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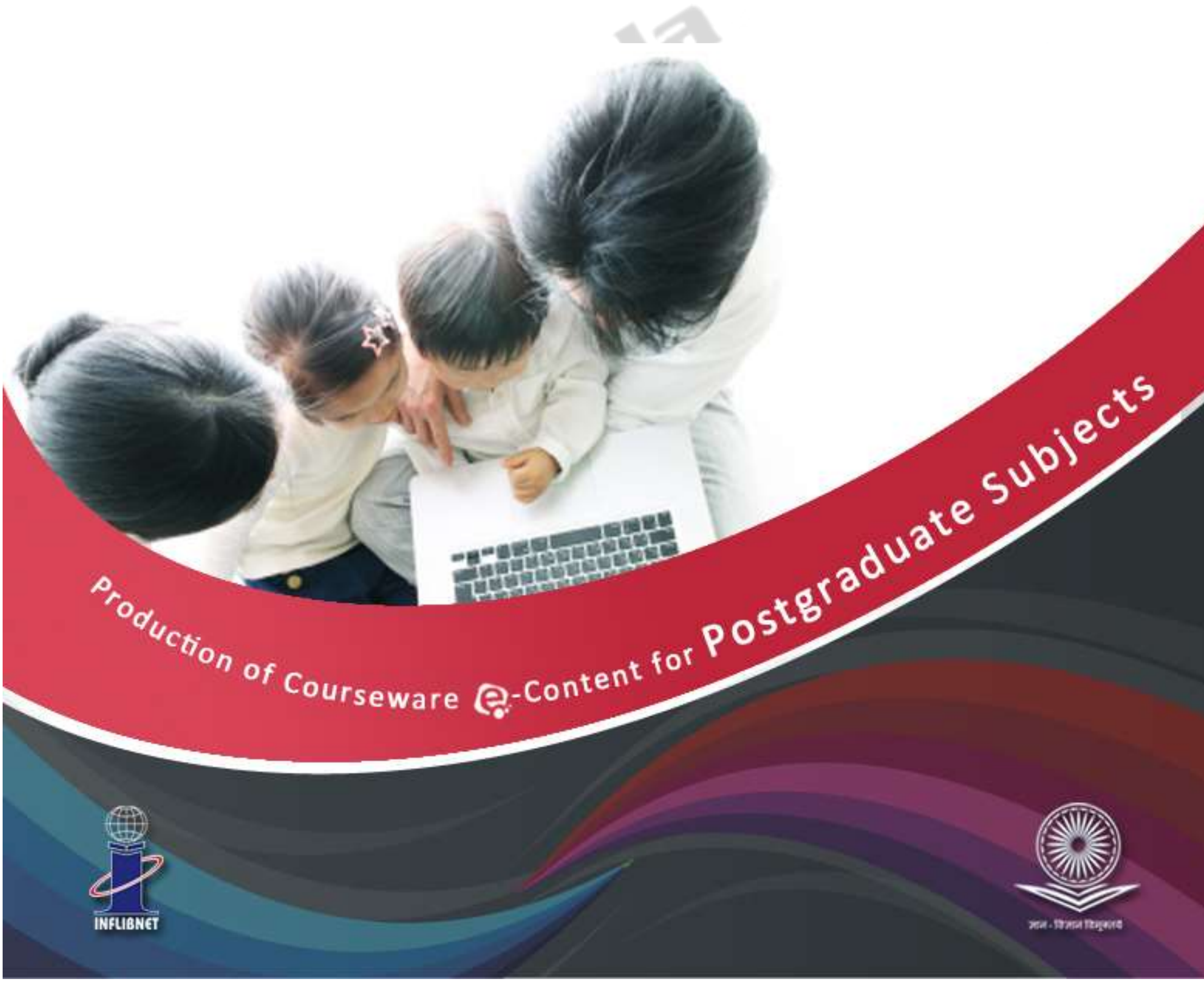

