3.1

The Ecosystem Concept

Experimental stand of beech trees "B1" in Solling. The experimental site was important in the International Biological Program (IBP). It was the first time that all the fluxes in a terrestrial forest ecosystem were investigated. Methods developed in the years 1965–1975 at this site served as a model for the global work of the IBP (Ellenberg 1971; Ellenberg et al. 1986). Photo E.-D. Schulze

Recommended Literature

To understand the processes taking place in the ecosystem the following literature is recommended:

- Brady and Weil: Elements of the nature and properties of soil, 2nd edn. Prentice-Hall, Englewood Cliffs, New Jersey, 2004
- Schlesinger: Biogeochemistry. Academic Press, London, 1997
- Schulze: Flux control in biological systems. Academic Press, San Diego, 1994
- Schulze: Carbon and nitrogen cycling in European forest ecosystems. Ecol Studies vol 142. Springer, Berlin Heidelberg New York, 2000.

In previous chapters the focus was on the responses of cellular processes (Chap. 1: Stress physiology) and the use of resources by individual plants (Chap. 2: Whole plant ecology). In the following, these responses will be related to conditions where plants:

- do not grow on their own but form stands, i.e. they compete with individual plants of the same species (perhaps even of the same rhizome) or with other species,
- are subject to use by other organisms (herbivory, pathogens),
- rely on resources and conditions which arise from the activity of other species. This concerns particularly feedback supply of nutrients by microorganisms from dead organic matter into forms which can be used by plants.

The botanical analysis of these diverse interactions deals with the temporal and spatial dynamics of vegetation (history of vegetation, distribution of plant species, competition and succession). This will be discussed in Chapter 4: Synecology. However, there are also processes dealing with the turnover and the distribution of resources at certain sites. This "ecosystem aspect" will be discussed in this chapter.

By moving from the level of the individual plant to the level of material turnover at a site, the following conditions are changed:

- the reference system, and
- the availability of resources.

Reference system: Turnover no longer depends on the concentration (g g^{-1} or mol g^{-1}) of material in certain organs or individual plants, but on the use of the habitat where the ground surface area is the only constant reference (g $m^{-2}{}_{ground}$ or mol $m^{-2}{}_{ground}$) based on which air and ground surface area may be used by different organisms. The density of individuals and the biodiversity are just as important and variable parameters in considering turnover per ground surface area as is turnover in different partial systems which relate to the ground area and are interconnected. These partial systems range from the living plant cover, via litter, to soil organisms. They may be individually or as a whole connected laterally with neighbouring systems.

Availability of resources: New system characteristics become important with the focus on the ground area of the stand. The plant does not exist on its own and independently in the space, but is incorporated into a complicated structure where the resources are also turned over by neighbours and made available, within limits, by soil organisms. The limitations of space also limit the use of external resources (light, water, CO_2).

3.1.1

What Is an Ecosystem?

The understanding that, at the level of the vegetation, additional higher order parameters were determined by the system itself led to the introduction of the term "ecosystem". Tansley (1935) realised, in his definition of the term, that it is not a description of a symbiosis or parts of a super-organism, but the interaction of plants and animals with the physical-chemical environment. Because of the importance of the basic concepts describing the development of the term "ecosystem", the original text is cited here:

I have already given my reasons for rejecting the term "complex organism" and "biotic community". Clements' earlier term "biome" for the whole complex of organisms inhabiting a given region is unobjectable, and for some purposes convenient. But the more fundamental conception is, as it seems to me, the whole system (in some sense of physics), including not only the organism complex, but also the whole complex of physical factors forming what we call the environment of the biome – the habitat factors in the widest sense. Though the organisms may claim our prime interest, when we are trying to think fundamentally, we cannot separate them from their special environment, with which they form one physical system.

It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth. Our natural human prejudices force us to consider organisms (in the sense of biologists) as the most important part of these systems, but certainly the inorganic "factors" are also part – there could be no system without them, and there is constant interchange of the most various kinds within each system, not only between the organisms but between the organic and inorganic. These ecosystems, as we may call them, are of the most various kinds and size. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom.

Ecosystems Are Thus Networks of Interrelations Between Organisms and Their Environment in a Defined Space

In this definition (1) boundaries of ecosystems and (2) their compartmentalisation remain unresolved. It is not resolved (3) whether new system characteristics occur which concern the system as a whole. Occasionally, ecosystems are defined as networks of interrelations without reference to space. In these cases, too, the interaction between organisms becomes only critical within the limitation of space.

3.1.2

Boundaries of Ecosystems

The size of an ecosystem is not pre-defined. The region should be uniform regarding the biogeochemical turnover, and contain all fluxes above and below the ground area under consideration. Likens (1992) considers river catchment areas as basic units for ecosystems within regional spaces, as material balance may only be completely quantified within such region. However, a river catchment area is subdivided into regions near brooks and those away from them and have, per ground area, very different turnover if peaty river valleys and dry woodlands are considered, for example. Considerable turnover occurs also in the flowing water itself, so that the balance of regions away from the flowing water appears almost impossible. River catchment areas integrate very heterogeneous parts of the region and would thus to be too wide a demarcation to be valid as a basic unit of ecosystems. The opposite extreme would be to consider a rotting tree in a forest as an ecosystem.

