Mendel University in Brno

Forest Ecology

Textbook

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INVESTICE DO ROZVOJE VZDĚLÁVÁNÍ

Content

Chapter 1. Introduction to Forest Ecology

1.1. Introduction

Human activities are affecting the global environment in myriad ways, with numerous direct and indirect effects on ecosystems. The climate and atmospheric composition of Earth are changing rapidly. Humans have directly modified half of the ice-free terrestrial surface and use 40% of terrestrial production. Our actions are causing the sixth major extinction event in the history of life on Earth and are radically modifying the interactions among forests, fields, streams, and oceans.

A community of species interacting among themselves and with the physical environment is an ecosystem. Ecosystems have the following distinguishing characteristics:

1. *A web of interactions and interdependencies among the parts.* Animals and microbes require the energy supplied by plants, and plants cannot persist without animals and microbes to cycle nutrients and regulate ecosystem processes. The interdependencies within ecosystems relate to function: there must be species that photosynthesize, species whose feeding results in nutrients being cycled, predators that keep populations of plant-eaters from growing too large, and so forth. Some system functions can be performed by more than one species (a property called redundancy); in other cases a single species plays a unique functional role (such species are called keystones).
2. Synergy is the "behavior of who1e systems unpredicted by the behavior or integral characteristics of any of the parts of the system when the parts are considered only separately" (Fuller 1981). Synergy characterizes any system whose components are tied together through interaction and interdependence (the human home is an example of a synergistic system; in fact the word ecology is derived from the Greek word for "home").
3. Stability is a simple yet complicated concept that does not mean 'no change" but rather is analogous to the balanced movement of a dancer or a bicycle rider (Mollison 1990). The processes of disturbance, growth, and decay produce continual change in nature. Stability means that (1) changes are maintained within certain bounds and (z) key processes (such as energy capture) and potentials (such as the productive potential of soil) are protected and maintained.
4. Diffuse boundaries. Unlike an organism, an ecosystem does not have a skin that clearly separates it from the external world. Ecosystems are defined by connectance, and connections extend through space and time, integrating every local ecosystem (one that is localized in time and space) within a network of larger and larger ecosystems that composes landscapes, regions, and eventually the entire earth. Any given forest both influences and is influenced by cities, oceans, deserts, the atmosphere, and forests elsewhere on the globe. Moreover, every local ecosystem produces patterns that propagate through time, communicating with and shaping the nature of future ecosystems. The interconnections among ecosystems that exist at many different spatial and temporal scales result in what is termed hierarchical structure, which simply means that each ecosystem that we can define in space comprise numerous smaller systems and at the same time is part of and in interaction with a hierarchy of larger systems (Fig. 1.1)

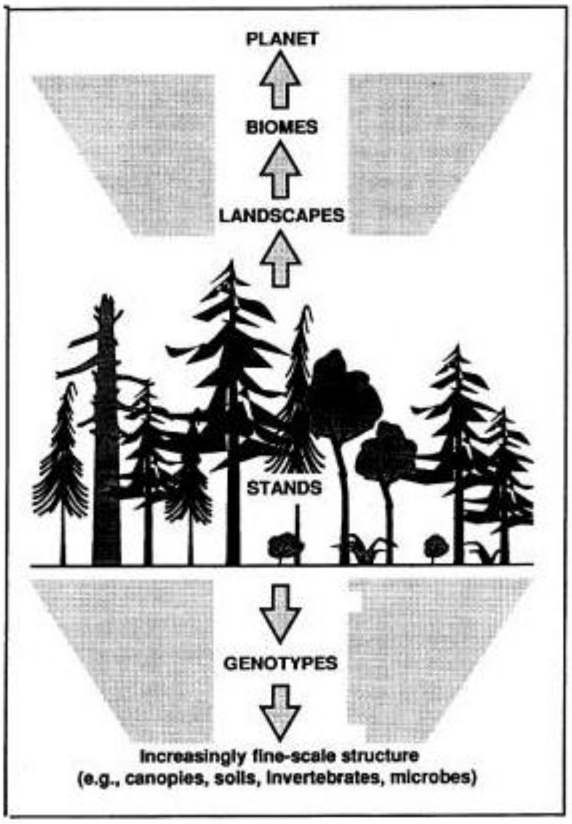


Figure 1.1. The hierarchy of nature. Every local ecosystem is part of a larger set of ecosystems that includes landscapes, regions, and ultimately the planet as a whole. Local ecosystems also comprise diversity at many scales, from individual plant and animal species and genotypes through microbes and the fine-scale structure of soils and canopies (Perry et al. 2008).

1.2. What is Ecology?

The term "ecology" was coined by Ernst Haeckel in 1869. However, while Haeckel in fact never contributed to ecology himself, ecological problems were studied well before the term came into existence. Ernst Haeckel's (1866) original definition of ecology, although focused on animals, was embracing and straightforward:

> *By ecology we mean the body of knowledge concerning the economy of nature – the investigation of the total relations of the animal both to its inorganic and to its organic environment; including above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact.*

There are two definitions of ecology in wide use in the United States today:

- "The scientific study of the distribution and abundance of organisms" (Andrewartha 1961)
- "The study of the relation of organisms or groups of organisms to their environment" (Odum 1959, 1971)

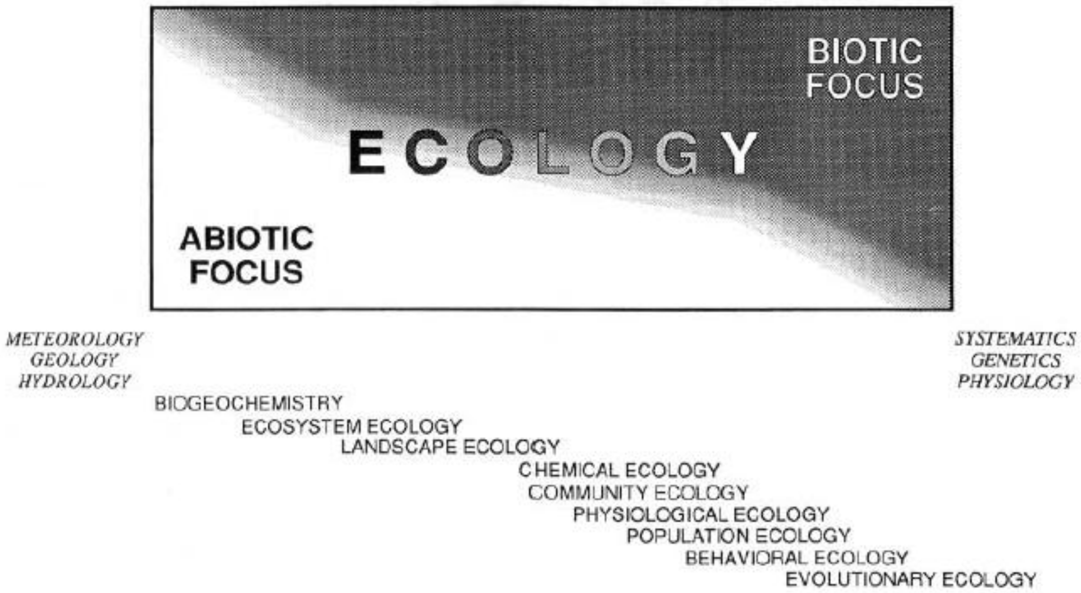


Figure 1.2. Ecological studies range from those focused on more abiotic relationships to those focused on more biotic relationships. Ecology, as represented by the box in this illustration, is softly bounded on one end of this spectrum by disciplines such as meteorology, geology and hydrology, and on the other end by systematics, genetics and physiology. The spectrum ranging from more abiotic to more biotic ecological subdisciplines then might include from left to right, biogeochemistry, ecosystem ecology, landscape ecology, chemical ecology, community ecology, physiological ecology, population ecology, behavioral ecology, evolutionary ecology. Obviously, the abioticbiotic focus is only one of the dimensional axes for subdisciplines in ecology. Another axis is the spatial or temporal scale of the ecological process or phenomenon being considered, e.g. landscape vs. organism (Likens 1992).

During the development of ecology there has been tension between different approaches or schools. In the beginning research in different branches, like plant and animal ecology, developed with out close contact, each developing according to their own praxis. Later the battleground was occupied by population and evolutionary ecology fighting against ecosystem-orientated research or a reductionistic or holistic approach. Today most of this tension has disappeared as an understanding of the value of different approaches in ecology has developed.

In order to stimulate and to bridge barriers, ecology needs to be defined in a manner that favours common thoughts and collaboration. We endorse a definition that has been expressed by a group of ecologists at the Institute of Ecosystem Studies, Millbrook, New York (Likens 1992):

> *Ecology is the scientific study of the processes influencing the distribution and abundance of organisms, the interactions among organisms, and the interactions between organisms and the transformation and flux of energy and matter.*

The purpose of this definition is to bring different fields of ecology together as a scientific discipline, organism as well as ecosystem orientated. The characteristic of ecology is its encompassing and synthetic view, not fragmented!

1.3. The Subdisciplines of Ecology

Ecology covers a wide range of phenomena, and, just as biologist group into physiologists. geneticists. taxonomists, and so on, different ecologists tend to concentrate on different aspects of ecosystems. In the following discussion, we delineate the types of things studied by the different subdisciplines of ecology and, in the process, preview some of the questions that we will concern ourselves with throughout the text. Although it is necessary for you to know what these subdisciplines are, remember that they are artificial distinctions, created by humans in order to aid understanding. No such neat divisions occur in nature. In fact, the trend in all natural sciences is increasingly integrative, especially at the level of ecosystems, landscapes, and the planet. Natural scientists still specialize - no single per son can understand all - but the important questions facing society require specialists to talk and work together.

- **Physiological Ecology** (ecophysiology) - is the study of how environmental factors influence the physiology of organisms.
- **Population Ecology** - is the study of the dynamics, structure, and distribution of populations.
- **Community Ecology** - is the study of interactions among individuals and populations of different species.
- **Evolutionary Ecology** - is linked closely to population ecology. The physical and biological environment acts as a filter that allows some individuals within a population to pass, and screens our others. Those who pass contribute genes to the next generation; thus, there is a continual inter-play between the environment and the generic composition of populations.
- **Ecosystem Ecology** (e.g. forest, river, ponds…) - is to a great extent about mass balances of elements and their interactions. The fluxes of elements are strongly coupled to each other, and often one limiting element regulates the fluxes of the others. This chapter gives an introduction to the most important elements and to some key concepts or cornerstones: mass balance, limiting nutrients, optimality and steady state. At the ecosystem level we are interested in structural and functional attributes of the system as a whole:
  - *The reciprocal influences between patterns and processes,* where patterns span scales from stands (e.g., the number of canopy layers) to landscapes (e.g., the distribution of community types or age classes across the landscape) to regions and the entire globe, and processes include all things that involve movement, change, or flux.
  - *Productivity* - the conversion of solar energy and nonliving chemicals to plant chemical energy and mass through photosynthesis **(primary productivity),** and conversion of the energy and mass in plants to energy and mass in animals and microbes **(secondary productivity).**
  - *Food webs* - the way in which energy is distributed among the organisms of the system.

  - *Cycling of matter.*
  - *Stability* or the processes that allow the system to adapt to uncertain and often catastrophic change in the environment.
  - *Interactions between land, air, and water.*
- **Landscape Ecology -** study these reciprocal interactions between spatial patterns and ecological processes (Turner et al. 2003). Though the term landscape is often used to denote our intuitive sense of what the word means - roughly an area humans can see when standing on a high point - for ecologists landscapes occur at a variety of scales; an eagle has one landscape, a ground squirrel another, a beetle yet another. Whatever the scale, the scientific focus is on linkages between spatial pattern and process.
- **Theoretical production ecology -** tries to quantitatively study the growth of crops. The plant is treated as a kind of biological factory, which processes light, carbon dioxide, water and nutrients into harvestable parts. Main parameters kept into consideration are temperature, sunlight, standing crop biomass, plant production distribution, nutrient and water supply.

1.4. Approaches to the Study of Ecosystem Ecology - cornerstones and scientific methodology

The goal of ecosystem science is to integrate information from studies of the interactions between individuals, populations, communities and their abiotic environments, including the changes in these relationships with time. Amid this complexity, several approaches have been used in attempts to synthesize understanding at the ecosystem level.

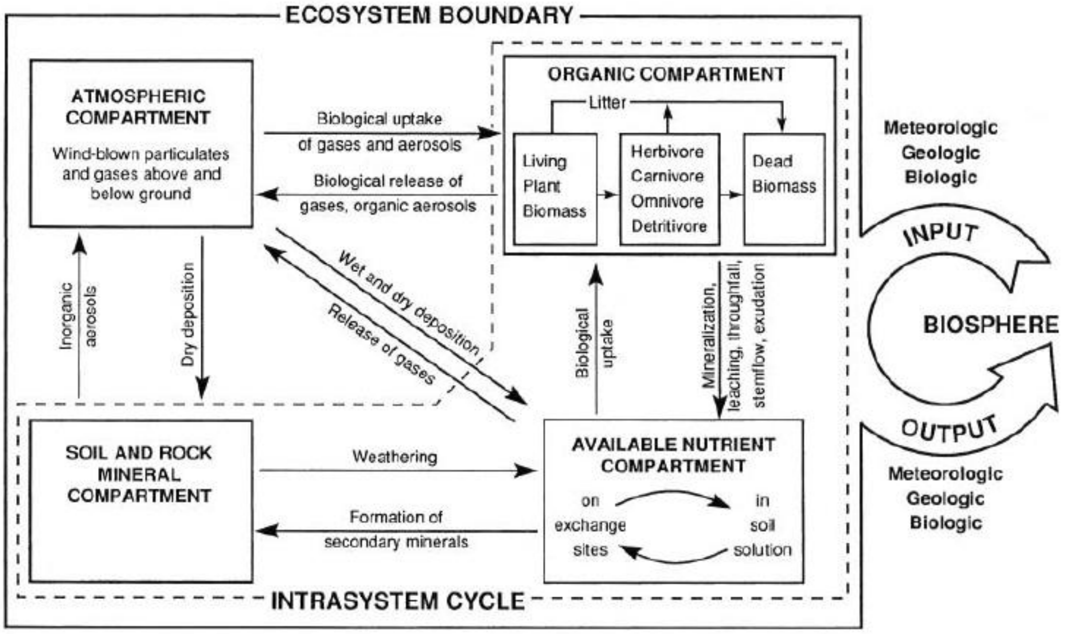


Figure 1.3. Model depicting nutrient relationships in a terrestrial ecosystem. Inputs and outputs to the ecosystem are moved by meteorologic, geologic and biologic vectors (Bormann and Likens 1967, Likens and Bormann 1972). Major sites of accumulation and major exchange pathways within the ecosystem are shown. Nutrients that, because they have no prominent gaseous phase, continually cycle within the boundaries of the ecosystem between the available nutrient, organic matter and primary and secondary mineral components tend to form an intrasystem cycle. Fluxes across the boundaries of

an ecosystem link individual ecosystems with the remainder of the biosphere. (From Likens et al. 1977; modified Likens 1992)

Studies of ecosystems should utilize all of the approaches described above in attempts to unravel complexity, develop ecological understanding and provide useful information for decision makers and managers. In all areas of ecology, and in science in general, the convergence and integration of information from different points of view, different disciplines and different approaches are what lead to major advances and breakthroughs in understanding. To gain comprehensive understanding about complex ecosystem function, including relationships among the integral components (e.g. Fig. 1.3), will require diverse talents and approaches.

1.5. Structure and functions of ecosystems

Most ecosystems gain energy from the sun and materials from the air or rocks, transfer these among components within the ecosystem, then release energy and materials to the environment. The essential biological components of ecosystems are plants, animals, and decomposers. Plants capture solar energy in the process of bringing carbon into the ecosystem. A few ecosystems, such as deep-sea hydrothermal vents, have no plants but instead have bacteria that derive energy from the oxidation of hydrogen sulfide (H_2S) to produce organic matter. Decomposer microorganisms (microbes) break down dead organic material, releasing CO_2 to the atmosphere and nutrients in forms that are available to other microbes and plants. If there were no decomposition, large accumulations of dead organic matter would sequester the nutrients required to support plant growth. Animals are critical components of ecosystems because they transfer energy and materials and strongly influence the quantity and activities of plants and soil microbes. The essential abiotic components of an ecosystem are water; the atmosphere, which supplies carbon and nitrogen; and soil minerals, which supply other nutrients required by organisms.

An ecosystem model describes the major pools and fluxes in an ecosystem and the factors that regulate these fluxes. Nutrients, water, and energy differ from one another in the relative importance of ecosystem inputs and outputs vs. internal recycling. Plants, for example, acquire carbon primarily from the atmosphere, and most carbon released by respiration returns to the atmosphere. Carbon cycling through ecosystems is therefore quite open, with large inputs to, and losses from, the system. There are, however, relatively large pools of carbon stored in ecosystems, so the activities of animals and microbes are somewhat buffered from variations in carbon uptake by plants. The water cycle of ecosystems is also relatively open, with water entering primarily by precipitation and leaving by evaporation, transpiration, and drainage to groundwater and streams. In contrast to carbon, most ecosystems have a limited capacity to store water in plants and soil, so the activity of organisms is closely linked to water inputs. In contrast to carbon and water, mineral elements such as nitrogen and phosphorus are recycled rather tightly within ecosystems, with annual inputs and losses that are small relative to the quantities that annually recycle within the ecosystem. These differences in the “openness” and “buffering” of the cycles fundamentally influence the controls over rates and patterns of the cycling of materials through ecosystems.

The pool sizes and rates of cycling differ substantially among ecosystems. Tropical forests have much larger pools of carbon and nutrients in plants than do deserts or tundra. Peat bogs, in contrast, have large pools of soil carbon rather than plant carbon. Ecosystems also differ substantially in annual fluxes of materials among pools, for reasons that will be explored in later chapters.

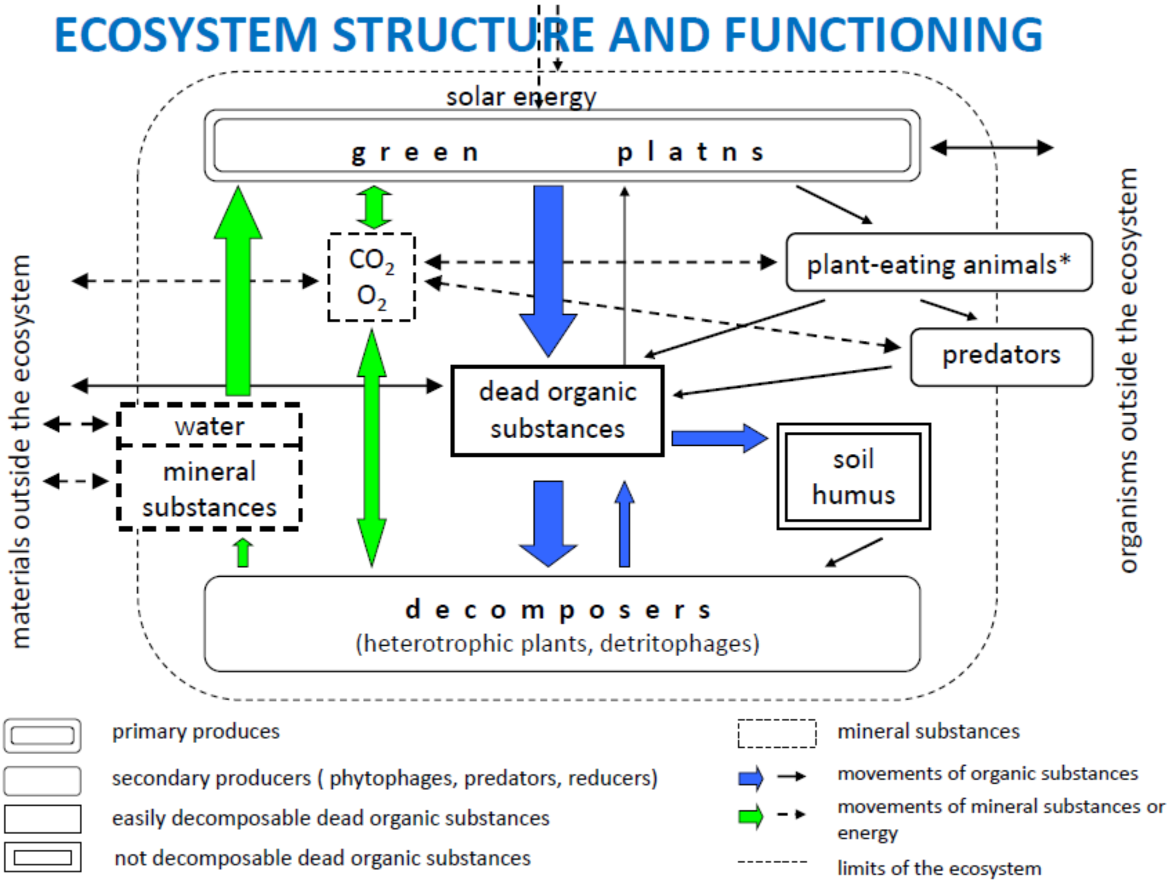


Figure 1.4. Model of ecosystem structure and functionig.