1. Details of Module and its Structure

Module Detail	
Subject Name	**<Botany>**
Paper Name	**<Ecology>**
Module Name/Title	**<Mechanisms of Succession>**
Module Id	
Pre-requisites	**<Basic knowledge about Succession and climax concept>**
Objectives	**<To make students aware about mechanisms of succession>**
Keywords	**Holistic concept /View, Relay Floristic theory, Facilitation model theory, Reductionist Concept/view, Initial floristic Composition Model, Tolerance model /theory,Inhibition Model, Mechanistic models, Resource Ratio Model, Individual Based Plant Model, General trends during succession**

Structure of Module / Syllabus of a module (Define Topic / Sub-topic of module)	
<Succession>	**Mechanisms of succession Holistic concept /View, Mechanistic models, General trends during succession**

2. Development Team

Role	Name	Affiliation
Subject Coordinator	**<Prof. Sujata Bhargava>**	**Savitribai Phule Pune University**
Paper Coordinator	**<Prof. NSR Krishnayya>**	**MS University Baroda**
Content Writer/Author (CW)	**< Prof. Nandita Ghoshal, Mr. Sunil Singh, Dr. MK Singh>**	**Banaras Hindu University, Varanasi**
Content Reviewer (CR)	**<Prof. NSR Krishnayya >**	
Language Editor (LE)	**<Prof. NSR Krishnayya>**	

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Mechanisms of succession

Mechanism of succession was although described earlier by Henry Thoreau (1860), Anton Kerner (1863) and HC Cowles (1899) yet it was FE Clements (1916) who first proposed a descriptive theory of succession and developed it as an ecological concept.

In general the two major concepts or views which explain the mechanism of succession in different situations are (i) Holistic Concept and (ii) Reductionist Concept. Although these models differ significantly in their predictions about the organizing principles of successional dynamics, it appears that none of them are correct all of the time.

I. Holistic concept /View

Holistic concept was first proposed by FE Clements in 1916.

Clements described ‘Climax vegetation’ as a ‘superorganism’ which arises, grows, matures and dies. It was analogous to the embryological development of an organism where seral stages are represented by various embryonic stages of this ‘superorganism’ i.e. each stage of succession represented a step in the development of a superorganism, the climax. This concept is also known as ‘Organismal theory’. The climax was an assemblage of vegetation that belonged to the highest type of vegetational community possible under the prevailing climate. The climax, according to Clements, is able to reproduce itself, “repeating with essential fidelity the stages of its development.” Each serial stage so modifies the environment that plants of that stage eventually can no longer exist there. Instead they prepare the site for the replacement plants of the next stage. The process continues until the vegetation arrives at the self-reproducing climax. That marks the end of succession. Each community occurs at a time and each community give way to the other community i.e. communities are discrete in time and succession is composed of several discrete seral communities. Course of succession thus can be predicted.

As per this hypothesis succession is driven by changes in attributes between pioneer and mature systems. Succession involves changes in the emergent properties that arise out of the organization of the ecosystem. Succession eventually leads to the formation of an emergent entity with unique characteristics involving nutrient flow, biomass accumulation, and species diversity (E. P. Odum 1969, 1983). Succession begins with the developmental stages of short-lived, shade-intolerant plant species and terminates with a mature stage dominated by long-lived, shade-tolerant species. Young stages so modify the environment that the existing community is replace by a more mature one, better able to exploit the changed environment.

There are two major theories based on this concept and they are:

a) Relay Floristic theory

b) Facilitation model theory

a) Relay floristic model /theory

This theory was proposed by Frank Egler (1954). As per this theory, groups of associated species marching together and disappearing through time as one group replaces another i.e. each community relays the site to the next community. The driving force behind succession is the reaction of the site to the plants leaving on it. Each seral stage so modifies the environment that plants of that stage eventually can no longer exist there. Instead they prepare the site for the replacement of plants of the next stage and the process continues until vegetation arrives at the self-reproducing climax i.e., the end of succession. Basic fundamentals of the theory are that of the total species which arrive in a bare area only a few are able to grow and mature. The early successional species modify the habitat in such a manner that it becomes more suitable for late successional species and less suitable for the early successional species.

