UNIT 10 COMMUNITY CHANGE

Structure

10.1 INTRODUCTION

You know ecosystems are dynamic entities in which a number of events take place. Associated with the biotic communities of the ecosystem are some changes, which may be either small-scale changes or large-scale changes. Small-scale changes may be brought about by natural causes or by the activities of man. One of the examples of small-scale changes is a stream, in which some sewage is accidentally dumped. In such a case there would be an increase in the organic and inorganic chemicals in the water. The organic molecules are consumed by bacteria. With the increased availability of organic matter, the number of bacteria would increase. Bacteria use up oxygen as they consume organic materials, thus the level of oxygen in the stream usually drops. This can kill the fish and other organisms or cause them to migrate to new areas. In due course of time, the stream will return to normal. The bacteria will die if the level of organic matter falls off, and dissolved oxygen will return to normal, thus allowing fish to return. This example, clearly shows that the biotic community of an ecosystem may be temporarily affected by the small scale changes.

On the other hand, there are certain long-term changes in the ecosystem which can permanently change the organisation and composition of biotic communities. These long-term changes may be caused by factors like volcanic eruptions, landslides, earthquakes, floods, hurricanes, and of course human interventions such as mining and deforestation. All these disturbances, change the habitat considerably. A variety of species invade the changed or disturbed site, and eventually over a period of time, a new community develops there. This process continues — one community replacing another community, until a stable, mature community develops.

In this unit, we shall focus our attention, primarily on the large-scale changes in a community. Such large-scale changes are collectively known as ecological succession. We shall discuss the basic processes involved in succession. Then we shall take up two specific examples to explain how succession takes place in nature. Subsequently you would study, models of succession. We shall also talk about the characteristics and trends in succession.

Objectives

After studying this unit, you would be able to :

- define succession
- recognise differences between primary and secondary succession
- contrast autogenic and allogenic succession
- compare autotrophic and heterotrophic succession
- describe the basic processes involved in succession
- describe the process and various stages of succession in aquatic and terrestrial habitats, and explain why animal life changes with seral stages
- discribe the facilitation, inhibition and cyclic models of succession
- discribes the characteristics and trends in succession.

Study Guide

While studying this unit, if you are not able to fully understand subsection 10.2.2 and 10.2.3, at the first instance, do not be disheartened. We advise you to continue your study of the subsequent sections, and after you have completed section 10.4, come back to these two subsections.

10.2 WHAT IS SUCCESSION?

As we have discussed in the previous section that factors like fire, floods and human interventions affect an ecosystem considerably. They often lead to the depletion or stripping off of original vegetation of an area. The eventual result is the formation of bare ground or area. But this bare area does not remain devoid of life for long. It is rapidly colonised by a variety of species that subsequently modify one or more environmental factors. This modification of the environment may in turn allow additional species to become established. So, a biotic community destroyed by natural or human causes is gradually replaced in a series of changes, until a mature or *climax community* is reached. The process of community development, through a series of intermediate successional stages leading to climax community is known as seral stage and all such intermediate stages from bare area to climax community are collectively referred as 'seres'.

Succession is a universal process of directional change in vegetation, on an ecological time scale. If said in another way, succession is a progressive series of changes which leads to the establishment of a relatively stable climax community.

Having discussed as to what succession is we shall now take up for discussion various kinds of succession in the following three subsections:

10.2.1 Primary and Secondary Succession

Succession occurring in bare areas where no community existed before is called Primary Succession. For instance, primary succession would take place on new volcanic flows, islands, deltas, dunes, bare rocks and in newly formed lakes. Secondary Succession occurs at a site from where an already developed community has been destroyed by some natural catastrophe such as fire or flooding; or by human activity (such as deforestation, ploughing, grazing etc. and a series of communities subsequently develop at the site. Secondary succession also occurs on abondoned farmlands, in overgrazed areas and construction projects.

In primary succession on a terrestrial site (see Fig. 10.1) the new site is first colonised by a few hardy pioneer species, that are often microbes, lichens and mosses. The pioneers over a few generations alter the habitat conditions by their growth and development.

These new conditions may be conducive to the establishment of additional organisms that may subsequently arrive at the site. The pioneers through their death any decay leave patches of organic matter in which protists and small animals can live. 'The organic matter produced by these pioneer species produce organic acids during decomposition that dissolve and etch the substratum releasing nutrients to the substratum. Organic debris accumulates in pockets and crevices, providing soil in

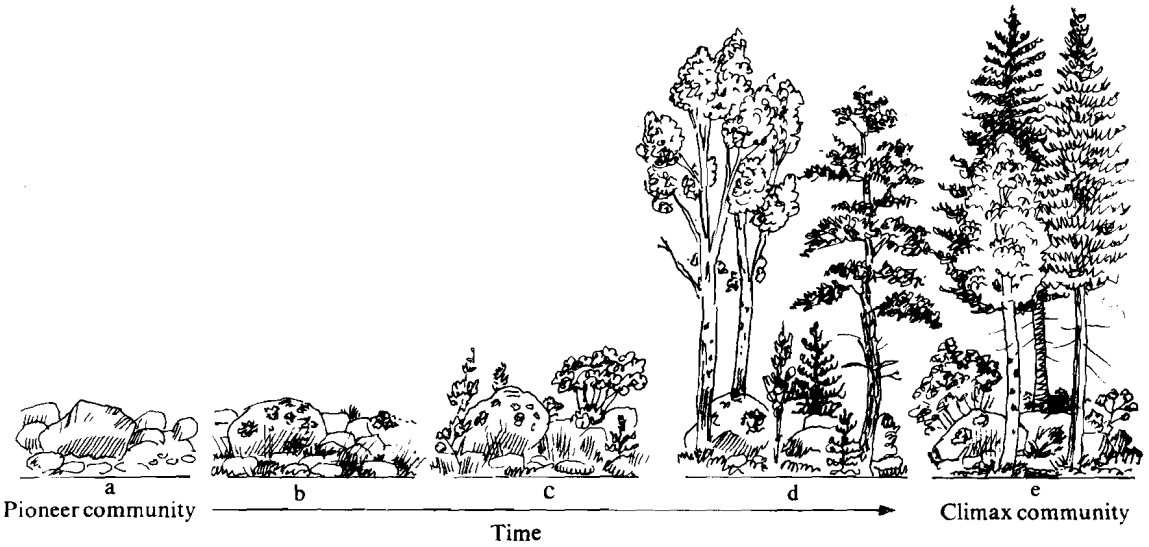


Fig. 10.1 : Primary succession on a terrestrial site developed through five seral stages (a-e), from left to right, beginning with bare rocks, colonised by lichens and mosses, and developing a relatively stable climax forest community.

