



Primary succession on bare rock, compressed into one view. Each community changes the soil, light and moisture in ways that make room for the next.

Ecological succession

How communities replace one another over time, from the first lichens on bare rock to a stable climax forest, and the theories that explain why.

- Pioneer stages
- Later seral stages and climax
- Water and hydrosere
- Disturbance and inhibition

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1. What succession is

Ecological succession is the gradual, directional change in the species composition of a community over time at a given place. Eugene Odum (1969) described it as an orderly process of community development that is reasonably predictable, results from the community modifying its own physical environment, and ends in a stabilised ecosystem.

Key terms

Term	Meaning
Sere	The whole sequence of communities from pioneer to climax at one site
Seral stage (seral community)	Each transitional community in a sere
Pioneer community	The first organisms to colonise a bare area (lichens on rock, phytoplankton in water)
Climax community	The final, relatively stable community in equilibrium with climate and soil
Ecesis	Successful establishment of a migrant species: germination, growth and reproduction
Nudation	Creation of a bare area
Ecotone	Transition zone between two communities, often rich in species (edge effect)

History of the idea

- **Eugenius Warming** (1895) described plant communities on Danish sand dunes.
- **Henry Cowles** (1899) read dune ages along Lake Michigan as a time sequence, founding the idea of succession in America.
- **Frederic Clements** (1916) saw succession as the development of a "superorganism" towards a single climatic climax.
- **Henry Gleason** (1926) countered with the **individualistic concept**: each species responds independently to the environment.
- **Arthur Tansley** (1935) proposed the polyclimax theory and coined "ecosystem".
- **Eugene Odum** (1969) listed the trends in ecosystem properties during development.
- **Joseph Connell and Ralph Slatyer** (1977) proposed three testable mechanisms.

2. Types of succession

Basis	Type	Description
Starting substrate	Primary	Begins on a surface never before occupied, with no soil: bare rock, lava, sand dunes, glacial moraine, new volcanic islands. Slow (often centuries to millennia)
	Secondary	Begins where an existing community has been removed but soil remains: abandoned fields, burnt or felled forest, flood plains. Faster (decades to a century), because soil, seeds and roots persist
Cause of change	Autogenic	Driven by the organisms themselves changing their environment (shade, litter, soil)
	Allogenic	Driven by external forces: silting, fire, climate change, grazing
Nutrition	Autotrophic	Dominated by green plants; organic matter accumulates
	Heterotrophic	Dominated by decomposers and consumers on an organic substrate; energy declines
Direction	Progressive	Towards greater biomass, complexity and diversity
	Retrogressive	Towards simpler communities, usually from disturbance (overgrazing, pollution)

Basis	Type	Description
Moisture of the starting habitat	Hydrosere (hydrarch)	Starts in water (pond, lake)
	Xerosere (xerarch)	Starts in a dry habitat: lithosere (bare rock), psammosere (sand)
	Halosere	Starts in saline soil or water (salt marshes)

Both hydrarch and xerarch series converge on a **mesic** (moderately moist) climax. Water-logged sites become drier as they fill; dry sites become moister as soil and litter build up.

3. The process: Clements's five steps

1. **Nudation:** formation of a bare area, by topographic causes (erosion, landslides, volcanic eruption), climatic causes (glaciers, drought) or biotic causes (clearing, fire, disease).
2. **Invasion:** arrival and establishment of species, in three steps: **migration** of seeds, spores and propagules by wind, water or animals; **ecesis**; and **aggregation**, the increase in numbers of established individuals.
3. **Competition and coaction:** as numbers grow, species compete for space, light, water and nutrients, and interact through predation, parasitism and mutualism.
4. **Reaction:** the organisms modify their environment: they build soil, add humus, change light and moisture. This makes the site less suitable for themselves and more suitable for others, and is the engine of autogenic succession.
5. **Stabilisation:** a climax community develops in equilibrium with the climate.

4. Hydrosere

A hydrosere begins in a freshwater pond or lake and ends in a forest. The main driver is the gradual filling of the basin with silt from runoff and with the remains of dead organisms, which makes the water shallower until it becomes land.

