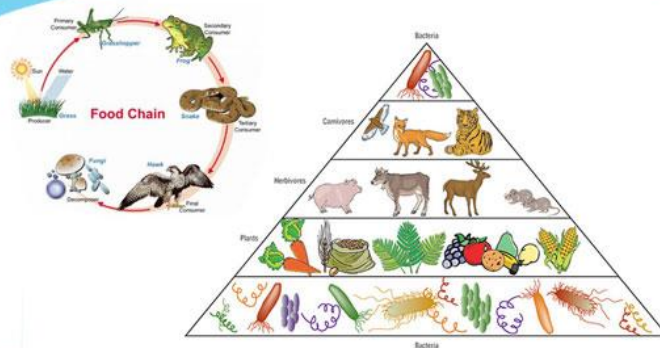


Subject: Environmental Sciences

**Production of Coursework
- Content for Post-Graduate Courses**



Paper No: 01 Ecosystem Structures & Functions

Module: 19 Ecological Succession – Part 1



Development Team

**Principal Investigator
&
Co- Principal Investigator**

**Prof. R.K. Kohli
Prof. V.K. Garg & Prof. Ashok Dhawan
Central University of Punjab, Bathinda**

Paper Coordinator

**Dr. Renuka Gupta, YMCA University of Science and
Technology, Faridabad, Haryana**

Content Writer

**Dr. Renuka Gupta, YMCA University of Science and
Technology, Faridabad, Haryana**

Content Reviewer

**Prof. V. K. Garg,
Central University of Punjab, Bathinda**

Anchor Institute



Central University of Punjab

Description of Module	
Subject Name	Environmental Sciences
Paper Name	Ecosystem Structure & Function
Module Name/Title	19. Ecological Succession – Part 1
Module Id	EVS/ESF-I/19
Pre-requisites	
Objectives	<ul style="list-style-type: none"> • To learn about process of ecological succession and ecosystem development. • To understand basic types of succession. • To learn about different steps and processes ecological succession. • To understand different Models of ecological succession. • To know about structural and functional changes during succession.
Keywords	Ecosystem, Ecological Succession, pioneer, climax, community, sere, seral stages, hydrosere, primary succession, secondary succession, autotrophic succession, heterotrophic succession, disturbance, xerosere, functional changes, models of succession.

Module 19: Ecological Succession – Part 1

Contents

1. Introduction
2. Type of Ecological Succession
3. Mechanism/Models of Ecological Succession
4. Structural and Functional changes during Succession

19. 1 Introduction

All ecosystems change in structure and function with time. Some changes are seasonal, e.g., rise or fall of a river and its effects on vegetation adjacent floodplain, seasonal growth and disappearance of plants in a forest, effects of stratification and mixing of water on plants in lakes and so on. Some other changes are long-term, progressive and non-cyclical which may result in a process “**Ecological Succession.**” It is a fundamental concept in ecology and refers to orderly and predictable changes in the community structure and function with time.

Environment is always changing with time by variations in climatic, physiographic factors or by interactions with existing species in an area. Each species in ecosystem has set of environmental conditions for its optimal growth and reproduction. As long as these conditions remain favorable, the particular species flourish in the environment. As the environmental conditions changes, they become optimal for other species and subsequently, first species may fail to flourish. In this way, a given community of organisms in an area is not permanently stable over time; rather it keeps on changing with the replacement of one community with another. The process of change continues until a stable community is reached which not only establishes itself in the given area, but also keeps on increasing in number by reproduction. All these changes are very orderly and predictable with time; the overall process is named as ecological succession. Thus, Ecological Succession may be defined as “**the orderly changes in community structure and function in an ecosystem with time mediated through the modifications in physical environment ultimately leading to a stable community over that area.**” Cowles (1899), Clements (1905, 1916) and many other early twentieth century botanists made significant contributions to establish the concept of succession.

Clements (1916) while studying plant communities defined succession as “*the natural process by which the same locality becomes successively colonized by different groups or communities of plants.*” As the process of succession proceeds, changes occur not only in the biotic community but also in physical environment and overall characteristics of the ecosystems changes in a holistic manner. Therefore, Odum (1969) preferred to designate the term as “**Ecosystem Development**” rather than ecological succession.

