Environmental Studies 30 -- The Global Ecosystem
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LECTURE 3: Principles of Biotic Adaptation

Purpose: We have seen in the previous two lectures that there is a strong correspondence between biomes and climates (and some other basic environmental variables). In order to understand why this correlation occurs, it is necessary to understand how plants and animals adapt to different environmental regimes. We will begin with the most general principles of population and community evolution and then consider the adaptive syndromes that have the most profound effect on the structure of biomes.

General Mechanisms: There are two classes of mechanisms that biologists think can account for all of the adaptive responses to the environment that can be observed in natural communities: the evolution of populations by natural selection and the evolution of communities by competitive exclusion.

I. Evolution by Natural Selection.

The Darwinian mechanism of natural selection is a very simple principle at the most general level, although complex in detail (Thomas Huxley is supposed to have exclaimed upon hearing Darwin describe it to him, "How stupid not to have thought of that!"). Darwin's reasoning was that 1) organisms possess heritable variations, 2) are forced to compete for scarce resources, and 3) that different variants are unlikely to be equally successful in competition under given conditions. The consequence should be a selective reproduction of these variants best able to compete. Darwin's principle, supplemented by a detailed knowledge of genetics, provides a very satisfactory account of the development of adaptations by populations of plants and animals.

II. Evolution by Competitive Exclusion

Darwinian evolution is a relatively slow process, whereas environments often change relatively rapidly. Usually communities respond to changing conditions by a change in their species composition before much Darwinian evolution occurs. This community process is generally called succession. Succession is governed by the competitive exclusion principle which is somewhat analogous to natural selection. It states that if two species populations are adapted to do more or less the same thing in a community, they will be forced to compete for scarce resources. Because generally, under given environmental conditions, one will be a little better at exploiting this scarce resource than the other, the superior competitor will come to prevail.

A community can be viewed as a system having many more potential entrants than successful competitors. If environmental conditions change, new species will be able to invade the community and displace some of the existing ones. As a rule, populations are physiologically capable of growing under a far wider set of conditions than they are actually found in nature because of competitive exclusion. You are all familiar with garden plants that grow perfectly well far outside their native habitats but fail to naturalize because they cannot compete with native plants. Figure 3.1 illustrates examples of relationships between physiological and ecological optima.

The relative amount of Darwinian evolution and succession during episodes of major environmental change is poorly understood. The Pleistocene (the last 2 million years) has been an extraordinarily turbulent period in the earth's history with much more rapidly changing climates than the norm. Some plants and animals responded to this environmental change with vigorous Darwinian evolution. This is especially obvious in herbaceous plants, some woody plants (e.g. the manzanitas and wild lilacs of California), and mammals. Other groups have responded almost completely by successional shifts in their distribution and in the kinds of communities they inhabit. The latter group includes most woody vegetation, especially trees which have hardly evolved at all for 20 to 30 million years, and beetles among which the same species are found throughout the Pleistocene.

Major Plant Adaptations

The adaptations that are especially important in explaining the form of biomes involve adaptations to water and temperature stress. Secondarily, competition for light and mineral nutrients plays a significant role. Perhaps the most convenient subdivision of adaptations is into anatomical, phenological and physiological responses.

I. Anatomical adaptation

A. Life Form

Life form may be simply classified as tree, shrub, and herb, although the shrub and herb categories are usually much subdivided into finer groups by ecologists. Grass and non-grass (forb) species are usually distinguished when discussing herbaceous plants for example. In general, life forms are limited by water availability, controlled by aridity or freezing temperatures. As water availability decreases, different life forms dominate communities. Along gradients of increasing aridity the usual pattern is for trees, then grasses, then shrubs to be most important in the vegetation. With the presence of permafrost soils, trees are replaced by low herbaceous plants.

A plant can have its buds or other resting stages in more or less protected positions during its dormant season, if any. Raunkiaer's classification with its peculiar terminology is commonly applied (see Figure 3.2 [from slide in lecture]). Annual herbs are dormant as seeds, the most resistant kind of resting adaptation, and are common where drought is the most serious environmental stress, as seeds require no water at all. Plants which experience relatively mild cold and drought stress carry their buds at the end of branches, exposed to the force of the weather as in trees and shrubs. Plants in more severely cold climates may have their buds more or less buried in soil or beneath snow protected from the wind and extreme cold, as in the bulb and corm forming perennial herbs.