The limits of an ecosystem must, clearly, extend so far that the essential parts of material turnover per ground area (e.g. carbon assimilation, nitrogen mineralisation, formation of ground water, etc.) are taken into account quantitatively. A rotting tree trunk is, considered from this point of view, only a partial system within a forest. Only the total turnover describes the characteristics and limits of, for example, a forest ecosystem. This is independent of the fact that some organisms (migrating birds) also have influence beyond these limits or that partial areas of the system possess their own dynamics.

3.1.3 Compartmentalisation

The division of ecosystems into different compartments depends on the question posed. The following divisions appear, amongst others, sensible:

- Above-ground and below-ground compartments: This division separates autotrophic and heterotrophic processes. In addition, it is possible to subdivide into soil horizons, and stems, branches and leaves. This classification describes material fluxes and separates the ecosystem regarding atmosphere and groundwater.
- Trophic level: Producers, consumers and decomposers describe energy flux.
- Functional groups: Groups of species which behave similarly regarding certain characteristics are often considered together (e.g. nitrogen-fixing plants, insects sucking phloem, parasites, and many others). They may reflect important interfaces within the trophic level.
- Structural characteristics: The structure of vegetation is particularly important in the coupling of exchanges of vegetation with the atmosphere. The division into trees, shrubs and herbaceous plants is important here.

3.1.4 System Characteristics

The network of interrelations is complex, i.e. it is determined by a multitude of factors and interactions. They are far away from an equilibrium and undetermined, i.e. there is no goal for certain dynamic change. Ecosystems behave linearly only within a short time span. Because there are no closed systems, there are always irregularities. Thus ecosystems may "break down" and make space available for new compositions of species. Open systems may be disturbed externally, particularly by anthropogenic and climatic influences.

In ecosystems, several new system characteristics occur, whereby all transitions to whole plant ecology are transient. This applies particularly to the structure (e.g. roughness of surface, climate of the stand, spatial compartmentalisation) already discussed in Chapters 2.1, 2.2 and 2.3. New characteristics occur regarding the use of resources at the level of the ecosystem, and regarding the interaction of specific functions of many species (**biodiversity**). From the point of view of the individual plant, the most important system characteristic is that there are neighbours, which, in contrast to the very variable physical-chemical environment, possess a multitude of options and thus codetermine the success or failure of an individual or a species. Because of the interaction between organisms the following system characteristics are particularly important:

- **Material balance**: This concerns all organisms of the ecosystem. Compared to whole plant ecology, material pools and material fluxes and the resulting ecosystem balance become increasingly important when studying ecosystems. Even in the future it will hardly be possible to trace and measure all processes. Thus the balance of material fluxes consisting of input and output remains as the most important quantitative characteristic at the scale of a stand. Similarly to whole plant ecology, the following quantities are observed:
  - amount of material (pool size; g m^{-2}),
  - material flux (g m^{-2} $time^{-1}$),
  - material balance, and here particularly loss and gain,
  - mechanisms regulating the size of the flux: regulation by substrate = **feed-forward**, regulation by products = **feed-back**, branching, modulation, Co-limitation (see also Chaps. 1 and 2),
  - in addition to material fluxes, there are also "information fluxes", i.e. material fluxes are started (e.g. pollination), without the amount becoming visible in the material fluxes.

- **Differentiation between species and individual plants**: Ultimately, it is individual plants that successfully dominate or die within an ecosystem. Depending on neighbouring individuals, differences occur between the course of growth of different plants in an ecosystem, even in clonal monocultures. In addition, individual species have different direct or indirect effects on the whole system (so-called keystone species). Behaviour under conditions of competition is difficult to predict, as slight differences between species may have far-reaching cumulative consequences.
- **Time scale**: Accumulation and consumption of resources change basic life conditions in the long term. Often seconds are sufficient to assess physiological reactions. Material balance is often determined on a yearly basis. However, if it concerns conditions at a site, then dependent on losses and gains, centuries or millennia are appropriate time scales (Chadwick et al. 1999; see Fig. 3.5.1).
- **Random events and interference**: Survival of individual plants in an ecosystem is not only determined by physiological characteristics of the species, but often also randomly by who the neighbour is (see also Chap. 4.1.4). The chance whether, in a microspatial mosaic of environmental conditions, a plant germinates or grows next to a less competitive neighbour may determine the success or failure of a species. The constitution of vegetation is decided during the seedling phase. With longer time scales individual processes, so-called interference, also become more important; storm damage, breakage caused by snow, drought, fire or economic measures of human beings may drastically change ecosystems within minutes. Material pools that accumulated over millennia may degrade within a very short time.

References

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