He elaborated the process of ecological succession in terms of the following parameters:

1. It is an orderly process of changes in species structure and function with time within a community. It is a directional and continuous process and thus, predictable.
2. It is a natural process and results from modifications in physical environment by the community species. These modifications may be brought by continuing struggle among species for physical factors (light and space) and resources for survival (energy and nutrients). Thus, the succession is a community controlled process even though the modifications in physical environment determine the patterns, rate of changes and development during the process.
3. It involves either change in abundance of dominant species or a complete replacement of species from immature to more mature and stable communities over a period of time.
4. It culminates in a stable ecosystem with a dominant species known as **climax** which is in more or less equilibrium with the surrounding environment.
5. The entire sequence of communities that replace one another in a given area is called as **sere** and the transitory communities are called as **seral stages** such as grass stage, herb stage, shrub stage, etc. The initial stage is called **pioneer** stage and is characterized by early successional pioneer plant community. The last or terminal stage is known as **climax**. The pioneer community may be replaced more easily by the next seral stage where as climax community is considered as more mature and stabilized stage of ecosystem.

Succession is a series of complex processes. There are three main causes of succession:

a) Initiating causes: these are climatic as well as biotic factors. The former includes landslide, volcanic activity, wind, soil erosion, etc. and the latter includes various activities of organisms. The

process of ecological succession is usually initiated by the formation of a bare area or habitat without any life form (e.g. by a landslide or lava flow) or formed from disturbance of an existing community (e.g. fires or land clearance).

b) Ecesis or continuing causes: these involve different processes like dispersal, migration, establishment, aggregation, competition, co-action, reaction, etc. which keep the pace of changes in community structure.

c) Stabilizing causes: According to Clements, climate is usually considered as one of the significant factor that causes stabilization of ecosystem.

19. 2 Types of Succession

Various types of succession have been grouped differently on the basis of different aspects as below:

Primary and Secondary Succession

On the basis of nutrient availability in the soil, succession is of two types: Primary and Secondary succession. **Primary Succession** starts in a newly formed area where environmental conditions are elementary, such as a bare area formed by lava flow, a new pond created by a landslide, sand dunes formation or bare rock surface formed by the retreating glaciers. The primary area contains no biological legacy, i.e., no vegetation, seed bank or organic matter. The area is not initially occupied by any community and the seeds or propagules for the first organism should arrive by immigration. For example, xerarch succession, beginning on a bare and dry land, imply a directional development from first stage “lichen” towards a mature and stable ecosystem, usually a “forest” (Fig. 19.1). Another example is formation of island from volcanic activity in ocean with pioneer species like bacteria, fungi and moss and followed by grasses, shrubs and trees in later stages.

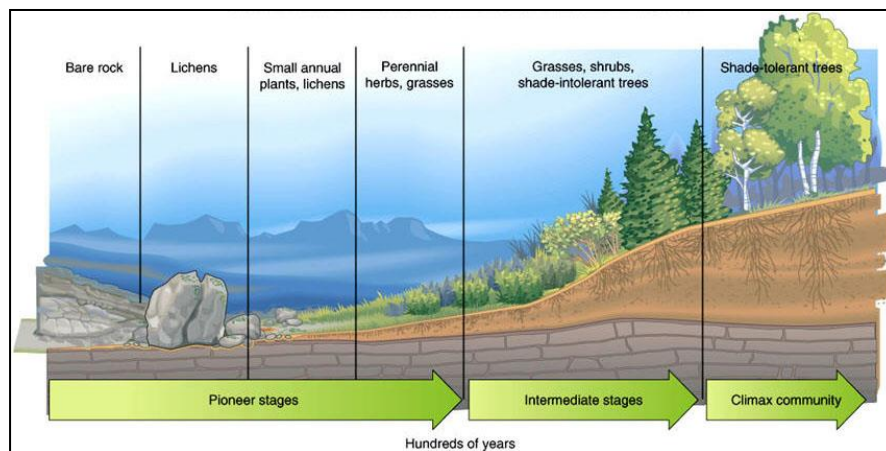


Fig. 19.1: Primary Succession

Source: <http://www.sciencescene.com/Environmental%20Science/02TheEnvironment&Ecosystems/02-Application.htm>

Secondary succession starts in an area previously occupied by a community, but now devegetated by some natural or human activities like fire, storms, tree cutting, disease outbreak, cultivation, biotic interventions, etc. After several years, some new community again occupies that area. It is called secondary succession (Fig. 19.2). The area is not having living matter above ground, but its substratum is built up with the nutrients, organic matter or propagules deposited by previously occupied community. Thus, the process of secondary succession is comparatively rapid than primary succession.

