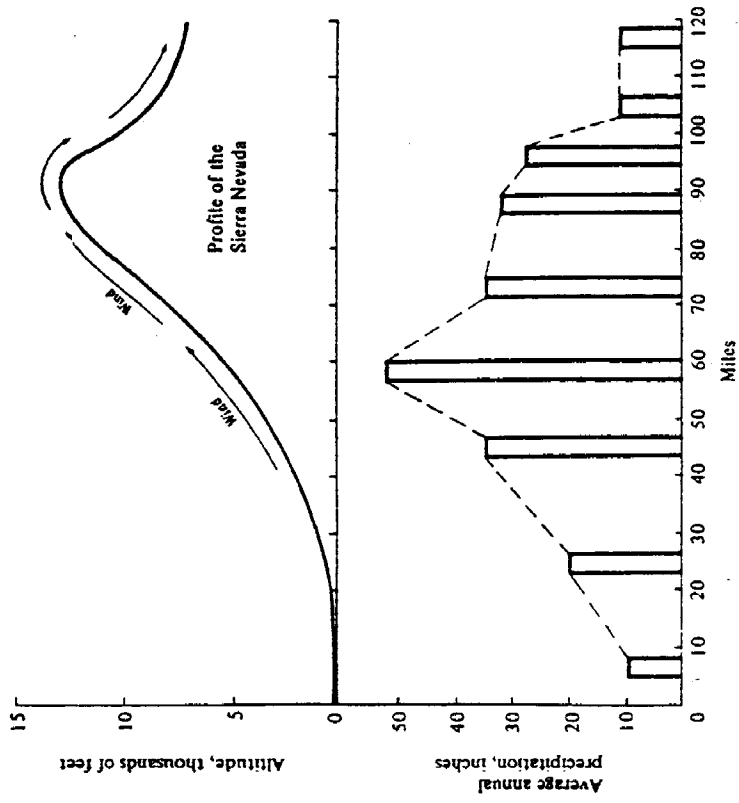
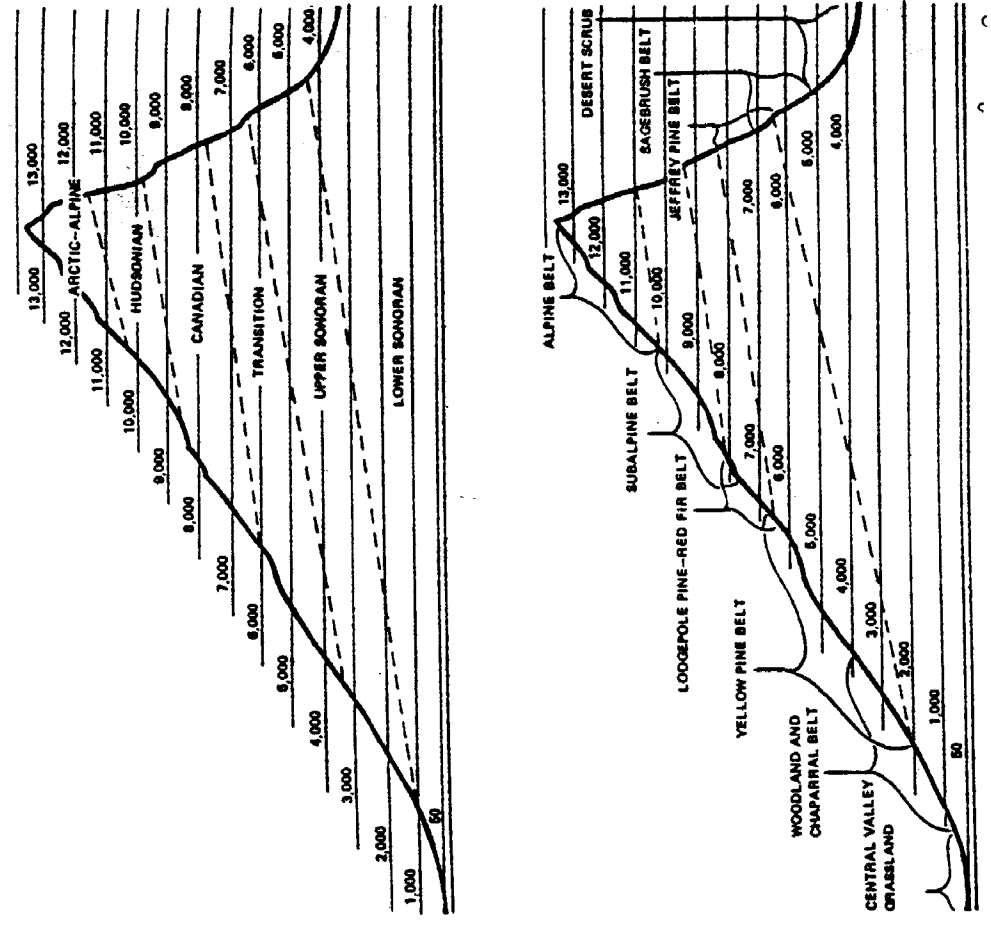