which seeds can become lodged and grow. As the community of organisms continues to develop, it becomes more diverse and competition increases, but at the same time new niche opportunities develop. The pioneer species disappear as the habitat conditions change and invasion of new species progresses, leading to the replacement of the preceding community. Similarly, primary succession in aquatic habitat also develops through a number of seral communities. We shall discuss this with an example in the Subsection 10.4.1.

Secondary succession is the sequential development of biotic communities after the complete or partial destruction of the existing community. A mature or intermediate community may be destroyed by natural events such as floods, droughts, fires, or storms or by human interventions such as deforestation, agriculture, overgrazing, etc. Let us look briefly at an example of secondary succession occurring on an abandoned agricultural farm where soil has been already formed before cultivation started (see Fig. 10.2).

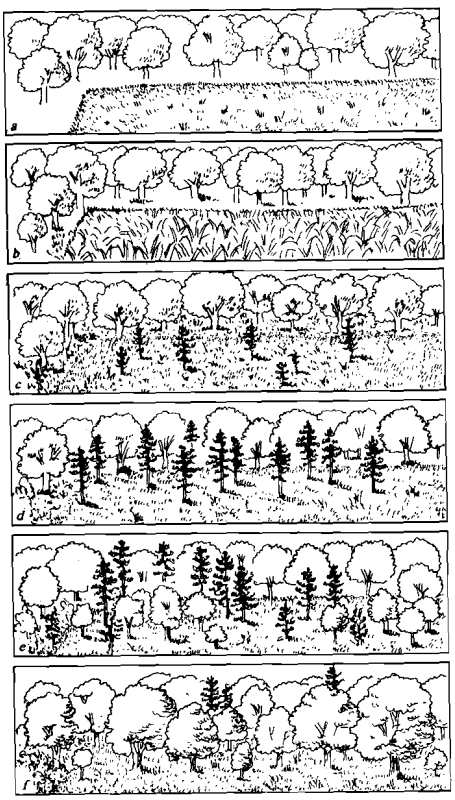


Fig. 10.2 : Secondary succession in an abandoned farmland shown in six stages (a-f). First grasses appear (a, b), and through the intermediate stages (b-e), finally a woodland ecosystem develops(f)

This abandoned farmland is first invaded by hardy species of grasses that can survive in bare, sun-baked soil. These grasses may be soon joined by tall grasses and herbaceous plants. These dominate the ecosystem for some years along with mice, rabbits, insects and seed-eating birds. Eventually, some trees may come up in this area, seeds of which may be brought by wind or animals. And over the years, a forest community develops. Thus an abandoned farmland over a period say 30 to 40 years becomes dominated by trees and is transformed into a forest.

When talk of the differences between primary and secondary succession, one obvious difference between the two is that the secondary succession starts on a well developed soil already formed at the site. Thus secondary succession is relatively faster as compared to primary succession which may often require hundreds of years.

10.2.2 Autogenic and Allogenic Succession

Autogenic = self-generated
Allogenic = externally generated

In many cases the living beings of an ecosystem, modify their environment considerably by their growth, death and decay. The changed conditions lead to the establishment of new kinds of species in that area. The whole process goes on and on, that is, there is replacement of one kind of community with another. Such a succession process is called **autogenic** succession. To sum up, autogenic succession results because of the changes brought about in the habitat by the members of the community themselves.

In some cases, the changes brought about in the habitat are caused by external agencies and not by the existing vegetation itself. This is called as allogenic succession. Such a succession may occur in a highly disturbed or eroded area or in ponds where nutrients and pollutants enter from outside and modify the environment and in turn the communities.

10.2.3 Autotrophic and Heterotrophic Succession

The succession where initially the green plants are much greater in quantity than the animals, is known as autotrophic succession. Such a succession takes place in a medium rich in inorganic substances. Since there are green plants, there is gradual increase in the organic matter content and energy flow in the ecosystem. On the other hand, in heterotrophic succession, the populations of heterotrophic organisms, like bacteria, actinomycetes, and fungi are present in greater quantity in the initial stages. Such a succession begins in a medium rich in organic matter such as the rivers and streams which are polluted heavily with sewage, or in small pools receiving leaf litter in large quantities. As indicated earlier, it begins, prominently in organic environment, and there is a progressive decline in the energy content.

SAQ 1

Put a tick (√) mark against the correct choice :

1) Succession involves the turnover of species during :
   a) the seasons of the year
   b) ecological time
   c) micro-evolutionary time
   d) macro-evolutionary time

2) Primary succession takes much longer than secondary succession because it involves :
   a) development of the soil
   b) accumulation of a wide variety of seeds
   c) colonisation by organisms that are farther away
   d) destruction of a habitat by some natural catastrophe

3) Most agriculture makes use of plants from :
   a) early primary succession
   b) early secondary succession
   c) late primary succession
   d) late secondary succession

4) Autogenic succession is brought about by :
   a) human activities
   b) physical conditions of the environment
   c) living inhabitants of that area
   d) natural disasters

5) The kind of succession, in which the green plants constitute the initial stages are known as :
   a) heterotrophic
   b) allogenic
   c) autotrophic
   d) both (a) and (b).