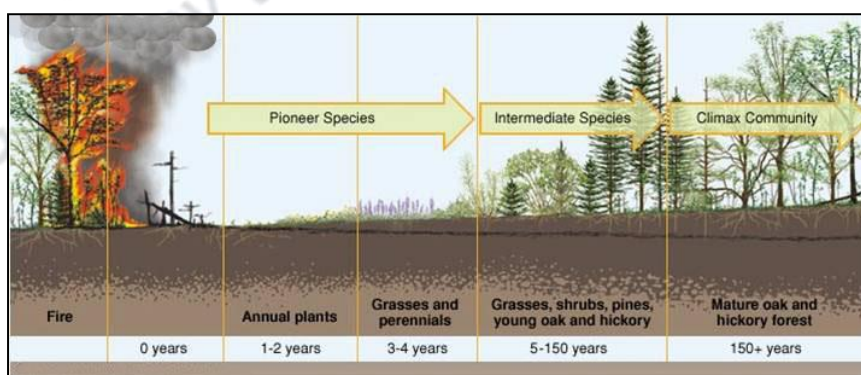


Fig. 19.2: Secondary Succession

Source: <http://www.sciencescene.com/Environmental%20Science/02TheEnvironment&Ecosystems/02-Application.htm>

Autogenic and Allogenic Succession

After the succession has begun, sometimes the community itself modifies its own environment which becomes unsuitable for that community, and its own replacement by new community takes place. This type of succession is known as autogenic succession, as it is self-made succession. In some cases, the replacement of existing community takes place due to some external force (e.g., fire or human activities) and not by the existing community. This is called as allogenic succession.

Autotrophic and Heterotrophic Succession

On the basis of successive changes in nutritional and energy requirements, succession is classified as autotrophic and heterotrophic succession. **Autotrophic succession** is characterized by the dominance of green plants and trees. It starts in a predominantly inorganic environment and energy flow is maintained indefinitely followed by increase in the organic matter content in the ecosystem. In this type of succession, rate of production (P) is more than rate of respiration (R). Initially primary producers are in majority but later on biomass of organisms increases and ratio of production and respiration remains one. The diversity of species increases with increase in organic matter content. In **heterotrophic succession**, heterotrophs dominate such as bacteria, actinomycetes, fungi and other consumers. It starts in a predominantly organic environment followed by progressive decline in energy content of ecosystem. Initially the rate of respiration is greater than production. For example, small areas of rivers and streams, which receives large amount of sewage or leaf litter.

Therefore, if the succession begins with $P > R$, it is autotrophic succession and if it starts with $P < R$, it is heterotrophic succession.

Hydrarch and Xerarch Succession

Depending upon the nature of environment where the process begins, the succession is hydrarch or hydrosere if it starts in substratum where water is in plenty, e.g., in ponds, lakes, streams, swamps, etc. It is xerarch or xerosere, if it begins in dry areas such as deserts, rocks, etc. Xerarch is sometimes classified in further groups - **the lithosere**: initiating in rocks, **psammosere**: on sand, and **halosere**: in saline soil. The succession starting in an area with moderate moisture conditions is called as **mesarch**.

19.3 Mechanism/Models of Ecological Succession

19.3.1 Clements Hypothesis

Clements, being the most influential ecologists to suggest the mechanism of succession, in *Plant Succession: An Analysis of the Development of Vegetation* (1916), stated the succession a universal process of community development. He believed firmly that climate was the main driving factor in determining the type of vegetation during succession. As per his philosophy, climates are like genomes, and vegetation is like an organism whose characteristics its genome determines. The final step in vegetation succession he referred to as a climax. Another major point in Clements hypothesis is that the entire vegetation develops together as a single unit like an organism. This is known as the **super-organism theory**. He considered climax community to be a super-organism and succession the embryonic development of that organism. As an organism, climax arises, grows, matures and dies. The climax is capable of reproducing itself and every time a climax is produced, the essential steps are similar. Thus, succession is orderly, predictable and developmental process. It represents the holistic view.