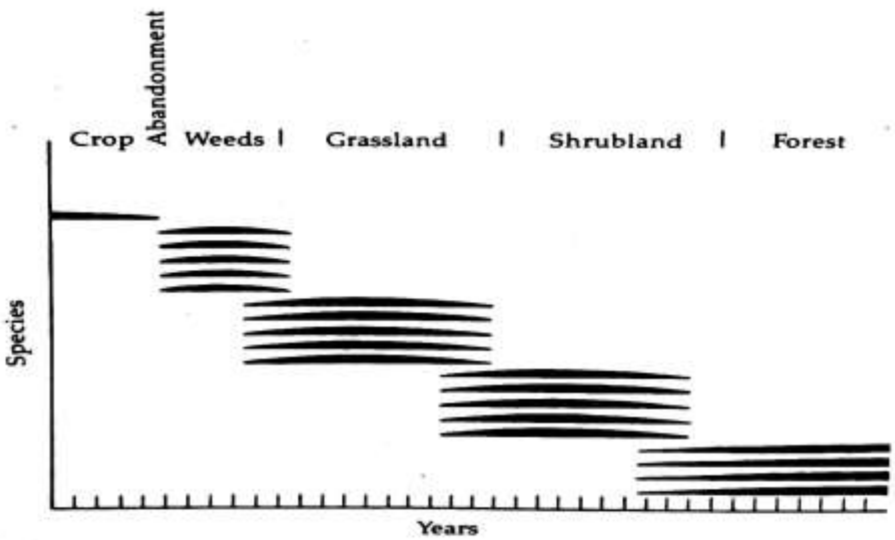

Fig. 1. Diagrammatic representation of the 'relay floristic model' of succession described in 'old-field succession'. The importance of the species at a given time is represented in terms of the thickness of the line.

b) Facilitation model theory

This theory was proposed by Connell and Slatyer (1977). The facilitation model, basically a Clementsian approach, is autogenic. Changes are brought about from within by the organisms themselves. Early stage species modify the environment and prepare the site for the later stage species, facilitating their success i.e. 1st seral stage facilitates the development of the next seral community. Facilitation model is seems to be most appropriate in explaining changes in many primary successions, but less so for secondary successions.

II. Reductionist Concept or Population approach:

Henry Gleason (1917) did not support the views of Clements on succession as he believed that the climax is not a superorganism. He thus proposed a new concept of succession and called it Reductionist Concept. As per this concept succession is a result of the independent responses to environmental conditions of individual species that constitute the community i.e. the individual responses of different species to environment. That is the reason this concept is often known asPopulation concept/approach. The course of succession is determined by the propagules of plants that arrived first on the site and were able to establish themselves under prevailing environmental conditions. Various types of interactions including competition among different species and the environment determine the course of succession. The resultant microenvironment, the potentiality of the plants to utilize various resources e.g. nutrients, moisture, light, space, etc. and other environmental inputs on the site regulate the occurrence of the final mature vegetation i.e. equivalent to climax. Course of succession thus cannot be predicted.

There are three major theories based on this concept and they are:

a) Initial floristic composition model or theory

b) Tolerance model or theory

c) Inhibition model or theory

The Initial floristic Composition model was proposed by Egler (1954) and is parallel to that of Relay Floristic model whereas Tolerance Model and Inhibition Model was described by Joe Connell and Ralph Slatyer, 1977 and were parallel to Facilitation model.

a) **Initial floristic Composition Model**

As per this model course of succession in many situations are governed by chance and differential longevity of the plants and thus in some way it is not predictable. Propagules of most species i.e. all of the pioneer species, many of the seral species and some of the climax species are present initially on site. Life history characteristics and competitive interactions will decide which species become dominant. Propagules of early successional community i.e. the pioneer species are generally quick growing and smaller or short in height whereas other seral species are larger, longer lived and growing slowly i.e. growing over a period of time and attain maturity later. Latter species which grow slow eventually dominates the site and out-compete the quick growing former species.

