CHAPTER 20
Principles of Biogeography

Introduction
Vegetation appears to the casual observer as a rather haphazard and random element of the Earth’s surface. Yet, on closer study, it is organized into well defined unities which operate at specific scales. Thus formations at the large scale subdivide into vegetation types, plant communities and populations of species at successively smaller scales. The vegetation–environment complex or ecosystem has come to be recognized as the fundamental unit of study in biogeography and ecology. At successively smaller scales the units of study are the biosphere or ecosphere, the biome, the regional ecosystem, the local ecosystem and the single organism–habitat system.

The ecosystem performs the role of harnessing the potential energy of the sun and converting it into chemical energy stored in the organic molecules of plants and animals. The distribution of ecosystems is explained by environmental controls, with all individual species in the ecosystems having a range of tolerance of each environmental factor. The niche of each species is defined by this range, and also by the function of each species in the ecosystem. Climate controls the distribution of the major vegetation regions of the Earth, and there has always been a close association between the subdivision of the Earth into climatic regions and vegetation regions.

Chapter summary
Units and scales of study

- Vegetation occupies a pivotal position in the natural landscapes of the world, owing to the variety of important functions it performs.
- A plant community has obligate symbiotic relationships which, according to the ideas of Clements, allow the community to act as a super-organism.
- Vegetation can be studied at a range of scales, from major vegetation formations to individual plants.
- Rowe suggests an equivalent scale of ecosystems ranging in size from the entire biosphere to single organism–habitat systems.
- Many modern studies of vegetation and ecosystems aim at the plant community and local ecosystem level, partly because it is an appropriate level for field investigations.

The concept of the ecosystem

- The Oxford botanist Tansley coined the term ‘ecosystem’ to emphasize that organisms cannot be separated from their environment, with which they form one physical system.
- The ecosystems are of various kinds and can exist at several scales.
- Tansley regarded the ecosystem as a self-regulating entity, maintaining specific internal conditions despite fluctuations in external environments.
• An ecosystem can be visualized in the form of a model like an electrical circuit, by which energy derived from the sun is transferred by means of chemical processes through soil and vegetation up the food chain, and then by decomposition through the cycle again.

• The ecosystem model adds a scientific dimension to ecology, giving access to the laws of thermodynamics and mathematics and incorporating biogeochemical cycles.

Environmental factors

Six factors are essential for successful plant growth – light, heat, moisture, air, nutrients and physical support.

• The environment of plants must always be beneficent enough to sustain the three major plant processes of photosynthesis, respiration and transpiration.

• Environmental factors are not themselves independent but act as a series of interdependent controls, with many mutual interactions.

• It is helpful to distinguish direct controls (e.g. water, nutrients) from indirect controls (e.g. aspect, slope, altitude), which influence a direct control and hence influence the plant only indirectly.

• A synergistic effect is one which is greater than the sum of the individual effects from the controlling factors.

Limiting factors and range of tolerance

• Autoecology is the study of a single species and its environment, whereas synecology studies whole communities and the links between the constituent organisms.

• According to Liebig’s law of the minimum, plant growth is governed by the factor in shortest supply.

• Plants have a tolerance range for each environmental factor, consisting of a lower limit of tolerance, an ecological optimum and an upper limit of tolerance.

• The sum total of all environmental gradients is referred to as the ecological amplitude.

• Competition is a vital process governing plant distributions and occurs as interspecific competition between species, and as intraspecific competition between individuals of a species.

The concept of the ecological niche

• The ecological niche of a species is defined as the functional role of the species in its community and the position of the species along all environmental gradients (ecological amplitude).

• The fundamental niche is the full space which a species can occupy according to all its environmental gradients.

• The realized niche is a small space occupied by the species in the face of competition from all other species.
• The spatial distribution of a species is a good indicator of its realized niche, but the position of the species within the ecological pyramid must also be considered.

**Vegetation zones of the earth**

• The German biogeographer Walter produced a listing of nine climatic zones which in turn correlated with eleven vegetation zones (formations or biomes).

• Walter’s classification of vegetation zones is a zonal one, and the units can be broadly correlated with zonal soils.

• Within each zone, it is recognized that regional variations will occur, owing to oceanity, exposure to winds and the presence of mountain ranges.

• Within these regions, local variations in the vegetation type will be related to topography, aspect and soil types.

• The English biogeographer Holdridge has produced a flexible model for classifying world vegetation based on mean annual temperature, mean annual precipitation and the ratio of potential to actual mean evapotranspiration.

• The Holdridge system can be modified for different locations and for different climatic scenarios, which explains its popularity among climate modellers.

**Succession and climax**

• The process whereby one plant community is succeeded by another through time is referred to as ecological succession.

• The final end point of the succession is the climax community or ecological climax.

• A succession which commences on a bare, previously unvegetated surface is a prisere or primary succession.

• A succession which commences on an area which was previously under human use, but which has now been abandoned, is a secondary succession.

• Successions modified by human actions are plagioseres, and their status is termed ‘plagioclimax’.