Forest ecosystem

- **Forest ecosystem - a community of species interacting among themselves and with the physical environment**
- Ecosystem may be used **concretely** for desribing a particular place on the ground or **abstractly** to decribe a type (e.g. Norway spruce ecosystem)
- **Biogeocenosis** is an equivalent (mostly in Europe)
- Main attributes are: **source of energy**, a **supply** (inputs) of row materials (e.g. nutrients in rainfall), **mechanisms for storing and recycling (cycling of matter and nutrients)**, **mechanisms** that allow it **to persist** (e.g. climatic fluctuations, periodic disturbance..)
- Ecosystem **is dynamic rather than static** (time and space dynamic - **succession**)
- **Synergy** – *the whole is greater than sum of the parts*
- **Stability** – it doesnt mean „*no change*“. Rather is analogous to the dynamic balance

1.6. Geographical distribution of forest in the world

Plant distributions is governed by a combination of historical factors, ecophysiology and biotic interactions. The set of species that can be present at a given site is limited by historical contingency. In order to show up, a species must either have evolved in an area or dispersed there (either naturally or through human agency), and must not have gone locally extinct. The set of species present locally is further limited to those that possess the physiological adaptations to survive the environmental conditions that exist. This group is further shaped through interactions with other species.

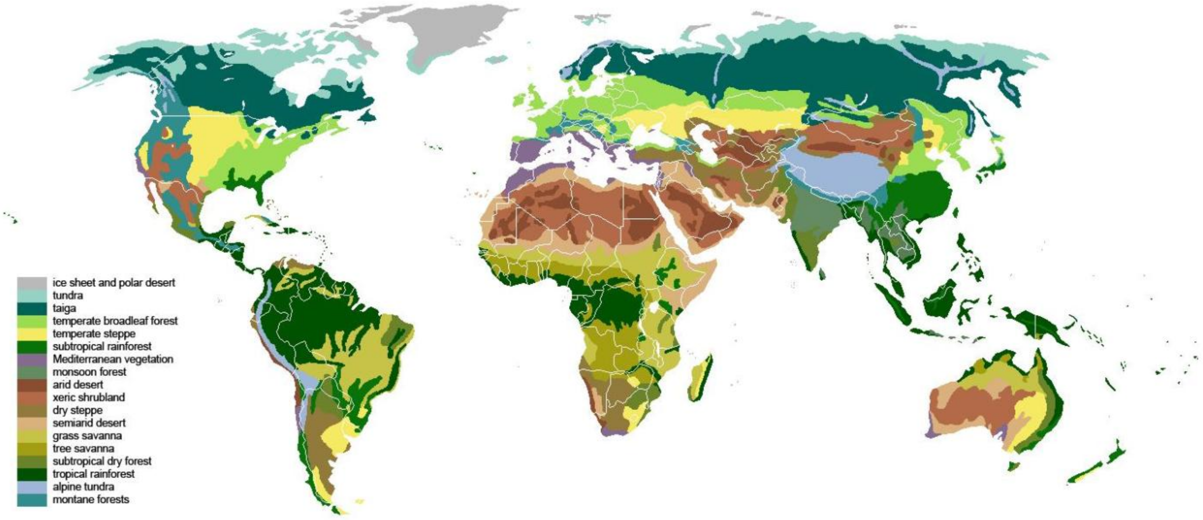
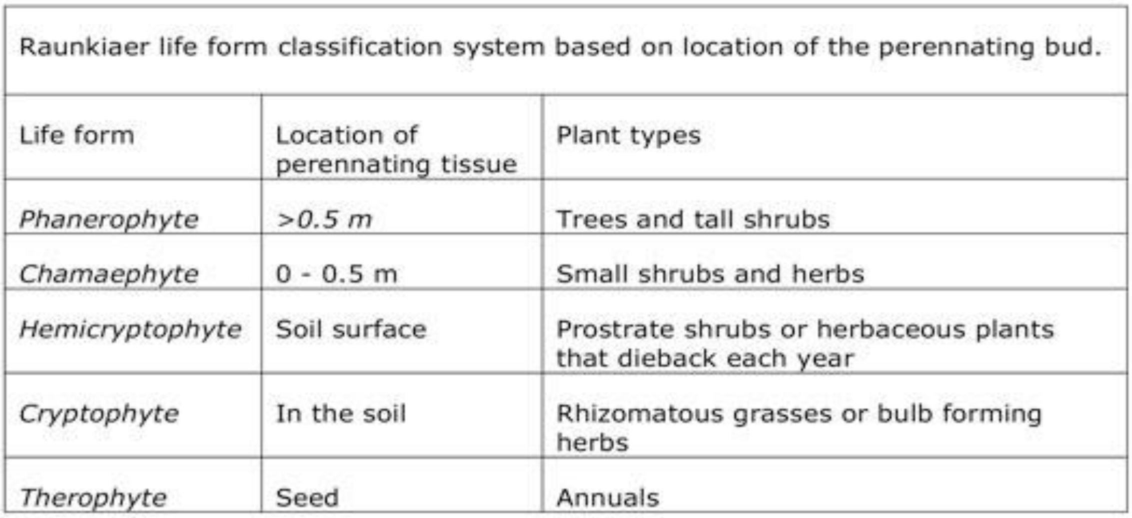


Figure 1.5. World biomes are based upon the type of dominant plant.

Plant communities are broadly distributed into biomes based on the form of the dominant plant species. For example, grasslands are dominated by grasses, while forests are dominated by trees. Biomes are determined by regional climates, mostly temperature and precipitation, and follow general latitudinal trends. Within biomes, there may be many ecological communities, which are impacted not only by climate and a variety of smaller-scale features, including soils, hydrology, and disturbance regime. Biomes also change with elevation, high elevations often resembling those found at higher latitudes.

Differences in temperature or precipitation determine the types of plants that grow in a given area (Fig. 1.6.). Generally speaking, height, density, and species diversity decreases from warm, wet climates to cool, dry climates. Raunkiaer (1934) classified plant life forms based on traits that varied with climate. One such system was based on the location of the perennating organ (Table 1). These are tissues that give rise to new growth the following season, and are therefore sensitive to climatic conditions. The relative proportions of different life forms vary with climate. In fact, life form spectra are more alike in similar climates on different continents than they are in different climates on the same continent. Regions of similar climate and dominant plant types are called biomes. This chapter describes some of the major terrestrial biomes in the world; tropical forests, savannas, deserts, temperate grasslands, temperate deciduous forests, Mediterranean scrub, coniferous forests, and tundra (Fig. 1.7., 1.8.).



Raunkiaer life form classification system based on location of the perennating bud.		
Life form	Location of perennating tissue	Plant types
Phanerophyte	*>0.5 m*	Trees and tall shrubs
Chamaephyte	0 - 0.5 m	Small shrubs and herbs
Hemicryptophyte	Soil surface	Prostrate shrubs or herbaceous plants that dieback each year
Cryptophyte	In the soil	Rhizomatous grasses or bulb forming herbs
Therophyte	Seed	Annuals

Table 1.1. Raunkiaer life form classification system based on location of the perennating bud Life forms can be classified by the location of perennating tissue and plant types (Forseth 2012).

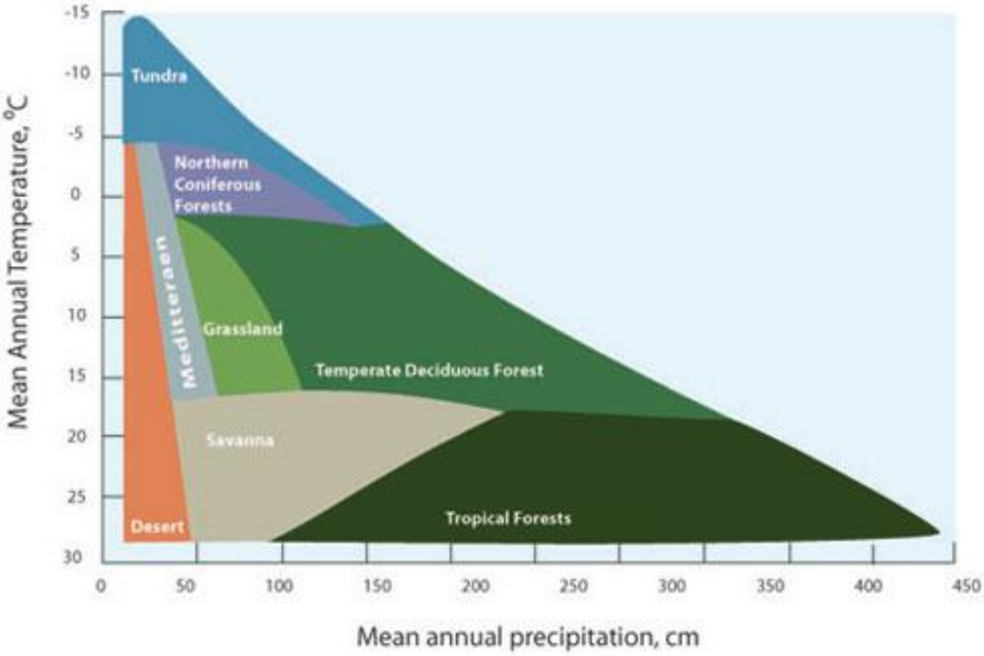


Figure 1.6. The distribution of vegetation types as a function of mean annual temperature and precipitation (Forseth 2012).

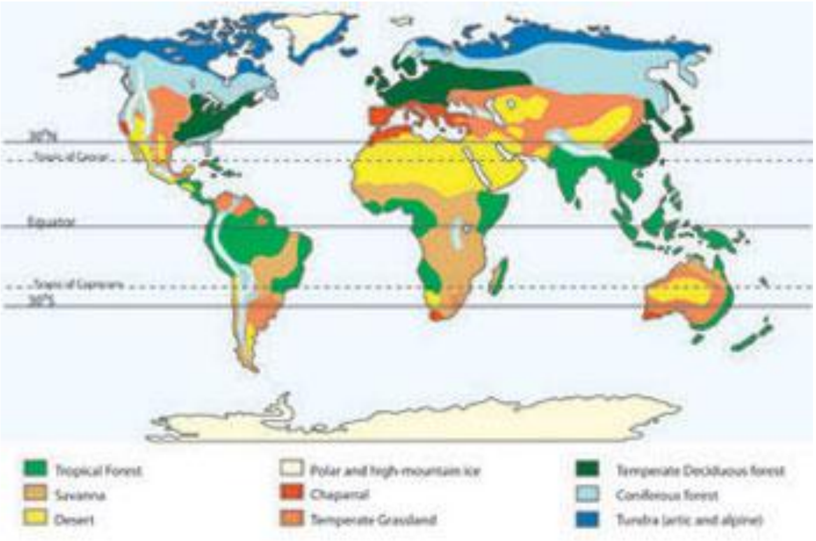


Figure 1.7. Biomes of the world. Biomes are regions of similar climate and dominant plant types (Forseth 2012).

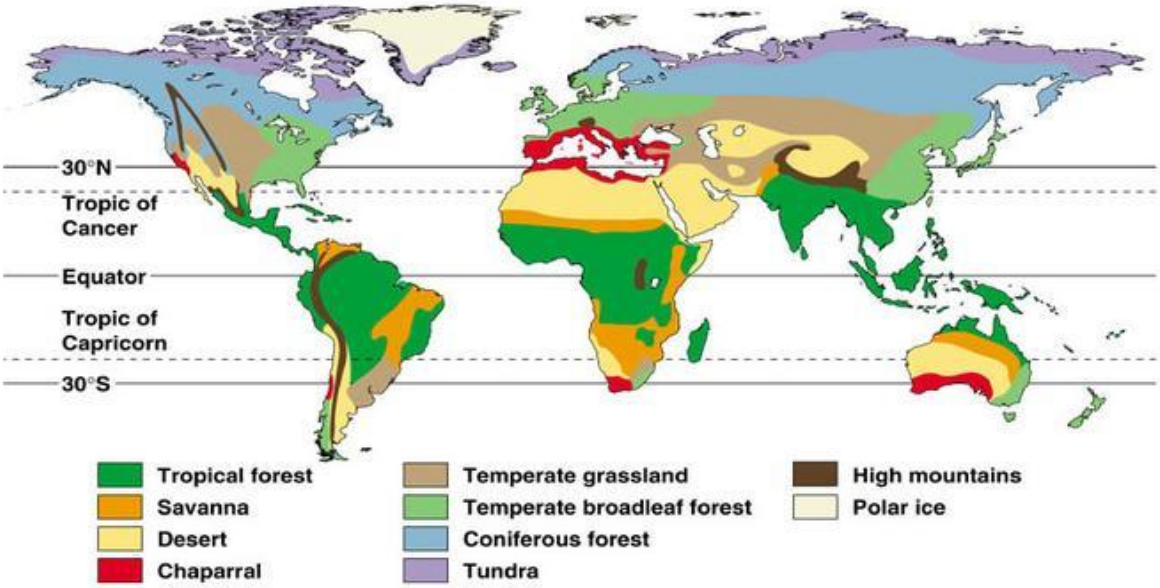


Figure 1.8. Biomes of the world (Source:http://bouchillonlifescience2.wikispaces.com/Coniferous+Forest+Key+Facts)

1.7. The man and the forest

Soil and forest development in Holocene

During the last ice age the most of the middle and northern part of Europe was covered by sediments that were formed by physical weathering of rocks: argillaceous shale, marl slate, sandy shales, debris shales. Alluvial sands, eolian sediments as loess covered more or less big bed of the rest of older geests and soils formed in the periglacial space. Ice age sediments and covered older beds were without humus as it documents present carbon analysis.

Humus reserves from older periods of soil formacion ion were at the beginning of the ice age mineralised (fungus decomposition): decline of KAK and saturation by base could be linked according to the ion balance. It is possible to come out of: at the beginning of Holocene the possible acid bottom layers that were if the form of alder liquid soils or rock geests (compare Fiedle and Hofmanu 1991), so these materials were over layered more or less thick covers of inacid ice age sediments.

The present plant and animal state in our country is the result of the fluctuation of the climate at the end or tertiary period and at the beginning of quaternary period. In the ice age (mainly third and fourth icing) reached our country northern glacier and in the mountains there were local glaciers, it was tundra (birches, osier, sporadically pines) on the rest of the territory. In interglacials the climate was similar to present northern Yugoslavia or Bulgaria. The man did not influence the nature in the beginnings: in the older and middle stone age man lived on gathering and hunting. Firstly 25 thousands years ago he started with group hunting of bigger animals. The man was as a hunter, also as a hunting object of big beasts and he did not have more important influence on the number of animals. 10 or 8 thousand years ago it started warming (2 or 3 degrees more that today). The forests expanded, they encountered to the first agriculture which advanced firstly in e.g. Praha-Louny and Příbram regions. The direct alteration of forests is in the beginning of 18th century.

For a new formation of ecosystems on the fresh and original material for soil formation (Ulrich 1994) there were crucial two processes from the view of substance balance:

- carbon and nitrogen accumulation from the atmosphere to organic matter,
- weathering of sificates and clay formation of sparse sediments with the rise of exchange reserves of nutrients and claying (rise of capacity of water maintenance),
- accumulation measure of organic matter could depend on the nitrogen income.

Results of antropogenic influence in the forest ecosystems

Periods	**Description**
5000-2000 BC	Husbandry with forest regeneration if lowlands (lowland area)
2000-1000 BC	Expansion to hillsides of mountains (upland area)
1000-0 BC	Settlement of mountains, beginning of charcoal burning
0-400 AD	Abandonment of settlements. afforestation
400-1400 AD	Grain farming, pasture in forests, in higher locations (submontaneous zone)
1400-1500 AD	Period of dilapidation, repeated afforestation in higher areas
1500-1750 AD	Rising of wood production (montaneous supermontaneous zone)
1 750-1 850 AD	Raking of litter. afforestation by conifers
1850-today	intensive forest management, harvesting of hroubí, acid income, nitrogen income etc.

Development of forestry and forest management

Forests were originally free goods for a long time which use was restricted only by the territorial demands of settlers. While the farmed lands became relatively individual property, distant Lands, pastures and forests were for a long time common property (allmends). In the middle ages the ownership of lands - and forests was secured by the estate law guaranteed by the sovereign. While in the 12^{th} century forests were in contracts of donation (e.g. 1169 king

Vladislav) bound by word, in the 13th century the land was measured. In 1369 forests were measured in Rožumberk domain. The later data about the forest area in the region of the present Czech Republic date from the statistic inquiry (published in 1924).

In the period till WWII. the lands were adapted by balance. From 1950 the data are the result of detailed inventory of all forests conducted by state organization (today The Department for Management Adaptation Brandýs nad Labem), from the beginning of 60s annually first as The Permanent Forest Inventory and from 1979 as The Collective Forest Management Plan (SLITP). In both cases the base was the data sum of valid forest maintenance plans.

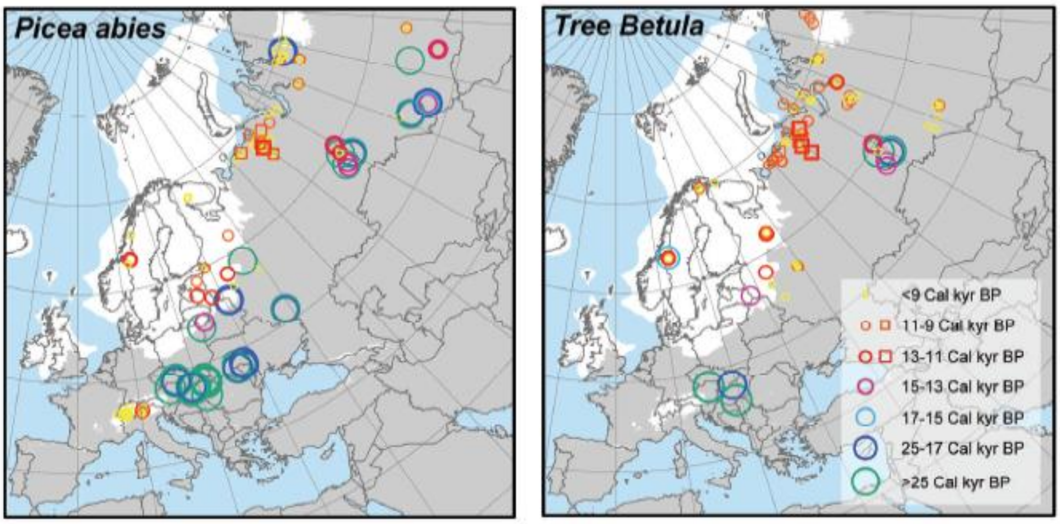


Figure 1.9. Distribution of macrofossil and stomata records for Picea and tree Betula in Eurasia. The macrofossil records from Väliranta et al. (2011) are indicated with squares. Additional data were compiled from the Northern Eurasian Macrofossil Database (Binney et al. 2009), the European Pollen Database (http://europeanpollendatabase.net/data/), Heikkilä et al. (2009), Koff (unpublished), and Willis & Van Andel (2004). The LGM ice sheet extent follows Ehlers & Gibbard (2004). Data were compiled with focus on late-glacial–early Holocene records in Eastern Europe and Eurasia but cannot be claimed to be complete.

Species composition

- In the period of older atlantica (5500 - 4000 BC) pines and other trees give from the boreal period and expand to mixed oakwood, spruce and beech tree.
- In the period of younger atlantica (4000 - 2500 BC) spruce trees expand and there ascend beech tree and fir. The colonizaíion starts with uprooting, pasture and thin forests.
- In the subboreal period between 2500 - 500 BC spruce trees and mixed oakwood fall back and beech trees and firs ascend. The spruce tree overweighs in Šumava, in Jizerské hory with the altitude 750 m spruce trees form one third of substituted wood.
- In younger subatlantica (500 BC - 1300 AD) the mixed forests formed of beech trees and firs are in uplands, however in higher places the spruce trees outweigh.