It is the chance and longevity of species that determine which species will dominate the community. Since the arrival of propagules is just a matter of chance, the course of succession in any way is not predictable. Therefore the site is not relayed from one community to another but there is a sorting out of species one at a time, based mainly on their longevity.

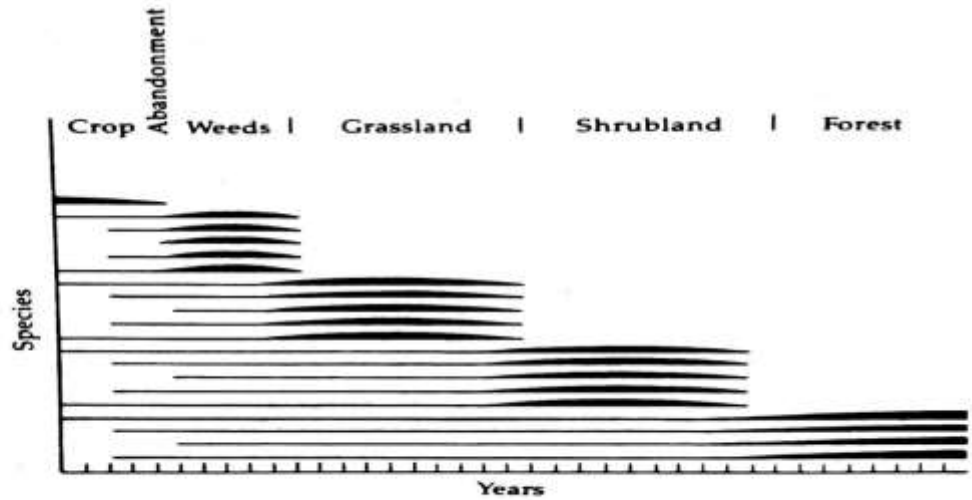

Fig. 2. Diagrammatic representation of the 'Initial floristic composition model' of succession described in 'old-field succession'. The importance of the species at a given time is represented in terms of the thickness of the line.

b) Tolerance Model

Of the species that arrive in the bare area any one of them can establish and survive as adult.

No initial selection pressure exists. The environment or habitat will be modified in such a manner that it becomes less suitable for the early species but will exert little or no effect on subsequent species. Juvenile of late successionals which invade the site can grow to maturity in continued presence of individual of early successionals. Later successional species are neither inhibited nor aided by species of earlier stages, i.e. they can grow to maturity in the presence of earlier stage species. Since the later species have a greater tolerance for the lower level of resources than the earlier ones. Such interaction (mainly competition) lead to community composed of those species which are most efficient in exploiting resources either by interference competition or by using resources unavailable to other species. In contrast with predictions of the facilitation model, the early occupants of the site do not change environmental conditions in ways that favor the subsequent invasion of later-successional species. Rather, with increasing time, the various species sort themselves out through their differing tolerances of the successionally increasing intensity of biological stresses associated with competition. In the tolerance model, competition-intolerant species are relatively successful early in succession when site conditions are characterized by a free availability of resources. However, these species are eliminated later on because they are not as competitive as later species, which eventually develop a climax community.Some of the course of secondary succession can be described by Tolerance model.

b) **Inhibition Model**

Of the species that arrive in bare area, any of them can establish and grow to maturity.No species is competitively superior to another, but the site belongs to those species that become established first and are able to hold their position against all the invaders. They make the site less suitable for both early and late successional species. As long as they continued to germinate they suppress or excludes the subsequent colonies of late arrivals i.e. as long as they live, they maintain their position. The ultimate winner is generally long lived plants, even though the early successional species may suppress later species for a long time. Such succession is not orderly and is less predictable. This model is purely Competitive in nature. Inhibition model can describe the course of succession of a number of secondary and primary successions.