10.3 PROCESSES IN SUCCESSION

Whether succession is primary or secondary, in terrestrial or aquatic ecosystems, the basic processes involved in succession are similar. There are a number of sequential steps in succession. In this section we shall discuss them in detail. These steps or processes are : *nudation; invasion* or *migration; ecesis; aggregation; competition, reaction;* and *stabilisation - climax.*

10.3.1 Nudation

The first step or requirement is the availability of the right kind of habitat, primary succession takes place in a bare area, that is, without any life form; and secondary succession occurs in area where soil is already formed, but the vegetation is destroyed. The bare area may develop due to several causes, some of them are :

i) *Topographic* — factors like soil erosion by gravity, water or wind, may destroy the existing vegetation thus creating a bare area. Other topographic causes include deposition of sand, landslide and volcanic activity.

ii) *Climatic* — glaciation, long dry periods, hails and storm, frost and fire are the agents that destroy vegetation.

iii) *Biotic* — One important agent is man that causes destruction of forests, grasslands and other stretches of vegetation for agriculture, industry, housing and several other purposes. Overgrazing by animals, diseases caused by organisms like bacteria, fungi and insects too destroy vegetation of an area to produce bare areas.

10.3.2 Invasion or Migration

When a habitat is changed it can be a potential site for the establishment of many organisms. Many species actually invade or reach this new site from any other area. The seeds, spores or other propagules of the plant species reach this area. This process is known as *migration,* and is generally brought about by air, water and various other agents.

10.3.3 Ecesis

After reaching the bare area, the process of successful establishment of the species as a result of adjustment with the conditions prevailing there is known as ecesis. In plants, after migration, seeds or propagules germinate and grow if the conditions are favourable. Ecesis is considered to be complete, if the plant is able to sexually reproduce in that particular area. As a result of reproduction, the number of individuals multiply rapidly and the species becomes established in that area.

10.3.4 Aggregation

After successful establishment of a species as a result of reproduction, the individuals of the species increase in number. So, as compared to earlier stages, there are a larger number of individuals of a species that have aggregated in the given area.

10.3.5 Competition

Interspecific competition : competition between two different species A and B. Interaspecific competition: competition amongst the individuals of the same species.

The aggregation of individuals in an area leads to interspecific and intraspecific competition. The competition is usually for i) *water,* particularly when there is shortage of water; ii) *nutrients,* particularly when they are in short supply; iii) *radiant energy,* if one plant grows in the shade of another plant; iv) *carbon dioxide;* v) *oxygen,* and vi) *space.* Success of a species during competition depends on several features, e.g., strong and efficient root system, capability to trap nutrients, endurance to drought and poor soil aeration, and efficiency of reproduction of the plant.

10.3.6 Reaction

This is the most important stage in succession. The mechanism of modification of environment, through the influence of living organisms on it is known as reaction. As a result of reaction, changes take place in soil, water, light conditions, temperature and many other factors of the environment. The environment thus gets modified, and becomes unsuitable for the existing community, and is eventually replaced by another community. The old occupants are ousted and fresh migrants establish themselves. Thus, through a series of invasions, a sequence of plant communities marked by changes from lower to higher forms establish themselves in the course of time. Each stage of succession plays some part in reducing the extreme conditions in which the sere began. Thus, gradually the conditions of the area are modified by the seral communities to suit the growth of a wider range of species.

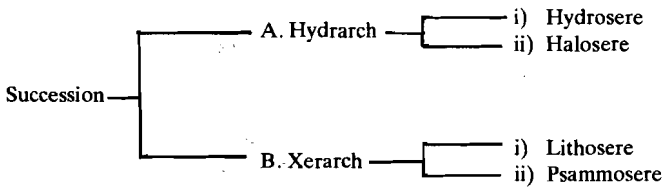
10.3.7 Stabilisation — Climax

The whole process of succession results in stabilisation of the vegetation which is now in complete harmony with the environmental complex of that place. And it is likely to persist as long as the climatic and physiographic conditions remain unchanged. The soil is fully occupied by plants and the community is closed. Only those species, which are capable of completing their life cycles, despite the intense competition, establish themselves, the homeostasis is thus attained. This final community is not replaced, and is known as climax community and the stage as climax stage.

The kind of succession that takes place from simple, few forms to complex, several kinds of forms are known as **progressive succession.** In some cases, reverse situation is seen, that is, the process of succession, instead of being progressive becomes retrogressive. This may be due to the destructive effects of organisms. For example, a forest changing into a grassland community is an example of **retrogressive succession.**

10.4 KINDS OF SUCCESSION

The ecological succession can be broadly classified into two kinds, on the basis of the nature of the habitat.



A. Hydrarch — When succession takes place in a wet area, that is, succession progresses from hydric to mesic conditions. This can be further subdivided as: i) hydrosere — when succession starts in fresh water ecosystems like ponds, pools, lakes and marshes; ii) halosere — when succession starts in saline water ecosystems, e.g., mangroves, coral reefs, estuaries.

B. Xerarch — When the succession takes place in drier area, i.e., the succession progresses from xeric to mesic conditions. It is further subdivided as : i) lithosere — when it takes place on bare rocks; ii) psammosere — when succession takes place in a sandy area, like sand dunes. In this section, we shall discuss in detail, an example each of Hydrarch and Xerarch.

10.4.1 Hydrarch

Its various stage are well studied in ecosystem like ponds, pools and lakes. In this subsection, we shall discuss, succession in a pond. Since pond is a fresh water ecosystem, the succession in it is also referred to as hydrosere. Succession in pond, begins by colonisation by the pioneers like the phytoplanktons, and finally terminates into a forest which is a climax community. As succession progresses, changes take place in the kind of vegetation as well the associated animal life (see Fig. 10.3). The whole process of succession or the hydrosere is further subdivided into a number of stages depending on the kind of organism(s) dominating a stage. We shall now discuss these stages one by one, in detail.