He recognized the following basic processes in succession (Fig. 19.3):

1. Nudation:

It is the formation of a bare area without any life form. It may be a primary bare area if it is a new geological formation or a secondary bare area if formed due to destruction of existing vegetation. It may occur due to topographic factors (soil erosion, landslide, volcanic activity etc.), climatic factors (glacier, drought, frost, fire etc.) or biotic factors (deforestation, cultivation, insect outbreak, agricultural practices, overgrazing, etc.).

2. Invasion:

It is invasion and successive establishment of species in the bare area. It has three stages: **a)**

Migration: In primary bare area, the seeds, spores or propagules of plants growing in adjacent areas arrive through dispersal by wind, water or animals. In secondary bare area, the propagules may already be present in the form of buried seeds or rootstocks - called as residuals. They are the pioneer stage of

succession. **b) Ecesis** - It is the process of successful establishment of the species as a result of their adaptation to new area. The seeds and spores germinate, grow into adult forms and then reproduce. **c) Aggregation** - It is the final maturation of colonizing species; that is the growth of the population of each individual species. As the species reproduce, their number increases and population grow denser.

3. Competition and Co-action:

As the species number and size increase, it leads to competition for water, space and food. There can be inter-specific or intra-specific competition. The species which do not succeed in competition will disappear and the species which succeed will establish in that area. The species interact and affect each other's life in various ways called co-actions.

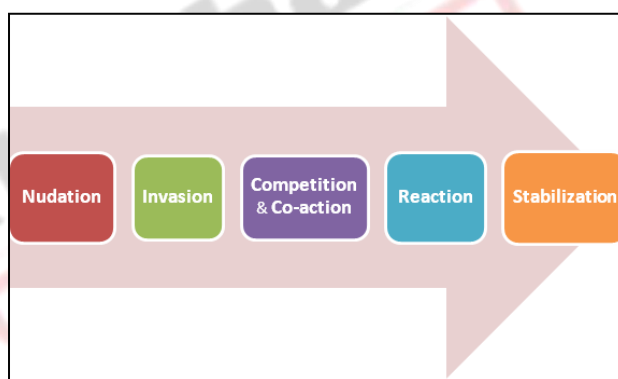


Fig. 19.3: Different processes of Ecological Succession

4. Reaction:

It is an important stage of succession and occurs between colonizing species and surrounding environment. The action of colonizing species changes the surrounding abiotic environment like soil, water, temperature and availability of nutrients. These changes make the place unfit for existing species and as a result they are replaced by a fit species.

For example, in a marshy area, reed swamp stage occur which includes amphibious plants with high evapo-transpiration rates. As a result, water availability in the area reduces and it will eventually become dry, thus becomes unsuitable for the existing plants. So, these autogenic changes by the plant species make them disappear and a new species which can grow in dry area will appear. This is termed

as reaction of surrounding environment. As a result, various communities form different seral stages. Each stage has its characteristic structure and species composition. A seral stage may last for 1 to 2 years or several decades.

5. Stabilization or Climax:

Eventually, a stage is reached when the final plant community becomes more or less stabilized for a longer period of time and maintains equilibrium with the surrounding environment. It is more mature, stable, self-maintaining and self-reproducing through development stages. Further, it is characterized by more or less equilibrium between gross primary production and total respiration, the energy captured from sunlight and energy released by decomposition, the uptake of nutrients and the return of nutrients by decomposition. This final stable community of the sere is the climax community. General process of succession with different developmental stages, viz., pioneer, seral and climax communities under the influence of physical environment, taking the examples of hydrosere and xerosere are shown in Fig. 19.4.