The relatively vigorous development of ecological communities during secondary succession means that competition rapidly becomes an organizing force in the community, so there is an intensification of interactions by which organisms interfere with and inhibit each other. Aspects of these interactions are more readily explained by the tolerance and inhibition models.

The concepts and their models described earlier are mainly based on the shifting patterns of species dominance as a product of responses of interaction of plants and the environment both at temporal and spatial level. A new approach based on experimental and computer simulation studies has now being conducted to explain the temporal and spatial dynamics of communities and ecosystems and such approaches are described as Mechanistic models.

Mechanistic models

Mechanistic models are relatively new approach where both the direct observations and the computer simulations are used toexplain the temporal and spatial dynamics of communities and ecosystems. This approach is based on both the direct process by which an interaction viz. competition occurs and also the influence of various traits of individuals mainly physiology, morphology and life history, on the course of succession.There are major two models or hypothesis under this approach:

(1) Resource Ratio Model

(2) Individual Based Plant Model

(1) **Resource Ratio Model**

This model was proposed by Tilman (1985, 1988)

As per this model there are two major components which are considered as drivers of succession: (a) interspecific competition for resources, and, (b) interspecific competition for limiting resources e.g. soil nutrients and light. The course of succession is regulated by the changes in relative availability of resources through time and results in **resource gradient**. Community composition changes along the gradient as the availability of resources changes. Resource gradient ranges from habitats with low soil nutrients but with high availability of light at the soil surface generally represented by early successional sites to habitats with nutrient rich but low availability of light represented by late successional sites.

(2) Individual Based Plant Model

This model was explained by Huston and Smith (1987) and somewhat based on reductionist approach. As per this model succession is a population process involving competition.

The model is based on competition among individual plants to explain species replacement on a spatial and temporal gradient.Huston and Smith gave their species the following five specific traits:

(i) Maximum size (height and diameter at breast height)

(ii) Maximum age

(iii) Growth rate

(iv) Tolerance for shade

(v) Rate of seed production

They consider light as the limiting resource.

It assumes that both relevant environmental resources and the intensity of competition changes through time and among communities. This model is based on the following three presumptions:

(i) As plant grows they alter the environment in such a way that the relative availability of resource changes, altering the rules of competition success.

(ii) The physiological traits of plants prevent any one species from achieving maximum competition ability under all circumstances.

(iii) The interaction between (i) and (ii) produces an inverse correlation between certain groups of traits, so species that are good competitors under one set of environmental conditions are poor competitor under another.

Huston and Smith by applying computer simulation could illustrate the various patterns of vegetational change that result from different combination of traits.

General trends during succession

During the course of succession there are considerable changes occur in vegetation and ecosystem traits. EP Odum (1969) was first to document these changes and presented a table of 24 ecosystem traits which according to him changes significantly during the course of succession. MG Barbour, JH Burk and WD Pitts in 1987 identified 14 important vegetation and ecosystem traits that generally change during course of progressive succession. They consider the status of each trait as early and late stages of succession and not the pioneer and climax stages and are presented below in the form of a table.

S.N.	Trait	Early stages	Late stages
1	Biomass	small	large
2	Physiognomy	simple	complex
3	Leaf orientation	multilayered	monolayered
4	Major site of nutrient storage	soil	biomass
5	Role of detritus	minor	important
6	Mineral cycles	open (leaky) rapid transfer	closed (tight) slow transfer
7	Net primary production	high	low
8	Site quality	extreme	mesic
9	Importance of macronutrient	great	Moderate, dependent, less
10	Stability (absence or slowness of change)	low	high
11	Plant species diversity	low	high
12	Species life history character	r	K
13	Propagule dispersal vector	wind	animal
14	Propagule longevity	long	short

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