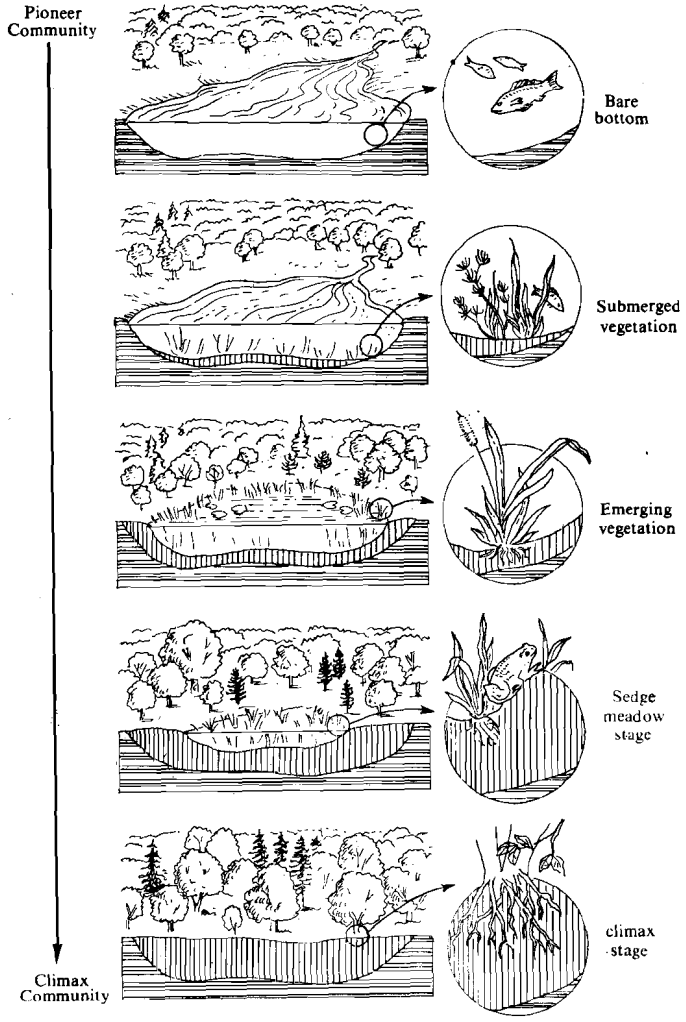


Fig. 10.3 : Hydrosere in a pond ecosystem. The pond is gradually converted into a forest ecosystem. Sediments begin to accumulate, and a series of biotic communities develop until the mature ecosystem is reached

i) **Phytoplankton Stage :** In this initial stage, the pond water is poor in nutrients and is devoid of much life. At this stage, the water is incapable of supporting larger life forms. So, in such situations, phytoplanktons consisting of microscopic algae, begin to multiply and they quickly become the pioneer colonisers. As the phytoplanktons and the dependent animal population dies, decomposer organisms like bacteria and fungi increase in number and bring about decomposition of the organic material. Decomposition results in the release of minerals and enrichment of aquatic habitats. Besides this, some silt may be brought to the pond, by the rain water from the surrounding land. By now the pond becomes shallower, and the mud at its bottom is rich in nutrients. Now it can support some rooted hydrophytes, thus initiating the next stage.

ii) **Submerged Stage :** This habitat which is now shallower and is richer in nutrients, and where light is available upto a certain depth, becomes suitable for the growth of rooted, submerged hydrophytes like *Myriophyllum, Elodea, Hydrilla, Potamogeton*,

Vallisneria, Utricularia and *Ceratophyllum.* These grow at various depths, mostly rooted in the muddy or sandy bottom depending on the species, and also on the clearness or turbidity of water. Year after year, this vegetation expands and covers large areas, and brings about marked changes in the habitat. Materials eroded by streams, rainwater or surface runoff are brought to the pond, and some of it are deposited on the plants because they form a direct obstacle in its advance, and especially because they slow down the currents, when the plants and the associated animals die, they sink to the bottom, where because of the insufficient oxidation, this organic matter is partially decomposed. Thus humus is formed which cements the mucky soil together making it firmer. The result of these reactions is the building up of substratum and shallowing of lake. Obviously, this process is disadvantageous to the present occupants and these are eventually replaced by another type of plants, which are of floating type.

iii) Floating Stage : The pond is now colonised by plant species which are rooted in mud but their leaves reach water surface and float. These are species of *Nelumbo, Nymphaea, Trapa, Monochoria.* Some free-floating species that are not fixed in the mud, also make their appearance. Examples are *Lemna, Wolffia, Pistia, Salvinia, Azolla* and *Eichhornia.* Due to the growth, and death and decay of these organisms, the water level by now becomes very much decreased, making the pond much more shallower. Evaporation of water, along with the addition of silt from the adjacent area also contribute in making the pond shallower. The pond, now does not remain suitable for this kind of plants and the next stage appears.

iv) Reed-Swamp Stage : This stage is also known as amphibious stage, as the plants of the community are rooted but most parts of their shoots remain exposed to air. Species of *Typha, Sagittaria* and *Phragmites* are some examples of this stage. These plants have well developed root system and they form dense patches of vegetation. The reaction of the reed-swamp plants is not only to shade the surface of the water but also to build up the pond margins by retaining the sedimentary materials washed into the lake and by the very rapid accumulation of plant remains. Not only is the plant population much denser than before but also mechanical tissues, which resist decay, are much more highly developed in plants with aerial organs. After the invasion and activities of these plants, the water level is very much reduced, and finally it becomes unsuitable for these plants also.

v) Sedge-Meadow Stage : Favoured by an increasing amount of light, as the former occupants disappear, they gradually change the reed swamp into a sedge meadow. And now species of Cyperaceae and Gramineae such as *Carex, Juncus, Cyperus* and *Eleocharis* colonise the area. They form a mat-like vegetation with the help of their much branched rhizomatous systems. All these react upon the habitat by binding water-carried and wind-borne soil, accumulating plant debris and transpiring enormous quantities of water. There is much rapid loss of water, and sooner or later the mud is exposed to air. As a result nutrients like ammonia, sulphides become oxidised to nitrates and sulphates. Thus the conditions in the area gradually change from marshy to mesic, and the marshy vegetation shows a decline. Upto the end of sedge-meadow stage, the climate of the region has no control over the succession because the water content of soil is high, irrespective of rainfall and climate of the region. At the end of this stage, the soil becomes dry and its water content will henceforth be dependent upon rainfall and climate of the region. The plants which succeed the sedge-meadow stage are therefore controlled by the climate to a very large extent. In dry climates the next stage may be grassland or some other xeric climax but in more moist climates it is woodland.