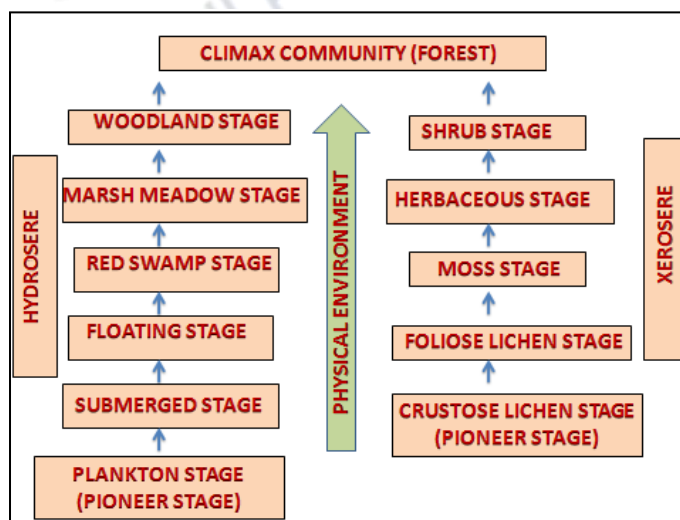


Fig. 19.4: Diagram to show process of succession with pioneer, seral and climax communities under the influence of physical environment, taking the examples of hydrosere and xerosere.

The concept developed due to Clements' work is termed as "Relay Floristics" (Egler, 1954). Species prepare area to make it more suitable for other species. As Clements indicated, if plant communities are super-organisms, they are capable of having a "strategy" as they hand over the site to the next community till a climax community is established. This is similar to a relay race where the runner at start of the race hands over the baton to next runner after covering a certain distance and so on till the final destination is reached.

19.3.2 Initial Floristic Model

Egler (1954) proposed 'Initial Floristics' concept by holding the view that most species are present right from the beginning of succession as seedlings or seeds (called as initial floristic pool), and succession merely represents changes in dominance over time. The groups of species grow and die depending upon their variable growth rates. The species dominating at climax stage can be present from the initial stages of succession; they may grow slowly and dominate the site later, replacing the earlier fast growing species.

Further, Drury and Nisbet (1973) stated that many species which characterize later successional stages are present but unremarkable at earlier stages. According to them, to begin with there are short-lived plants with high relative growth rate, then, herbaceous perennials with rapidly growing short-lived trees, followed by slowly growing long-lived trees. They viewed succession as a resource gradient process in which each species requires an optimum set of resources for growth or reproduction, and as the resource availability changes through time, species replacement occurs. This model holds true only for the secondary succession and not for primary succession.

19.3.3 Connell and Slatyer's Models

Three different models of ecological succession were proposed by Connell and Slatyer (1977) (Table 19.1).

Facilitation Model: The facilitation model suggests that the disturbed area is first exploited by certain pioneer species that are most capable of invading and establishing on the site. These initial species

modify the site, making it more suitable for invasion by other species, for example, by adding nutrients to the soil. Thus the early species 'facilitate' colonization by later species. Once established, the later species eliminate the early species through competition. These ecological dynamics proceed through different stages in which earlier species are eliminated by later species, until the climax stage is reached and there is no longer net change in the community.

Tolerance Model: The tolerance model suggests that sequence of species in succession is solely a function of life history. The later species can invade and grow to maturity despite the presence of early species. With passage of time, the early species will be excluded. Modification of environment by the early species has little or no effect on the arrival and growth of later successional species.

Inhibition Model: The inhibition model suggests that as long as early species persist undamaged or continue to regenerate, they exclude or suppress subsequent colonists of all species. Modification of the environment by the early species makes it less suitable for both existing species as well as arrival of later species. If external stresses are present, early colonists may be damaged (or killed) and replaced by species which are more resistant. For example, some plants are known to secrete toxic biochemicals into soil (allelochemicals), which inhibit the establishment and growth of other species. Eventually when the inhibitory species die, the later successional species can then establish in the area. These gradual changes eventually culminate in development of climax community.

Studies indicate that all of three models may be correct but applicable in different situations.

19.3.4 Individualistic concept

According to Individualistic Concept given by Gleason (1926), the succession is an extraordinary mobile process whose processes are not fixed and do not occur in a definite predictable ways. Moreover, it occurs due to individual response of different species. All communities are unique and ever changing due to internal species variations occurring as a result of disturbances, competition or new arrivals. Therefore, succession is considered as a multidirectional process with different pathways and endpoints.

Table 19.1: Three different models of ecological succession proposed by Connell and Slatyer (1977) – 1) Facilitation Model 2) Tolerance Model 3) Inhibition Model.