**Classification of successions**

• Successions are classified into four types – psammoseres, lithoseres, hydroseres and haloseres – depending on the nature of the original land – or water – surface.

• The principle of competitive replacement means that a plant community in a succession creates conditions more and more favourable for a competitor, which will replace it.

• Clements did much to establish the principles of succession, and he divided successional processes into five types: nudation, migration, ecesis, reaction and stabilization.
• Concepts have developed since Clements’s work, so that now it is recognized that there are three successional models: facilitation model, tolerance model and inhibition model.

• Allogenic successions are driven by external controls whereas autogenic successions proceed largely on the basis of internally caused changes.

**Lithoseres**

• A lithosere starts on a bare rock surface, e.g. cliff, quarry or scree.

• The dominant ecological problem for plants is aridity on the soilless surface.

• Soil formation proceeds very slowly beneath successive plant covers of lichen, mosses, grasses and shrubs.

• Hydrolysis and chelation are the main weathering processes which produce soil, liberate nutrients and allow a larger water-holding capacity.

• The invasion of the proto-soil by soil fauna and soil micro-organisms greatly speeds up the rates of soil formation.

**Psammoseres**

• A psammosere starts on bare loose sand on the sea- or lake-shore.

• Aridity is a severe ecological problem, owing to the inability of the sand to hold water.

• Secondary ecological problems are nutrient deficiency, unstable surfaces, abrasive quartz grains and soil alkalinity on seashores.

• The role of greater humus content and increasing thickness of humus surface horizons is vital in regulating the succession.

• Other soil changes during the succession involve leaching and a decline in pH and salt content, an increase in the organic population of the soil, and an increase in the thickness of the A, E and B soil horizons.

**Hydroseres**

• Hydroseres start in freshwater lakes and pools, which become progressively shallower by processes of siltation.

• Rushes, reeds and sedges dominate the early stages of hydroseres, owing to their hydrophytic nature and ability to use oxygen even in waterlogged conditions.

• Waterlogged soils also pose problems of nutrient unavailability and the possible toxicity of a range of organic and inorganic chemicals.

• Some plants in the hydrosere, e.g. alder and bog myrtle, are able to fix atmospheric nitrogen and thus play a pivotal role in the hydrosere.

• Only when the soil level builds up significantly above the water table are the wide range of terrestrial shrubs and trees able to become established.

**Haloseres**

• Haloseres commence in salt water on the salt marshes of estuaries, bays or inland drainage areas.
• The zonation of plant communities in the halosere is governed largely by height above sea level, which in turn controls the length of time of inundation by saline water.

• Halophytes are plants which have ecophysiological mechanisms which enable them to tolerate the high salt content of saline soils in haloseres.

• Height above sea level allows more salt to be leached from the soil, leading to a lowering of pH, greater rooting depth for non-halophytes, and a lessening of the problems of waterlogging and anaerobism.

• The invasion of European salt marshes by the cord grass, *Spartina anglica*, in the past two centuries has greatly speeded up the rates of succession in haloseres.

**Ecosystem changes through succession**

• General changes during a succession involve increasing height of plants, increasing biomass, increasing stratification, though not usually increasing species diversity.

• Soils usually deepen, contain more humus and show more horizons.

• E.P. Odum has recorded changes in the basic ecology of communities during succession which involve many fundamental properties such as nutrient conservation, increasing role of detrivores, narrower niches, complex interactions and greater stability.

• High rates of net primary production in the early stages of successions become lower in the later stages.

• In the early stages of succession, the communities are dominated by fast-growing r-species, whereas slow-growing k-species dominate in the later stages.

**Theories of climax vegetation**

• Clements introduced the monoclimax theory of succession, which emphasizes the dominance of climate in his so-called climatic climax.

• Tansley supported the polyclimax theory of succession, emphasizing that other factors, e.g. soil or topography, may be dominant and may thus permanently prevent the climatic climax.

• Whittaker put forward the mosaic theory, which emphasizes the patterning of vegetation communities.

• Aubréville suggested the theory of cyclic climax, based on his observations in tropical forest vegetation and the processes of invasion and closure of gaps in the vegetation which he observed there.

• All these four theories of climax have points of relevance in understanding modern climax vegetation, though the work of Tansley would appear to be especially favoured.
CASE STUDY  Woodland History of the UK and Europe: Unresolvable Controversies?

The concept of equifinality in systems theory is very relevant to physical geography. It states that similar endpoints may be reached from different initial states and via different lines of development. This partly explains why physical geography is rich in debates about the genesis of landscape elements such as landforms, soils and vegetation communities. Debates over origins and evolutionary pathways can be civilised or acrimonious; they have been a feature of the history of physical geography.