vi) Woodland Stage : When the lowland has been built upto an extent where the soil is saturated perhaps only in spring and early summer, certain species of shrubs and trees may appear. Those that can tolerate waterlogged soil around their roots will be the pioneers. Various species of *Salix, Cornus, Cephalanthus, Alnus* and *Populus* may form dense thickets. Some shade-tolerant herbs may also grow among the trees and shrubs. These woody plants react upon the habitat by producing shade and by lowering the water table both by further building up the soil and by vigorous transpiration. By this time of succession there is much accumulation of humus wit rich flora of microorganisms like bacteria, fungi and others. Thus mineralisation o the soil favours the arrival of new tree species in the area leading to climax stage.

vii) Climax Stage : A variety of trees invade the woodland community which soon develop into the climax community. The nature of the climax is dependent upon the climate of the region. In tropical region, where rainfall is high, dense rain forests develop, and in temperate regions, mixed forests of trees like *Quercus, Ulmus, Acer* may develop. In regions of moderate rainfall the climax stage consists of deciduous forests or monsoon forests.

Thus in the hydrosere you have just studied, stage i) is the pioneer community stage, vii) the climax community, and stages ii) to vi) as the seral communities or seral stage.

Successive Changes in Animal Life During Hydrosere

So far, we have discussed the successive changes in plant communities in the different seral communities of a hydrosere. The question arises, is there any change in the animal life along with the different seres. There are certainly changes in the animal life also, but these may not be as obvious as in case of plant community. In an aquatic ecosystem like this, protozoans like *Paramecium, Amoeba, Euglena* and many others are the pioneers. When the planktonic growth forms are very rich, then animals like blue gill fish, sun fish, large mouth bass etc. start appearing. Some caddisflies are also found. In the second stage, that is, the submerged stage, the caddisflies are replaced by other animals that may creep over the submerged vegetation. Thus dragonflies, mayflies and some crustaceans as *Asellas, Gammarus, Daphnia, Cypris, Cyclops* inhabit the pond at this stage. At the floating stage, the animals life is chiefly represented by *Hydra* spp., gill breathing snails, frogs, salamanders, diving beetles, and other insects. There also appear some turtles and snakes.

At the reed-swamp stage, the pond becomes shallower, and the bottom starts becoming exposed. The floating animals are replaced by different species of mayflies and dragonflies, whose nymphs remain attached to submerged parts of the vegetation, and adults present on the surfaces of exposed parts of vegetation. Gill-breathing animals like snails are replaced by lung breathers as *Lymnea, Physa* and *Gyraulus*. Among insects, water scorpion, giant water bug, scavenger beetles etc. are present at this stage. The bottom of the pond is now inhabited by some annelids, mud pickrel and bull-heads. Red-winged black birds, kingfisher, great blue heron, swamp sparrow, ducks, musk rats, and beavers become common in the area.

At the sedge-meadow stage, the animals like snails as *Anodonta, Psidium* become common. Finally, at the woodland stage, under terrestrial conditions, most of the terrestrial forms of animal life appear in the area.

10.4.2 Xerarch

Successions initiated on bare rock, wind-blown sand, rocky talus slopes, or other situations where there is an extreme deficiency of water are termed xerarch. Here, we shall discuss the example of a bare rock. It is not only deficient in water but also lacks any organic matter, having only minerals in disintegrated, unweathered state. The pioneers to colonise this primitive substratum are crustose type of lichens, and through a series of successive seral stages, the succession finally terminates into a forest which constitutes the climax community (also see Fig. 10.1). As in the hydrarch, successive changes take place in both plants as well as animals, but changes in plants are more obvious than animals. Now, we shall take up the various stages of xerosere for discussion.

i) Crustose Lichen Stage : On bare rocks, conditions are inhospitable for life, as there is extreme deficiency of water and nutrients, great exposure to sun, and extremes of temperature. Crustose lichens alone are usually able to grow in such situations. Some examples of these pioneering species are, *Rhizocarpon, Rhinodina, Lecidea* and *Lecanora*. These plants flourish during periods of wet weather and remain in a state of desiccation for very long periods during drought. During the wet weather they rapidly absorb moisture by their sponge-like action. Mineral nutrients are obtained by the secretion of carbondioxide which, with water forms a weak acid that slowly eats into the rock into which the rhizoids sometimes penetrate for a distance of several millimetres. Nitrogen is brought by rain or by wind-blown dust. Thus all the life requirements of this simple, crust-like species is met with. Thus, lichens help corrode and decompose the rock, supplementing the other forces of weathering. And by mixing the rock particles with their own remains, make conditions favourable for

Lichen — an alga and a fungus that live in symbiosis, forming a distinctive structure or thallus that may be crusty or leafy; Lichens are pioneers on rock or other surfaces.

growth of other organisms. Thus, a thin layer of soil is formed. The rapidity with which a small amount of soil is formed is controlled largely by the nature of the rock and by the climate. On quartzite or basalt rocks in a dry climate, the crustose-lichen stage might persist for hundreds of years. But on limestone or sandstone in a moist climate, sufficient changes permit the invasion of foliose lichens, and all this may occur within a life time.

ii) Foliose Lichen Stage : As mentioned earlier, the weathering of the rocks and the decaying of the crustose lichens results in the formation of soil on the otherwise bare rocks. The foliose lichens make their appearance on such spots on the rocks which have accumulated some soil. These lichens include *Dermatocarpon, Parmelia* and *Umbilicaria.* These lichens have large, leaf-like thalli, which overlap the crustose lichens. The latter are thus cut-off from direct light. This results in death and decay of the crustose lichens. The mass of foliaceous lichens can absorb and retain more water to some extent. Wind and water-borne dust particles are trapped by these lichens. This helps in the further building up of substratum. All these processes result in the accumulation of more and more humus. The rocks are weathered by the acids secreted by the living and the decaying plants. The weathering of the rocks and the rapid addition of humus to it result in the increase in thickness of soil layer. Thus, a considerable change in habitat is brought about.