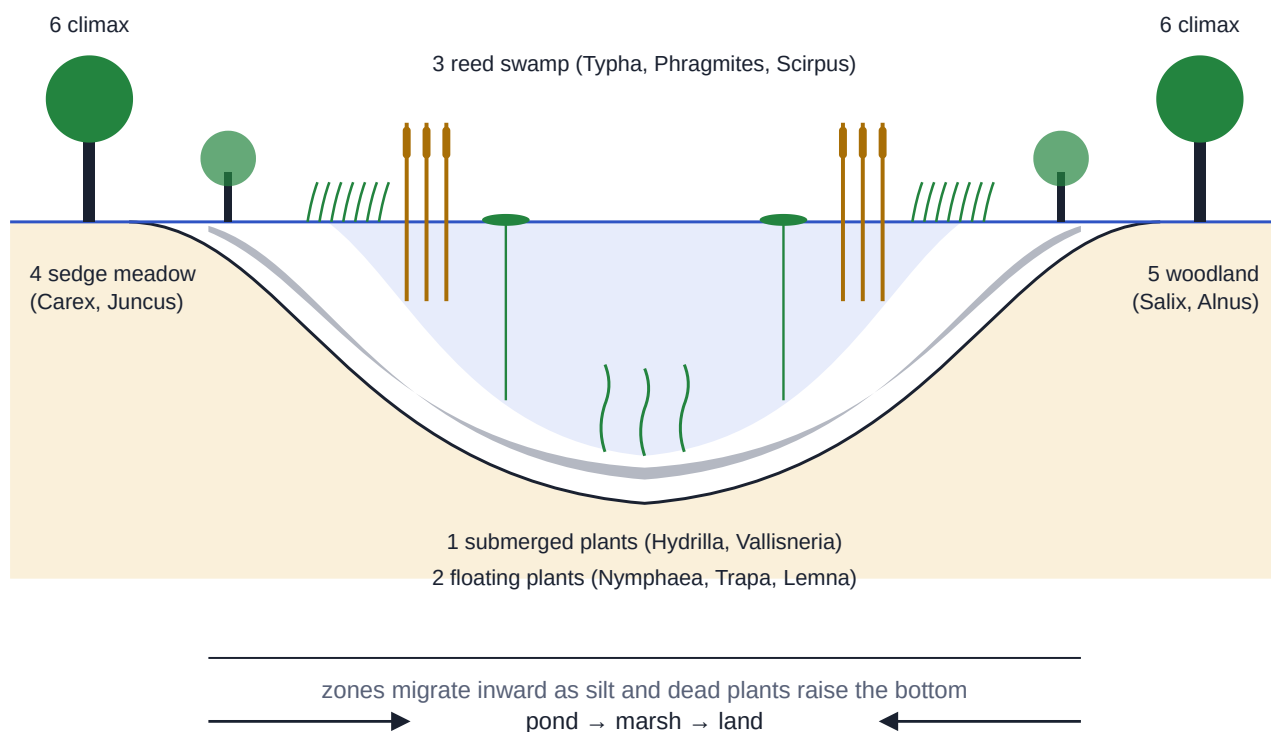


Figure 1. The hydrosere as seen in a lake cross-section. At any moment all the stages can be found side by side as concentric zones; over time each zone advances towards the centre until the lake disappears.

Stage	Typical organisms	Changes brought about
1. Phytoplankton	Diatoms, green algae, cyanobacteria; zooplankton	Organic matter from dead plankton begins to settle
2. Rooted submerged	<i>Hydrilla</i> , <i>Vallisneria</i> , <i>Potamogeton</i> , <i>Utricularia</i> , <i>Ceratophyllum</i>	Trap silt; decay raises the bottom
3. Floating	Rooted: <i>Nymphaea</i> , <i>Nelumbo</i> , <i>Trapa</i> . Free-floating: <i>Pistia</i> , <i>Eichhornia</i> , <i>Lemna</i> , <i>Salvinia</i>	Shade out submerged plants; water becomes shallower
4. Reed swamp (amphibious)	<i>Typha</i> , <i>Phragmites</i> , <i>Scirpus</i> , <i>Sagittaria</i>	Dense rhizomes and high transpiration; water table falls
5. Sedge meadow (marsh meadow)	<i>Carex</i> , <i>Juncus</i> , <i>Cyperus</i> , <i>Eleocharis</i>	Soil exposed in dry season; humus accumulates
6. Woodland	Shrubs and small trees: <i>Salix</i> , <i>Alnus</i> , <i>Cornus</i> , <i>Cephalanthus</i>	Drier soil; shade; more litter

