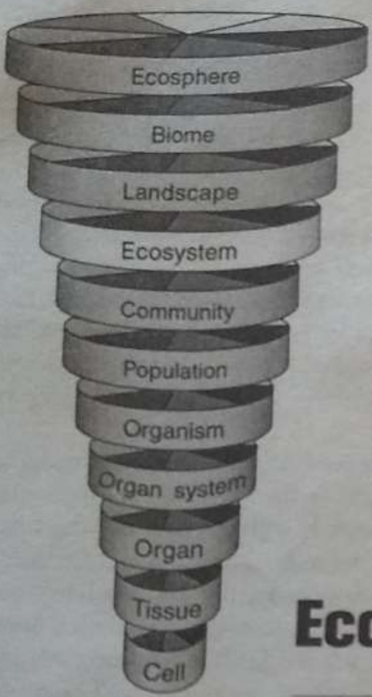
8



Ecosystem Development

1 Strategy of Ecosystem Development
2 Concept of the Climax
3 Evolution of the Biosphere
4 Microevolution Compared with Macroevolution, Artificial Selection, and Genetic Engineering
5 Relevance of Ecosystem Development to Human Ecology

1 Strategy of Ecosystem Development

Statement

Ecosystem development, more often known as **ecological succession**, involves changes in energy partitioning, species structure, and community processes over time. When not interrupted by outside forces, succession is reasonably directional and, therefore, predictable. It results from the modification of the physical environment by the community and from competition-coexistence interactions at the population level—that is, succession is community controlled even though the physical environment determines the pattern and the rate of change and often limits the extent of development. If successional changes are largely determined by internal interactions, the process is known as **autogenic** ("self-generated") **succession.** If outside forces in the input environment (such as storms and fire) regularly affect or control change, there is **allogenic** ("externally generated") **succession**.

When new territory is opened or becomes available for colonization (for example, after a volcanic lava flow, in an abandoned crop field, or in a new water impoundment), autogenic succession usually begins with an unbalanced community metabolism, where gross production, P, is either greater than or less than community respiration, R, and proceeds toward a more balanced condition, where $P = R$. The ratio of biomass to production (B/P) increases during succession until a stabilized ecosystem is achieved, in which a maximum of biomass (or high information content) and symbiotic function between organisms are maintained per unit of available energy flow.

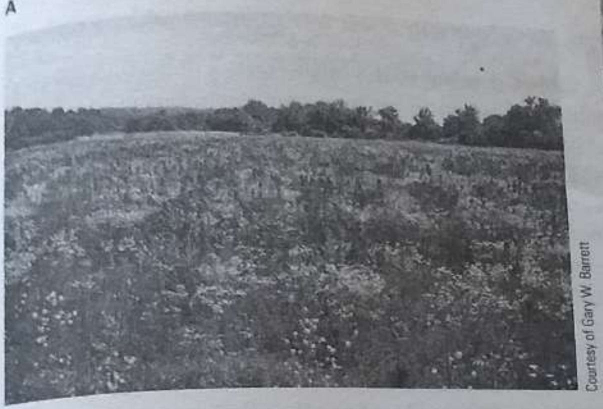
The whole sequence of communities that replace one another in a given area is termed the **sere;** the relatively transitory communities during succession are variously termed **seral stages** or **developmental stages.** The initial seral stage is termed the **pioneer stage** and is characterized by early successional *pioneer plant species* (typically annuals), which exhibit high rates of growth, small size, short life span, and production of a great number of easily dispersed seeds. The terminal stage or mature, stabilized system is the **climax**, which persists, in theory, until affected by major disturbances. Succession beginning with $P > R$ is **autotrophic succession**, contrasting with **heterotrophic succession**, which begins with $P < R$. Succession on a previously unoccupied substrate (such as a new lava flow) is termed **primary succession,** whereas succession starting on a site previously occupied by another community (such as a clear-cut forest or abandoned crop field) is known as **secondary succession.**

It is to be emphasized that the mature or *climax stage* is best recognized by the state of the community metabolism, $P = R$, rather than by species composition, which varies widely with topography, microclimate, and disturbance. Even though, as already emphasized, ecosystems are not "superorganisms," their development has many parallels in the developmental biology of individual organisms and in the development of human societies, in that they progress from "youth" toward "maturity."