iii) Moss Stage : The accumulation of soil, particularly in the crevices and depressions of rock favours the growth of certain xerophytic mosses., e.g., species of *Polytrichum, Tortula* and *Grimmia.* The spores of these mosses are brought by the blowing wind. They have more or less the same power of withstanding desiccation as that of foliose lichens. The lichens and mosses grow together and compete with one another. The rhizoids of mosses and foliose lichens compete for water and nutrients, and the stems of the former attain greater height than the latter. The plants in the lower strata, i.e., the lichens die, and the mosses grow. The mosses form cushion-like structure, that may be a few centimeters in thickness. The substratum is thus gradually built up and is widened. The foliose lichens gradually give way to mosses that overtop the lichens. Many times, all three stages may be found on a single rock surface, the pioneers occupying the most exposed places.

iv) Herb Stage : The Soil-forming and soil-holding reactions of the mosses are so pronounced that the seeds of various xerophytic herbs, especially short-lived annuals, are soon able to germinate and grow. The plants mature, although the first generations, because of the drought and sterility of the soil, may make only a stunted growth. Their roots continue the process of corroding the rock, and each year the humus from their decaying remains enriches the soil. Gradually, biennials and perennials begin to invade the area and with the habitat becoming more and more favourable, their numbers also increase.

The processes of rock disintegration and humus and nutrient accumulations are greatly increased, as the tangled network of roots increases and the soil becomes shaded. Evaporation and temperature extremes are decreased, humidity is slightly increased, and drought periods are shortened. The bacterial, fungal and animal populations of the soil increase and conditions gradually become less xeric. Upto now, some xerophilous, shallow rooted grasses like *Aristida, Festuca* and *Poa* were growing. As the conditions improve, then some drought-enduring species like *Potentilla, Solidago and many others invade the area. As a result of growth of the herbs, the smaller plants like mosses and lichens do not get enough light. So these conditions are detrimental for their growth, they gradually start perishing.*

v) Shrub Stage : Sufficient soil is formed in the herbs stage, for supporting the woody plants or the shrubs. They migrate with the help of seeds or rhizomes from the adjacent areas. Examples are : species of *Rhus* and *Phytocarpus.* The shrubs soon develop into dense vegetation. The habitat is considerably modified. The herbs are shaded by the overgrowing shrubs. They no longer find it possible to thrive in such a situation and are, therefore, completely replaced by the shrubs. The shrubby vegetation adds a lot of organic matter to the soil, through leaves and other plant parts. The soil is thus enriched with considerable amount of humus. The huge mass of roots of the shrubs corrode the rocks. The enriched soil attains greater capacity for holding water. The soil is shaded, and, therefore, evaporation of water is considerably reduced. The humidity is increased over such areas. All these favour the growth of seedlings of trees which start invading the area.

vi) Climax Forest : First, some xerophytic species of trees, establish in this area. They are sparsely distributed and are stunted because the conditions are still not very congenial for them. With passage of time, the rocks are further weathered and a deep layer of soil is formed. This favours vigorous growth of a much larger number of trees. The moisture in the soil is conserved because of the shading of soil. The climax forest is thus developed. The vegetation becomes more and more mesophytic with the accumulation of humus.

Thus, in the xerosere, as in the hydrosere the habitat has changed from one extreme condition to a medium situation which permits the development of a mesophytic type of vegetation.

Changes in Animal Life During Xerosere

Just like the hydrosere, there occur successive changes in animal life during the xerosere. A few mites are usually found associated with the lichens. Initially, the fauna is sparse in terms of species composition. There are a few ants or a few spiders present in the cracks and crevices of rock. These pioneer animals are exposed to harsh environment particularly the thermal extremes. As succession progresses, the mites become more varied in terms of species and small spiders, springtails as well as tradigrades become associated with the mosses. At later stage of succession, when grasses start appearing, the fauna increases markedly, both in qualitative and quantitative terms. Nematodes, larvel insects, collembola, ants, spiders and mites appear in this new environment. With the development of forest climax community, there develops a rich fauna consisting of invertebrates as well as vertebrates. These include springtails, mices, squirrels, shrews, mammals like fox, chipmunk, mouse and mole, birds, reptiles like turtles, snakes, and amphibians like salamenders and frogs.

SAQ 2

1) Which of the following organisms will be the first to colonise a bare rock?
   a) annual plant
   b) biennial plant
   c) perennial plant
   d) lichen

2) The kind of climax community in an area depends most on the area's:
   a) pool of available colonists
   b) soil organisms
   c) climate
   d) bed rock

3) This is a thought puzzle — put it together. Here are the pieces:
   (Write the correct sequence of the numbers of the pieces arranged by you in the space provided.)
   a) inter, and intra-specific competition
   b) aggregation of species in a given area
   c) development of bare area
   d) stabilised vegetation, likely to persist long
   e) reaching to the new site
   f) sexual reproduction, increase in number and establishment of organisms
   g) modification of the environment through the influence of living organisms.

10.5 MODELS OF SUCCESSION

After studying the processes and kinds of succession, there remains a question as to why succession happens; what mechanisms operate so that a bare rock is colonised by lichens and mosses; why does shrub stage succeed grassland; and some type of woodland (that is often predictable) succeeds shrub stage? This is an area of long-standing controversy in ecology, its resolution is hampered because of lack of sufficient field data and experimentation. Currently, it is believed that different mechanisms operate at different stages during primary succession and for different types of secondary succession, but there is disagreement about the relative importance of these different mechanisms.

