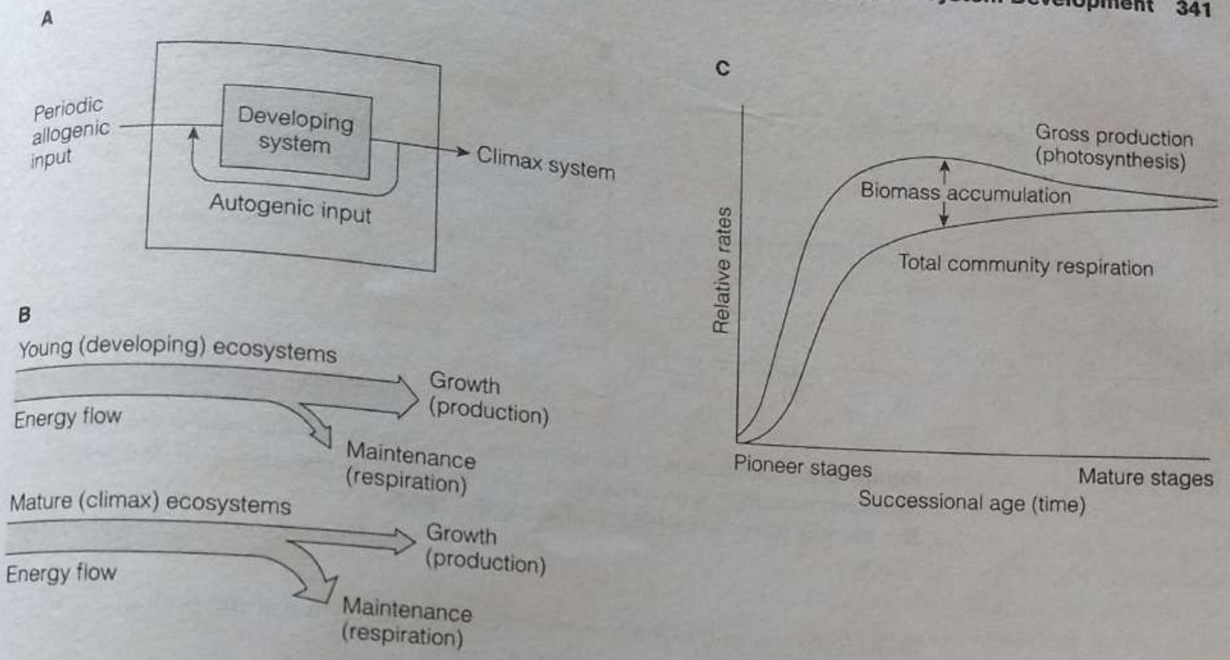


Figure 8-2. Ecosystem development models. (A) Systems (cybernetic) model; (B) Energy flow model; and (C) Production/respiration (*P*/*R*) maintenance model.

During the first 40 to 60 days in the microcosm experiment, daytime net production, *P*, exceeds nighttime respiration, *R*, so that biomass, *B*, accumulates in the system. After an early "bloom" at about 30 days, both rates decline and become approximately equal at 60 to 80 days. The *B*/*P* ratio, in terms of grams of carbon supported per gram of daily carbon production, increases from less than 20 to more than 100 as the steady state is reached. Not only are autotrophic and heterotrophic metabolism balanced in the climax stage, but also a large organic structure is supported by small daily production and respiration rates. The relative abundance of species also changes, so that different kinds of bacteria, algae, protozoa, and small crustaceans dominate at the end than at the beginning of the 100-day succession (Gorden et al. 1969).

Direct projection from small laboratory microcosms to natural systems is not possible, because the former are limited to small organisms with simple life histories and, of necessity, have a reduced species and chemical diversity. Nevertheless, the same basic trends seen in the microcosm are characteristic of succession on land and in large bodies of water. Seasonal succession also often follows the same pattern—an early seasonal bloom, characterized by rapid growth of a few dominant species, followed later in the season by the development of high *B*/*P* ratios, increased diversity, and a relatively steady, although temporary, state in terms of *P* and *R*. Open systems may not experience a decline in total or gross productivity at maturity, as the space-limited microcosms do, but the general pattern of bioenergetic change in microcosms seems to mimic nature quite well.