- Total species composition of wood was influenced in the 1411 century by the settlement of suitable regions, that is of oakwood, pine trees, alders, lime trees and birch trees.
- In the first half of the 16th century the experiments of alien trees took place (sawn chestnut). It is spoken in the 20th century about the preference of some trees spoken during the 19th century as a mama (pine then spruce) and it is adverted to that owners, were not able to enlighten from insect and wind damages that were happening in the monocultures.
- In the half of the 19th century it is generally recommended "the forest ideally mixed by vegetation that is soil protecting". The result of improvement of species composition of our forests is the increase of the broadleaf tree proportion between 1950 and 2000 almost to its double.

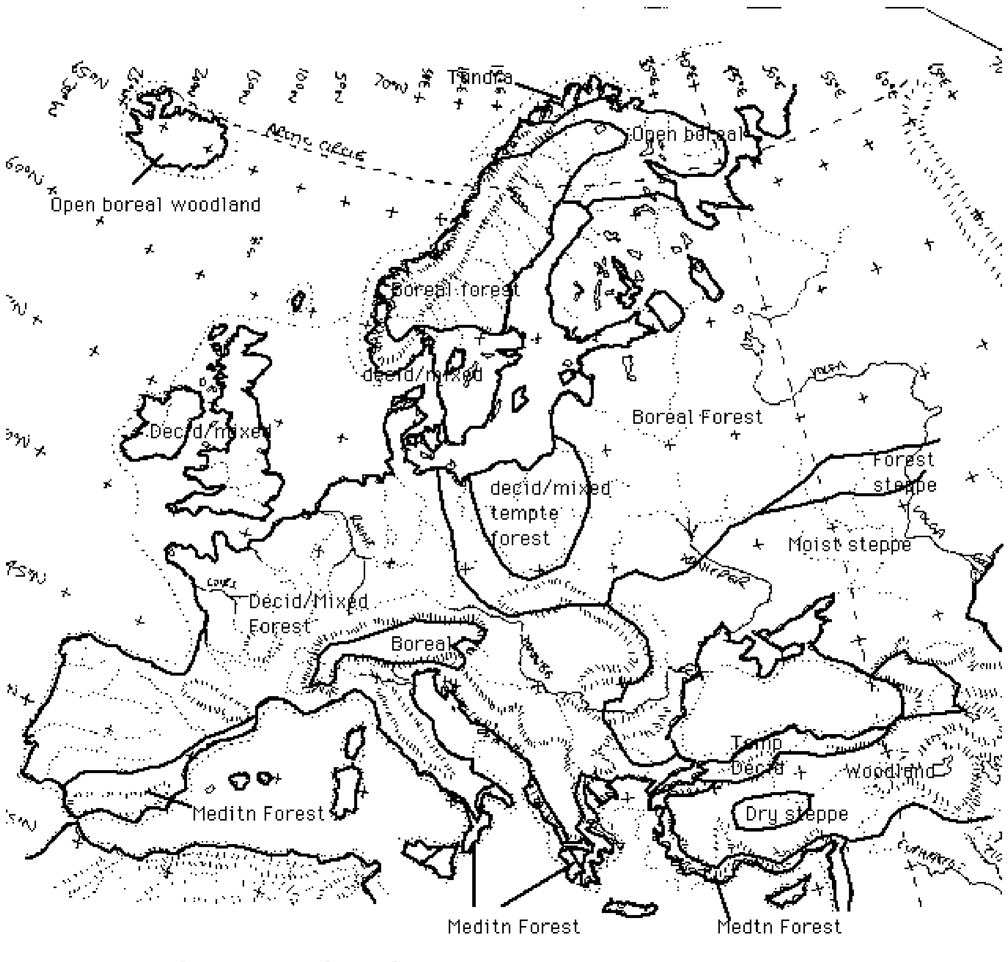


Figure 1.10. Potential vegetation boundaries in Europe (Source:http://www.esd.ornl.gov/projects/qen/NEW_MAPS/europe0.gif)

<u>Main problems in the forest management in the Czech Republic</u>

- inappropriate species composition
- tong-time action effect of air pollution (high percentage of defoliation) and
- the influence of acid deposition on soil
- decrease of resilience of forest ecosystems
- low representation of natural recovery

- inappropriate vegetation structure (high part of the same-age vegetations)
- high part of pasture maintenance
- decreased retention ability of unafforested drainage areas
- biodiversity protection
- necessity of increasing of the importance of the public function of forests
- low awareness of the exercise of principles of sustained forest management on the ecosystem level
- necessity of the higher economical evaluation of wood material

Importance of the forest ecology for sustained exploiting of forests

- necessity of forest recognition as a difficult interactive system (ecosystem) in its principle function and service (holistic approach)
- necessity of understanding of the forest life in its ongoing substance circulations, fluxes and information transitions (necessity of multidisciplinary approach in its recognition)
- necessity of trend recognition of its development in various time and space criterions (microscopic and macroscopic, short-termed and long-termed) and on different levels of the biotic organisation (molecular, cell, organismal, population, biocenotic and ecosystemic)
- necessity of detailed knowledge of the forest ecosystem functioning for correction of our actions in using and management of forests in the sense of permanent sustenance.

1.8. Review questions

1. What is an ecosystem?
2. How does it differ from a community?
3. What is the difference between a pool and a flux?
4. Which of the following are pools and which are fluxes: plants, plant respiration, rainfall, soil carbon, consumption of plants by animals?
5. What are the state factors that control the structure and rates of processes in ecosystems?

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Chapter 2. Analyses of Changes in Forest Structure and Function at Multiple Time and Space Scales

2.1. Introduction

Forests currently cover about 40% of Earth`s ice-free land surface (52.4 x 106km^2), a loss of 10 x 106km^2 from that estimated were it not for the presence of humans.

Ecosystem ecology addresses the interactions between organisms and their environment as an integrated system. The ecosystem approach is fundamental in managing Earth's resources because it addresses the interactions that link biotic systems, of which humans are an integral part, with the physical systems on which they depend. This applies at the scale of Earth as a whole, a continent, or a farmer's field. An ecosystem approach is critical to resource management, as we grapple with the sustainable use of resources in an era of increasing human population and consumption and large, rapid changes in the global environment.

The flow of energy and materials through organisms and the physical environment provides a framework for understanding the diversity of form and functioning of Earth's physical and biological processes.

2.2. Ecosystems analyses

Ecosystem analysis seeks to understand the factors that regulate the pools (quantities) and fluxes (flows) of materials and energy through ecological systems. These materials include carbon, water, nitrogen, rock-derived minerals such as phosphorus, and novel chemicals such as pesticides or radionuclides that people have added to the environment. These materials are found in abiotic (nonbiological) pools such as soils, rocks, water, and the atmosphere and in biotic pools such as plants, animals, and soil microorganisms.

Francis C. Evans (1956) used the first original definition of ecosystems analyses:

> *Ecosystem analysis is a mix of biogeo-chemistry, ecophysiology, and micrometeorology that emphasizes "the circulation, trans-formation, and accumulation of energy and matter through the medium of living things and their activities".*

For example, rather than concentrating on the growth of individual trees, the ecosystem ecologist often expresses forest growth as net primary production in units of kilograms per hectare per year. Ecosystem ecology is less concerned with species diversity than with the contribution that any complex of species makes to the water, carbon, energy, and nutrient transfer on the landscape (Waring, Running 1996).

An initial step in ecosystem analysis is to measure the amount of material stored in different components of the system, for example, the carbon stored in stem biomass, water stored in the snowpack, and nutrients stored in the soil. In systems terminology, these are the state variables that can be directly measured at any given time. Innumerable studies have been published measuring the current state of forest ecosystems. Frequently, however, the rates of change of these system states, or flows of material, are of greatest interest. What is the rate of snowmelt, stem biomass accumulation, or nutrient leaching in a particular system? These questions require study of the processes controlling energy and matter transfer, a much more difficult undertaking. In these process studies, we wish to identify the cause-effect relationships controlling system activity, which is often called a mechanistic approach. This identification of system states and multiple cause-effect relationships that operate in a forest ecosystem to regulate material flows can be quantified and organized with an ecosystem simulation model. This type of model becomes the starting point of our space/time scaling of ecosystem principles.

Ecosystem processes can be studied at many spatial scales. How big is an ecosystem? The appropriate scale of study depends on the question being asked (Fig. 2.1).

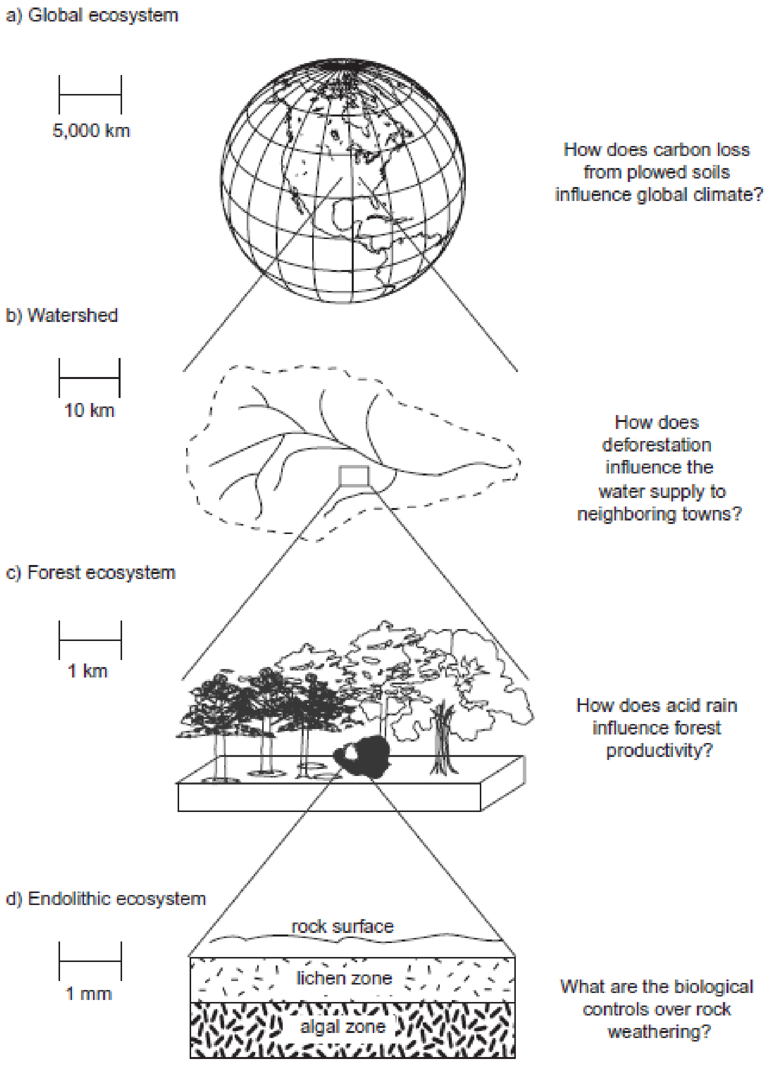

Figure 2.1. Examples of ecosystems that range in size by 10 orders of magnitude: an endolithic ecosystem in the surface layers of rocks, 1 ¥ 10-3m in height (d); a forest, 1 ¥ 103m in diameter (c); a watershed, 1 ¥ 105m in length (b); and Earth, 4 ¥ 107m in circumference (a). Also shown are examples of questions appropriate to each scale (Chapin et al. 2011).

The impact of zooplankton on the algae that they eat might be studied in the laboratory in small bottles. Other questions such as the controls over productivity might be studied in relatively homogeneous patches of a lake, forest, or agricultural field. Still other questions are best addressed at the global scale. The concentration of atmospheric CO_2, for example, depends on global patterns of biotic exchanges of CO_2 and the burning of fossil fuels, which are spatially variable across the globe. The rapid mixing of CO_2 in the atmosphere averages across this variability, facilitating estimates of long-term changes in the total global flux of carbon between Earth and the atmosphere.

2.3. Hierarchy and behaviour of the system in space and time

Multiscale analysis of forest ecosystems with the stand as our reference level, which includes the vegetation and surrounding physical environment, linked together through a variety of biological, chemical, and physical processes. Most scientific under-standing of ecosystem processes has been gained by direct field measurements and experiments on small study plots usually <1 ha (10,000 m^2) over a period from a few days to at most a few years (Levin 1992; Karieva, Andersen 1988).

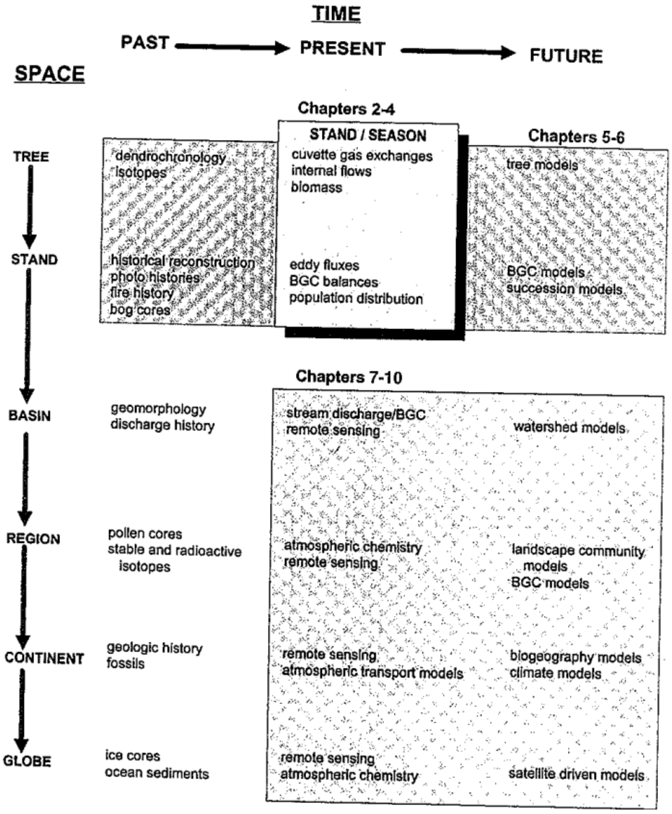

Figure 2.2. Examples of measurement techniques available for forest ecosystem analysis at different time and space scales. Temporal analysis of past ecosystem activity is possible from quasi-permanent records obtained by (issue or elemental analysis, such as tree rings, isotopic ratios, and pollen records from ice and bog cores. Spatial analysis beyond the stand level requires some type of remote sensing technology, and temporal analysis into the future requires some form of modelling (Waring, Running 1996).

From an ecological scaling point of view, we like to refer to these studies as the stand/seasonal level of analysis (Fig. 2.2). Such studies are designed to clarify the ecological processes and controls on the forest without regard to the spatial heterogeneity of the surrounding landscape, or the temporal changes that forests have undergone or will undergo in future years.

2.4. Models in Ecosystem Analysis - data extrapolation, simulation and mathematic modelling

Models have been an integral tool of ecosystem analysis since the earliest days of systems ecology (Odum 1983). Ecosystems are too complex to describe by a few equations; current ecosystem models have hundreds of equations which present interactions in non-continuous and nonlinear ways. Furthermore, these models provide the organizational basis for interpreting ecosystem behavior. Swartzman (1979) identified six primary objectives for ecosystem simulation models: (1) to replicate system behavior under normal conditions by comparison with field data, (2) to further understand system behavior, (3) to organize and utilize information from field and laboratory studies, (4) to pinpoint areas for future field research, (5) to generalize the model beyond a single site, and (6) to investigate effects of manipulations or major disturbances on the ecosystem over a wide range of conditions. Active ecosystem modeling programs pursue all of these objectives, although relevance to land management is attained only in objectives 5 and 6 (Waring, Running 1996).

A comprehensive biogeochemical model should treat all of the processes presented in Table 2.1, although we are aware of no current model that does so completely. It is essential that energy, carbon, water, and elemental cycles all be represented, even if simplistically. It is precisely the interactions among the cycles that are the core of ecosystem analysis. The inherent differences in time dynamics among these cycling processes should also be acknowledged, although not necessarily by explicit calculations. Leaf energy balances change within minutes, system gas fluxes change diurnally, tissue growth and carbon allocation dynamics are observable at weekly to monthly intervals, whereas nutrient mobilization may be measurable seasonally. Different forest ecosystem models have time steps ranging from an hour to a year, and newer models contain sections that represent processes at different time steps.

Of equal importance is that each process is treated with approximately the same level of detail. A model that computes photosynthesis of each age class of needles but fails to couple the nitrogen cycle to photosynthetic capacity is not balanced. Most forest biogeo-chemical models suffer some deficiencies in balance because they began as single process models and only later, often in much less detail, added other processes critical to ecosystem operation. Beyond some of these basic properties of good ecosystem modeling, every model differs depending on the specific objectives pursued. Some ecosystem models optimize energy partitioning as part of a climate model, whereas others focus on forest productivity, hydrology, or elemental cycles.

Ecosystems, because of their dynamic and interconnected properties, cannot be subjected to classic experimentation where one variable at a time is modified (Rastetter 1996). Computer simulation models of ecosystem behavior offer a valuable experimental alternative because they allow multivariant interactions to be traced and analysed. With simulated experiments, the accuracy with which different variables need to be measured can also be estimated. Such ecosystem models establish mathematical relationships in a simple but increasingly mechanistic way, to clarify causal connections and integrate system operation. On this basis, models can predict responses to new conditions that do not yet exist. For example, computer simulation models can predict how stream discharge may respond to harvesting in a watershed and identify possible flood problems before any logging commences. Computer simulation models have been the primary means for evaluating potential responses of natural ecosystems to future climate changes.

Table 2.1. Component Processess of a Comprehensive Ecosystem Biogeochemical Model (Waring, Running 1996).

Energy balance
- Short-wave radiation balance (incoming—outgoing)
- Long-wave radiation balance (incoming—outgoing)
- Sensible heat fiux
- Latent heat flux
- Soil heat flux

Water balance
- Precipitation partitioning (snow versus rain)
- Canopy and litter interception and storage
- Soil surface infiltration
- Soil water content
- Subrooting zone outflow
- Hili slope hydrologie routing
- Evaporation
- Transpiration

Carbon balance
- Photosynthesis, gross primary production
- Maintenance respiration
- Growth respiration
- Photosynthate storage
- Net primary production
- Carbon allocation - Leaves, stem/branches, roots, defensive compounds, reproduction
- Phenological timing - Canopy growth/senescence Litlerfall of leaves, turnover of stems and roots
- Decomposition
- Net ecosystem production

Elemental balance
- Sources (atmosphere, rock weathering, biological fixation)
- Soil solution transformation
- Immobilization, nitrification, denitrification
- Mineralization
- Root uptake
- Tissue storage
- Internal recycling
- Volatilization
- Leaching
- Export through harvesting and erosion

Examples of Ecological Model – application of system analyses

FOREST-BGC originated as a stand-level model of forest biogeochemical cycles, in effect, a model quantifying our understanding of the mechanistic processes of energy and mass fluxes in the stand/season space/time domain. Other forest ecosystem models are also available, and results from these will be illustrated (see reviews by Ágren et al. 1991; Tiktak, van Grinsven 1995; Ryan et al. 1996; Thornley, Cannell 1996). FOREST-BGC is a process-level simulation model that calculates the cycling of carbon, water, and nitrogen through forest ecosystems (Fig. 2.3; Running, Coughlan 1988; Running, Gower 1991).