Stage	Typical organisms	Changes brought about
7. Climax forest	Depends on climate: tropical rain forest, deciduous forest, or temperate forest	Mesic conditions, deep mature soil

Human nutrient pollution (**cultural eutrophication**) greatly speeds up the early stages: algal blooms and weeds such as water hyacinth (*Eichhornia*) can choke Indian ponds and wetlands within years.

5. Xerosere (lithosere)

A lithosere begins on bare rock: no soil, little water, extreme temperatures and strong light. Only a few organisms can survive there.



- 1. Crustose lichen stage:** the pioneers. Lichens such as *Rhizocarpon*, *Lecidea* and *Lecanora* form flat crusts and secrete organic acids (oxalic, carbonic) that slowly dissolve the rock surface. Their decaying remains mix with rock particles to form the first soil.
- 2. Foliose lichen stage:** leaf-like lichens (*Parmelia*, *Dermatocarpon*) trap dust and hold more water, shading out the crustose forms.

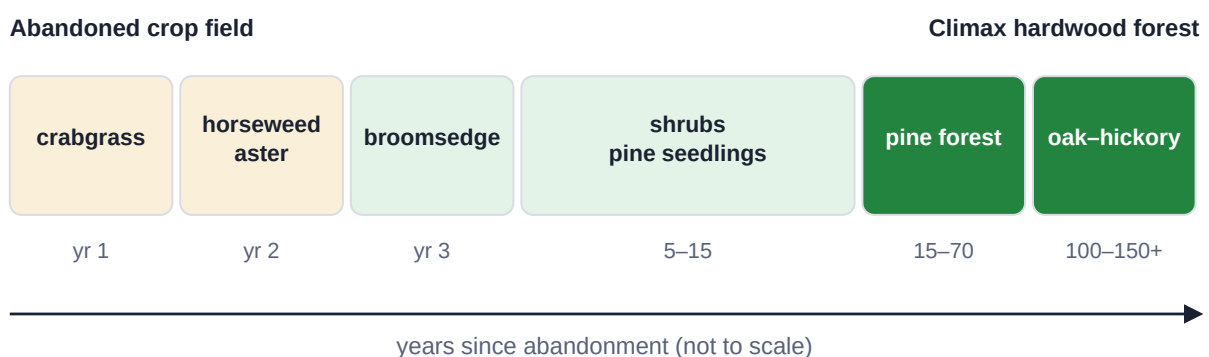
3. **Moss stage:** xerophytic mosses (*Polytrichum*, *Tortula*, *Grimmia*) form mats; their rhizoids penetrate the rock crevices and the soil layer thickens.
4. **Herb stage:** annual herbs appear first, followed by biennials and perennial grasses (*Aristida*, *Poa*, *Festuca*). Their roots break the rock further and add humus.
5. **Shrub stage:** woody shrubs (*Rhus*, *Zizyphus*, *Capparis*) shade out herbs; leaf litter enriches the soil.
6. **Climax forest:** trees take over as the soil becomes deep enough; the forest type depends on regional climate.

Psammosere and halosere

On sand dunes, sand-binding grasses (marram, *Ammophila*; in India *Spinifex* and *Ipomoea pes-caprae*) stabilise the sand, followed by herbs, shrubs and eventually woodland. In saline habitats, halophytes such as *Salicornia*, *Suaeda* and, along tropical coasts, mangroves (*Rhizophora*, *Avicennia*) start the sere, trapping silt and reducing salinity.

6. Secondary succession

Secondary succession follows disturbances that remove the vegetation but leave the soil. Because soil, seed banks, roots and nearby seed sources persist, it skips the slow pioneer stages and proceeds much faster.



Pines need open sun; their own shade prevents their seedlings, but oak and hickory seedlings tolerate it.

Figure 3. Old-field succession in the Piedmont region of North Carolina (studied by Oosting in the 1940s and Keever in 1950). A cleared cotton or maize field returns to hardwood forest in roughly 150 years.