It is also interesting to note that peak net primary production (P_N), which represents the maximum yield possible, comes at 30 days in the microcosm and at 30 years

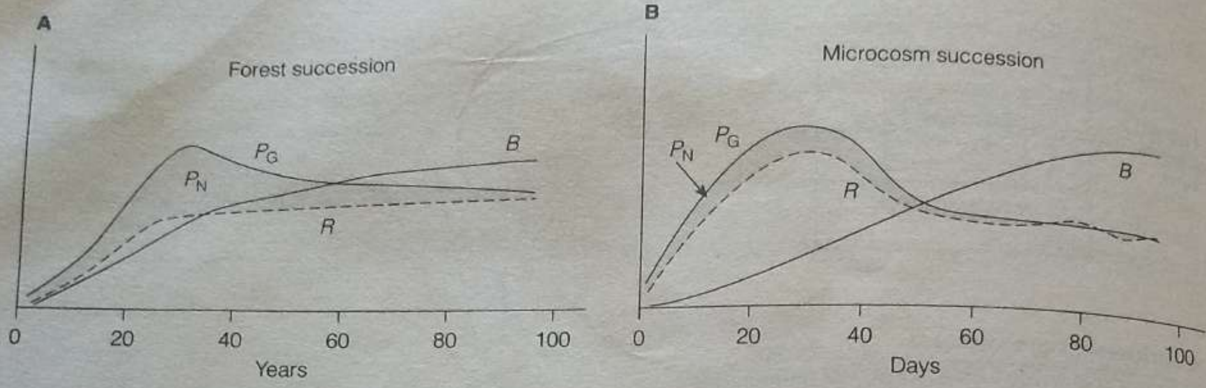


Figure 8-3. Comparison of the energetics of ecosystem development in (A) forests and (B) microcosms. P_G = gross production; P_N = net production (shaded area); R = respiration; B = biomass (after Cooke 1967; Kira and Shidei 1967).

in the forest. Short-rotation forestry is based on harvesting at the peak of P_N, which on many sites comes between 20 and 40 years.