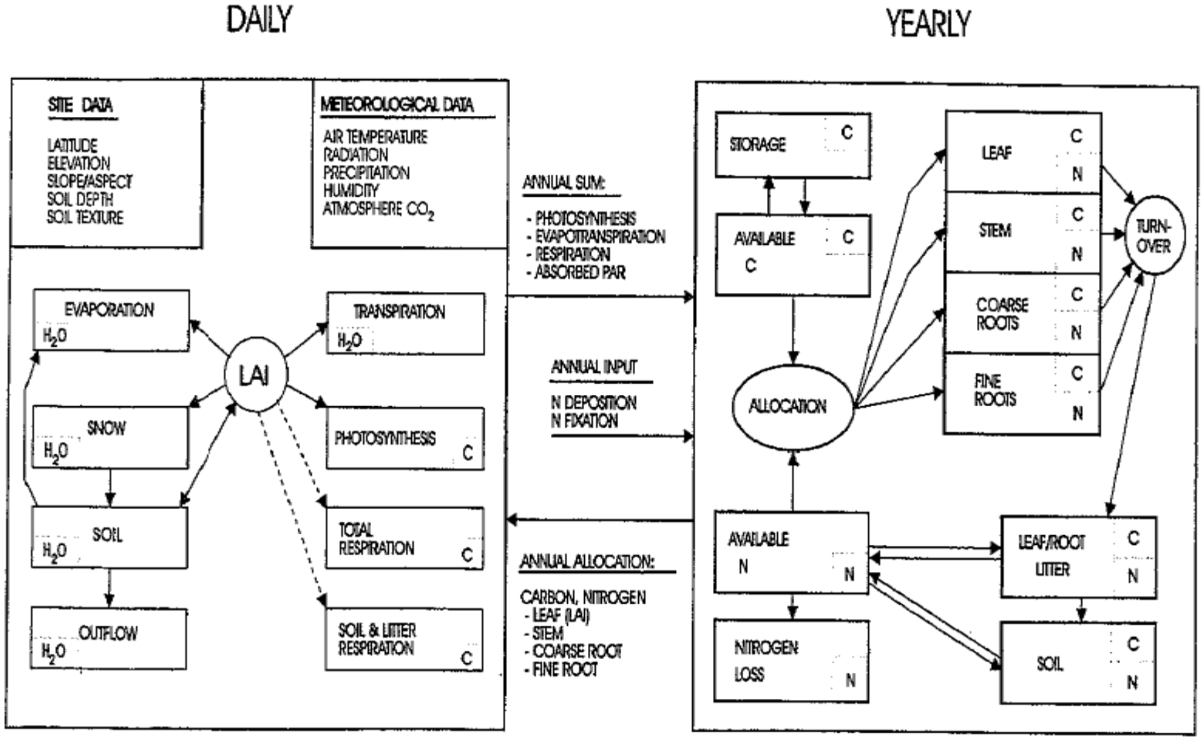

Figure 2.3. Compartment flow diagram for the FOREST-BGC ecosystem simulation model. This diagram illustrates the state variables of carbon, water, and nitrogen, the critical mass flow linkages, the combined daily and annual time resolution, and the daily meteorological data required for executing the model. The major variables and underlying principles associated with the model were developed specifically for application at multiple time and space scales, and for compatibility with remote-sensed definition of key ecosystem properties (Waring, Running 1996).

2.5. Management Applications of Ecosystem Analysis

Management applications of ecosystem analysis commonly encompass large areas, which imposes a requirement that the types and accuracy of data match the available sources. Ecosystem analysis can provide through model simulations some estimates of important variables that are difficult to measure directly. For example, using hydrologic equilibrium theory, one can infer a balance that is commonly established among climatic properties, soil water holding capacity, and the maximum leaf area that forests will support. It is a seeming contradiction that these rather sophisticated ecosystem models and analytic tools are particularly valuable in data-poor areas. A handful of key measurements, some acquired by satellite and synthesized with a model, can allow an inference of ecosystem activity that would be nearly impossible to acquire through standard ground surveys. The first requirement in preparing for regional scale assessments is to construct a coordinated, geographically specific information base that includes the most important system attributes such as weather data, satellite imagery of the mosaic of vegetation and soils, snowpack depth, streamflow, and location of wildlife populations. Most established land management agencies have acquired a tremendous amount of these kinds of data, but they are often not available in a consistent, geographically referenced format. The second requirement is to maintain the array of ecosystem and environmental data in an immediately accessible form. Finally, ecological process models are needed that use the archived data sets and real-time information to project both near and long-term ecosystem responses.

2.6. Dynamic of processes in forest ecosystems - energy and material transfer

Ecosystem structure and functioning are governed by at least five independent control variables. These state factors, as Jenny and co-workers called them, are climate, parent material (i.e., the rocks that give rise to soils), topography, potential biota (i.e., the organisms present in the region that could potentially occupy a site), and time (Fig. 2.4) (Jenny 1941, Amundson, Jenny 1991). Together these five factors set the bounds for the characteristics of an ecosystem. These can be summarised in the following expression:

$$\mathbf{E = f\,(c, o, r, p, t\ \ldots)}$$

where:

E = ecosystem
c = climate
o = organisms
r = topography
p = parent material or bedrock, with changes into soil
t = time

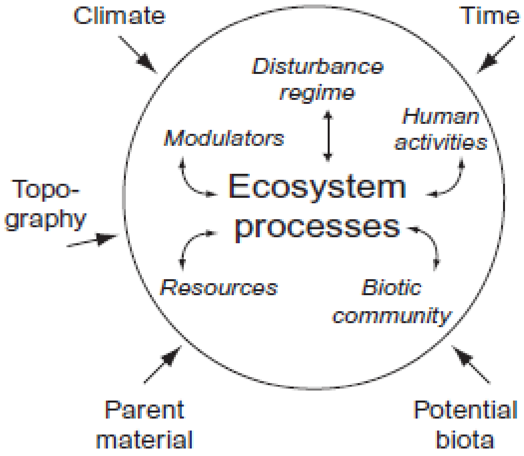

Figure 2.4. The relationship between state factors (outside the circle), interactive controls (inside the circle), and ecosystem processes. The circle represents the boundary of the ecosystem. (Modified with permission from American Naturalist, Vol. 148 © 1996 University of Chicago Press, Chapin et al. 2011).

This expression and Fig. 2.5 show in a simplified way how these major factors affect a terrestrial ecosystem and resulting effects. Of prime importance for the organisms and the ecosystem is the climate, in terms of its physical and chemical components. Light as a component of the physical climate is necessary for organisms, in particular plants. Further, the energy coning from light and expressed in temperature or heat is fundamental as a rate regulator of all biological activities. A part of the physical climate is also water. With its double importance through its physiological action and its function as a carrier of substances in the plants, as well as in the whole ecosystem. There is also a chemical dimension to the climate. The air contains not only gases such as oxygen, carbon dioxide and nitrogen, but also acids such as carbonic and sulfuric acid. The soil contains mineral or nutrient elements essential to the organisms. Over time there are also changes as a consequence of Man's actions or from natural causes. The topography or slope determines the incoming radiation to the ecosystems and also affects the ways water passes through the ecosystem. In addition, there are mechanical factors acting in and on the ecosystem: wind, fire, grazing and Man's activities, such as harvesting in fields and forests. Finally, time is an essential factor, sometimes forgotten. It is always a question of the time perspective in which different factors should be considered - short term vs. long term.

The soil has a key role in terrestrial ecosystems as its properties determine the type of species and ecosystem that can and will develop under specific climatic regimes. To understand what shapes the structure of terrestrial ecosystems we need some insight into and under-standing of basic soil properties and processes.

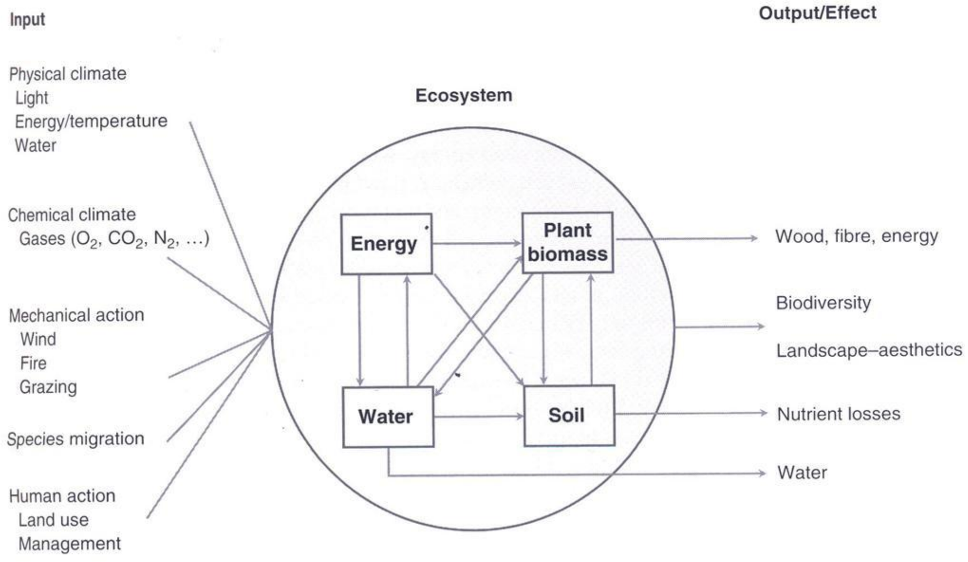

Figure 2.5. Factors shaping terrestrial ecosystems (Agren, Anderson 2012).

Ecosystem processes both respond to and control the factors that directly govern their activity. For example, plants both respond to and influence their light, temperature, and moisture environment. Interactive controls are factors that both control and are controlled by ecosystem characteristics (Fig. 2.4) (Chapin et al. 2011). Important interactive controls include the supply of resources to support the growth and maintenance of organisms, modulators that influence the rates of ecosystem processes, disturbance regime, the biotic community, and human activities.

Resources are the energy and materials in the environment that are used by organisms to support their growth and maintenance (Field et al. 1992). The acquisition of resources by organisms depletes their abundance in the environment. In terrestrial ecosystems these resources are spatially separated, being available primarily either aboveground (light and CO_2) or belowground (water and nutrients). Resource supply is governed by state factors such as climate, parent material, and topography. It is also sensitive to processes occurring within the ecosystem. Light availability, for example, depends on climatic elements such as cloudiness and on topographic position, but is also sensitive to the quantity of shading by vegetation. Similarly, soil fertility depends on parent material and climate but is also sensitive to ecosystem processes such as erosional loss of soils after overgrazing and inputs of nitrogen from invading nitrogen-fixing species. Soil water availability strongly influences species composition in dry climates. Soil water availability also depends on other interactive controls, such as disturbance regime (e.g., compaction by animals) and the types of organisms that are present (e.g., the presence or absence of deep-rooted trees such as mesquite that tap the water table). In aquatic ecosystems, water seldom directly limits the activity of organisms, but light and nutrients are just as important as on land. Oxygen is a particularly critical resource in aquatic ecosystems because of its slow rate of diffusion through water.

Modulators are physical and chemical properties that affect the activity of organisms but, unlike resources, are neither consumed nor depleted by organisms (Field et al. 1992). Modulators include temperature, pH, redox state of the soil, pollutants, UV radiation, etc. Modulators like temperature are constrained by climate (a state factor) but are sensitive to ecosystem processes, such as shading and evaporation. Soil pH likewise depends on parent material and time but also responds to vegetation composition.

Landscape-scale disturbance by fire, wind, floods, insect outbreaks, and hurricanes is a critical determinant of the natural structure and process rates in ecosystems (Pickett, White 1985, Sousa 1984). Like other interactive controls, disturbance regime depends on both state factors and ecosystem processes. Climate, for example, directly affects fire probability and spread but also influences the types and quantity of plants present in an ecosystem and therefore the fuel load and flammability of vegetation. Deposition and erosion during floods shape river channels and influence the probability of future floods. Change in either the intensity or frequency of disturbance can cause long-term ecosystem change. Woody plants, for example, often invade grasslands when fire suppression reduces fire frequency. The nature of the biotic community (i.e., the types of species present, their relative abundances, and the nature of their interactions) can influence ecosystem processes just as strongly as do large differences in climate or parent material. These species effects can often be generalized at the level of functional types, which are groups of species that are similar in their role in community or ecosystem processes. Most evergreen trees, for example, produce leaves that have low rates of photosynthesis and a chemical composition that deters herbivores. These species make up a functional type because of their ecological similarity to one another. A gain or loss of key functional types for example, through introduction or removal of species with important ecosystem effects can permanently change the character of an ecosystem through changes in resource supply or disturbance regime. Introduction of nitrogen-fixing trees onto British mine wastes, for example, substantially increases nitrogen supply and productivity and alters patterns of vegetation development. Invasion by exotic grasses can alter fire frequency, resource supply, trophic interactions, and rates of most ecosystem processes (D’Antonio, Vitousek 1992). Elimination of predators by hunting can cause an outbreak of deer that overbrowse their food supply. The types of species present in an ecosystem depend strongly on other interactive controls, so functional types respond to and affect most interactive controls and ecosystem processes.

Human activities have an increasing impact on virtually all the processes that govern ecosystem properties (Vitousek 1994). Our actions influence interactive controls such as water availability, disturbance regime, and biotic diversity. Humans have been a natural component of many ecosystems for thousands of years. Since the Industrial Revolution, however, the magnitude of human impact has been so great and so distinct from that of other organisms that the modern effects of human activities warrant particular attention. The cumulative impact of human activities extend well beyond an individual ecosystem and affect state factors such as climate, through changes in atmospheric composition, and potential biota, through the introduction and extinction of species. The large magnitude of these effects blurs the distinction between “independent” state factors and interactive controls at regional and global scales. Human activities are causing major changes in the structure and functioning of all ecosystems, resulting in novel conditions that lead to new types of ecosystems. The major human effects are summarized in the next section.

2.7. Review questions

1. Ecosystems analyses?
2. Hierarchy and behaviour of the system in space and time?
3. Models in Ecosystem Analysis?
4. Dynamic of processes in forest ecosystems?
5. Factors shaping terrestrial ecosystems?

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Chapter 3. Primary production

3.1. Introduction

Productivity is the accrual of matter and energy in biomass. The first step in this process (termed primary productivity) is performed by green plants, which are the only organisms capable of capturing the electro-magnetic energy of the sun and converting it to the chemical energy of reduced car-bon compounds (i.e., photosynthates). Secondary productivity results when heterotrophic organisms consume plant tissues and convert some proportion of that matter and energy to their own biomass. Secondary producers, which are associated with the detrital and the grazing energy transfer pathways, compose a small proportion of total forest productivity, but are critically important regulators of ecosystem processes, particularly nutrient cycling. Gosz et al. (1978) give a relatively thorough balance sheet for energy transfers in a temperate deciduous forest.

3.2. Climate, water and nutrients as a main driving force of primary productivity

The availability of water and nutrients is the major factor governing carbon input to ecosystems. Photosynthesis is the process by which most carbon and chemical energy enter ecosystems. The proximate controls over photosynthesis by a single leaf are the availability of reactants such as light energy and CO_2; temperature, which governs reaction rates; and the availability of nitrogen, which is required to produce photosynthetic enzymes (Fig. 3.1).

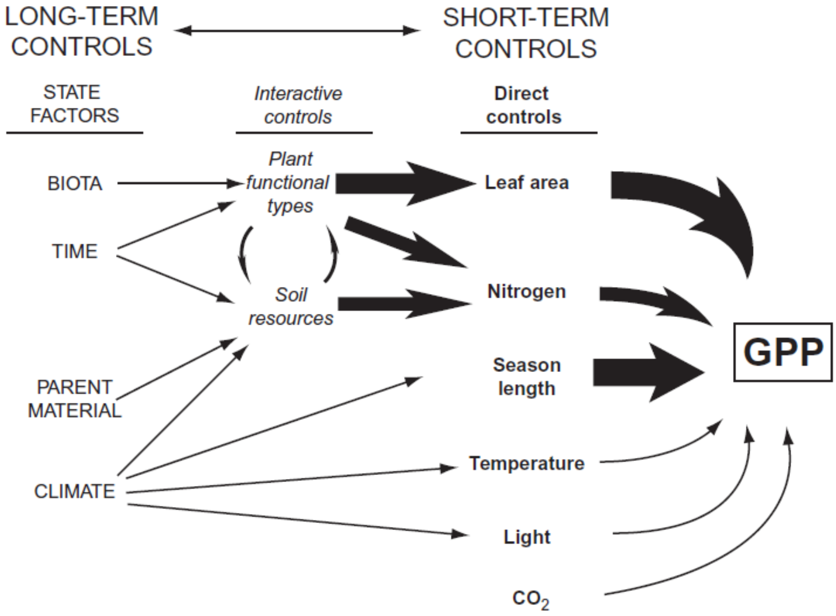

Figure 3.1. The major factors governing gross primary production (GPP) in ecosystems. These controls range from the direct controls, which determine the diurnal and seasonal variations in GPP, to the interactive controls and state factors, which are the ultimate causes of ecosystem differences in GPP. Thickness of the arrows associated with direct controls indicates the strength of the effect. The factors that account for most of the variation in GPP among ecosystems are leaf area and length of the photosynthetic season, which are ultimately determined by the interacting effects of soil resources, climate, vegetation, and disturbance regime (Chapin et al. 2011).

Photosynthesis at the scale of ecosystems is termed gross primary production (GPP). Like photosynthesis by individual leaves, GPP varies diurnally and seasonally in response to changes in light, temperature, and nitrogen supply. Differences among ecosystems in annual GPP, however, are determined primarily by the quantity of leaf area and the length of time that this leaf area is photosynthetically active. Leaf area and photosynthetic season, in turn, depend on the availability of soil resources (water and nutrients), climate, and time since disturbance.

3.3. Global Carbon Cycle and Productivity

The global carbon cycle is a complex set of processes involving three main components: the land; the oceans; and the atmosphere. Through natural flows, hundreds of billions of tons of carbon are exchanged with the atmosphere. However, this number pales in comparison to the amount of carbon stored in stocks (Houghton 2001). The carbon cycle is the biogeochemical cycle by which carbon is exchanged among the biosphere, pedosphere, geosphere, hydrosphere, and atmosphere of the Earth. Along with the nitrogen cycle and the water cycle, the carbon cycle comprises a sequence of events that are key to making the Earth capable of sustaining life; it describes the movement of carbon as it is recycled and reused throughout the biosphere.

Carbon is also present in the Earth's atmosphere, soils, oceans, and crust. When viewing the Earth as a system, these components can be referred to as carbon pools (sometimes also called stocks or reservoirs) because they act as storage houses for large amounts of carbon. Any movement of carbon between these reservoirs is called a flux. In any integrated system, fluxes connect reservoirs together to create cycles and feedbacks. An example of such a cycle is seen in Fig. 3.2 where, carbon in the atmosphere is used in photosynthesis to create new plant material.

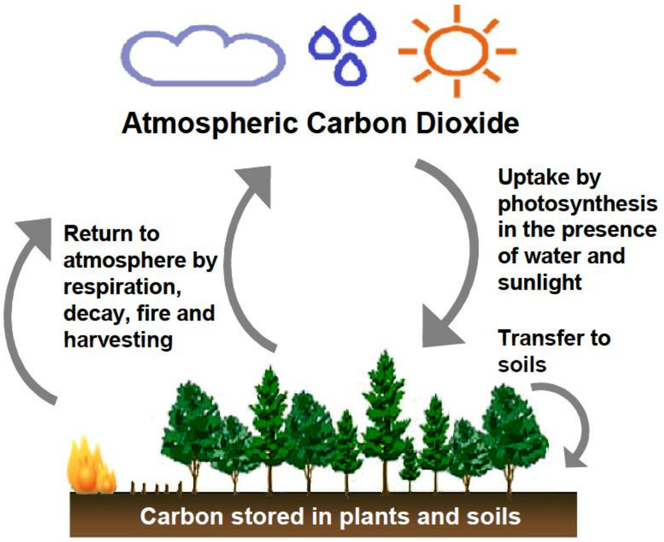

Figure 3.2. A sub-cycle within the global carbon cycle. Carbon continuously moves between the atmosphere, plants and soils through photosynthesis, plant respiration, harvesting, fire and decomposition.

On a global basis, this processes transfers large amounts of carbon from one pool (the atmosphere) to another (plants). Over time, these plants die and decay, are harvested by humans, or are burned either for energy or in wildfires. All of these processes are fluxes that can cycle carbon among various pools within ecosystems and eventually releases it back to the atmosphere. Viewing the Earth as a whole, individual cycles like this are linked to others involving oceans, rocks, etc. on a range of spatial and temporal scales to form an integrated global carbon cycle (Fig. 3.3).