Unexpectedly, cold climates stress plants by having both the potential to freeze and to desiccate bud tissue -- exposed dormant buds have a small but significant water loss which cannot be replaced from the roots if the water translocation system is frozen. On the other hand, cold climates with short, cool growing seasons put a premium on rapid deployment of photosynthetic tissue during the growth season, so trees persist despite their handicaps until the climate is quite cold indeed. A variety of tradeoffs are involved in life form adaptation, which we will examine in detail for each biome.

B. Leaf form

Leaves display the plant's photosynthetic tissue to light, and for this purpose broad, thin leaves with a minimum of support and protective tissue are ideal. However, such leaves lose water very rapidly, and are easily eaten by herbivores. Leaves are variously toughened to slow the rate of transpiration. Small size, light color, hairy surface, and vertical orientation are also among many leaf adaptations plants in arid environments may have.

Typically, different compromises are reached in different environments. Many trees and shrubs even have different kinds of leaves on the same plant: for example, thick, small leaves in the upper story where heat load is high and thinner ones deeper in the canopy where light levels fall and humidity increases. The thin shade leaves spread out the photosynthetic tissue to make best use of light, but high surface area and a thin covering of water proof cuticle leads to high water loss. Sun leaves are thicker and have a thick cuticle. They are more resistant to water loss, but more expensive to make and are less efficient at photosynthesis because cells on the upper surface partly shade cells on the bottom of a leaf. Alternatively, the toughest leaves may be near the ground where they are subject to browsing. The term <u>sclerophyll</u> is applied to thick, hardened leaves. Such leaves are common in California vegetation because they resist desiccation during the summer drought.

C. Root architecture

Root systems are described as <u>intensive</u> and <u>extensive</u>. Intensive roots fill a small volume of soil with fine roots, as in many grasses. This system is well adapted to exploiting small amounts of rainfall that do not penetrate very deeply into the soil. Extensive root systems invade a large volume of soil, but not very densely. Such roots are well adapted to very dry and to wet conditions. We will see why later.

II. Phenological adaptations

"Phenology" refers to adaptations to climatic rhythms, particularly the seasonality of temperature, rainfall, and light.

A. Deciduous leaves

Under conditions of cold temperature or drought stress (and the two have similar effects on plant tissue), leaves can be shed, at some considerable cost of lost nutrients and energy. Moreover, leaves take time and energy to regrow. The deciduous habit predominates in two widely separated biomes, the **Tropical Deciduous Forest biome (due to drought)** and the **Temperate Deciduous Forest biome (due to cold)**. In addition, communities dominated by deciduous plants occur in some deserts and in extremely cold parts of boreal forests.

B. Flowering and Fruiting

Plants must time reproduction to the climatic cycle to make best use of the growing season. Moreover, a large portion of flowering plants depend upon animals for pollination and seed dispersal and must adjust their flowering and seeding to the habits of the animals. The color of flowers often reflects a pollination strategy; flowers visited by insects are generally blue or yellow, those visited by hummingbirds are usually red. You may have noticed the inordinate attention hummingbirds pay to the unlikeliest red objects, such as cars and shirts on the clothesline.

Biome-scale patterns are evident. For example, evergreen tropical forests have mostly aperiodic flowering and high diversity of these forests makes individuals of the same species rather rare (and thus far apart). For this reason, many plants in the deep tropics depend on strong-flying insects, birds and bats for pollination, and have large colorful flowers to attract them.

III. Physiological adaptations

A. Homeohydric and poikilohydric plants

To function, the protoplasm of plants must contain a lot of water. Many of the physiological and anatomical adaptations of terrestrial plants exist to maintain the hydrature of protoplasm. Poikilohydric plants, the so-called **"lower plants,"** are dependent on atmospheric humidity to maintain hydrature. These include the terrestrial algae, lichens, mosses and so forth. These plants have weak or nonexistent organs to transport water from the ground to leaves.

Homeohydric plants, including the ferns and seed plants (conifers and flowering plants) have elaborate mechanisms to maintain moisture in their photosynthetic tissues when the humidity of the air is far less than saturated, which is the usual case. Homeohydric plants have a large vacuole in each leaf cell full of water and dissolved substances to buffer their internal environment and to exert an osmotic potential of several atmospheres to keep the cells full of water. Osmotic potential in root cells also serves to suck water out of the ground.

A leaf's water is lost to the atmosphere by evaporation through controllable pores called stomata (stoma, singular). This loss of water is called transpiration. A plant can control water loss by closing the stomata, but the stomata need to be open for carbon dioxide needed for photosynthesis to enter the leaf. If water is lost faster than it can be taken up by the roots, the leaf protoplasm dehydrates, photosynthesis stops, and the plant wilts (the turgor pressure of cell water that gives structural support is lost). **Figure 3.3** (from slide in lecture) shows a schematic diagram of a plant to illustrate the parts involved in this process.