There are two main points of debate in successional mechanism; one, whether the effects of early species on the environment is the critical factor determining succession of species; or whether what matters most are life history characteristics of species, such as longevity. Below, we describe three mechanisms, (see Fig. 10.4) the first one emphasises on environmental modification, while the other two emphasise on the life-history characteristics.

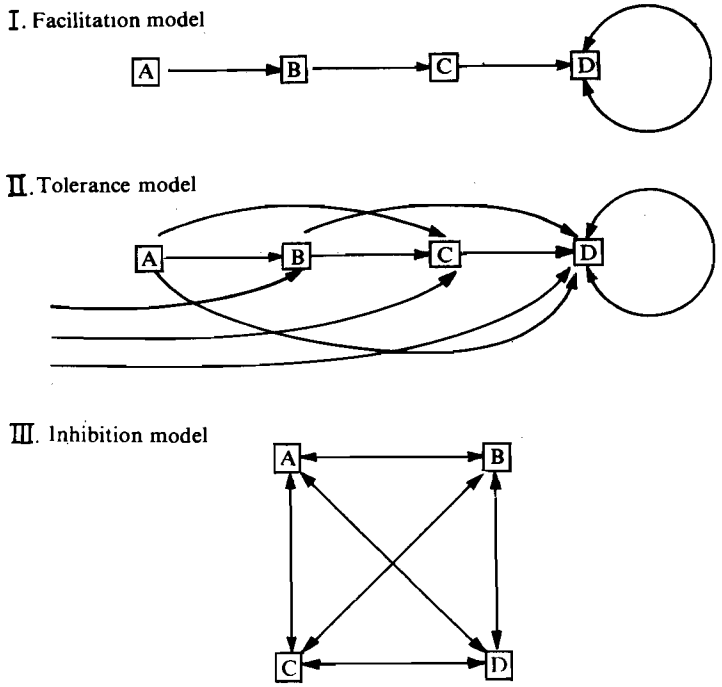


Fig. 10.4 : Three Models of Succession. The four species are represented by A,B,C and D. The arrows indicate 'is replaced by'. (After Krebs, C.J., 1985).

10.5.1 The Facilitation Model

This is considered as the classical model of succession. It is based on the assumption that species of a previous stage are replaced by the succeeding stage. And at each stage the species modify their own environment to make it progressively less suitable for themselves and increasingly more suitable for succeeding colonisers. Based on these characteristics Connell and Slayter (1977) proposed the facilitation model (see Fig. 10.4, I). To explain it better let us consider the example of succession in a pond. You may have noticed that due to the death and decay of different species of plants, siltation takes place and bottom of ponds is raised and the conditions become less suitable for their own survival and more suitable for the establishment of succeeding species. The essence of the facilitation model is that species of early stages of succession modify their own environment in a way that inhibits their own regeneration but facilitates the entry and survival of species of next higher stage of succession.

For many years this model was considered to be the only one. For the early stages of primary succession, it still seems to provide the best explanation of what is actually observed. But for later stages of primary succession and for secondary succession in forests or grasslands this model is not fully tenable.

10.5.2 The Tolerance Model

In this model, the presence of early successional species is not essential, that is, any species can start succession (see Fig. 10.4, II). Some species are competitively superior and they eventually predominate in the climax community. Species that are more tolerant of limited resources, replace the other species. Succession proceeds either by the invasion of later species or by a thinning out of the initial colonists, depending on the starting conditions. The crux of the whole thing is that there is a competitive hierarchy in which later species can outcompete earlier species (see Fig. 10.4, II) and can also invade in their absence.

10.5.3 The Inhibition Model

According to this model, succession is very heterogenous because the development at any one site depends on who gets there first. Species replacement is not necessarily orderly (see Fig. 10.4, III) because each species tries to exclude or suppress any new colonists. Thus succession becomes more individualistic and less predictable because communities are not always converging at climatic climax. In this model, no species is competitively superior than another. Whoever colonises the site first holds it against all new comers. Succession in this model proceeds from short-lived species to long-lived species and is not an orderly replacement. The essence of this model is that during succession, all replacements are possible, and much depends on who gets there first.

The three models of succession agree that the pioneer species will appear first because these species have evolved certain colonising characteristic such as rapid growth, abundant seed production, and means of efficient dispersal. Early colonising species are not well adapted to establish in occupied sites, on account of root competition with the established species and the reduced availability of light. In the different models of succession, the early colonisers, are fugitive species that create conditions which makes the habitat progressively unsuitable for themselves.

The main distinction between the three models is in the mechanisms that determine subsequent establishment. In the facilitation model, species replacement is facilitated by the species of the preceding stage. In the inhibition model, species replacement is inhibited by the present residents until they are damaged or killed. In the third model, species replacement is not affected by the present residents.

10.6 TRENDS IN SUCCESSION

Succession is an important aspect of change in ecosystems and a simple description of successional communities (as in Section 10.3 and 10.4) is only the beginning of the story. We need to know at a more fundamental level *what is happening* during succession because this might give some *clue* as *to why it happens.*

During primary succession, for example, from an aquatic habitat or a bare rock to climax woodland, there are certain obvious changes in the vegetation and soil. For example, increase in community biomass, and development of soil containing dead organic matter mainly from a largely mineral substrate. These changes are linked with many other ecosystem features. For instance, energy flow and nutrient cycling.

Succession may begin with a bare area colonised by small plants and may culminate in a community of large plants whose growth form results in increased vertical stratification and a marked influence on the environmental conditions within the community. Many such changes, enumerated in Table 10.1, are quite characteristic of ecological succession.

You have learnt from your study of Section 10.4 that the early successional stages are characterised by a few species, low biomass, and dependence on abiotic sources for nutrients. In the early stages, the net primary production is greater than respiration, resulting in increased biomass over time. Energy is channelled through relatively few pathways to many individuals of a few species, and production per unit biomass is high. Food chains are short, linear and largely grazing.