Allogenic Compared with Autogenic Influences

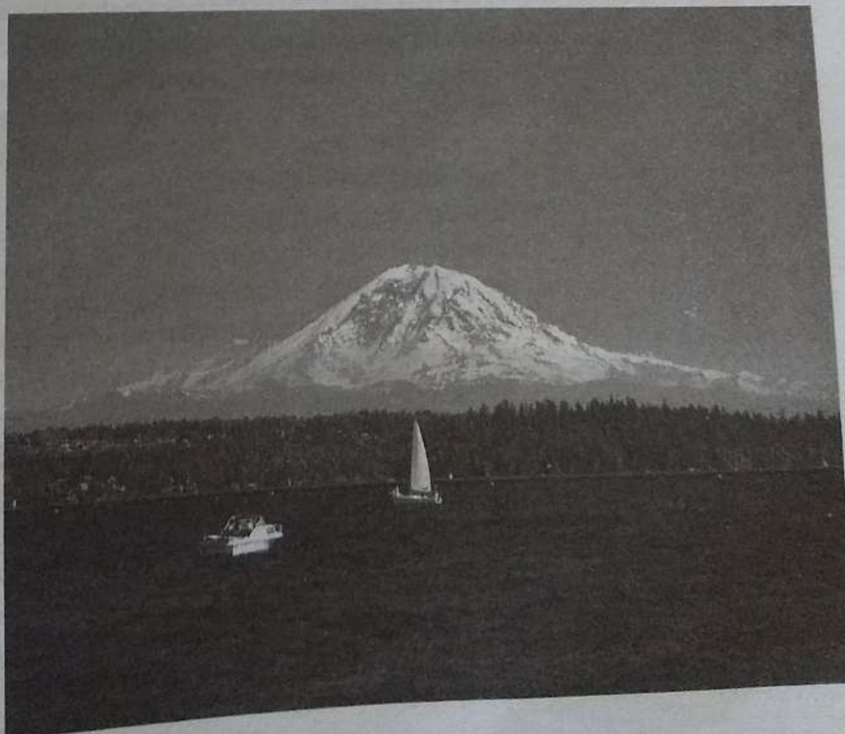
Imported materials or energy, geological forces, storms, and human disturbances can and do alter, arrest, or reverse the trends shown in Table 8-1. For example, eutrophication of a lake, whether natural or cultural, results when nutrients and soil enter the lake from outside—that is. from the watershed. This is equivalent to adding nutrients to a laboratory microecosystem, or fertilizing a field; the system is "set back" in successional terms, to younger, "bloom" states. Brewer et al. (1994) noted, for example, that nutrient enrichment in an old-field community for 11 years resulted in a system that continued to be dominated by annual plant species, rather than the perennials that dominated mature (control) plots. *Allogenic succession* of this type is, in many aspects, the reverse of autogenic succession. When the effect of allogenic processes consistently exceeds that of autogenic ones, as in the case of many ponds and small lakes, the ecosystem not only cannot stabilize but also may become "extinct" by filling up with organic matter and sediments and becoming a bog or a terrestrial community. Such is the ultimate fate of human-made lakes subjected to accelerated erosion within the watershed.

Lakes can and do progress to a more *oligotrophic* (less enriched) condition when nutrient input from the watershed slows or ceases. Thus, there is hope that the troublesome cultural eutrophication, which reduces water quality and shortens the life of the water body, can be reversed if the inflow of nutrients from the watershed can be greatly reduced. An example is the recovery of Lake Washington (Fig. 8-4), located in Seattle, described by W. T. Edmondson (1968, 1970). For 20 years, treated, nutrient-rich sewage was discharged into the lake, which became increasingly turbid and full of nuisance algal blooms. As a result of public outcry, sewage effluent was diverted from the lake, which quickly returned to a more oligotrophic condition (clearer water and no blooms).

The interaction of external and internal forces can be summarized in a general systems model (Fig. 8-2A) of the form first introduced in Figure 1-5. Autogenic forces are depicted as internal input or feedback, which, in theory, tends to drive the system toward some sort of equilibrium state. Allogenic forces are depicted as periodic, external input disturbances, which set back or otherwise alter the developmental trajectory.

Where ecosystem development takes a long time to run its course—as in a forest development starting from bare ground—periodic disturbances will affect the successional process, especially in the variable environments of the temperate zones. Oliver and Stephens (1977) reported on a study of the vegetational history of a small area of the Harvard Forest located in Massachusetts. Fourteen natural and human-caused disturbances of varying magnitudes occurred, at irregular intervals, between 1803 and 1952. There was also evidence of two hurricanes and a fire before 1803. Small disturbances did not bring in new species of trees but often allowed species already in the understory, such as black birch (*Betula lenta*), red maple (*Acer rubrum*), and hemlock (*Tsuga canadensis*), to emerge into the canopy. Large-scale disturbances (such as a hurricane or a large fire) created openings, into which early successional species (such as pin cherry, *Prunus pennsylvanica*) invaded, where a new age class developed from seeds or seedlings already present on or in the forest floor (northern red oak, *Quercus rubra*, was a species that often filled such openings and grew to canopy dominance after several decades). Replacement and succession in forest clearings has been termed **gap phase succession.** Oliver and Stephens concluded from their study that the composition of the forest in the 1970s was more the result of allogenic influences than of autogenic development. In a subsequent review paper, Oliver (1981) concluded that severity and frequency of disturbance are the major factors determining forest structure and species composition in many areas of North America. More recently, Dale et al. (2001) noted that climate change can affect forest structure and function by altering the frequency, intensity, duration, and timing of fire, drought, introduction of exotic species, and insect or pathogen outbreaks.

