though the community began on a very dry and sterile sort of habitat, development eventually results in a closed canopy forest, moist and cool in contrast with the bare dunes. The deep, humus-rich soil, with earthworms and snails, contrasts with the dry sand that it replaced. Thus, the original, relatively inhospitable pile of sand is eventually transformed completely by the action of a succession of communities.

Succession on dunes in the early stages is often arrested when the wind piles up the sand over the plants, and the dune begins to move, entirely covering the vegetation in its path. This is an example of the arresting or reversing effect of allogenic perturbations discussed earlier in this section. Eventually, however, as the dune moves inland, it becomes stabilized, and pioneer grasses and trees again become established. Using carbon dating, Olson (1958) estimated that about 1000 years are required to reach a forest climax on the dunes of Lake Michigan—about five times longer than required for mature forest development starting from a more hospitable site, as seen in the next example.

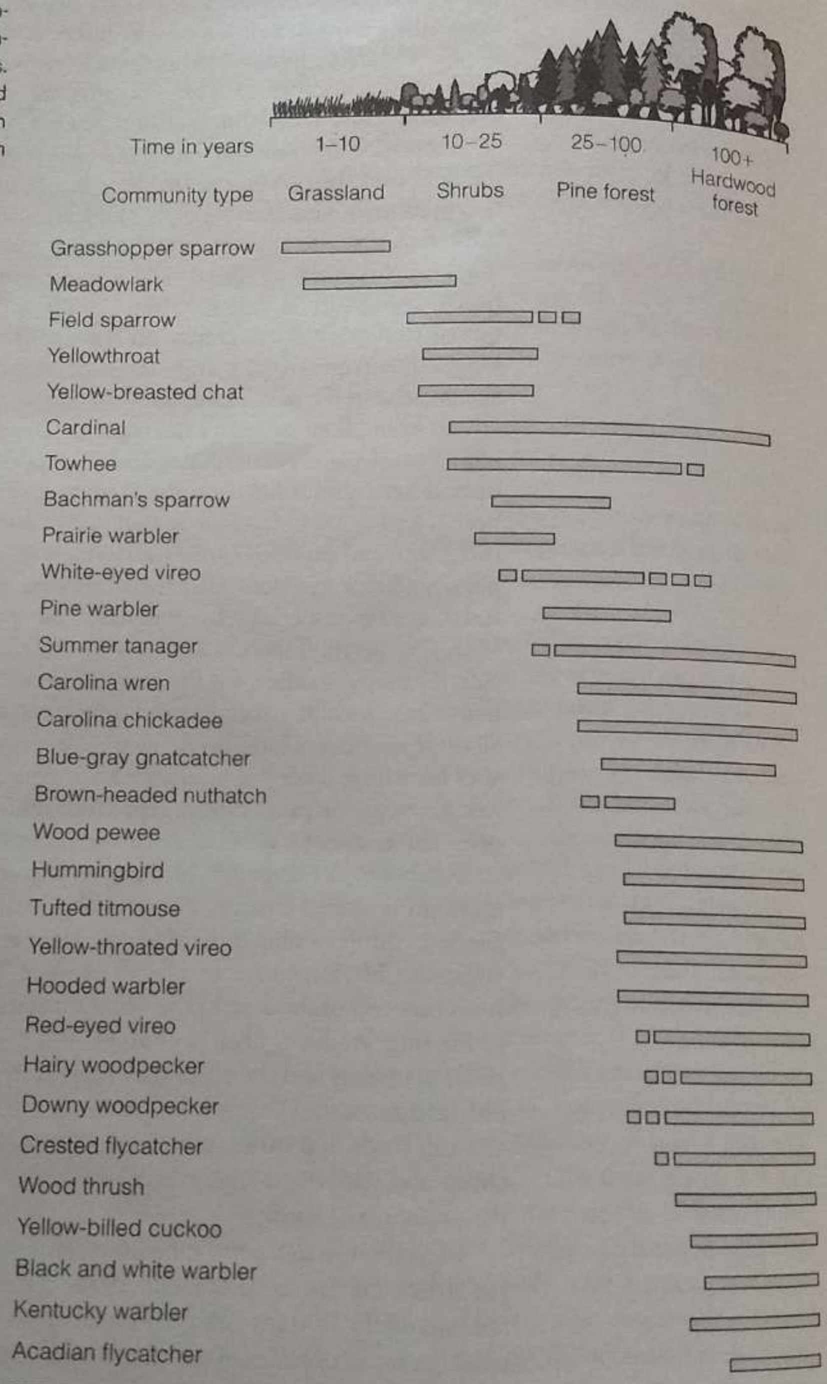
An example of *secondary succession* is illustrated in Figure 8-7, which shows the sequence of plant communities and bird populations that develop on abandoned upland agricultural fields on the Piedmont of the southeastern United States. Pioneer colonists are *r*-strategist annual plants, such as crabgrass (*Digitaria*), horseweed (*Erigeron*), and ragweed (*Ambrosia*), which spend a large part of their energy on dispersal and reproduction. After two or three years, perennial forbs (asters and goldenrods), grasses (especially broomsedge, *Andropogon*), and shrubs such as blackberry (*Rubus*) move in. If there is a good seed source nearby, pines invade and soon form a closed canopy, shading out the early pioneers. Several species of fast-growing deciduous trees, such as sweetgum and tulip trees, often come in with the pines. Because all these species are long-lived, the pine stage (with scattered broad-leaved trees) persists for a long time, but gradually an understory of shade-tolerant oaks and hickories develops. As pines cannot reproduce under their own shade, the oaks and hickories rise to canopy dominance as the pines die from disease, old age, and storms.