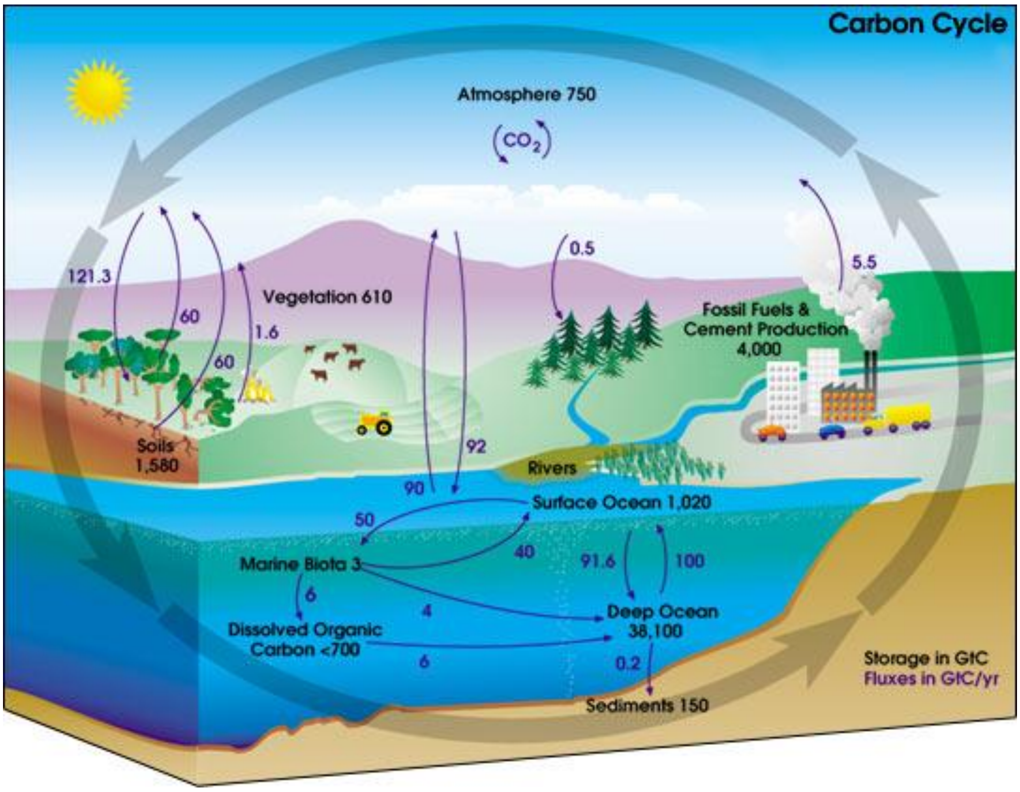

Figure 3.3. A simplified diagram of the global carbon cycle. In any given year, tens of billions of tons of carbon move between the atmosphere, hydrosphere, and geosphere. Human activities add about 5.5 billion tons per year of carbon to the atmosphere. The illustration above shows total amounts of stored carbon in black, and annual carbon fluxes in purple. (Illustration courtesy NASA Earth Science Enterprise). Source: http://earthobservatory.nasa.gov/Library/CarbonCycle/carbon_cycle4.html

On the shortest time scales, of seconds to minutes, plants take carbon out of the atmosphere through photosynthesis and release it back into the atmosphere via respiration. On longer time scales, carbon from dead plant material can be incorporated into soils, where it might reside for years, decades or centuries before being broken down by soil microbes and released back to the atmosphere. On still longer time scales, organic matter[1] that became buried in deep sediments (and protected from decay) was slowly transformed into deposits of coal, oil and natural gas, the fossil fuels we use today. When we burn these substances, carbon that has been stored for millions of years is released once again to the atmosphere in the form of carbon dioxide (CO_2).

The carbon cycle has a large effect on the function and well being of our planet. Globally, the carbon cycle plays a key role in regulating the Earth's climate by controlling the concentration of carbon dioxide in the atmosphere. Carbon dioxide (CO_2) is important because it contributes to the greenhouse effect, in which heat generated from sunlight at the

Earth’s surface is trapped by certain gasses and prevented from escaping through the atmosphere. The greenhouse effect itself is a perfectly natural phenomenon and, without it, the Earth would be a much colder place. But as is often the case, too much of a good thing can have negative consequences, and an unnatural buildup of greenhouse gasses can lead to a planet that gets unnaturally hot. In recent years CO_2 has received much attention because its concentration in the atmosphere has risen to approximately 30% above natural background levels and will continue to rise into the near future. Scientists have shown that this increase is a result of human activities that have occurred over the last 150 years, including the burning of fossil fuels and deforestation. Because CO_2 is a greenhouse gas, this increase is believed to be causing a rise in global temperatures. This is the primary cause of climate change and is the main reason for increasing interest in the carbon cycle. The Earth’s carbon reservoirs naturally act as both sources, adding carbon to the atmosphere, and sinks, removing carbon from the atmosphere. If all sources are equal to all sinks, the carbon cycle can be said to be in equilibrium (or in balance) and there is no change in the size of the pools over time. Maintaining a steady amount of CO_2 in the atmosphere helps maintain stable average temperatures at the global scale. However, because fossil fuel combustion and deforestation have increased CO_2 inputs to the atmosphere without matching increases in the natural sinks that draw CO_2 out of the atmosphere (oceans, forests, etc.), these activities have caused the size of the atmospheric carbon pool to increase. This is what has been responsible for the present buildup of CO_2 and is believed to cause the observed trend of increasing global temperatures. How far will CO_2 levels rise in the future? The answer depends both on how much CO_2 humans continue to release and on the future amount of carbon uptake and storage by the Earth's natural sinks and reservoirs. In short, it depends on the carbon cycle.

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[1] *We often refer to carbon occurring in “organic” versus “inorganic” forms. This is a simple way of grouping different forms of carbon into biologically derived compounds (complex substances produced only by the growth of living organisms) and mineral compounds that can be formed in the absence of biological activity (but can sometimes be formed with the assistance of living things, as in the case of sea shells). Organic compounds includes such things as sugars, fats, proteins and starches and are contained in both living organisms and the material that remains after their death and partial decomposition (including the organic matter in soils as well as the deposits of coal and oils we refer to as fossil fuels). Note that complete decomposition of organic matter results in a return to mineral forms, often as CO_2. Mineral forms of carbon include carbonates contained in rock and seawater as well as CO_2 itself.*

3.4. Photosynthesis

Photosynthesis is a process used by plants and other organisms to convert light energy, normally from the sun, into chemical energy that can be used to fuel the organisms' activities. Carbohydrates, such as sugars, are synthesized from carbon dioxide and water. Oxygen is also released, mostly as a waste product. Most plants, most algae, and cyanobacteria perform the process of photosynthesis, and are called photoautotrophs. Photosynthesis maintains atmospheric oxygen levels and supplies all of the organic compounds and most of the energy necessary for all life on Earth.

Although photosynthesis is performed differently by different species, the process always begins when energy from light is absorbed by proteins called reaction centres that contain green chlorophyll pigments. In plants, these proteins are held inside organelles called chloroplasts, which are most abundant in leaf cells, while in bacteria they are embedded in the plasma membrane. In these light-dependent reactions, some energy is used to strip electrons from suitable substances such as water, producing oxygen gas. Furthermore, two further compounds are generated: reduced nicotinamide adenine dinucleotide phosphate (NADPH) and adenosine triphosphate (ATP), the "energy currency" of cells.

In plants, algae and cyanobacteria, sugars are produced by a subsequent sequence of light-independent reactions called the Calvin cycle, but some bacteria use different mechanisms, such as the reverse Krebs cycle. In the Calvin cycle, atmospheric carbon dioxide is incorporated into already existing organic carbon compounds, such as ribulose bisphosphate (RuBP). Using the ATP and NADPH produced by the light-dependent reactions, the resulting compounds are then reduced and removed to form further carbohydrates such as glucose.

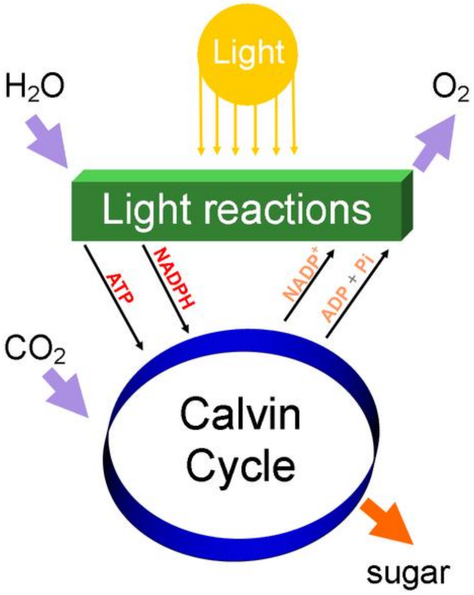

Figure 3.4. A simplified diagram of photosynthesis. Photosynthesis changes sunlight into chemical energy, splits water to liberate O_2, and fixes CO_2 into sugar.
(Source: http://en.wikipedia.org/wiki/File:Simple_photosynthesis_overview.svg)

3.5. Autotrophic respiration

Autotrophic respiration (Ra) involves the oxidation of organic substances to CO_2 and water, with the production of ATP and reducing power (NADPH):

$$O_2 + CH_2O \text{ ---» } CO_2 + H_2O$$

Total autotrophic respiration consists of two major components associated with the metabolic energy expended in the synthesis of new tissue and in the maintenance of living tissue already synthesized.

3.6. Heterotrophic respiration

The detritus produced by autotrophic plants serves as food or substrate for heterotrophic organisms which respire CO_2 or methane (CH_4). In estimating carbon balances of ecosystems, the rate that litter (including large woody components) decomposes (above and belowground) is important to quantify. We discuss how the activities of micro- and macroorganisms respond to changes in the size, biochemical composition, and physical environment associated with different substrates, with the goal of estimating CO_2 evolution from the breakdown and decomposition of all forms of detritus. In this section, we focus on leaf and fine-root detritus because these components turn over rapidly and are therefore likely to contribute the most to seasonal fluctuations in heterotrophic respiration.

When heterotrophic respiration is monitored by enclosing samples of fresh leaf oř fine-root litter within small-mesh nylon bags, the mass loss per unit time can be measured, and, because organic matter is approximately 50% carbon, the CO_2 evolved can be calculated. Alternatively, under laboratory conditions, litter samples may be placed in chambers with controls on moisture and temperature and CO_2 effíux directly monitored. From a combination of studies, three major variables have been identified as limiting heterotrophic respiration: substráte quality, relative water content, and temperature.

3.7. Gross and Net production

To understand the global carbon cycle, a basic knowledge of primary productivity must be reached. All ecosystems on Earth contain a wide variety of plants in various densities. The amount of living organisms within a particular area is referred to as biomass and is usually expressed in units of dry organic matter (tons) or units of energy in joules. Through photosynthesis, plants fix carbon as illustrated by the following formula:

$$6CO_2 + 6H_2O + \text{light energy} = C_6H_{12}O_6 + 6O_2$$

Gross primary production (GPP) is the amount of chemical energy as biomass that primary producers create in a given length of time. (GPP is sometimes confused with Gross Primary productivity, which is the rate at which photosynthesis or chemosynthesis occurs.) Some fraction of this fixed energy is used by primary producers for cellular respiration and maintenance of existing tissues (i.e., "growth respiration" and "maintenance respiration"). The remaining fixed energy (i.e., mass of photosynthate) is referred to as net primary production (NPP).

NPP = GPP - respiration [by plants]

Net primary production is the rate at which all the plants in an ecosystem produce net useful chemical energy; it is equal to the difference between the rate at which the plants in an ecosystem produce useful chemical energy (GPP) and the rate at which they use some of that energy during respiration. Some net primary production goes toward growth and reproduction of primary producers, while some is consumed by herbivores.

Both gross and net primary production are in units of mass per unit area per unit time interval. In terrestrial ecosystems, mass of carbon per unit area per year (g C m^{-2} yr^{-1}) is most often used as the unit of measurement (Fig. 3.4.)

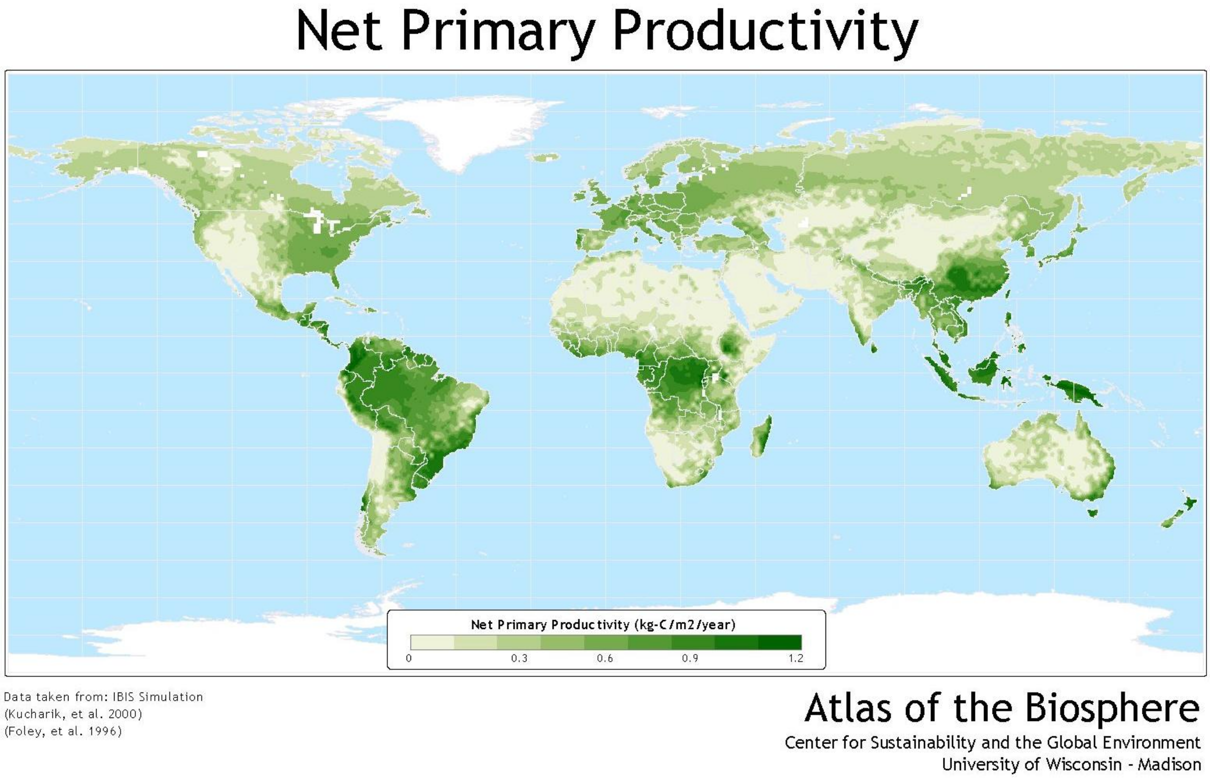

Figure 3.4. Net Primary Productivity (NPP).

Carbon is a constituent of all terrestrial life. Carbon begins its cycle through forest ecosystems when plants assimilate atmospheric CO_2 through photosynthesis into reduced sugars (Fig. 3.4). Usually about half the gross photosynthetic products produced (GPP) are expended by plants in autotrophic respiration (Ra) for the synthesis and maintenance of living cells, releasing CO_2 back into the atmosphere. The remaining carbon products (GPP - Ra) go into net primary production (NPP): foliage, branches, stems, roots, and plant reproductive organs. As plants shed leaves and roots, or are killed, the dead organic matter forms detritus, a substrate that supports animals and microbes, which through their heterotrophic metabolism (Rh) release CO_2 back into the atmosphere. On an annual basis, undisturbed forest ecosystems generally show a small net gain in carbon exchange with the atmosphere. This represents net ecosystem production (NEP). The ecosystem may lose carbon if photosynthesis is suddenly reduced or when organic materials are removed as a result of disturbance. Soil humus represents the major accumulation of carbon in most ecosystems because it remains unoxidized for centuries. It is the most important long-term carbon storage site in ecosystems.

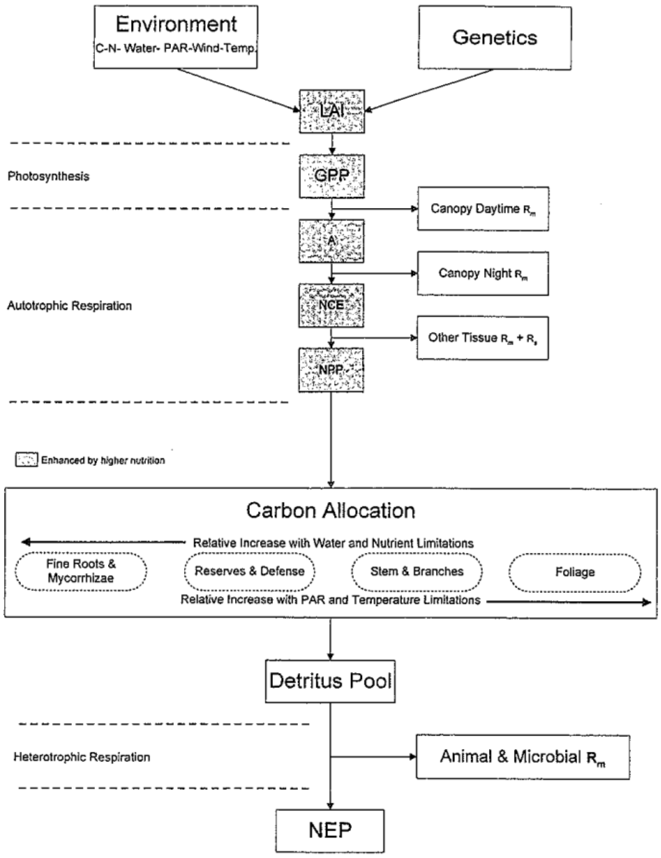

Figure 3.4. Carbon balance models that are coupled to water and nutrient cycling operate by predicting carbon uptake and losses through a series of processes, starting with photosynthesis and the absorption of solar radiation by leaves. Gross primary production (GPP) is further limited by other environmental variables affecting canopy stomatal conductance. Deducting foliar maintenance respiration during the daylight hours provides an estimate of net assimilation (A). Including canopy respiration at night yields an estimate of daily net canopy exchange (NCE) for a 24-hr period. Net primary production (NPP) is calculated by accounting for additional autotrophic losses associated with synthesis (Rs and maintenance (Rm) throughout each day. NPP is partitioned into various components based on schemes associated with C:N ratios which change with the availability of water and nutrients. Leaf and fine-root turnover are the major contributors to litter on a seasonal basis, but all biomass components eventually enter the detrital pool. The annual turnover of leaves and roots is correlated with seasonal variation in LAI, specific leaf area, and nitrogen content. Decomposition of litter and release of CO; by heterotrophic organisms are functions of substrate quality (C:N ratio), temperature, and moisture conditions Net ecosystem production (NEP) is calculated as the residual, after deducting heterotrophic respiration (Rh) (Waring, Running 1996).

3.8. Review questions

1. Characterize photosynthesis and their limiting factors in forest ecosystem.
2. Explain diferences between primary and secondary productivity.
3. Define Net primary productivity and biomass allocation in different forest type.
4. Explain how climate change will influence the NPP of forest ecosystem.
5. What are the main principles and explanations for global climatic changes-

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http://en.wikipedia.org/wiki/Photosynthesis
http://globecarboncycle.unh.edu/CarbonCycleBackground.pdf

Chapter 4. Water cycle in forest ecosystem

4.1. Introduction

The water cycle, also known as the hydrologic cycle or the H_2O cycle, describes the continuous movement of water on, above and below the surface of the Earth. The mass water on Earth remains fairly constant over time but the partitioning of the water into the major reservoirs of ice, fresh water, saline water and atmospheric water is variable depending on a wide range of climatic variables. The water moves from one reservoir to another, such as from river to ocean, or from the ocean to the atmosphere, by the physical processes of evaporation, condensation, precipitation, infiltration, runoff, and subsurface flow. In so doing, the water goes through different phases: liquid, solid (ice), and gas (vapor). The water cycle involves the exchange of energy, which leads to temperature changes. For instance, when water evaporates, it takes up energy from its surroundings and cools the environment. When it condenses, it releases energy and warms the environment. These heat exchanges influence climate. The evaporative phase of the cycle purifies water which then replenishes the land with freshwater. The flow of liquid water and ice transports minerals across the globe. It is also involved in reshaping the geological features of the Earth, through processes including erosion and sedimentation. The water cycle is also essential for the maintenance of most life and ecosystems on the planet.

The hydrologic cycle is an important feature of all ecosystems, and particularly forests, which generally grow in climates where precipitation provides more water than the vegetation can use or soils can store. The excess water contributes to stream flow, which provides for irrigation and urban needs far from the source of precipitation. Vegetation is a major factor in the hydrologic cycle. Before precipitation reaches the soil, water is intercepted and evaporated from the surface of vegetation and the litter layer. The rate at which water infiltrates into the soil, runs off the surface, or percolates through to the water table is affected by the density and depth of root channels and organic residue incorporated into the soil.