Figure 8-4. Lake Washington, Seattle, where W. T. Edmondson conducted his classic research in the field of restoration ecology.



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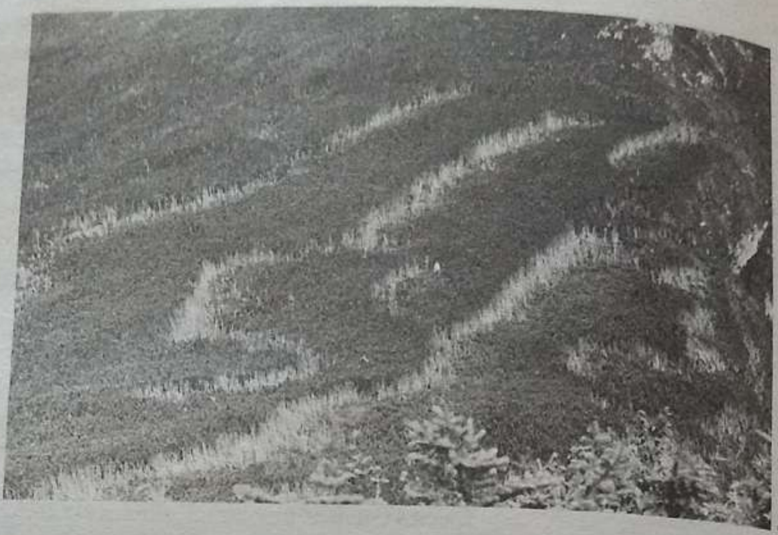

Figure 8-5. Wave-generated succession in a balsam fir forest. Bands of different shades represent successive waves of development (Sprugel and Bormann 1981).

Courtesy of D. G. Sprugel and F. H. Bormann

If disturbances are rhythmic (come at more or less regular intervals), either because of a cyclic input environment or because of periodicities in the community development itself, the ecosystem undergoes what can logically be termed **cyclic succession.** The historic 1988 fire in Yellowstone National Park, for example, appears to be a cyclic phenomenon, occurring every 280 to 350 years (Romme and Despain 1989; see the November 1989 issue of *BioScience* entitled "Fire Impact on Yellowstone" for details). The fire-chaparral vegetation cycle described previously (Chapter 5) is an example of a self-generated cyclic succession, because the accumulation of undecomposed litter builds up fuel for the periodic fires in the dry season.

Another example of cyclic succession is the *wave-generated succession* in balsam fir (*Abies balsamea*) forests at high altitudes in the northeastern United States (Sprugel and Bormann 1981). As trees reach their maximum height and density in the thin soils, they become vulnerable to strong winds that uproot and kill old trees, thereby starting a secondary succession. As shown in Figure 8-5, a series of bands of young, mature, and dead trees (the latter appearing as light-colored bands in the figure) cover the mountainside. Because of the continuous cyclic succession, the bands move as "waves" across the landscape in the general direction of the prevailing winds. At any one time, all stages of succession are present, providing a variety of habitats for animals and smaller plants. The whole mountainside constitutes a *cyclic climax* in equilibrium with the surrounding environment.

The natural pattern of alternating bands of young and mature stands suggests that strip or patch clear-cutting could prove to be a good commercial harvest procedure for large forested areas, because natural regeneration would be facilitated (thus avoiding expensive tree replanting), and soil and animal populations would be little disturbed compared with the disturbance in a massive clear-cut of the whole forest. Furthermore, mixtures of different successional stages provide an abundance of *edges* (see Chapter 2) that benefit many forms of wildlife.

Still another example of cyclic succession is the cycle of spruce and budworms (described in Chapter 6). In this case, the periodic disturbance is not a physical force but a herbivore that defoliates and kills older growth, thus bringing on a succession of young growth.