The mature stages in succession are characterised by a greater species diversity, greater biomass, gross production that almost equals total community respiration

Table 10.1 : Changes in Ecosystems During Succession (Modified from Odum, 1969)

Characteristics	Immature (early) ecosystem	Mature (late) ecosystem
Gross production/Respiration (P/R ratio)	High, > 1, (P>R)	Approaches 1, balance (P=R)
Net community production	High	Low
Food Chains	Linear, mainly grazing	Web-like, mainly detritus
Total organic matter (biomass)	Small	Large
Species diversity	Low	High
Structure of community	Simple	Complex (stratification with many microhabitats)
Total organic matter	Small	Large
Inorganic nutrients	Mostly found in physical environment	Large amounts, locked in organic matter
Mineral cycles	Open	Closed
Stability	Low	High
Size of Organisms	Small	Large
Gross Production/standing crop biomass (P/B ratio)	High	Low

(P=R), substratum rich in organic matter. Food chains are complex and largely detrital. Large amounts of inorganic nutrients locked in organic matter in the soil, and the vegetation.

The trend of most successions is towards a more complex and longer-lasting ecosystem, in which less energy is wasted and hence, a greater biomass can be supported without further increase in the supply of energy. Actually, succession may be very complicated because stages may be skipped, telescoped or extended. Human activities retard or reverse this succession back — due to agriculture, farming, lumbering, urbanisation and environmental pollution. If any habitat is left undisturbed, then eventually a stable climax community will be formed.

SAQ 3

I) Fill in the blank spaces with appropriate words:

1) Three mechanisms may influence the path of succession, ... in which early species alter the environment in ways that improve the area for later species; ..... in which early species make it more difficult for later species to colonise; and ..... in which early species have no influence over colonisation by later species.

2) During a succession, the number of species ....., the community biomass ....., and the community's ratio of respiration to production ..... At climax, the rate of production is ..... the rate of respiration.

10.7 SUMMARY

- Succession occurs when a series of communities replace one another, as each community changes the environment to make conditions favourable for a subsequent community, and unfavourable for itself. The first plants to colonise an area make up the pioneer community. The final stage of succession is called the climax community. The stage leading to the climax community are called successional stages or seres.
- Primary succession occurs when plants colonise bare rocks or other areas where there is no soil. Secondary succession occurs when plants recolonise an area in which the climax community has been disturbed.
- When succession is brought about by living inhabitants, the process is called autogenic succession, while change brought about by outside forces is known as allogenic succession.

- Succession in which, initially the green plants are much greater is quantity is known as autotrophic succession; and the ones in which the heterotrophs are greater in quantity is known as heterotrophic succession.
- The basic processes of succession are more or less the same for any kind of succession. These processes are; nudation; invasion or migration; ecesis; aggregation; competition: reaction: and stabilisation — climax.
- Succession in aquatic ecosystems like pond begins with increased nutrient sediments, encroachment by shore plants, and a general increase in both numbers and kinds of organisms. The continued trend results in the pond filling in and later blending in with the surrounding terrestrial community.
- Succession in xeric habitat like a bare rock begins by pioneer plants. These establish on the substratum with hostile conditions, like deficiency of water, too much exposure to sun. By the activity of the pioneers, some soil is formed on the bare area. This area is subsequently colonised by various kinds of plants, and a considerable amount of soil builds. The overall xeric conditions change to mesic conditions.
- There are three popular models to explain the mechanism of succession. The facilitation model suggests that the species in the early stages of succession modify the habitat in a way that inhibits their own regeneration, but is suitable for the growth of species of the subsequent stages of succession. The toleranace model says that there is a competitive hierarchy in which the later species can outcompete earlier species and can also invade in their absence. The inhibition model suggests that during succession, all replacements are possible and much depends on who gets there first.
- Succession is characterised by the following: increased productivity, the shift of nutrients from the reservoirs, increased diversity of organisms with increased niche development, and a gradual increase in the complexity of food webs.

10.8 TERMINAL QUESTIONS

1) Give an example that illustrates each of the following: (Do not use examples given in the text).

   a) Primary succession

   .....

   .....

   b) Secondary succession

   .....

   .....

   c) Progressive succession

   .....

   .....

   d) Retrogressive succession

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   .....

2) Explain how primary succession on land differs from succession in a lake or pond.

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   .....

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   .....

3) Where would one expect to look for signs of secondary succession? What does secondary succession end?

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4) Essentially what determines the rate of succession in fresh water bodies?

.....

.....

.....

5) Imagine two volcanic areas, both the same size. In both areas, a fresh lava flow has spread newly formed rock over the land. One area is an island, far from land, and the entire island has been covered with lava. The second area exists in the middle of a large continent. Would succession occur faster on island or on the continent; or would the two be the same? Defend your answer.

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10.9 ANSWERS

Self-Assessment Questions

1) 1) b 2) a 3) b 4) c 5) c

2) 1) d 2) c 3) c, e, f, b, a, g, d

3) 1) facilitation, inhibition, tolerance
2) increases, increases, increases, equal

Terminal Questions

1) Write the examples from your experiences.

2) Primary succession on land occurs in areas, where there is deficiency of water, and the soil is not formed. Succession in this case proceeds from xeric to mesic conditions. On the other hand, succession in lake or pond proceeds from a situation where there is plenty of water and very less soil to the mesic conditions.

3) Secondary succession occurs in disturbed areas, where soil is often in place, eliminating the long soil building stages as seen in primary succession. Some plants like weeds grow profusely and their growth is not checked. As secondary succession progresses, the initial invaders are eventually replaced by plants from the surrounding community. Larger, fast growing trees block the sunlight and a new generation of shade-tolerant shrubs emerges below the conopy, eventually the lines between the area in succession and the surrounding community begins to fade. At this stage the last stage of secondary succession is reached.

4) The availability of nutrients determine the rate of succession in fresh water bodies. By the growth and development of different seres, the nutrient content in the ecosystem increases. The rate of succession is also enhanced if the nutrient supply is increased; such as in the case of eutrophication in ponds and lakes.

5) Succession would occur faster in area existing in the middle of the large continent. This is because, here all propagules or seeds of plants belonging to the different seres would reach much faster, establish and ultimately result in climax community.