Explanation and Examples

Descriptive studies of succession on sand dunes, grasslands, forests, marine shores, or other sites—and more recent functional considerations—have led to a partial understanding of the developmental process and generated a number of theories about

A



B

Figure 8-1. Photographs of (A) a young old-field community located in Union County, Indiana, and (B) a sugar maple tree. The maple tree is in a mature beech-maple climax forest in Hueston Woods State Park near Oxford, Ohio. The boiled concentrated sap of the sugar maple (*Acer saccharum*) is the commercial source of maple sugar and syrup.

its cause. H. T. Odum and Pinkerton (1955), building on the Lotka law of the maximum energy in biological systems (Lotka 1925), were the first to point out that succession involves a functional shift in energy flows, with increasing energy relegated to maintenance (respiration) as the standing crop of biomass and organic matter accumulates. Margalef (1963b, 1968) documented this bioenergetic basis for succession and extended the concept. The role that population interactions play in shaping the course of *species replacement*—a characteristic feature of ecological succession—was discussed during the 1970s and 1980s (see Connell and Slayter 1977; McIntosh 1980; for reviews). Much of the controversy considering these reviews is reduced if the stages of development are based on energetics rather than on species composition, as noted in the Statement.

Changes that may be expected to occur in major structural and functional characteristics of autogenic development are listed in Table 8-1, in which 24 attributes of ecological systems are grouped for convenience of discussion under four headings. Trends contrast the situation in early and in late development. Figure 8-1A illustrates a young ecosystem (old-field community) in the early stage of development and Figure 8-1B shows a mature ecosystem (beech-maple forest) in the late stage of development. The degree of absolute change, the rate of change, and the time required to reach a mature status may vary not only with different climatic and physiographic conditions but also with different attributes of the ecosystem in the same physical environment. When good data are available, rate-of-change curves are usually convex, with changes occurring most rapidly at the beginning of development, but bimodal or cyclic patterns may also occur.

The trends listed in Table 8-1 represent those that are observed to occur when internal, autogenic processes predominate. The effect of external, allogenic disturbances may reverse or otherwise alter these developmental trends, as will be discussed later.

Bioenergetics of Ecosystem Development

The first seven attributes in Table 8-1 relate to the bioenergetics of the ecosystem. In the early stages of autotrophic succession in an inorganic environment, the rate of primary production or total (gross) photosynthesis, P, exceeds the rate of community respiration, R, so that the P/R ratio is typically greater than 1. The P/R ratio is less than 1 in the special case of an organic environment (such as a sewage pond), so succession in such cases is termed *heterotrophic*, because bacteria and other heterotrophs are the first to colonize the environment. In both cases, however, the theory is that P/R approaches 1 as succession proceeds. In other words, the energy fixed by production tends to be balanced by the energy cost of maintenance (total community respiration) in the mature or climax ecosystem. The P/R ratio, therefore, is a functional index of the *relative maturity* of the system.

As long as P exceeds R, organic matter and biomass, B, will accumulate in the system, with the result that the ratios B/P, B/R, and B/E (where $E = P + R$) will increase (or conversely, the P/B ratio will decrease). Recall that these ratios were discussed in Chapter 3 in terms of the laws of thermodynamics. Theoretically, then, the amount of standing crop biomass supported by the available energy flow, E, increases to a maximum in the mature or climax stage. As a consequence, the net community production, or *yield*, in an annual cycle is large in the early stages and small or zero in mature stages.

A simplified systems (cybernetic) model is shown in Figure 8-2A, in which internal, autogenic processes are considered as inputs that are modified by periodic allogenic inputs. Figure 8-2B, an energy flow model, shows the basic change in energy partitioning between P and R mentioned earlier. As the organic structure builds up, more and more energy is required to maintain this structure and dissipate disorder, and so less energy is available for production. This shift in energy use has parallels in the development of human societies, and it greatly affects attitudes about how the environment is treated, as we shall see later in this chapter. Figure 8-2C is a summary of how the three main factors—production, respiration, and biomass—change over time.

Comparison of Succession in a Laboratory Microcosm and a Forest

One may observe bioenergetic changes by initiating succession in experimental laboratory microecosystems of the type derived from natural systems, as described in Chapter 2. In Figure 8-3, the general pattern of a 100-day autotrophic succession in a typical flask-microcosm experiment, based on data from Cooke (1967), is compared with a hypothetical model of a 100-year forest succession presented by Kira and Shidei (1967).