A disturbance develops a relatively large bare area		
Facilitation Model	Tolerance Model	Inhibition Model
Only certain “Pioneer species” are capable of becoming established in the bare area.	Individuals of any species in the succession could establish and exist as adults under the prevailing conditions.	Individuals of any species in the succession could establish and exist as adults under the prevailing conditions.
Modification of the environment by the early species in terms of availability of water, nutrients, etc. makes it more suitable for the arrival of later species. These early species ‘facilitate’ colonization by later species.	Modification of environment by the early species has little or no effect on the arrival and growth of later successional species.	Modification of the environment by the early species makes it less suitable for both existing species as well as arrival of later species.
Early species are eliminated through competition for resources with established later species.	Species sequence is solely a function of life history. The later species can invade and grow to maturity regardless of the presence of early species. With passage of time, the early species will be excluded.	As long as early species persist undamaged or continue to regenerate, they exclude or suppress subsequent colonists of all species.
The sequence continues until the current resident species no longer facilitates the invasion and growth of other species. This final stage is climax community.	Juveniles of species dominating at climax can be present from the earliest stages of succession.	If external stresses are present, early colonists may be damaged (or killed) and replaced by species which are more resistant.
This model follows Clement’s hypothesis described earlier.	The sequence continues until no species is there that can invade and grow in presence of the residents.	The model assumes that later successional species come to dominate the area simply because they live a long time and resist damage by physical and biological factors.

19.3.5 Three-Plant Strategy model

Grime (1979) recognized three categories of plants: **ruderals** - these species are fast growing, rapidly complete their life cycles, and produce large amounts of seeds, **competitors** - these species are able to outcompete other plants by efficiently tapping into available resources, and **stress tolerant** - these species are tolerant to shortages of resources (stress). According to his theory, ruderals form early successional stage and competitive species dominate later stages in succession. A superior competitor is capable of capturing all the resources, e.g. light as well as nutrients, at the same time more efficiently than its neighbours. The rapid growth of strong competitors translates into a rapid development of absorptive surface area which enables them to pre-empt both above and below ground resources. Stress tolerant species are not efficient in resource capture. Grime expanded his theory to describe secondary succession. At the onset, ruderals are established in a disturbed site. Then after, in a favourable environment, with potential for high productivity, competitive species play an important role and result in successive species changes. When conditions are stressful, (nutrient poor soil or climate change), competitive species play less important role and species changes are less. Stress tolerant species replace competitive species as stress increases.

19.3.6 Vital Attribute Model

According to Noble and Slatyer (1980), vital attributes are those attributes of a species which are vital to its role in a vegetation replacement sequence. These are: 1) the method of arrival or persistence of the species at the site during and after a disturbance 2) the ability to establish and grow to maturity in the developing community 3) the time taken for the species to reach critical life stages.

More than one biological mechanism or phenomenon may be responsible for a particular vital attribute displayed by a species, and for a given vital attribute the biological mechanisms may differ from species to species. The vital attribute reflects only the outcome of these mechanisms. These three attributes in turn can be related to (a) duration of their dormancy in the seed bank b) their age at first fruiting and c) their longevity as adults.

19.3.7 Resource Ratio Hypothesis of Competition

This model was proposed by Tilman (1985). According to him, inter-specific competition for resources and patterns of long-term supply of limiting resources are the key factors for plant establishment and growth in an area. Limiting resources give rise to competition among species and a resource ratio level is set, new species adapted to it succeeds. It suggests that if multiple species are competing for a single limiting resource, then species that can survive at the lowest equilibrium resource ratio level outcompete all other species. If two species are competing for two resources, then coexistence is possible only if each species has a lower resource ratio level on one of the resources. For example, two phytoplankton species may be able to coexist if one is more limited by nitrogen, and the other is more limited by phosphorus.