Keever showed that each early stage has a reason: horsetweed (*Conyza*) germinates in autumn and dominates the first summer, but its decaying roots inhibit its own seedlings; aster then takes over, and in turn is out-competed for water by broomsedge (*Andropogon*), a drought-tolerant grass.

Examples in India include regeneration after **shifting cultivation (jhum)** in the north-eastern hills, recovery of forests after fire, and vegetation development on abandoned farmland. When the jhum cycle is shortened from 20–30 years to under 5, the sere cannot reach forest and degrades into bamboo or weedy scrub.

Feature	Primary succession	Secondary succession
Starting site	Never occupied; no soil	Previously vegetated; soil present
Pioneers	Lichens, mosses, algae	Annual weeds, grasses from seed bank
Soil formation	Must happen from scratch	Already there
Time to climax	Hundreds to thousands of years	Decades to about 200 years
Examples	Bare rock, lava flows, glacial moraine, new islands	Abandoned fields, burnt or logged forests, after floods

7. Classic field studies

Site	Event	What was learned
Glacier Bay, Alaska	Glacier retreat of about 100 km over 250 years exposed moraine of known ages	A chronosequence: pioneer mat plants and <i>Dryas</i> → alder thickets → Sitka spruce → spruce–hemlock forest. Chapin and colleagues (1994) showed nitrogen-fixing <i>Dryas</i> and alder raise soil nitrogen and organic matter (facilitation), but alder also competes with spruce seedlings (inhibition): both mechanisms act at once
Krakatau, Indonesia	1883 eruption sterilised the remaining island	Recolonised by ferns, grasses and then forest within 50 years; arrival order depended on dispersal (wind and sea first, animal-dispersed later)

Site	Event	What was learned
Surtsey, Iceland	New volcanic island formed 1963	Protected from human visitors; first vascular plant within two years; seabird colonies later added nutrients and sped up plant establishment
Mount St. Helens, USA	1980 eruption	Survivors ("biological legacies") such as buried roots and pocket gophers accelerated recovery; the nitrogen-fixing lupine was an early colonist

8. Mechanisms: Connell and Slatyer's models

Why does one community give way to another? Connell and Slatyer (1977) proposed three models, which differ in how early species affect later ones.

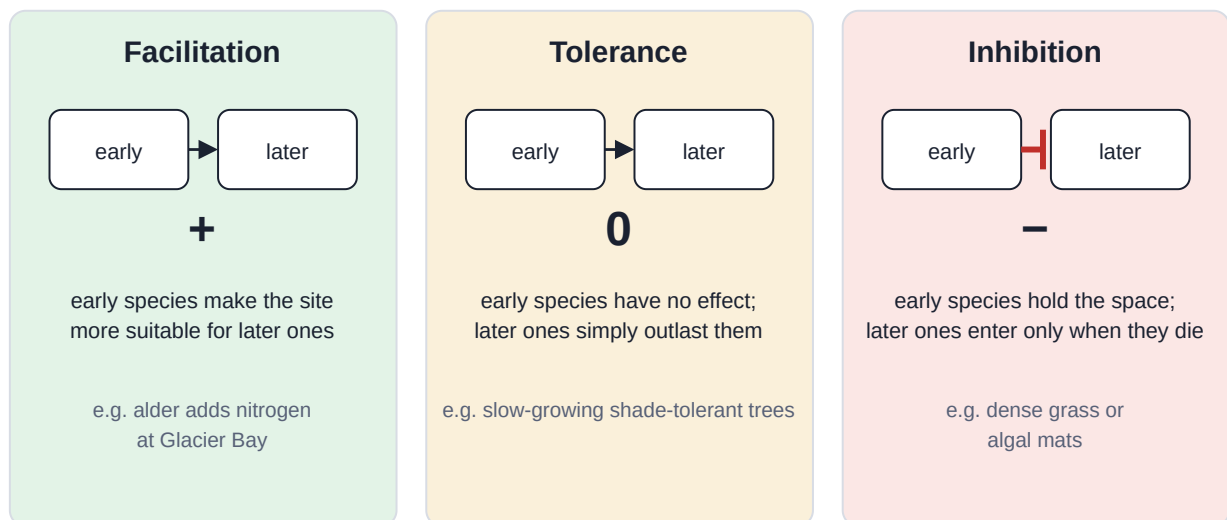


Figure 4. The three models. In real seres, different species pairs and stages often follow different models.