As shown in Figure 8-7, bird populations change with each major seral stage; the most pronounced changes occur as the life-form of the dominant plants changes (herb to shrub to pine to hardwood). Habitat selection by birds is more targeted to vegetative life-form than to species of plant. No species of plant or bird can thrive from one end of the sere to the other. Species have their maxima at different points in the time gradient. Ostfeld et al. (1997) documented a similar relay succession of small mammals and the effect they had on the survival of tree seeds and seedlings in old-field secondary succession. Animals are not just passive agents in community change. Birds and other animals disperse seeds necessary for the establishment of shrub and hardwood stages, and herbivores, parasites, and predators often control the sequence of species.

In shallow-water marine habitats, large animals rather than plants often provide the structural matrix. Glemarec (1979) described a secondary succession of benthic animals off the Brittany coast of France. A period of relative calm followed after storms caused a redistribution of sediments and disruption of bottom fauna. During this period, in the absence of outside interference, a more or less directional and predictable sequence of populations established dominance. First came bivalve suspension feeders, then bivalve deposit feeders, and finally, the benthos became dominated by polychaete worm detritus feeders, thus confirming the theory that uninterrupted succession converts an inorganic environment to a more organic one.

Secondary plant succession is as striking in grassland regions as in forests regions,

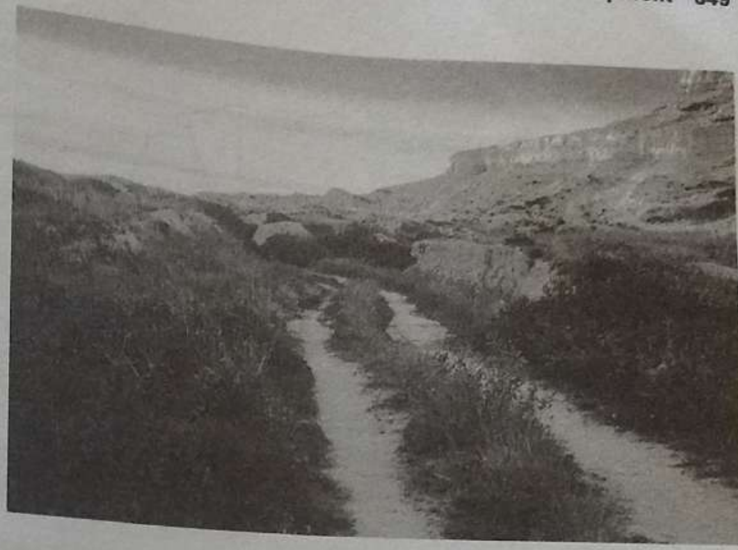
Figure 8-7. General pattern of ecological succession on abandoned farmland in the southeastern United States. The graph shows changes in songbird populations that accompany changes in vegetation (after Johnston and Odum 1956; E. P. Odum 1997).



	Grassland	Shrubs	Pine forest	Hardwood forest
Number of common species[a]	2	8	15	19
Density (pairs per 100 acres)	27	123	113	233

[a] A common species is arbitrarily designated as one with a density of five pairs per 100 acres or greater in one or more of the four community types.

Figure 8-8. The Oregon Trail near Scottsbluff, Nebraska, where a trace etched by the wheels of wagons that carried settlers during the 1840–1860 westward migrations between Missouri and Oregon is still evident.



Courtesy of Terry L. Barrett

even though only herbaceous plants are involved. Shantz (1917) described succession on the abandoned wagon roads used by pioneers crossing the grasslands of the central and western United States (Fig. 8-8), and virtually the same sequence has been described many times since. Although the species vary geographically, the same pattern holds everywhere. This pattern involves four successive seral stages: (1) an *annual weed* stage (2–5 years); (2) a *short-lived grass* stage (5–10 years); (3) an *early perennial grass* stage (10–20 years); and (4) a *climax grass* stage (reached in 20–40 years). Thus, starting from bare or plowed ground, 20 to 40 years is required for nature to "build" a climax grassland—the actual time depending on the limiting effect of moisture, grazing, and other factors. A series of dry years or overgrazing causes the succession to revert toward the annual weed stage; how far back depends on the severity of the effect. Increased nutrient enrichment, either with commercial fertilizer or with municipal sludge, will also arrest secondary succession in the annual weed stage of development (W. P. Carson and Barrett 1988; Brewer et al. 1994).