As the osmotic potential of a plant's cells reaches dangerous levels, a series of feedback responses is triggered. In the short run, the stomata simply close. Over the longer term, new leaves may have different morphologies (more sclerophyllous leaves are produced) or the plant may shed leaves. Few plants, even in deserts, can tolerate osmotic potentials much above 30 atmospheres. Only plants that live in salty soils (halophytes) have higher osmotic potentials (generated by the uptake of inorganic salts) and these plants are an exception. In such plants, high osmotic potentials are necessary to remove water from the salty soil. Such plants can usually be recognized by their succulent leaves; you may be familiar with Salicornia, pickleweed, of coastal salt marshes and inland salt pans.

B. Hardiness

To resist cold, especially freezing, plants must undergo a physiological process of hardening in advance. Plants that survive quite severe winters can be killed if they are subjected to winter temperatures during periods of active growth.

C. C-3, C-4, and CAM Plants

Recently, it has been discovered that plants have three different photosynthetic pathways that differ substantially in how CO_2 is taken up. The C-3 system characterizes most plants but it obliges the plant to take up CO_2 while photosynthesizing during the daytime when water stress is greatest. Some plants in arid and semi-arid areas have C-4 photosynthesis which like the C-3 system requires CO_2 uptake during the day, but is much more proficient in its ability to take CO_2 out of the air so the plant's stomata do not need to be open as much and water loss is limited. In addition, C-4 plants are able to have greater photosynthesis than C-3 plants at high light intensities common in arid regions. Some other plants in desert areas have CAM photosynthesis, which permits the uptake and storage of CO_2 during the night. These plants can photosynthesize during the day with stomata closed, economizing on water.

D. **Secondary Plant Compounds**

Plants produce a wide variety of substances of no obvious use in growth and reproduction. These include tannins, alkaloids (such as caffeine), cyanogenic substances, essential oils and so forth. Most of these substances appear to be defenses against herbivores, e.g., tannins, common in acorns, complex proteins which makes them undigestable, encouraging most animals to avoid them. However, a few animals typically defeat the defenses of each plant. Evolutionists picture the coevolution of herbivores and their victims as a kind of arms race of adaptation followed by counter-adaptation. Plants often seem to calibrate the dose of secondary compounds in fruits to attract animals that effectively spread them, but discourage "thieves" that are inefficient dispersers, or who digest too many seeds. Humans make a wide variety of uses of secondary plant compounds (spices and drugs, for example). Some leaves are also defended from herbivore attack because they are very low in protein and other essential nutrients. Eucalyptus defends itself from insect attack in this way; the insects cannot eat enough leaf mass to grow when leaves are mature. Crop plants are often more susceptible to insect attack because we select them for maximum production at the expense of secondary compounds and because we find these compounds noxious.

Major Animal Adaptations

There is less unity in animal adaptations than in plant adaptations. Animals do a wider variety of things in ecosystems than do plants. If we confine the discussion mainly to herbivores, some simplifying generalizations are possible.

I. Body Size

Large size is a general advantage to herbivores for avoiding predation and for metabolic efficiency. Its penalties include an inability to specialize on the smallest bits of tender plant tissue and being stuck on the ground. Hence large herbivores are largely confined to grassland and shrub biomes, leaving the forests to small herbivores.

II. Cellulose Use

Most of the energy available in plant tissue is in the form of cellulose, which animals cannot digest directly. Some form of microbial symbiont is required. The most efficient herbivores are the ruminants and other herbivores that have anatomical "reaction vessels" for microbial digestion of cellulose. Few small, tree dwelling herbivores have solved this problem effectively, largely confining forest herbivores to fruit and seed eating, and specialization on the softer, more nutritious parts of the plants, as in most insects. You may have noticed that, except in grasslands, herbivore damage tends to be confined to young leaves and tender shoots. Mature leaves usually do not show much damage.

III. Water and Temperature Economy

Animals have problems with cold and drought stress similar to plants, but their adaptations are different. Behavioral adaptations play a major role -- migration, use of shade and burrows, torpor and hibernation, and so forth. Color is sometimes used to regulate temperature as in black birds and insects. Physiological mechanisms are also common, e.g., sweating or panting to lose heat, or adapting to severe water economy and urine-concentrating kidneys to avoid the need to drink water, as in desert rodents.