4.2. What is hydrology?

The scientific discipline in the field of physical geography that deals with the water cycle is called hydrology. It is concerned with the origin, distribution, and properties of water on the globe. Consequently, the water cycle is also called the hydrologic cycle in many scientific textbooks and educational materials. In a broad context, the sciences of meteorology and oceanography describe parts of a series of global physical processes involving water that are also major components of the science of hydrology. Geologists describe another part of the physical processes by addressing groundwater movement within the planet's subterranean features. Hydrologists are interested in obtaining measurable information and knowledge about the water cycle. Also important is the measurement of the amount of water involved in the transitional stages that occur as the water moves from one process within the cycle to other processes. Hydrology, therefore, is a broad science that utilizes information from a wide range of other sciences and integrates them to quantify the movement of water. The fundamental tools of hydrology are based in supporting scientific techniques that originated in mathematics, physics, engineering, chemistry, geology, and biology. Consequently, hydrology uses developed concepts from the sciences of meteorology, climatology, oceanography, geography, geology, glaciology, limnology (lakes), ecology, biology, agronomy, forestry, and other sciences that specialize in other aspects of the physical, chemical or biological environment.

Hydrology, therefore, is one of the interdisciplinary sciences that is the basis for water resources development and water resources management.

4.3. Energy and Water

Water and solar energy are essential for the functioning of the Earth System. Since neither is distributed evenly around the globe, the mechanisms by which they are redistributed (the global hydrologic cycle and energy budget) are important. These processes are so tightly intertwined that they cannot be treated separately. Solar energy drives the hydrologic cycle through the vertical transfer of water from Earth to the atmosphere via evapotranspiration, the sum of evaporation from surfaces and transpiration, which is the water loss from plants. Conversely, evapotranspiration accounts for 75% of the turbulent energy transfer from Earth to the atmosphere and is therefore a key process in Earth's energy budget (see Fig. 4.1). The hydrologic cycle also controls Earth's biogeochemical cycles by influencing all biotic processes, dissolving nutrients, and transferring them within and among ecosystems. These nutrients provide the resources that support growth of organisms. The movement of materials that are dissolved and suspended in water links ecosystems within a landscape.

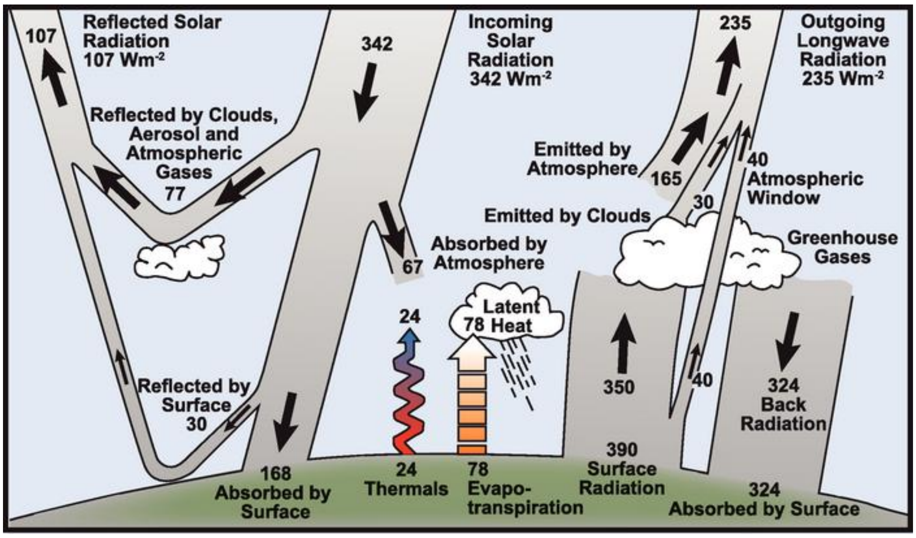


Figure 4.1: Estimate of the Earth's annual and global mean energy balance. Over the long term, the amount of incoming solar radiation absorbed by the Earth and atmosphere is balanced by the Earth and atmosphere releasing the same amount of outgoing longwave radiation. About half of the incoming solar radiation is absorbed by the Earth's surface. This energy is transferred to the atmosphere by warming the air in contact with the surface (thermals), by evapotranspiration and by longwave radiation that is absorbed by clouds and greenhouse gases. The atmosphere in turn radiates longwave energy back to Earth as well as out to space. IPCC (2007). Units are W.m^{-2}. Source: Kiehl and Trenberth (1997).

The Sun can with high accuracy be described as a black body emitting energy at 5800 K (5530 °C) with a maximum at a wavelength of 0.5 µm (see Fig. 4.1). Averaged over the year and all surfaces of the Earth this amounts to 342 w m^2 As this shortwave radiation hits the Earth's atmosphere, 77 W.m^2 (23%) is directly reflected back into space, 67 W.m^2 (20%) is absorbed by molecules in the atmosphere, heating it. The remaining part is partly reflected (30

W.m^2 or 9%) and partly absorbed (168 W.m^2 or 49%) by the Earth's surface (see Fig. 4.1). The total annual energy flux from the Sun that is absorbed by the surface of the Earth is, therefore, $168 \times 365 \times 24 \times 3600 \times 4 \times n \times (6371 \times 10^3)^2 = 2.7 \times 10^{24}$ J.

The gross photosynthesis on Earth is 220 Pg (C) yr^{-1}. The heat of combustion of 1 g in the form of glucose (C) is 38.9 kJ and the gross photosynthesis corresponds to 7.84×10^{21} J. The solar energy trapped in photosynthesis is thus a negligible component (3‰) in the Earth's energy budget.

The radiation balance includes both short-wave (0.3-4 μm) and long-wave (4-80 μm) components of radiation. About 95% of solar radiation is short-wave, which contains about equal proportions of visible light (0.4-0.7 μm; the photosynthetically active component of radiation, PAR) and near-infrared radiation (NIR). Short-wave radiation incident on vegetation or other surfaces may be reflected or absorbed; the absorbed radiation may heat the surface and be transformed into sensible heat, or it may evaporate water (latent heat). All surfaces above absolute zero emit long-wave radiation at a rate proportional to the fourth power of the temperature (Stefan-Boltzmann law). The total radiation incident on any surface is the sum of (1) direct short-wave radiation from the sun; (2) diffuse short-wave radiation from the sky; (3) reflected short-wave from nearby surfaces; (4) long-wave radiation from atmospheric emission; and (5) long-wave emitted from nearby surfaces (Fig. 4.2).

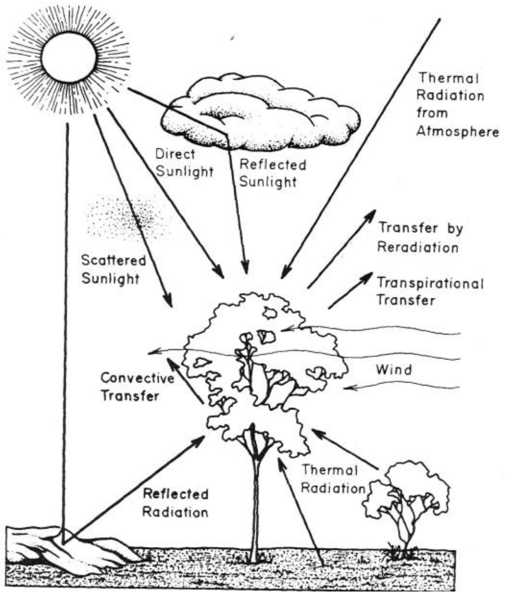


Figure 4.2: Energy exchange between vegetation and the environment involves a number of processes. Solar radiation reaches plant canopies as direct, scattered, and reflected sunlight, all of which contain some short-wave components important for photosynthesis. On partly cloudy days, reflection from clouds can increase incident short-wave radiation at the ground surface by as much as 30%. On clear days, less than 10% of the short-wave radiation is scattered by the atmosphere; on overcast days, incident short-wave radiation is reduced and diffuse, casting no shadows. Plant and other surfaces absorb and reflect short-wave and long-wave radiation, and they emit thermal radiation as a function of their absolute (Kelvin) temperature. The bulk of the heat load on plants is reradiated; evaporative cooling by transpiration and heat transfer by convection and wind (advection) remove the rest. Some heat is stored temporarily in the soil and plant tissue, which is later reradiated. (Gates 1980; Waring, Running 1996).

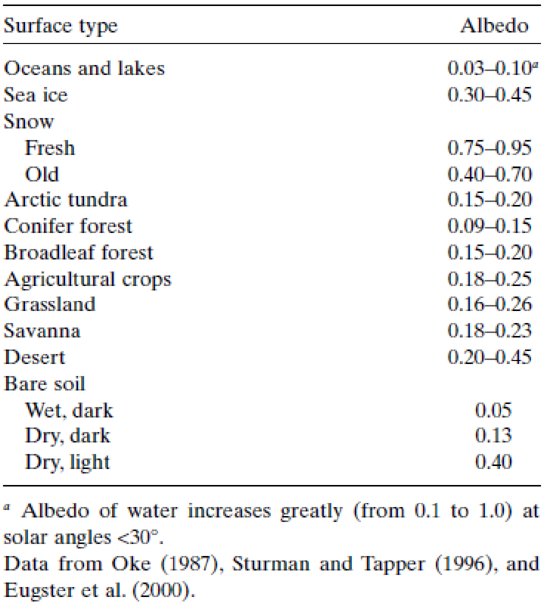
Net radiation (Rnet) is quantified according to the following equation:

$$R_n = (1 + \alpha)I_s - \varepsilon_L\, \sigma T^4\ (\text{surface}) + \sigma T^4\ (\text{sky})$$

where α is the albedo or reflectivity of the surface as a fraction of intercepted incident short-wave radiation (Is); ε_L is emissivity compared to a perfect black body, with ε_L for most soils and vegetation being between 0.9 and 0.98; T is the Stefan-Boltzmann constant (5.67 x 10^{8} W m^{-2} K^{-4}); and *T* is Kelvin temperature in reference to absolute zero (10°C = 283K).

Depending on the reflective properties of leaves, the net radiation above dense forests is typically about 80-90% of incident short-wave radiation (Landsberg, Gower 1997). If soils or snow intercept a major part of incoming solar radiation, more precise calcula-tions are required, based on the fractions of short- and long-wave radiation that penetrate through the canopy. Reflectivities (albedos) for a wide range of surfaces are presented in Table 4.3.

Table 4.1. Typical values of albedo of major surface types on earth (Chapin et al. 2002).



Surface type	Albedo
Oceans and lakes	0.03–0.10[a]
Sea ice	0.30–0.45
Snow	
Fresh	0.75–0.95
Old	0.40–0.70
Arctic tundra	0.15–0.20
Conifer forest	0.09–0.15
Broadleaf forest	0.15–0.20
Agricultural crops	0.18–0.25
Grassland	0.16–0.26
Savanna	0.18–0.23
Desert	0.20–0.45
Bare soil	
Wet, dark	0.05
Dry, dark	0.13
Dry, light	0.40

[a] Albedo of water increases greatly (from 0.1 to 1.0) at solar angles <30°.

Data from Oke (1987), Sturman and Tapper (1996), and Eugster et al. (2000).

4.4. Main components of water balance

Storage - water in soil and aboveground and belowground biomass.
Inputs - Precipitation, Interception, Throughfall, Stemflow, Infiltration, Percolation, Underground water
Outputs - Transpiration, Evaporation Surface Runoff, Base Flow
Precipitation - Condensed water vapor that falls to the Earth's surface . Most precipitation occurs as rain, but also includes snow, hail, fog drip, graupel, and sleet.
Canopy interception - The precipitation that is intercepted by plant foliage, eventually evaporates back to the atmosphere rather than falling to the ground.

Snowmelt - The runoff produced by melting snow.

Runoff - The variety of ways by which water moves across the land. This includes both surface runoff and channel runoff. As it flows, the water may seep into the ground, evaporate into the air, become stored in lakes or reservoirs, or be extracted for agricultural or other human uses.

Infiltration - The flow of water from the ground surface into the ground. Once infiltrated, the water becomes soil moisture or groundwater.

Subsurface flow - The flow of water underground, in the vadose zone and aquifers. Subsurface water may return to the surface (e.g. as a spring or by being pumped) or eventually seep into the oceans. Water returns to the land surface at lower elevation than where it infiltrated, under the force of gravity or gravity induced pressures. Groundwater tends to move slowly, and is replenished slowly, so it can remain in aquifers for thousands of years.

Evaporation - The transformation of water from liquid to gas phases as it moves from the ground or bodies of water into the overlying atmosphere. The source of energy for evaporation is primarily solar radiation. Evaporation often implicitly includes transpiration from plants, though together they are specifically referred to as evapotranspiration.

Sublimation - The state change directly from solid water (snow or ice) to water vapor.

Deposition - This refers to changing of water vapor directly to ice.

Advection - The movement of water in solid, liquid, or vapor states through the atmosphere. Without advection, water that evaporated over the oceans could not precipitate over land.

Condensation - The transformation of water vapor to liquid water droplets in the air, creating clouds and fog.

Transpiration - The release of water vapor from plants and soil into the air. Water vapor is a gas that cannot be seen.

Percolation - Water flows horizontally through the soil and rocks under the influence of gravity

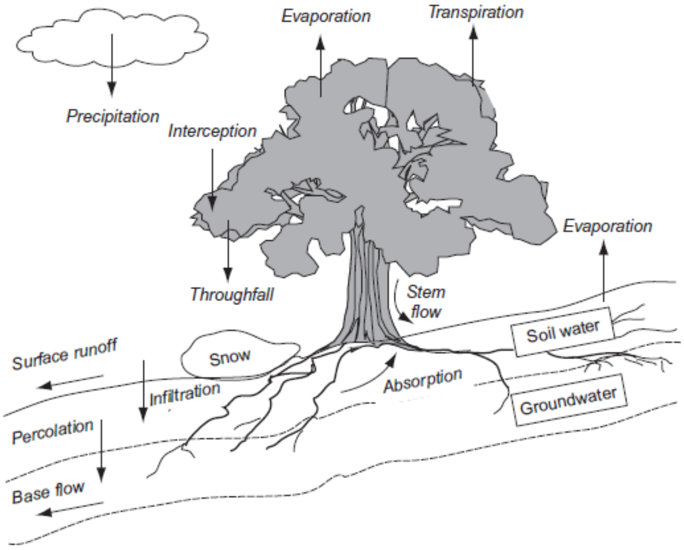


Figure 4.3. Water balance of an ecosystem (Waring and Running 1998).

4.5. Review questions

1. What are the main input and output components of water balance in forest ecosystems.
2. How the solar radiation influenced hydrological cycle and exchange of water between soil, vegetation and atmosphere.
3. How we define evapotranspiration and what are the main factors influenced it.
4. Describe movement water within the soil and availability of water for plant (trees).

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Chapter 5. Biotic interactions and biodiversity

5. 1. Producers, Consumers and Decomposers

The three basic ways in which organisms get food are as producers, consumers and decomposers.

Producers (*autotrophs*) are typically *plants* or *algae*. Plants and algae do not usually eat other organisms, but pull nutrients from the soil or the ocean and manufacture their own food using *photosynthesis*. For this reason, they are called ***primary producers***. In this way, it is energy from the sun that usually powers the base of the food chain. An exception occurs in deep-sea *hydrothermal ecosystems*, where there is no sunlight. Here primary producers manufacture food through a process called *chemosynthesis*.

Consumers (*heterotrophs*) are species which cannot manufacture their own food and need to consume other organisms. Animals that eat primary producers (like plants) are called *herbivores.* Animals that eat other animals are called *carnivores*, and animals that eat both plant and other animals are called *omnivores.*

Decomposers (*detritivores*) break down dead plant and animal material and wastes and release it again as energy and nutrients into the ecosystem for recycling. Decomposers, such as *bacteria* and *fungi* (mushrooms), feed on waste and dead matter, converting it into inorganic chemicals that can be recycled as mineral nutrients for plants to use again.

5. 2. Food chain

A **food chain/web** is a linear consequence of links in a ***food web*** starting from a species that are called producers in the web and ends at a species that is called decomposers species in the web. A food chain differs from a food web, because the complex ***polyphagous*** network of feeding relations are aggregated into trophic species and the chain only follows linear ***monophagous*** pathways. A common metric used to quantify food web trophic structure is food chain length. In its simplest form, the length of a chain is the number of links between a trophic consumer and the base of the web and the mean chain length of an entire web is the arithmetic average of the lengths of all chains in a food web.

The food chain's length is a continuous variable that provides a measure of the passage of energy and an index of ecological structure that increases in value counting progressively through the linkages in a linear fashion from the lowest to the highest ***trophic (feeding) levels*.** Food chains are often used in ecological modeling (such as a three species food chain). They are simplified abstractions of real food webs, but complex in their dynamics and mathematical implications. Ecologists have formulated and tested hypotheses regarding the nature of ecological patterns associated with food chain length, such as increasing length increasing with ecosystem size, reduction of energy at each successive level, or the proposition that long food chain lengths are unstable. Food chain studies have had an important role in ecotoxicology studies tracing the pathways and biomagnification of environmental contaminants.

Food chains vary in length from three to six or more levels. A food chain consisting of a flower, a frog, a snake and an owl consists of four levels; whereas a food chain consisting of grass, a grasshopper, a rat, a snake and finally a hawk consists of five levels. ***Producers***, such as plants, are organisms that utilize solar energy or heat energy to synthesize starch. All food chains must start with a producer. In the deep sea, food chains centered around *hydrothermal vents* exist in the absence of sunlight. *Chemosynthetic* bacteria and archaea can use hydrogen sulfide from hydrothermal vents as an energy source (just as plants use sunlight) to produce carbohydrates; they form the base of the food chain. ***Consumers*** are organisms that eat other organisms: in most food chains, all the organisms in a food chain are consumers. In a deep-sea food chain, tube worms, clams, and mussels harbor the chemosynthetic bacteria and make use of the food they produce. They are all eaten by crabs, which are in turn consumed by octopuses.

Trophic levels can be represented by numbers, starting at level 1 with plants. Further trophic levels are numbered subsequently according to how far the organism is along the ***food chain***.

- Level 1: Plants and algae make their own food and are called primary producers.
- Level 2: Herbivores eat plants and are called primary consumers.
- Level 3: Carnivores which eat herbivores are called secondary consumers.
- Level 4: Carnivores which eat other carnivores are called tertiary consumers.
- Level 5: *Apex predators* which have no predators are at the top of the food chain.

In real world *ecosystems*, there is more than one food chain for most organisms, since most organisms eat more than one kind of food or are eaten by more than one type of predator. A diagram which sets out the intricate network of intersecting and overlapping food chains for an ecosystem is called its ***food web***. Decomposers are often left off food webs, but if included, they mark the end of a food chain. Thus food chains start with primary producers and end with decay and decomposers. Since decomposers recycle nutrients, leaving them so they can be reused by primary producers, they are sometimes regarded as occupying their own trophic level.

Biomass transfer efficiency

Generally, each trophic level relates to the one below it by absorbing some of the energy it consumes and in this way can be regarded as resting on, or supported by, the next lower trophic level. Food chains can be diagrammed to illustrate the amount of energy that moves from one feeding level to the next in a food chain. This is called an *energy pyramid*. The energy transferred between levels can also be thought of as approximating to a transfer in biomass, so energy pyramids can also be viewed as biomass pyramids, picturing the amount of biomass that results at higher levels from biomass consumed at lower levels.

The efficiency with which energy or biomass is transferred from one trophic level to the next is called the *ecological efficiency*. Consumers at each level convert on average only about 10% of the chemical energy in their food to their own organic tissue (the *ten percent law*). For this reason, food chains rarely extend for more than 5 or 6 levels. At the lowest trophic level (the bottom of the food chain), plants convert about 1% of the sunlight they receive into chemical energy. It follows from this that the total energy originally present in the incident sunlight that is finally embodied in a tertiary consumer is about 0.001%.

5. 3. Ecological pyramid

An ecological pyramid (also **trophic pyramid** or **energy pyramid**) is a graphical representation designed to show the biomass or biomass productivity at each trophic level in a given ecosystem.

Biomass is the amount of living or organic matter present in an organism. ***Biomass pyramids*** show how much biomass is present in the organisms at each trophic level, while ***productivity pyramids*** show the production or turnover in biomass.

Ecological pyramids begin with producers on the bottom (such as plants) and proceed through the various trophic levels (such as herbivores that eat plants, then carnivores that eat herbivores, then carnivores that eat those carnivores, and so on). The highest level is the top of the food chain.

An **ecological pyramid of biomass** shows the relationship between biomass and trophic level by quantifying the biomass present at each trophic level of an ecological community at a particular time. It is a graphical representation of biomass (total amount of living or organic matter in an ecosystem) present in unit area in different tropic levels. Typical units are grams per meter^2, or calories per meter^2.