Succession is equally apparent in aquatic as in terrestrial habitats. However, as already emphasized, the community development process in shallow-water ecosystems (ponds and small lakes) is usually complicated by strong inputs of materials and energy from the watershed that may speed up, arrest, or reverse the normal trend of community development that would occur in the absence of such strong allogenic influences. The complex interaction of autogenic and allogenic succession is illustrated by the rapid changes in artificial ponds and impounded lakes. When a reservoir is created by flooding rich soil or an area with a large amount of organic matter (as when a forested area is flooded), the first stage in development is a highly productive bloom stage, characterized by rapid decomposition, high microbial activity, abundant nutrients, low oxygen levels at the bottom, but often rapid and vigorous growth of fish. People who fish are very pleased with this stage. However, when the stored nutrients are dispersed and the accumulated food used up, the reservoir stabilizes at a lower rate of productivity, with higher benthic oxygen and lower fish yields. Those who fish may be displeased with this stage (Fig. 8-9). However, this system and fish yield will likely remain stable on a long-term basis.

If the watershed is well protected by mature vegetation, or if the soils of the water-

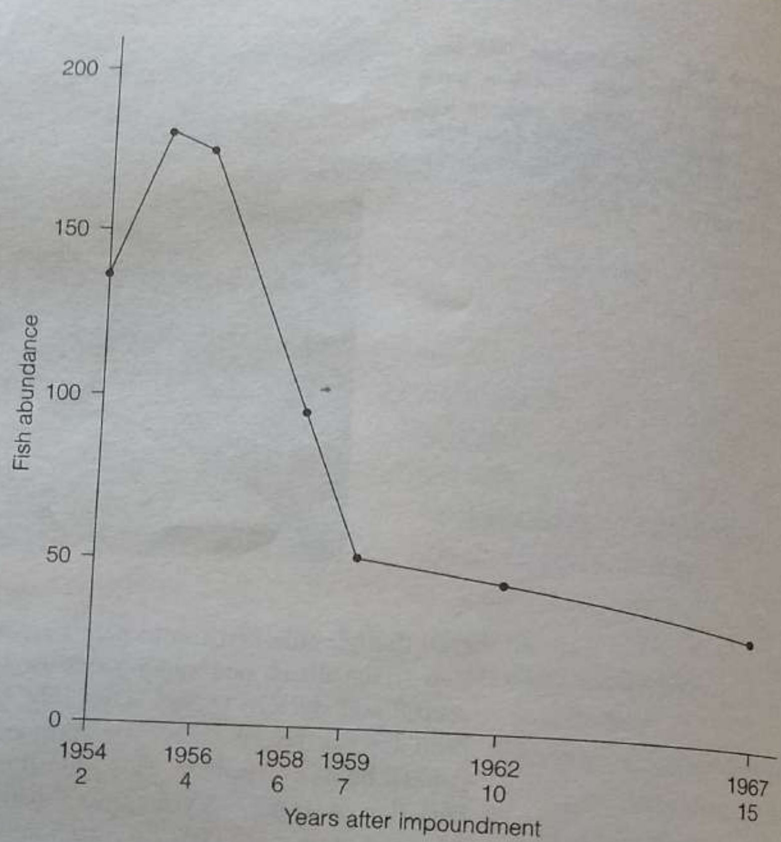


Figure 8-9. Fish abundance in a mainstream reservoir on the upper Missouri River from the second to the fifteenth year after completion of a dam in Lake Francis Case, South Dakota (data from Gasaway 1970).

shed are infertile, the stabilized stage in bodies of water may last for some time—a "climax" of sorts. However, erosion and various human-accelerated nutrient inputs usually produce a continuing series of transient states until the basin fills up. Impoundments in impoverished watersheds or primary, sterile sites will, of course, have a reverse pattern of low productivity at the start. Failure to recognize the basic nature of ecological succession and the relationships between the watershed and the impoundment has resulted in many failures and disappointments in human attempts to maintain such artificial ecosystems.

Because the oceans are, generally speaking, in a mature state and have been chemically and biologically stabilized for centuries, oceanographers have not been concerned with ecological succession. However, with pollution threatening to disturb equilibria in the sea, the interaction of autogenic and allogenic processes is starting to receive greater attention from marine scientists. Successional changes are evident in coastal waters, as already noted in the example of the development of benthic communities after severe storms have disrupted the sea bottom. Changes that occur in such a successional gradient in the coastal water column can be summarized as follows:

- The relative abundance of mobile forms among the phytoplankton increases;
- Productivity slows down;
- The chemical composition of the phytoplankton, as exemplified by the plant pigments, changes;
- The composition of the zooplankton shifts from passive filter feeders to more active and selective hunters, in response to a shift from numerous small suspended