IV. Homeothermy and Poikilothermy

These two physiological types of thermal regulation have very different metabolic energy requirements. Homeotherms operate at high energy levels, often making them superior food gatherers, if rather inefficient converters of what they eat. Poikilotherms need much less energy to support a unit of biomass, but often cannot compete with the speedier homeotherms. Poikilotherms dominate in the niches for small animals; small size imposes high heat loss burdens for homeotherms. Insects dominate most of these niches in the terrestrial realm. Poikilotherms also compete well in warm, very low productivity environments like deserts where a slow metabolic rate is a great advantage when food supplies are minimal. Thus reptiles do best in deserts.

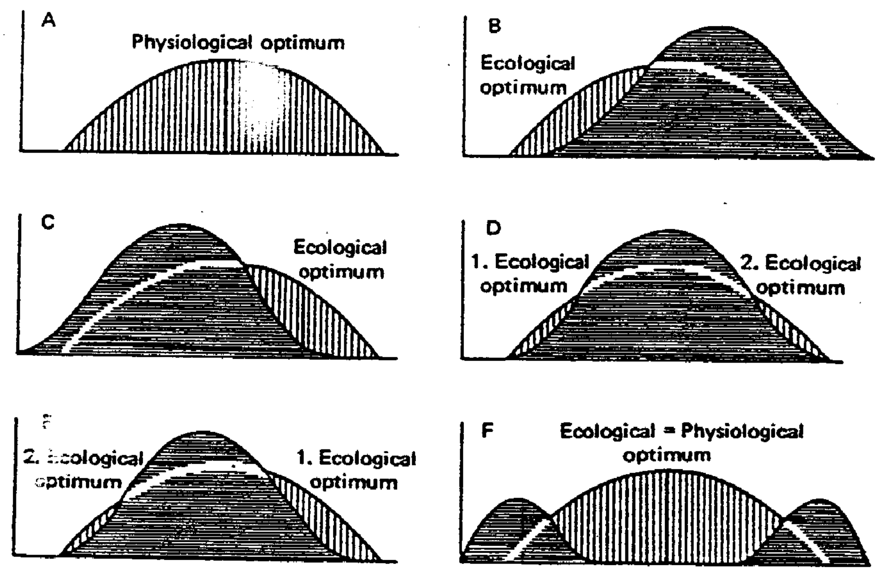

Fig. 3. Growth curves (vertical shading) of one species without (A) or under pressure due to competition (B — F, horizontal shading). Ordinate: Growth intensity and production of organic matter; abscissa: variable habitat factors.

Figure 3.1

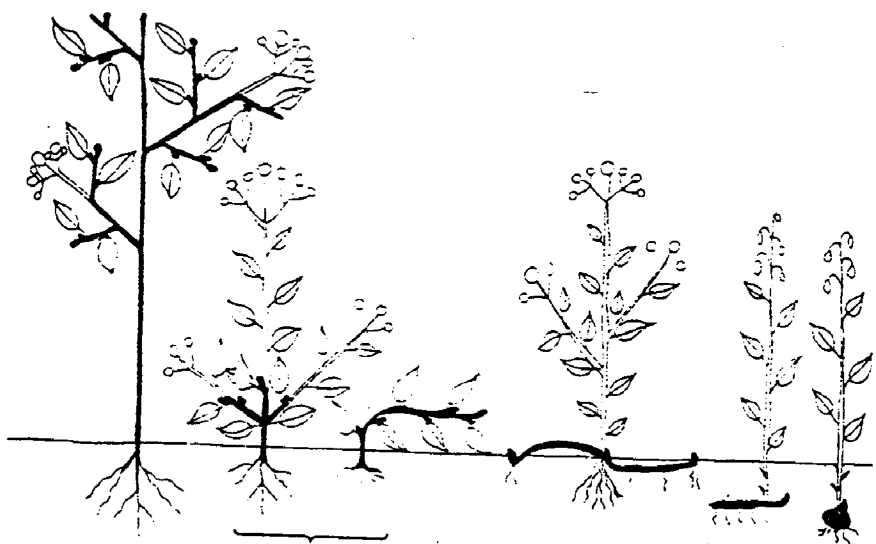

Figure 12-4. Diagrammatic representation of Raunkiaer's life forms. Unshaded parts of the plant die during unfavorable seasons, while the solid black portions persist and give rise to the following year's growth. Proceeding from left to right, the buds are progressively better protected (after Raunkiaer 1937).