Illustration of the "rainshadow" effect of the Sierra Nevada mountains in central California. (Pianka, 1974)



Comparison of two types of zone identification for the Sierra Nevada. (Bakker 1971)

Figure 2.6

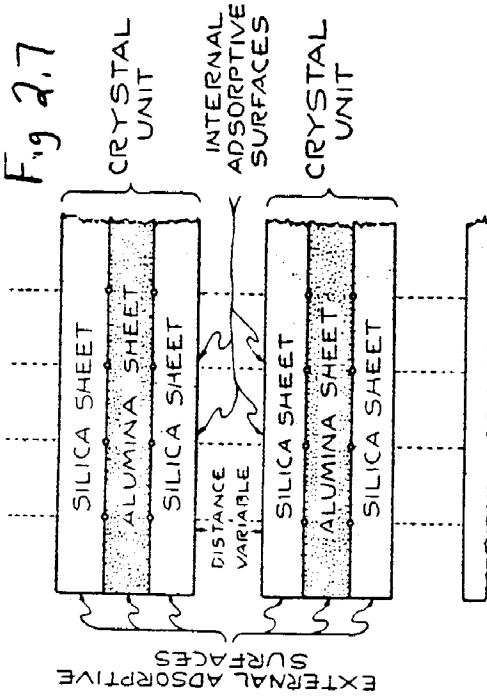


Figure 4.5. A schematic representation of the lattice structure that characterizes montmorillonite crystals. This is an edge-wise view of two of the innumerable units that make up a crystal of this clay. Each crystal unit is composed of two sheets of silica and one of alumina (2 to 1 type of lattice) tightly bound together by mutually shared oxygen atoms (represented by small circles). The respective crystal units in turn are loosely bound to one another by weak oxygen linkages (represented by dots) which allow a ready and comparatively wide expansion of the lattice (quite in contrast to kaolinite). This bellows-like spread of the lattice insures a very high internal adsorption of water and cations much greater than that ascribed to the external surfaces.

Illite has the same general structural organization as does montmorillonite except in respect to the linkages between the crystal units. Here potassium atoms supply additional connecting linkages between the crystal units, thus supplementing the oxygen bonding. These potassium linkages lessen sharply the expansion that the illite crystals are able to exhibit. As a result, the adsorptive capacity of this clay is considerably lower than that of montmorillonite. Illite, nevertheless, exceeds kaolinite in this respect.

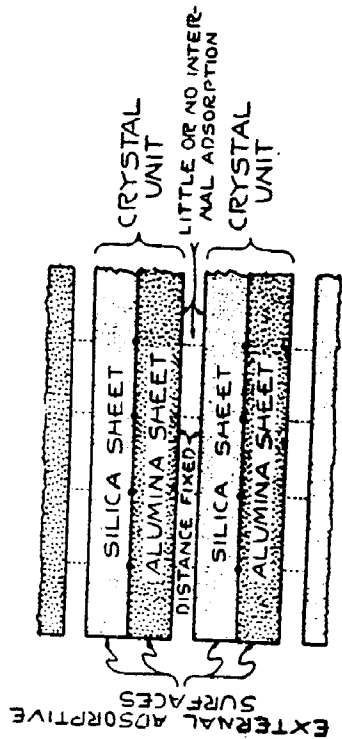


Figure 4.4. A schematic diagram showing the lattice structure characteristic of kaolinitic crystals. The section is a vertical one and gives an edge-wise view of two of the innumerable units that make up a crystal of this clay. Each of the crystal units is composed of one silica sheet and one alumina sheet (1 to 1 type of lattice) bonded very tightly by mutually shared oxygen atoms (represented by small circles). The respective crystal units are, in turn, bonded to each other rather tightly by an oxygen-hydroxyl linkage (denoted by dots) thereby giving a restricted and non-expanding lattice. As a result, ions as well as water molecules penetrate