- **Facilitation** fits the classical Clementsian view: early species "prepare the way", as in primary succession where soil must be built.
- **Tolerance:** later species can establish at any time; they come to dominate because they tolerate lower resource levels (shade) and live longer.
- **Inhibition:** whichever species arrive first hold the site and resist invasion. Change happens only when they die or are damaged, so short-lived species are replaced by long-lived ones. Sousa's studies of boulders in intertidal zones found this pattern.

Other mechanisms emphasised since include differences in **life history** (colonisers are r-selected, good dispersers with rapid growth; late species are K-selected, competitive, long-lived), the **initial floristic composition** model (Egler, 1954: most species are present from the start and dominate in turn), and Tilman's **resource-ratio** hypothesis (changes in the ratio of soil nutrients to light drive replacement).

9. Trends during succession

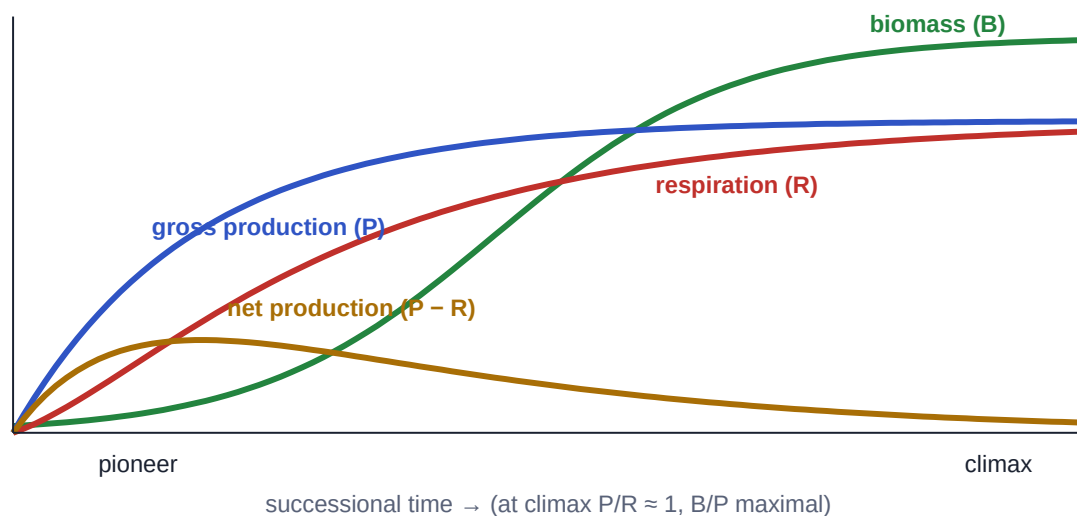


Figure 5. Energy flow during succession. Early on, production greatly exceeds respiration, so biomass accumulates. As the community matures, respiration rises to match production and net production falls towards zero: the climax is a steady state.

Ecosystem attribute	Developmental (early) stages	Mature (climax) stages
Gross production / respiration (P/R)	> 1 (or < 1 in heterotrophic succession)	≈ 1
Production / biomass (P/B)	High	Low
Biomass supported per unit energy (B/E)	Low	High
Net community production (yield)	High	Low
Food chains	Short, linear, grazing-based	Web-like, detritus-based

Ecosystem attribute	Developmental (early) stages	Mature (climax) stages
Total organic matter	Small	Large
Species diversity	Low	High (often peaks at mid-succession)
Structural stratification	Simple	Well-organised layers
Niche specialisation	Broad	Narrow
Size of organisms	Small	Large
Life cycles	Short, simple; r-selection	Long, complex; K-selection
Mineral cycles	Open; nutrients lost	Closed; nutrients retained in biomass
Role of detritus in nutrient regeneration	Unimportant	Important
Stability (resistance to perturbation)	Low	High
Entropy	High	Low

Odum summed this up as a shift from a strategy of **maximum production** (quantity) to one of **maximum protection** (quality, homeostasis). Agriculture deliberately holds ecosystems in the productive early state, which is why crops give high yields but need constant input to fight the return of succession.