The history of woodlands in the UK is an area of knowledge rich in hypothesis but short on proof. Figure 20.14 shows the extent of wildwood in 4000 BP just at the beginning of the widespread clearances by the first farmers. The woodland provinces of this map denote the principal species of woodland tree, but not their density of coverage. One can ask the question: was it wall-to-wall forest, as Sir Arthur Tansley (1939) claimed, or was it more open woodland, something more like a parkland savanna of slowly shifting groves and wide expenses of grass, kept open by large herds of big grazing animals, as proposed by Frans Vera (2000)?

The problem is usually discussed in the context of the Oak-Hazel province of the north and west of England and Wales which also came to dominate much of the south and east after lime declined relatively from c2500 BP onwards. Vera concludes that oaks can only regenerate in light, thorny thickets away from grazing animals, where they will eventually produce an oak grove. Oaks did not regenerate beneath themselves, but their acorns were carried to other groves in the savanna by woodland fauna such as birds and squirrels. Eventually the grove would collapse through senescence (old age), animals would be able to get in as it became grass, and the cycle would begin again. Oak and hazel require light to flower and fruit. Vera gives examples from across Europe of oaks failing to reproduce in present-day forests, which he believes to be due to the exclusion of grazing animals to prevent browsing damage.

Rackham (2007) presents an opposing view, and gives examples of oaks regenerating in the Middle Ages in Britain. He believes that oaks were able to reproduce successfully within existing woods prior to the arrival of American oak mildew early in the 20th century, which made oaks need more light than previously. Smout (2007) believes that there is a middle-ground in this debate, and that the effects of human activities are being underestimated in the ecology of the wildwood. Mesolithic hunter-gathers probably enlarged grassy areas for grazing animals by clearing and burning, practices which also encouraged nuts and berries on the trees of woodland edges. Also, the ancient practice of coppicing woodland for fuel and small timber would have had a great effect on light levels. The controversy is covered in many unknowns, but Rackham agrees that “the numbers, habits, tastes and effects of wild beasts are the most important unanswered question.”

References
One of the difficulties in studying the ecological history of woodlands is to know (a) the influence of human activities and (b) the intensity of grazing by animals. Figure 1a shows coppicing in Grass Woods in Wharfedale, North Yorkshire. Coppicing is a form of woodland management that takes advantage of the tendency of deciduous trees to regrow from the stump after felling, and became much more common from the 14th century onwards. Coppice woods were felled on a rotation to produce a regular crop of poles, and the woods were enclosed against stock to prevent damage to the young growth. Figure 1b shows red deer (*Cervus elaphus*) grazing on the Isle of Arran, Scotland. Deer were important features of the Medieval economy and landscape in Britain. The British natural wildwood had a plethora of grazers and browsers, but the hunt and wolves kept down numbers, so that no one place became overgrazed. Nowadays the high density of red deer is regarded as the main factor accounting for the lack of regeneration in Scotland’s native woodlands.

Source: Ken Atkinson

### Essay questions

1. To what extent can world vegetation patterns be explained by a study of world climatic types?
2. With reference to two contrasting world biomes, discuss in each case how environmental factors limit vegetation growth, and describe some of the adaptations made by plants to cope with the conditions.
3. Explain the factors which influence the range of tolerance of the following species, at the regional and local scales:
   a) oak (*Quercus robur*)
   b) heather (*Calluna vulgaris*)
   c) bracken (*Pteridium aquilinum*)
   d) the otter (*Lutra lutra*)
   e) the polar bear (*Thalarctos maritimus*)

### Discussion topics

1. Discuss and illustrate how the ecological concepts of *competition*, *range* and *niche* are related in the real world.
2. For the different types of succession (psammoseres, lithoseres, hydroseres, haloseres), discuss how human activities can influence the successions and their endpoints.
3. Discuss, with examples, how different models explain how climax vegetation can be formed. What do these models tell us about the nature of the wildwood of the British Isles prior to its clearance for farming?
4. What ecological lessons can be learned from the work of Robert J. Whittaker on the re-invasion of the island of Krakatao, Indonesia, by plants and animals since 1883?
Further reading


Archibold, O. W. (1995) Ecology of World Vegetation, London: Chapman & Hall. An up-to-date textbook on world vegetation regions and their flora. Clearly written and well illustrated. The approach is ecological with the emphasis on present-day processes. A modern treatment of the classical models of vegetation succession will be found in chapter 1, and there are examples of successions from different biomes throughout the book.


**Web resources**

This Department of Environment, Food and Rural Affairs (DEFRA) website discusses the policy of ‘managed retreat’ or ‘managed realignment’ for coastal ecosystems in England.

http://www.english-nature.org.uk/livingwiththesea
A major statement of the policy towards coastal ecosystems by the chief government adviser on wildlife matters, English Nature (the forerunner of the present Natural England).

http://www.naturalengland.co.uk
Natural England is the present-day successor to the former English Nature. It manages National Nature Reserves (NNRs), and carries out research in ecology and biogeography, and advises Government in England.

http://www.snh.org.uk
Scottish Natural Heritage maintains the network of National Nature Reserves in Scotland, and carries out research into ecology and biogeography. It is the foremost Government adviser on Scottish wildlife.