Generally, the major limiting resources for terrestrial habitats are soil nutrient - nitrogen and light. These resources are naturally inversely related, the habitats with poor nitrogen soils have high light availability and the habitats with nitrogen rich soils have low light availability. The life history of a plant should depend on the point along the nitrogen concentration: light gradient at which the plant is a superior competitor. To elaborate, when succession begins on a nitrogen poor soil, the species that has lowest nitrogen requirement may outcompete other species with high nitrogen requirements. As succession proceeds the soil may become rich in nitrogen, but light at the soil surface becomes limiting with increasing plant biomass. Thus, the early successional species which are superior competitors for nitrogen should be inferior competitor for light, while the later successional species would be superior competitor for light and inferior competitor for nitrogen. Because of trade-off, a good competitor for nutrients cannot be a good competitor for light, as they require contrasting traits – more biomass allocation to roots for more nutrient capture, and more allocation to shoots for light capture. This is the directional change in supply of limiting resources that result in directional replacement of one species by the other.

Tilman's model reflects that succession is tightly linked with interactions between plants. It is a complex process, and therefore cannot be described with one model for all situations and locations.

19.4 Structural and Functional changes during Succession

Odum and Pinkerton (1955) were the first to mention the functional shift of energy during the process of succession in addition to the changes in species structure and composition. Margalef (1968) documented this bioenergetic basis of succession and extended the concept. Odum (1969) has given the list of major structural and functional changes that are expected to occur during autogenic succession (Table 19.2). Twenty four different characteristics of ecological systems were analysed by contrasting the situation in early and later stages. The degree of absolute change, the rate of change, and time required to reach a mature and steady stage vary not only with different climatic and physiographic conditions but also with different attributes of ecosystem in the same physical environment. Further, the effect of external disturbances, as the case of allogenic succession, may change the trend of development.

The functional changes include variations of energy flow and nutrient cycling with time. As depicted from the table 19.2, in the early stages of autotrophic succession, the rate of primary production or gross photosynthesis (P) exceeds the rate of community respiration (R), so that the P/R ratio is greater than 1. Whereas in case of heterotrophic succession, e.g., a sewage pond with organic matter load where the bacteria and other heterotrophs are first to colonize, the P/R ratio is typically less than 1. In both cases, however, the P/R ratio approaches 1 as succession proceeds. The P/R ratio is a functional index of the relative maturity of the system. The energy fixed by the producers tends to be balanced by the energy consumption during maintenance (i.e., total respiration) in the mature or climax ecosystem.

So long as P exceeds R, organic matter and biomass (B) will accumulate in the system. As a result, the P/B ratio will tend to decrease or, the B/P or B/R ratio will increase. In such cases, the amount of standing crop biomass supported by the available energy flow increases to a maximum in the mature or climax stages. As a consequence, the net community production is more in young stages and small or zero in mature stages in an annual cycle.

Table 19.2: Different structural and functional changes occurring in an autogenic succession.

S No.	Ecosystem Characteristics	Trend in ecosystem development Early Stages → Later Stages Youth → Maturity
Energy Flow		
1	Gross Production (P)	Increases during early phase of primary succession; little or no increase during secondary succession
2	Net Community Production (yield)	Decreases
3	Community Respiration (R)	Increases
4	P/R ratio	P>R to P =R
5	P/B ratio	Decreases
6	B/P and B/R ratios (biomass supported per unit energy)	Increase
7	Food Chains	From linear food chains to complex food webs
Community structure		
8	Species Composition	Changes rapidly at first, then more gradually
9	Size of individuals	Tends to increase
10	Species diversity	Increases initially, then stabilizes or declines in older stages as size of individuals increases
11	Total Biomass (B)	Increases
12	Nonliving organic matter	Increases
Biogeochemical cycles		
13	Mineral Cycles	Become more closed
14	Turnover time and storage of essential elements	Increases
15	Internal cycling	Increases
16	Nutrient conservation	Increases
Natural Selection and Regulation		
17	Growth form	From r-selection (rapid growth) to K-selection (feedback control)
18	Life cycles	Increasing specialization, length and complexity
19	Symbiosis (Living together)	Increasing mutualism
20	Entropy	Decreases
21	Information	Increases
22	Overall efficiency of energy and nutrient use	Increases
23	Resilience	Decreases
24	Resistance	Increases

Source: Odum and Barrett (2005). *Fundamentals of Ecology*. Cengage Learning, New Delhi