10. Climax theories

Theory	Proponent	Main idea
Monoclimax	Clements (1916)	In any climatic region there is only one climax, determined by climate. All seres converge on it given enough time; other stable communities are temporary deviations
Polyclimax	Tansley (1935)	A region can have several climaxes, controlled by climate, soil, topography, fire or animals

Theory	Proponent	Main idea
Climax pattern	Whittaker (1953)	Communities vary continuously along environmental gradients; the climax is a pattern of populations matching a pattern of habitats, not a set of discrete types
Information theory	Margalef (1968)	Ecosystems develop towards maximum information (complexity, organisation) per unit of energy

Types of climax (polyclimax terms)

- **Climatic climax:** controlled by regional climate; the only true climax in Clements's view.
- **Edaphic climax:** held by soil conditions, such as waterlogged or saline soil.
- **Topographic climax:** held by slope, aspect or drainage.
- **Fire climax (pyric):** maintained by recurrent fire, such as savannas and some pine forests.
- **Disclimax (disturbance climax, plagioclimax):** maintained by human activity or domestic animals, such as grazed pastures, lawns, tea gardens.
- **Subclimax:** a long-lasting seral stage just before climax, arrested by some persistent factor.
- **Preclimax and postclimax:** communities of drier (preclimax) or wetter (postclimax) conditions than the regional climax, found in local patches.

When a disturbance diverts succession so that it does not reach the normal climax, this is called **deflected succession**, and the resulting community is a plagioclimax.

11. Heterotrophic succession

When succession happens on dead organic matter, the energy source is not renewed by photosynthesis but is steadily consumed. Communities change as the substrate is broken down, and the sere ends when the resource is exhausted rather than in a stable climax. P/R is less than 1 throughout.

- **Decaying log:** bark beetles and fungi first, then wood-boring insects and bacteria, then termites and earthworms, until the log becomes humus.
- **Hay infusion** (a classic lab exercise): bacteria bloom first, then flagellates and small ciliates such as *Colpoda*, then *Paramecium*, predatory ciliates and rotifers; in light, algae may eventually appear.
- **Animal carcass:** a predictable sequence of blowflies, flesh flies, beetles and mites, used in **forensic entomology** to estimate time since death.

12. Applications

- **Ecological restoration:** planting nitrogen-fixing pioneers (*Acacia*, *Prosopis*, *Leucaena*) to speed up recovery of mine spoils, degraded land and fly-ash dumps.
- **Forestry and range management:** controlled burning or grazing to keep useful seral stages.
- **Wetland management:** removing weeds and dredging to slow the hydrosere in reservoirs and lakes.
- **Agriculture and weed control:** weeds are early-successional species; farming is the continual resetting of succession.
- **Conservation:** many rare species depend on specific seral stages, so protecting them may require managed disturbance.
- **Climate change:** shifting climate may move the climatic climax itself, as seen in tree lines advancing upslope in the Himalaya.

13. Quick revision

Remember	Fact
Definition	Orderly, directional change in community composition over time, ending in a climax
Clements's steps	Nudation → invasion (migration, ecesis, aggregation) → competition and coaction → reaction → stabilisation
Hydrosere	Phytoplankton → submerged → floating → reed swamp → sedge meadow → woodland → forest
Lithosere	Crustose lichens → foliose lichens → mosses → herbs → shrubs → forest
Primary vs secondary	No soil vs soil present; slow vs fast
Mechanisms	Connell and Slatyer 1977: facilitation, tolerance, inhibition
Energy	$P/R > 1$ early (autotrophic), ≈ 1 at climax, < 1 in heterotrophic succession
Climax theories	Monoclimax (Clements), polyclimax (Tansley), climax pattern (Whittaker)
Climax types	Climatic, edaphic, topographic, fire, disclimax, subclimax

Remember	Fact
Classic sites	Lake Michigan dunes (Cowles), Glacier Bay, Krakatau, Surtsey, Mount St. Helens, Piedmont old fields

14. End-semester question bank

Long answer (10–15 marks)

1. Define ecological succession. Describe the different types of succession and the general process according to Clements.
2. Describe the stages of a hydrosere with suitable examples and a labelled diagram.
3. Describe the stages of a xerosere (lithosere) and explain how each stage modifies the environment.
4. Distinguish between primary and secondary succession, with examples. Describe old-field succession.
5. Explain the facilitation, tolerance and inhibition models of succession, with field evidence.
6. Discuss the trends in ecosystem structure and function during succession, as described by Odum.
7. What is a climax community? Compare the monoclimax, polyclimax and climax pattern theories.
8. Write an essay on the practical importance of succession in ecological restoration and resource management.