The pyramid of biomass may be "inverted". For example, in a pond ecosystem, the standing crop of phytoplankton, the major producers, at any given point will be lower than the mass of the heterotrophs, such as fish and insects. This is explained as the phytoplankton reproduce very quickly, but have much shorter individual lives.
One problem with biomass pyramids is that they can make a trophic level appear to contain more energy than it actually does. For example, all birds have beaks and skeletons, which despite having mass are not eaten by the next trophic level.

An **ecological pyramid of productivity** is often more useful, showing the production or turnover of biomass at each trophic level. Instead of showing a single snapshot in time, productivity pyramids show the flow of energy through the food chain. Typical units are grams per meter^2 per year or calories per meter^2 per year. As with the others, this graph shows producers at the bottom and higher trophic levels on top.

When an ecosystem is healthy, this graph produces a standard *ecological pyramid*. This is because in order for the ecosystem to sustain itself, there must be more energy at lower trophic levels than there is at higher trophic levels. This allows organisms on the lower levels to not only to maintain a stable population, but also to transfer energy up the pyramid. The exception to this generalization is when portions of a food web are supported by inputs of resources from outside the local community. In small, forested streams, for example, the volume of higher levels is greater than could be supported by the local primary production.
When energy is transferred to the next trophic level, typically only 10% of it is used to build new biomass, becoming stored energy (the rest going to metabolic processes). In this case, in the *pyramid of productivity* each step will be 10% the size of the previous step (100, 10, 1, 0.1, 0.01).

The advantages of the *pyramid of productivity* as a representation:

- It takes account of the rate of production over a period of time.
- Two species of comparable biomass may have very different life spans. Thus a direct comparison of their total biomasses is misleading, but their productivity is directly comparable.
- The relative energy chain within an ecosystem can be compared using pyramids of energy; also different ecosystems can be compared.
- There are no inverted pyramids.
- The input of solar energy can be added.

The disadvantages of the *pyramid of productivity* as a representation:

- The rate of biomass production of an organism is required, which involves measuring growth and reproduction through time.

- There is still the difficulty of assigning the organisms to a specific trophic level. As well as the organisms in the food chains there is the problem of assigning the decomposers and detritivores to a particular trophic level.

Nonetheless, productivity pyramids usually provide more insight into an ecological community when the necessary information is available.

An **ecological pyramid of numbers** shows graphically the population of each level in a food chain. The diagram to the right shows a (fictional) example of a five level pyramid of numbers: 10,000 fresh water shrimps support 1,000 bleak, which in turn support 100 perches followed by 10 northern pikes and finally one osprey. However this is inconsistent with the scenario that 10% of each trophic level passes to the next one, since mature individuals of each of these species have very different masses.

Secondary production

Secondary production is the generation of ***biomass of heterotrophic (consumer) organisms*** in a system. This is driven by the transfer of organic material between trophic levels, and represents the quantity of new tissue created through the use of assimilated food. Secondary production is sometimes defined to only include consumption of primary producers by herbivorous consumers[2] (with tertiary production referring to carnivorous consumers),[3] but is more commonly defined to include all biomass generation by heterotrophs. Organisms responsible for secondary production include animals, protists, fungi and many bacteria.

Secondary production can be estimated through a number of different methods including increment summation, removal summation, the instantaneous growth method and the Allen curve method. The choice between these methods will depend on the assumptions of each and the ecosystem under study. For instance, whether cohorts should be distinguished, whether linear mortality can be assumed and whether population growth is exponential.

5. 4. Biological interactions

Biological (Biotic) interactions are the effects *organisms* in a *community* have on one another. In the natural world no organism exists in absolute isolation, and thus every organism must interact with the environment and other organisms. An organism's interactions with its environment are fundamental to the survival of that organism and the functioning of the ecosystem as a whole.

In ecology, biological interactions can involve individuals of the same species (intraspecific interactions) or individuals of different species (interspecific interactions). These can be further classified by either the mechanism of the interaction or the strength, duration and direction of their effects.[3] Species may interact once in a generation (e.g. pollination) or live completely within another (e.g. endosymbiosis). Effects range from consumption of another individual (predation, herbivory, or cannibalism), to mutual benefit (mutualism). Interactions need not be direct; individuals may affect each other indirectly through intermediaries such as shared resources or common enemies.

Neutralism

Neutralism describes the relationship between two species which interact but do not affect each other. It describes interactions where the fitness of one species has absolutely no effect whatsoever on that of the other. True neutralism is extremely unlikely or even impossible to prove. When dealing with the complex networks of interactions presented by ecosystems, one cannot assert positively that there is absolutely no competition between or benefit to either species. Since true neutralism is rare or nonexistent, its usage is often extended to situations where interactions are merely insignificant or negligible.

Amensalism

It is a relationship in which a product of one organism has a negative effect on another organism.[4] It is specifically a population interaction in which one organism is harmed, while the other is neither affected nor benefited. Usually this occurs when one organism exudes a chemical compound as part of its normal metabolism that is detrimental to another organism. The bread mold penicillium is a common example; penicillium secrete penicillin, a chemical that kills bacteria. A second example is the black walnut tree (*Juglans nigra*), which secrete juglone, an allelochemical that harms or kills some species of neighboring plants. This interaction may nevertheless increase the fitness of the non-harmed organism by removing competition and allowing it greater access to scarce resources. In this sense the impeded organism can be said to be negatively affected by the other's very existence, making it a +/- interaction. A third example is when sheep or cattle make trails by trampling on grass, thereby destroying a food source.

Competition

Competition is an interaction between organisms or species, in which the fitness of one is lowered by the presence of another. Limited supply of at least one resource (such as food, water, and territory) used by both can be a factor. Competition both within and between species is an important topic in ecology, especially community ecology. Competition is one of many interacting biotic and abiotic factors that affect community structure. Competition among members of the same species is known as ***intraspecific competition***, while competition between individuals of different species is known as ***interspecific competition***. Competition is not always straightforward, and can occur in both a direct and indirect fashion.

- According to the ***competitive exclusion principle*****,** species less suited to compete for resources should either adapt or die out, although competitive exclusion is rarely found in natural ecosystems. According to evolutionary theory, this competition within and between species for resources plays a very relevant role in natural selection, however, competition may play less of a role than expansion among larger groups such as families.

Types of competition:

a) By mechanism

Interference competition

Occurs *directly* between individuals via aggression etc. when the individuals interfere with foraging, survival, reproduction of others, or by directly preventing their physical establishment in a portion of the habitat. An example of this can be seen between the *Novomessor cockerelli* species and Red Harvester Ants, where one species interferes with the others' ability to forage by plugging the entrances to their colonies with small rocks.

Exploitation competition

Occurs *indirectly* through a common *limiting resource* which acts as an intermediate. For example, use of resources depletes the amount available to others, or they compete for space. Also known as exploitative competition.

Apparent competition

Occurs *indirectly* between two species which are both preyed upon by the same predator. For example, species A and species B are both prey of predator C. The increase of species A may cause the decrease of species B, because the increase of As may aid in the survival of predator Cs, which will increase the number of predator Cs, which in turn will hunt more of species B.

b) By species

Intraspecific competition

Intraspecific competition occurs when members of the same species compete for the same *resources* in an ecosystem. The organism that obtains less resources, will usually perform less well than if it lives alone, Although in this situation it may actually be more useful to think in terms of resource availability than competition.

Interspecific competition

Interspecific competition may occur when individuals of two separate species share a limiting resource in the same area. If the resource cannot support both populations, then lowered fecundity, growth, or survival may result in at least one species. Interspecific competition has the potential to alter populations, communities and the evolution of interacting species. An example among animals could be the case of cheetahs and lions; since both species feed on similar prey, they are negatively impacted by the presence of the other because they will have less food, however they still persist together, despite the prediction that under competition one will displace the other. In fact, lions sometimes steal prey items killed by cheetahs. Potential competitors can also kill each other, and this phenomenon is called '*intraguild predation*'. For example, in southern California coyotes often kill and eat gray foxes and bobcats, all three carnivores sharing the same stable prey (small mammals).

Predation

In ecology, predation describes a biological interaction where a **predator** (an organism that is hunting) feeds on its **prey** (the organism that is attacked). Predators may or may not kill their prey prior to feeding on them, but the act of predation often results in the death of its prey and the eventual absorption of the prey's tissue through consumption. Other categories of consumption are ***herbivory*** (eating parts of plants), ***mycophagy*** (eating parts of fungi) and ***detritivory***, the consumption of dead organic material (detritus). All these consumption categories fall under the rubric of consumer-resource systems. It can often be difficult to separate various types of feeding behaviors. For example, some parasitic species prey on a host organism and then lay their eggs on it for their offspring to feed on it while it continues to live or on its decaying corpse after it has died. The key characteristic of predation however is the predator's direct impact on the prey population. On the other hand, detritivores simply eat dead organic material arising from the decay of dead individuals and have no direct impact on the "donor" organism(s).

Selective pressures imposed on one another often leads to an evolutionary arms race between prey and predator, resulting in various ***antipredator adaptations***. Ways of classifying predation surveyed here include grouping by trophic level or diet, by specialization, and by the nature of the predator's interaction with prey.

Classification of predators by the extent to which they feed on and interact with their prey is one way ecologists may wish to categorize the different types of predation. Instead of focusing on what they eat, this system classifies predators by the way in which they eat, and the general nature of the interaction between predator and prey species. Two factors are considered here: How close the predator and prey are physically (in the latter two cases the term *prey* may be replaced with *host*). Additionally, whether or not the prey are directly killed by the predator is considered, with true predation and parasitoidism involving certain death.

True predation

A true predator can commonly be known as one which kills and eats another living thing. Whereas other types of predator all harm their prey in some way, this form certainly kills them. Predators may hunt actively for prey, or sit and wait for prey to approach within striking distance, as in *ambush predators*. *Seed predation* and egg predation are other forms of true predation, as seeds and eggs represent potential organisms. Predators of this classification need not eat prey entirely. For example, some predators cannot digest bones, while others can. Some may eat only part of an organism, as in grazing (see below), but still consistently cause its direct death.

Grazing

Grazing organisms may also kill their prey species, but this is seldom the case. While some herbivores like zooplankton live on unicellular phytoplankton and therefore, by the individualized nature of the organism, kill their prey, many only eat a small part of the plant. Grazing livestock may pull some grass out at the roots, but most is simply grazed upon, allowing the plant to regrow once again. Kelp is frequently grazed in subtidal kelp forests, but regrows at the base of the blade continuously to cope with browsing pressure. Animals may also be 'grazed' upon; female mosquitos land on hosts briefly to gain sufficient proteins for the development of their offspring. Starfish may be grazed on, being capable of regenerating lost arms.

Parasitism

Parasites can at times be difficult to distinguish from grazers. Their feeding behavior is similar in many ways, however they are noted for their close association with their host species. While a grazing species such as an moose (*Alces alces*) may travel many kilometers in a single day, grazing on many plants in the process, parasites form very close associations with their hosts, usually having only one or at most a few in their lifetime. This close living arrangement may be described by the term *symbiosis*, "living together", but unlike *mutualism* the association significantly reduces the fitness of the host. Parasitic organisms range from the macroscopic mistletoe, a parasitic plant, to microscopic internal parasites such as cholera. Some species however have more loose associations with their hosts. Lepidoptera (butterfly and moth) larvae may feed parasitically on only a single plant, or they may graze on several nearby plants. It is therefore wise to treat this classification system as a continuum rather than four isolated forms.

Parasitoidism

Parasitoids are organisms living in or on their host and feeding directly upon it, eventually leading to its death. They are much like parasites in their close symbiotic relationship with their host or hosts. Like the previous two classifications parasitoid predators do not kill their hosts instantly. However, unlike parasites, they are very similar to true predators in that the fate of their prey is quite inevitably death. A well-known example of a parasitoids are the ichneumon wasps, solitary insects living a free life as an adult, then laying eggs on or in another species such as a caterpillar. Its larva(e) feed on the growing host causing it little harm at first, but soon devouring the internal organs until finally destroying the nervous system resulting in prey death. By this stage the young wasp(s) are developed sufficiently to move to the next stage in their life cycle. Though limited mainly to the insect order Hymenoptera, Diptera and Coleoptera parasitoids make up as much as 10% of all insect species.

Commensalism

Commensalism benefits one organism and the other organism is neither benefited nor harmed. It occurs when one organism takes benefits by interacting with another organism by which the host organism is not affected. A good example is a remora living with a shark. Remoras eat leftover food from the shark. The shark is not affected in the process as remoras eat only leftover food of the shark which doesn't deplete the shark's resources.

Mutualism

It is an interaction between two or more species, where species derive a mutual benefit, for example an increased carrying capacity. Similar interactions within a species are known as ***co-operation***. Mutualism may be classified in terms of the closeness of association, the closest being symbiosis, which is often confused with mutualism. One or both species involved in the interaction may be *obligate*, meaning they cannot survive in the short or long term without the other species. Though mutualism has historically received less attention than other interactions such as predation, it is very important subject in ecology. Examples include *cleaner fish*, *pollination* and *seed dispersal*, *gut flora* and *nitrogen fixation by fungi*.

5. 5. Biodiversity

5. 5. 1. Definition of Biodiversity

Biodiversity is the degree of variation of life. This can refer to genetic variation, species variation, or ecosystem variation within an area, biome, or planet. Terrestrial biodiversity tends to be highest at low latitudes near the equator, which seems to be the result of the warm climate and high primary productivity. Biologists most often define biodiversity as the "totality of genes, species, and ecosystems of a region". An advantage of this definition is that it seems to describe most circumstances and presents a unified view of the traditional three levels at which biological variety has been identified:

- *species diversity*
- *ecosystem diversity*
- *genetic diversity*

Species diversity is the effective number of different species that are represented in a collection of individuals (a dataset). The effective number of species refers to the number of equally-abundant species needed to obtain the same mean proportional species abundance as that observed in the dataset of interest (where all species may not be equally abundant). Species diversity consists of two components, ***species richness*** and ***species evenness***. Species richness is a simple count of species, whereas species evenness quantifies how equal the abundances of the species are.

Localized *species richness* at a particular place is called **alpha diversity**, bud the biotic community often changes in a traverse of the landscape as soil, slope or disturbance such as fire changes, frequently creating locally different habitats within a forest: **beta diversity** measures the extent of such change along a gradient and can be thought of as the diversity within a landscape. **Gamma diversity** is similar to alpha diversity but is a measure of species richness across a range of habitats within a larger geographical area and is often used to show regional diversity, which may include forests and other types of vegetation.

Ecosystem diversity refers to the diversity of a place at the level of *ecosystems*. The term differs from biodiversity, which refers to variation in species rather than ecosystems. Ecosystem diversity can also refer to the variety of ecosystems present in a biosphere, the variety of species and ecological processes that occur in different physical settings.

Genetic diversity, the level of biodiversity, refers to the total number of genetic characteristics in the genetic makeup of a species. It is distinguished from *genetic variability*, which describes the tendency of genetic characteristics to vary. Genetic diversity serves as a way for populations to adapt to changing environments. With more variation, it is more likely that some individuals in a population will possess variations of alleles that are suited for the environment. Those individuals are more likely to survive to produce offspring bearing that allele. The population will continue for more generations because of the success of these individuals.

5. 5. 2. Methods for biodiversity evaluation

Measures of genetic diversity

Genetic Diversity of a population can be assessed by some simple measures.

- *Gene Diversity* is the proportion of *polymorphic* loci across the *genome*.
- *Heterozygosity* is the fraction of individuals in a population that are heterozygous for a particular locus
- *Alleles per locus* is also used to demonstrate variability.

Measures of species diversity

Diversity indices

Species diversity can be calculated by one or more diversity indices to quantify species diversity. Such indices include *species richness*, the *Shannon index*, the *Simpson index* and the complement of the Simpson index (also known as the Gini-Simpson index). When interpreted in ecological terms, each one of these indices corresponds to a different thing, and their values are therefore not directly comparable. Species richness quantifies the actual rather than effective number of species. The Shannon index equals $\log({}^{q}D)$, and in practice quantifies the uncertainty in the species identity of an individual that is taken at random from the dataset. The Simpson index equals $1/{}^{q}D$ and quantifies the probability that two individuals taken at random from the dataset (with replacement of the first individual before taking the second) represent the same species. The Gini-Simpson index equals $1 - 1/{}^{q}D$ and quantifies the probability that the two randomly taken individuals represent different species.

Species richness is the number of different species represented in an *ecological community*, landscape or region. Species richness is simply a count of species, and it does not take into account the abundances of the species or their relative abundance distributions. In contrast, species diversity takes into account both species richness and species evenness.

The Shannon index has been a popular diversity index in the ecological literature, where it is also known as Shannon's diversity index, the Shannon-Wiener index, the Shannon-Weaver index and the Shannon entropy. The idea is that the more different letters there are, and the more equal their proportional abundances in the string of interest, the more difficult it is to correctly predict which letter will be the next one in the string. The Shannon entropy quantifies the uncertainty (entropy or degree of surprise) associated with this prediction. It is most often calculated as follows:

$$H' = -\sum_{i=1}^{R} p_i \ln p_i$$

where $p_i$is the proportion of characters belonging to the *i*th type of letter in the string of interest. In ecology, $p_i$is often the proportion of individuals belonging to the *i*th species in the dataset of interest. Then the Shannon entropy quantifies the uncertainty in predicting the species identity of an individual that is taken at random from the dataset.

The Simpson index was introduced in 1949 by Edward H. Simpson to measure the degree of concentration when individuals are classified into types. The measure equals the probability that two entities taken at random from the dataset of interest represent the same type. It equals:

$$\lambda = \sum_{i=1}^{R} p_i^2$$

This also equals the weighted arithmetic mean of the proportional abundances $p_i$of the types of interest, with the proportional abundances themselves being used as the weights. Proportional abundances are by definition constrained to values between zero and unity, but their weighted arithmetic mean, and hence λ, can never be smaller than 1/*S*, which is reached when all types are equally abundant.

By comparing the equation used to calculate λ with the equations used to calculate true diversity, it can be seen that 1/λ equals ^2D, i.e. true diversity as calculated with $q = 2$. The original Simpson's index hence equals the corresponding basic sum.

5. 5. 3. Ecological effects of biodiversity

The diversity of species and genes in ecological communities affects the functioning of these communities. These ecological effects of biodiversity in turn affect both climate change through enhanced greenhouse gases, aerosols and loss of land cover, and biological diversity, causing a rapid loss of ecosystems and extinctions of species and local populations. The current rate of extinction is sometimes considered a mass extinction, with current species extinction rates on the order of 100 to 1000 times as high as in the past.

The two main areas where the effect of biodiversity on ecosystem function have been studied are the ***relationship between diversity and productivity***, and the ***relationship between diversity and community stability***. More biologically diverse communities appear to be more productive (in terms of biomass production) than are less diverse communities, and they appear to be more stable in the face of perturbations.

5. 5. 3. Conservation of forest biodiversity, population integrity and uniqueness

The conservation of biodiversity is an essential part of sustainable forest management. Forests cover nearly one-third of the world’s total land area and are vital in ensuring environmental functions such as climate regulation and soil conservation in addition to biodiversity. They provide habitats for a large array of plants and animals, many of which are rare or threatened. Biologically diverse forests also contribute to the sustainability of the wider landscape and provide a range of other ecosystem services.

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Chapter 6. Biogeochemical cycles of nutrients

6.1. Introduction

Nutrients move through the ecosystem in biogeochemical cycles. A biogeochemical cycle is a circuit/pathway by which a chemical element moves through the biotic and the abiotic factors of an ecosystem. It is inclusive of the biotic factors, or living organisms, rocks, air, water, and chemicals. The elements that are moving through the biotic or abiotic factors may be recycled, or they may be accumulated in a place called a sink/reservoir where they are held for a long period of time. The amount of time that a chemical is held in one place is called residence.

A biogeochemical cycle or inorganic-organic cycle is a circulating or repeatable pathway by which either a chemical element or a molecule moves through both biotic ("bio-") and abiotic ("geo-") compartments of an ecosystem. In effect, an element is chemically recycled, although in some cycles there may be places (called "sinks") where the element accumulates and is held for a long period of time. In considering a specific biogeochemical cycle, we focus on a particular element and how that element participates in chemical reactions, moving between various molecular configurations.

6.2. Principles and definitions

All of the chemical elements in an organism are part of the biogeochemical cycle. The chemicals travel not only through the biotic and abiotic components of an ecosystem, but they also travel through an organism. The abiotic factors of an ecosystem include: (1) water (hydrosphere), (2) land (lithosphere), and (3) air (atmosphere). All of the living factors that are found on Earth make up the biosphere.