The structural changes during progression of ecological succession mainly include changes in species composition and species diversity. Odum (1969, 1971) put forth the concept of ecosystem strategy. According to this concept, ecosystems tend to be in a state of homeostasis under the influence of unfavorable external environment. In an autotrophic succession, species diversity tends to increase, with an increase in organic matter content and biomass supported by available energy. Therefore, in a climax community, the available energy and biomass increases. But in a heterotrophic succession, rates of respiration always exceed production, so there is a gradual decline of energy. In nature, both these types of succession are going hand in hand. The autotrophic ones take nutrients from the soil, water and air, whereas the heterotrophic ones return them back to soil, water or air through decomposition of complex dead organic matter. Thus, succession reaches a stage where the amount of energy and nutrients taken by the producers from surrounding environment is returned in more or less similar amount to the environment by decomposition. This stage may be a climax stage. E.P. Odum has described this stage as a strategy of increased control of the physical environment toward achieving a homeostasis which provides maximum protection from environmental disturbances.

19.5 Summary

1. Ecological Succession is an orderly process of changes in community structure and function in an ecosystem with time mediated through the modifications in physical environment ultimately leading to a stable community over that area.
2. It is a directional, continuous process and predictable.
3. Succession is a series of complex processes. There are three main causes of succession: initiating causes (climatic and biotic factors), ecesis or continuing causes (dispersal, migration, establishment, aggregation, competition, etc.), and stabilizing causes (climate).
4. On the basis of nutrient availability in the soil, succession is of two types: Primary and Secondary succession. Primary Succession starts in a newly formed area not initially occupied by any community. Secondary succession starts in an area previously occupied by a community, but devegetated by some natural or human activities.
5. Autogenic succession is self-created succession, while allogenic succession takes place due to external forces.

6. Autotrophic succession is characterized by the dominance of green plants and trees. In heterotrophic succession, heterotrophs dominate such as bacteria, actinomycetes, fungi and other consumers. Therefore, if the succession begins with $P > R$, it is autotrophic succession and if it starts with $P < R$, it is heterotrophic succession.
7. Clements recognized five basic processes in succession – Nudation: formation of a bare area without any life form, Invasion: successful establishment of species in a bare area, Competition: competition among species for water, space and food, results in disappearance of failure species, Reaction: modifications in surrounding abiotic environment by the species, leading to a number of seral communities, and Stabilization; Eventually a stage is reached when the final plant community becomes more or less stabilized for a longer period of time in the equilibrium with the environment of that area.
8. Different botanists and ecologists have given different models to describe various factors responsible for the continuity of succession like climate, species characteristics, species interactions, etc.
9. Not only species composition and diversity varies with time during succession, functional changes including energy flow also takes place. .

References

- Clements, F.E. (1905). *Research methods in ecology*. Lincoln, NB: University Publishing Company.
- Clements, F.E. (1916). *Plant succession: an analysis of the development of vegetation*. Washington, DC: Carnegie Institution of Washington.
- Connell, J.H. and Slatyer, R.O. (1977). Mechanism of succession in natural communities and their role in community stability and organization. *American Naturalist*. 111: 1119-1144.
- Cowles (1899). *Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan*. University of Chicago Press, Chicago.
- Drury, W.H. and Nisbet, I.C.T. (1973). Succession. *Journal of the Arnold Arboretum*. 54 (3), pp. 331-368.
- Egler, F.E. (1954). Vegetation Science Concepts. I. Initial floristic composition – a factor in old-field vegetation development. *Vegetatio* 4: 412-417.

Gleason (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*. 53, 1-20.

Grime, J.P. (1979). *Plant Strategies and Vegetation Processes*. Wiley, Chichester, UK.

Margalef, R. (1968). *Perspectives in Ecological Theory*. University of Chicago Press, Chicago.

Noble and Slatyer (1980). The use of vital attributes to predict successional changes in plant communities to recurrent disturbances. *Vegetatio*. 43: 5-21.

Odum and Pinkerton (1955). Time's speed regulator, the optimum efficiency for maximum output in physical and biological systems. *American Scientist*. 43, 331.

Odum, E.P. (1969). The strategy of ecosystem development. *Science*. 164: 262-270.

Odum, E.P. (1971). *Fundamentals of Ecology*. Third Edition. Saunders College Publishing, Philadelphia.

Odum and Barrett (2005). *Fundamentals of Ecology*. Cengage Learning, New Delhi.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press. Princeton, New Jersey.



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