Short notes (5 marks)

1. Ecesis
2. Pioneer community
3. Reaction in succession
4. Reed swamp stage
5. Lichens as pioneers
6. Disclimax
7. Heterotrophic succession
8. Glacier Bay chronosequence
9. Autogenic and allogenic succession

10. Psammosere

Differentiate between

1. Primary and secondary succession
2. Hydrosere and xerosere
3. Autogenic and allogenic succession
4. Autotrophic and heterotrophic succession
5. Monoclimax and polyclimax theories
6. Early and mature stages of an ecosystem

Draw and label

1. Stages of a hydrosere in a pond cross-section
2. Stages of a lithosere
3. The three Connell-Slatyer models
4. Changes in biomass, production and respiration during succession

▼ Very short answer (2 marks), with answers

1. Who proposed the monoclimax theory? **F. E. Clements**
2. Who proposed the polyclimax theory? **A. G. Tansley**
3. Successful establishment of a migrant species is called? **Ecesis**
4. Pioneers of a lithosere? **Crustose lichens**
5. Pioneers of a hydrosere? **Phytoplankton**
6. Succession beginning in a saline habitat? **Halosere**
7. Succession on sand? **Psammosere**
8. P/R ratio at climax? **About 1**
9. Climax maintained by human activity? **Disclimax (plagioclimax)**
10. Who studied succession on Lake Michigan dunes? **H. C. Cowles**
11. Reed-swamp genus? ***Typha*** (also *Phragmites*, *Scirpus*)
12. Year of Connell and Slatyer's models? **1977**

15. Case-based MCQs

Ten hard questions that test application rather than recall. Choose an answer before opening the explanation.

Q1. A granite quarry abandoned 40 years ago in Jharkhand still has only lichen crusts and scattered mosses, while a paddy field abandoned for the same time nearby is now shrubland with young trees. The main reason for the difference is:

- A. The quarry receives less rainfall
- B. The quarry began primary succession with no soil, while the field began secondary succession with soil and a seed bank
- C. Lichens inhibit all later species
- D. The paddy field was fertilised by farmers

▼ **Show answer**

Answer: B. A freshly exposed rock face has no soil, so pioneers must slowly create it: this is primary succession, which is very slow. The abandoned field kept its soil, nutrients, seed bank and roots, so it began secondary succession and passed rapidly through the herb and shrub stages.

Q2. In a field experiment, researchers remove early-arriving grasses from plots. Tree seedlings then establish much faster than in control plots where the grasses are left. This result supports which model?

- A. Facilitation
- B. Tolerance
- C. Inhibition
- D. Monoclimax

▼ **Show answer**

Answer: C. If removing early species speeds up the arrival of later ones, the early species were holding the site against invasion: this is the inhibition model. Under facilitation, removal would slow later species down; under tolerance, removal would make little difference.

Q3. At Glacier Bay, spruce seedlings planted in alder thickets grow faster than those planted in the pioneer stage, yet their survival is lower inside alder thickets than in open alder-free plots on the same-aged soil. These findings show that:

- A. Only facilitation operates
- B. Alder both facilitates (by adding nitrogen) and inhibits (by competing for light and roots) spruce, so the models are not mutually exclusive
- C. Spruce is a pioneer
- D. Succession at Glacier Bay is heterotrophic

▼ **Show answer**

Answer: B. Chapin and colleagues found that alder raises soil nitrogen and organic matter, helping spruce grow, but alder shade and litter also reduce spruce establishment. Real successions often combine several mechanisms, and their balance can shift over time.

Q4. Measurements in a young forest show gross primary production of 20 000 kcal/m²/yr and community respiration of 12 000 kcal/m²/yr. What does this indicate?