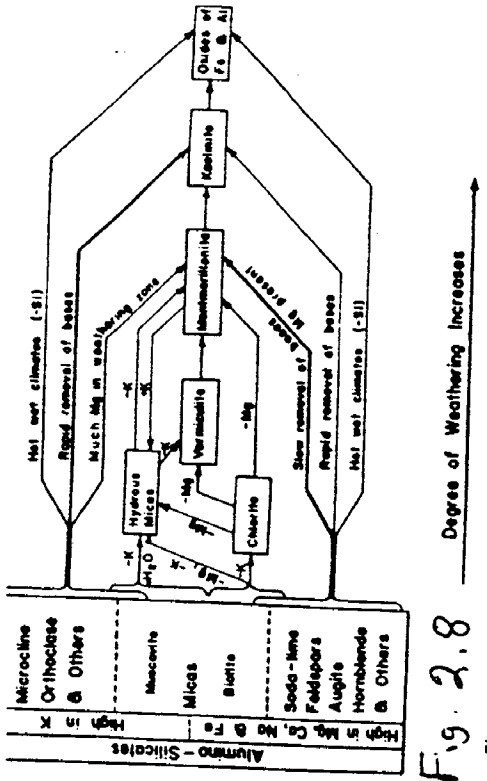


Figure 4.6. Diagram showing the general conditions for the formation of the various silicate clays and the oxides of iron and aluminum. In each case, genesis is accompanied by the removal of soluble elements such as K, Na, Ca, and Mg.

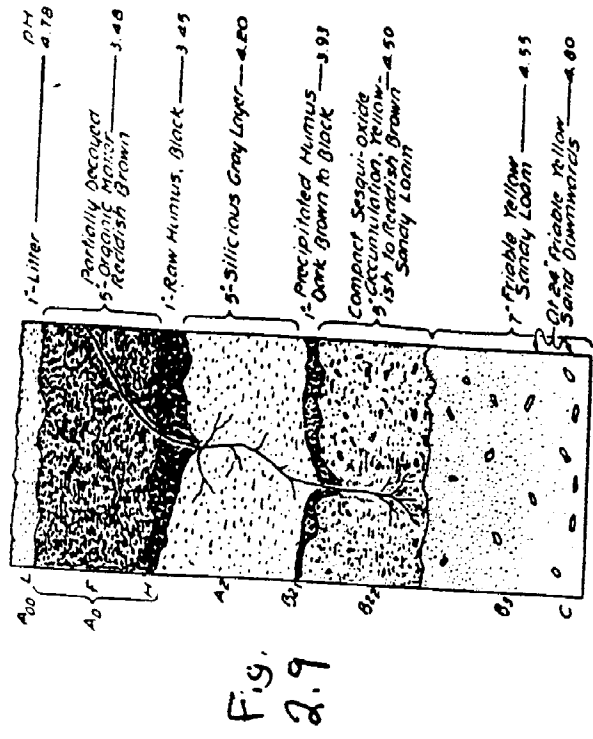


Figure 19.4. A well-developed podzol profile at White Lake Lodge, New York, on the southwestern edge of the Adirondack Mountains. The soil is very loam, furnished with birch, hemlock, and spruce. Note the thickness of the organic layers (minor or difficult to see) and the marked acidity of the whole.

TABLE 2-1: Vegetation, Climate and Soils of the Major Biomes

<u>BIOOME</u>	<u>VEGETATION</u>	<u>CLIMATE</u>	<u>SOILS</u>
I. Equatorial	Evergreen Broadleaf Forest	Rainy and hot year-round	Latosols
II. Tropical	Deciduous Broadleaf Forest	Summer rain - winter drought, hot year-round	Red Clays (lateritic)
III. Subtropical	Desert Vegetation or Barren	Low to extremely low rainfall, mild to hot	Red desert or undeveloped
IV. Mediterranean	Sclerophyll Shrublands	Winter rain - summer drought, mild winters	Unleached noncalcic brown soils
V. Warm-temperate	Evergreen Broadleaf and Needleleaf Forests	Year-round rain, mild winters	Red and yellow podzols
VI. Temperate	Deciduous Broadleaf Forests	Year-round rain, short-cold winters	Grey brown podzols
VII. Arid-temperate	Grasslands (Steppe) or Desert Shrublands	Semi-arid to arid, mild to cold winters	Chernozem, chestnut, grey desert soils
VIII. Cold-temperate (Boreal)	Evergreen and Deciduous Needleleaf Forests	Summer rain, long-cold to extremely cold winters	Podzols
IX. Arctic/Antarctic	Low, Herbaceous Plants (Tundra)	Ample rain, very short summer growing season	Permafrost, tundra soils

Discussion Questions

1. Why is it necessary to have separate environmental and historical hypotheses in biogeography? Are these hypotheses competing, complementary or both?
2. Why is climate the single most important set of physical factors in biogeography?
3. Why are vegetation belts on mountains usually inclined in the direction of prevailing winds?