Figure 3.2

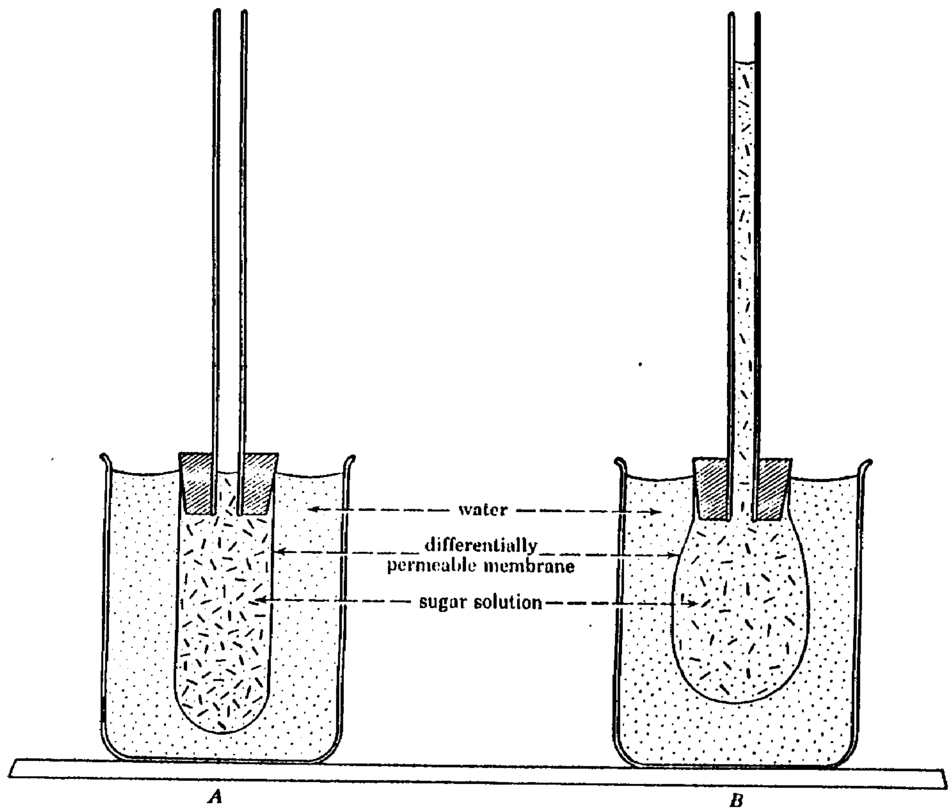

Diagram of osmometer and diffusion through a differentially permeable membrane. A, before osmosis has occurred; B, after osmosis.

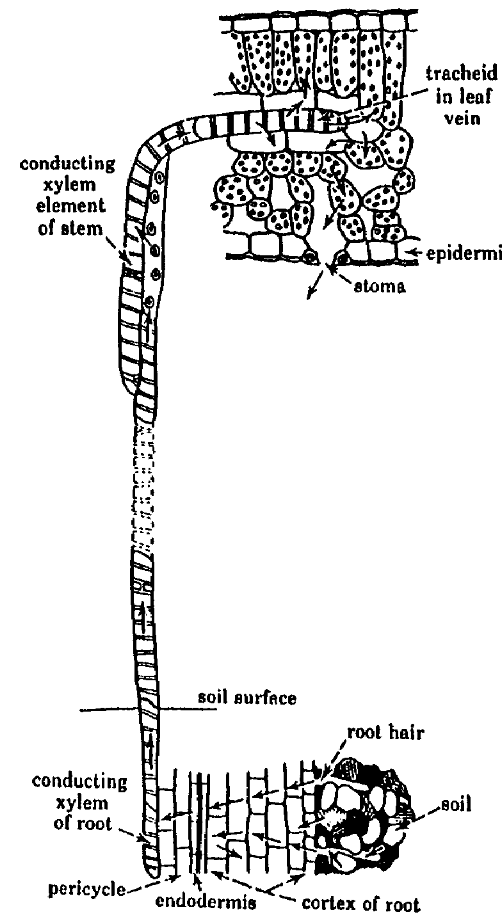

Diagram showing entry of water from the soil to the root hair and its path of movement through the plant to parenchyma leaf cells, thence escaping as water vapor into intercellular spaces, from whence it passes to the atmosphere, mainly through stomata.

Figure 3.3

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Lecture 3: Discussion Questions

1. Compare the evolutionary processes of natural selection and competitive exclusion. Why do you suppose different groups of organisms seem to respond very differently to these processes?

2. In what way is poikilohydry and homeohydry in plants analagous to poikilothermy and homeothermy in animals?

3. Why are plant adaptations more closely reflective of climatic conditions than animal adaptations?