- A. The ecosystem is at climax
- B. The ecosystem is in a developmental stage, accumulating biomass
- C. The ecosystem is in heterotrophic succession
- D. Productivity is declining

▼ **Show answer**

Answer: B. $P/R = 20\,000 / 12\,000 \approx 1.7$. A ratio well above 1 means the community fixes more energy than it uses, so organic matter and biomass accumulate, as in early autotrophic succession. At climax P/R approaches 1; in heterotrophic succession it is below 1.

Q5. A pond in West Bengal receives untreated sewage. Within ten years it becomes covered with water hyacinth, much shallower and fringed by *Typha*. This change is best described as:

- A. Retrogressive, autogenic succession
- B. Hydrosere accelerated by allogenic nutrient input (cultural eutrophication)
- C. Primary xerosere
- D. A stable edaphic climax

▼ **Show answer**

Answer: B. Sewage adds nitrogen and phosphorus from outside the system (an allogenic factor), fuelling rapid growth of floating plants whose decay speeds up silting. The pond is moving through the normal hydrosere stages, but far faster than it would naturally.

Q6. A grassland in a region with a climate suitable for forest remains grassland for centuries because cattle graze it continuously. When grazing stops, shrubs and trees invade within 20 years. The grassland was a:

- A. Climatic climax
- B. Edaphic climax
- C. Disclimax (plagioclimax)
- D. Postclimax

▼ **Show answer**

Answer: C. Its stability depended on a biotic disturbance maintained by people and livestock, not on climate or soil. When the disturbance was removed, succession resumed towards the climatic climax. This is a disclimax (plagioclimax), and the grazing had caused deflected succession.

Q7. Which of the following trends would you **not** expect as an ecosystem proceeds from early succession to climax?

- A. Nutrient cycles become more closed
- B. Food chains become more web-like and detritus-based
- C. Net community production increases
- D. Species become more K-selected

▼ **Show answer**

Answer: C. Net community production ($P - R$) is highest early and falls towards zero at climax, because respiration rises to match production. The other trends are all part of Odum's list of changes during ecosystem development.

Q8. A decaying tree trunk in a forest shows, over 30 years, a sequence of bark beetles, fungi, wood-boring beetles, termites and finally earthworms, until it becomes humus. Which statement about this sequence is correct?

- A. It is autotrophic succession ending in a climax
- B. It is heterotrophic succession with $P/R < 1$ throughout, ending when the energy source is used up
- C. It is secondary succession of the forest
- D. It is an example of the tolerance model only

▼ **Show answer**

Answer: B. The community depends entirely on stored energy in the dead wood. With no photosynthesis to replace it, the energy declines steadily, so respiration exceeds production ($P/R < 1$). The sequence ends when the substrate is exhausted rather than in a self-sustaining climax.

Q9. On the island of Surtsey, formed in 1963, plant colonisation was slow until seabird colonies became established; within their nesting areas plant cover and species richness then increased sharply. This illustrates:

- A. Inhibition by seabirds
- B. Facilitation by allochthonous nutrient input from animals
- C. Heterotrophic succession
- D. A fire climax

▼ **Show answer**

Answer: B. Seabirds carry marine nutrients (in guano, food remains and carcasses) onto the nutrient-poor lava, fertilising the soil. Their colonies became hotspots of plant establishment, a clear case of facilitation, where one group of organisms makes the site more suitable for others.

Q10. Two ecologists study vegetation along a mountain slope. One recognises distinct climax forests on north- and south-facing slopes and a separate climax on waterlogged soils; the other argues these all represent a continuous gradient of populations matching a gradient of environments. Their views correspond respectively to:

- A. Monoclimax and polyclimax
- B. Polyclimax and climax-pattern theory
- C. Climax-pattern and monoclimax
- D. Monoclimax and information theory

▼ **Show answer**

Answer: B. Recognising several discrete climaxes, each controlled by different factors such as aspect or soil, is Tansley's polyclimax view. Treating vegetation as a continuous pattern along environmental gradients, without discrete climax types, is Whittaker's climax-pattern hypothesis, rooted in Gleason's individualistic concept.

For further reading: Odum and Barrett, *Fundamentals of Ecology*; P. D. Sharma, *Ecology and Environment*; Smith and Smith, *Elements of Ecology*; Begon, Townsend and Harper, *Ecology*.