The cycling of minerals through forest ecosystems is closely linked with those of water and carbon. Precipitation washes minerals from the atmosphere and deposits them on leaves and other surfaces. Water carries dissolved minerals into the soil where they are taken up by roots and transported in the transpiration stream. Water also carries minerals out of the system through erosion and by leaching. Plants respire carbon obtained through photosynthesis to convert minerals from elemental to biochemical forms, and to recycle nutrients internally from older to newer tissues. Heterotrophic and symbiotic organisms rely on carbon supplied from roots and that extracted from detritus to acquire their energy supply and nutrients. Low molecular weight acids produced as metabolic products enhance the release of additional minerals from soil and rock. Other products of microbial decomposition contribute to the accumulation of soil humus. A general picture of the processes involved in the cycling of minerals through forest ecosystems is presented in Fig. 6.1.

Model (Fig. 1.3 – Chapter 1) accounts for the quantitative movement of matter across the boundaries of such a watershed ecosystem by the three principal vectors-meteorologic (movement by atmospheric forces), geologic (movement by alluvial or colluvial forces) and biologic (movement by animals). We consider the release and storage of materials inside the boundaries, for example by weathering, or biomass accumulation and release, as internal features of the ecosystem rather than input/output fluxes but in any event they must be quantitatively accounted for in the bookkeeping of mass balance determinations. All of these vectors and transformations must be carefully considered in quantitative evaluations of biogeochemical cycles.

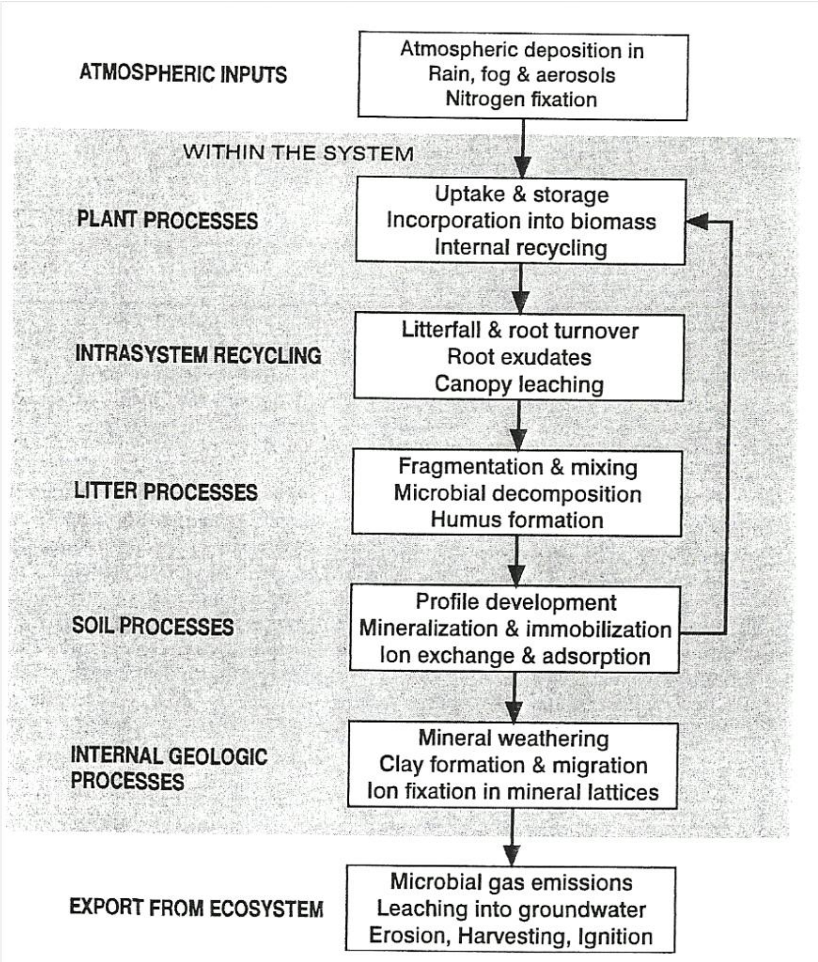


Figure 6.1 Minerals that cycle through a forest ecosystem have variable sources. Many are sequestered from the atmosphere; others are derived from geologic weathering of minerals. Plants modify the cycling of many elements through their selective uptake, internal redistribution, and the fraction returned annually to the forest floor. Litter on the forest floor is utilized by many soil organisms, but eventually a small fraction accumulates as soil humus. During the decomposition process, minerals are converted from organic to inorganic forms. Whether the elements are immobilized in microbial biomass, made available on soil exchange sites, adsorbed to clay surfaces, or fixed permanently into mineral lattices depends on a variety of soil and geologic processes that differ within the soil profile. Eventually some minerals are again taken up by plants and recycled through the system, while others may be lost as gases or in leachate (Waring, Runnig 1998).

6.3. Essentials elements

Of the 90-odd elements known to occur in nature, some 30 or 40 are thought to be required by living organisms (Odum 1959). We will be considering only a few of these, mainly those utilized in fairly large quantities by living organisms. The principal elements of life are carbon, hydrogen, oxygen, and nitrogen. However, a number of others are certainly important to understand as well, notably phosphorus and sulphur. Some "non-essential" elements participate in biogeochemical cycles, entering organism tissues because of chemical similarity to essential elements. For example, strontium can behave like calcium in the body.

In addition to C, H, and O, all plants require certain macronutrients. Nitrogen (N) is a major constituent of proteins, nucleic acids, and chlorophyll; phosphorus (P) is most important as a component of the energy currency in biochemical reactions, and sulphur (S) is found in many amino acids. Specific roles are known for potassium (K) in controlling stomatal function and the charge balance across plant membranes, for calcium (Ca) as a constituent of cell walls, and for magnesium (Mg) in chlorophyll. These nutrients also stimulate the rate of various enzymatic reactions. The micronutrients iron (Fe), copper (Cu), zinc (Zn), and manganese (Mn) are widely involved as coenzymes, whereas the essential roles of boron (B) and chlorine (Cl) are still poorly known. Grasses and some other plants accumulate silicon (Si) in cell walls, which provides strength and reduces tissue palatability to herbivores. Molybdenum (Mo) is essential for N metabolism in plant tissues, as well as for N fixation by symbiotic bacteria. Cobalt (Co) is essential for the microorganisms involved in N fixation. Although higher plants all require the same macronutrients, they differ in their selective accumulations, their microbial associations, and in the exudates and residues they produce. As a consequence, the amount and balance of nutrients sequestered in plant biomass affects soil fertility and forest productivity. Nutrients must be available in appropriate forms and in sufficient amounts to meet growth requirements. Most plants exhibit rapid growth at the beginning of the growing season. To maintain a constant relative growth rate, even for a short period, requires that the flux of nutrients to growing points match the rate of expansion. Any reduction in the rate at which nutrients are supplied causes nutrient concentrations to drop in expanding tissue (Ingestad 1982).

6.4. Source and uptake of nutrients

One of the most important principles of plant nutrition is the “law of limiting factors.” This law states that yield or plant growth is limited by the factor, which is in shortest supply. This concept is illustrated below. The water level in the barrel is limited by the lowest stave. Yield is similarly limited by the nutrient or other growth factor, such as water, which is most limiting (Fig. 6.2).

This law applies not only to nutrients and other growth factors, but to management variables as well. Applying high rates of fertilizers to crops is of no value unless the proper varieties, plant populations and weeds, insects and disease control are used. Nutrient uptake precedes dry matter accumulation because nutrients are required for plant growth and hence dry matter accumulation. The pattern of growth (dry weight) and nutrient accumulation with growth of sorghum plants points out that the nutrient uptake curves are above the dry matter curve for most of the growth period. For example, the half-bloom stage occurs at 60 days after the emergence and about one-half of the total plant weight has been produced; however, nearly 60 percent of the phosphorus, 70 percent of the nitrogen and 80 percent of the potassium the plant will utilize already have been taken up.

Those percentages emphasize how important proper fertility is at early growth stages in the nutrition of the sorghum plant.

Under field conditions, the concentration of nutrients in the soil solution is reduced during the period of exponential plant growth. Nutrients are supplied to plant root surfaces through three mechanisms: (1) the growth of roots and mycorrhizae into the soil; (2) the mass flow of ions with the movement of soil water as a result of transpiration; and (3) the diffusion of ions toward the root surface when uptake rates exceed supply (Eissenstat, Van Rees 1994). The relative mobility and concentration of nutrients in soil solution and the rate of plant uptake determine which of these mechanisms predominates. Uptake of Ca is often the result of the interception of ions in newly exploited soil zones. Mass flow is important for Mg, SO_4^{-2}, and Fe. Plant demand for N, P, and K often exceeds delivery by mass flow, such that diffusion is the dominant process that supplies these macronutrients (Eissenstat, Van Rees 1994).

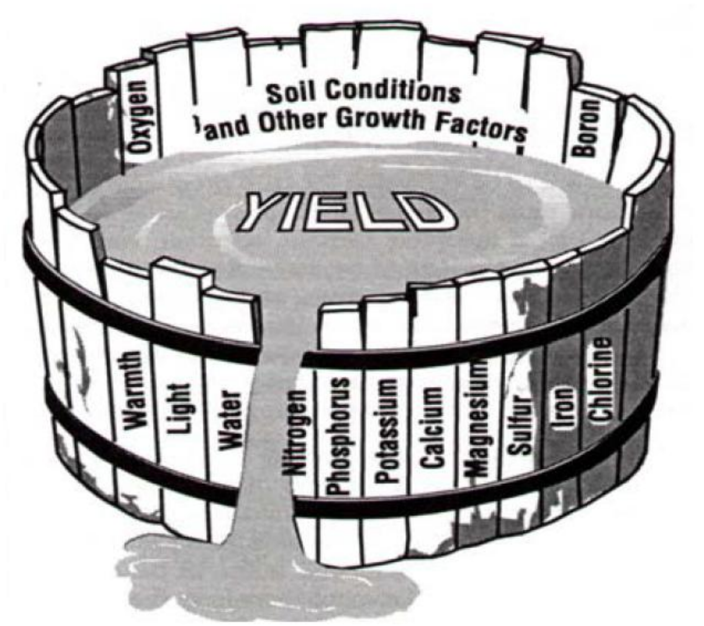
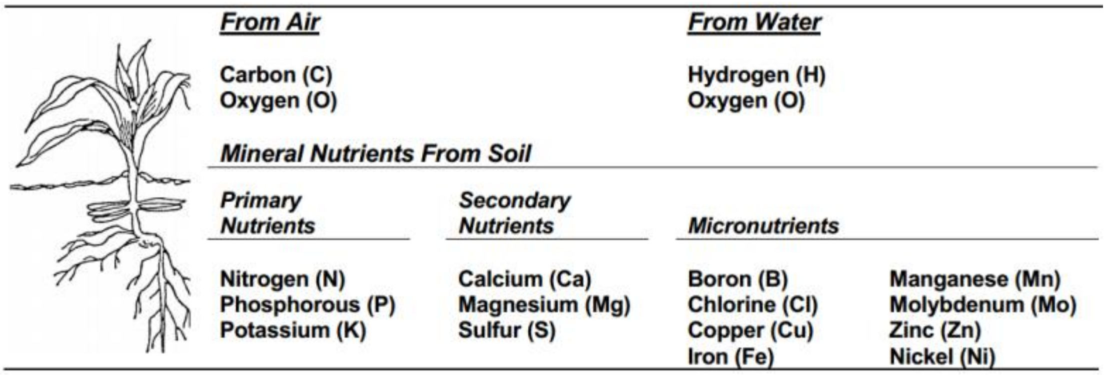
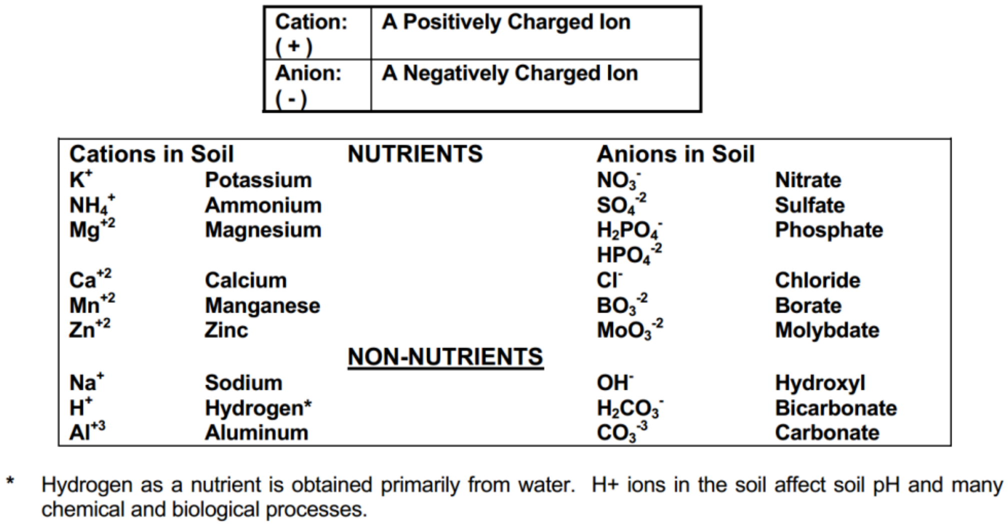


Figure 6.2. Principles of plant nutrition - "law of limiting factors".
(Source: http://www.agronomy.ksu.edu/extension/doc2146.ashx).



From Air		***From Water***	
Carbon (C) **Oxygen (O)**		**Hydrogen (H)** **Oxygen (O)**	
Mineral Nutrients From Soil			
Primary Nutrients	***Secondary Nutrients***	***Micronutrients***	
Nitrogen (N)	**Calcium (Ca)**	**Boron (B)**	**Manganese (Mn)**
Phosphorous (P)	**Magnesium (Mg)**	**Chlorine (Cl)**	**Molybdenum (Mo)**
Potassium (K)	**Sulfur (S)**	**Copper (Cu)**	**Zinc (Zn)**
		Iron (Fe)	**Nickel (Ni)**

Figure 6.3. Source of plant nutrients.
(Source: http://www.agronomy.ksu.edu/extension/doc2146.ashx).



Cation: (+)	A Positively Charged Ion
Anion: (-)	A Negatively Charged Ion

Cations in Soil		NUTRIENTS	Anions in Soil	
K^+	Potassium		NO_3^-	Nitrate
NH_4^+	Ammonium		SO_4^{-2}	Sulfate
Mg^{+2}	Magnesium		$H_2PO_4^-$ HPO_4^{-2}	Phosphate
Ca^{+2}	Calcium		Cl^-	Chloride
Mn^{+2}	Manganese		BO_3^{-2}	Borate
Zn^{+2}	Zinc		MoO_3^{-2}	Molybdate
		NON-NUTRIENTS		
Na^+	Sodium		OH^-	Hydroxyl
H^+	Hydrogen*		$H_2CO_3^-$	Bicarbonate
Al^{+3}	Aluminum		CO_3^{-3}	Carbonate

* Hydrogen as a nutrient is obtained primarily from water. H+ ions in the soil affect soil pH and many chemical and biological processes.

Figure 6.4. Ion forms of nutrients utilized by plants.
(Source: http://www.agronomy.ksu.edu/extension/doc2146.ashx).

All chemical elements, including plant nutrients exist in nature in an electrically charged form called ions. Ions carry either a positive or negative electrical charge. Ions with positive charges are called cations while those with negative charges are anions. Plants can only utilize nutrients in an ion form although some nutrients are utilized by plants in more than one ionic form. A partial list of common soil cations and anions is shown below (Fig. 6.3; 6.4)

6.5. Storage and interval recycling

Total nutrient demands are highly variable from species to species. Within a species, nutrient concentrations also vary depending on growth rates and the availability of nutrients. When nutrients are added to deficient soils the growth rate of trees usually increases, often without inducing a change in foliar nutrient concentrations. When one nutrient or other factors limit growth, nutrients may be taken up in excess of immediate metabolic requirements. This results in high concentrations in foliage a condition that is called luxury consumption. Differences in leaf nutrient concentrations form one basis for diagnosing deficiencies, but foliar analyses must be interpreted with care because much variation occurs with season, canopy position, and growth rate (Linder, Rook 1984; Van den Driessche 1984). More insight is gained when foliar composition is compared seasonally than judged from a single sampling and when account is taken for changes in carbohydrate reserves that alter the specific leaf weight over time (Linder 1995).

The optimum balance of nutrients is determined experimentally by varying nutrient concentrations in hydroponic solutions or sand cultures and observing the relative concentrations found in plants with maximum growth rates. At maximum growth rate the balance of nutrients in solution and those in leaf tissue are the same (Ingestad 1979). The optimum nutrient balance differs only slightly among tree species when referenced to nitrogen content (Ingestad 1979; Ericsson 1994; Linder 1995).

Total plant nutrient contents reflect long-term nutrient uptake but tell us little about seasonal nutrient circulation. Mature foliage and other organs may exhibit relatively stable

ratios of nitrogen with other elements, but this balance is often accomplished through internal reallocation. Reallocation of nutrients from twigs and older foliage helps sustain rapid shoot elongation when root uptake is inadequate to meet the demand. The actual flux, however, is difficult to estimate accurately unless isotopic tracers are used (Mead, Preston 1994).
The reserves of nutrients available for export from a particular tissue can often best be measured by assessment of metabolically active forms (Attiwill, Adams 1993). The biochemical composition of plants becomes even more important when considering plant-animal interactions because the nutritional value of the vegetation to animals is largely dependent on the extent to which nitrogen is present in a digestible form.

6.6. Return in litter and leachate

Return of nutrients in litterfall is the major route of recycling from vegetation to soil. Aboveground litterfall can be measured through periodic collection, weighing, and chemical analysis of twigs, leaves, fruits, and other products that fall into nets or trays positioned just above the ground surface. Annual additions of coarse woody debris can be estimated by recording the amount that fall across string lines laid out annually in a large grid under a forest canopy. Nutrient return in litterfall can vary seasonally from year to year depending on forest composition and the leaf abscission process. In a temperate deciduous forest, Gosz et al. (1972) found that premature abscission of leaves in summer storms resulted in a small amount of litterfall with relatively high nutrient concentrations because nutrient reabsorption had not occurred.

Small amounts of most nutrients are leached from living plant tissues. Potassium, an element which is highly soluble and concentrated in stomatal guard cells, is particularly easily removed through leaching. In general, K > P > N > Ca in regard to leaching losses from foliage. Differences in the rates at which nutrients are leached from foliage and bark may explain variation in epiphyte loads on forest species (Schlesinger, Marks 1977). Fine roots also lose nitrogen and potassium through exudation and leaching.

6.7. Forest floor, soil and decomposition processes

The soil in forest ecosystems usually consists of a number of layers, or horizons, that collectively comprise the complete soil profile. Recognition of the processes that occur in these horizons is an essential part of understanding nutrient cycling in forest ecosystems. A characteristic property of forest soils is a nearly permanent cover of leaf litter and woody debris. Beneath this surface organic layer, distinct soil horizons usually develop with different chemical, physical, and biological properties. Humans have altered the development of soil horizons by changing the natural sequence of disturbance, the kinds of plants, animals, and microbes present, and the nutrient capital in forest soils. The basic processes, however, remain the same by which nutrients are made available in the soil, taken up by plants, and eventually returned in organic residues.

The forest floor is often easy to separate from the underlying layers of mineral soil, but these two major categories may be further subdivided. The forest floor often consists of L, F, and H layers. The L layer consists of fresh, undecomposed litter. The F layer lies immediately below the L layer and consists of fragmented organic materials in a stage of partial decomposition. This layer is dominated by organic materials in cellular form, and fungi and bacteria are common. Beneath the F layer lies the H or humus layer, primarily consisting of amorphous, resistant products of decomposition and with lower proportions of organic matter in cellular form. The lower portion of the H layer often shows an increasing proportion of inorganic mineral soil constituents, but organic components still dominate (Waring, Runnig 1998).

The humus form is the part of the topsoil that is strongly influenced by organic matter and coincides with the sequence of organic (Ol, Of, Oh, H) and underlying organo-mineral horizons (A, Ae, Aa). Plant remains like leaves, needles, wood, root exudates, etc., form a prominent part of the primary production of forest ecosystems (Zanella et al. 2011).

Within the general description of temperate forest soil, ecologist have long differentiated between mor and mull forest floors. In broad geologist terms, mors develop in cooler climates, often characterized by coniferous vegetation. Decomposition in the forest floor is slow and incomplete, resulting in a thick organic layer. Moreover, the litter of coniferous species contains high concentrations of phenolic substances and lignin that field acid decomposition residues. As a result, the soil solution often has a pH as low as 4.0. In these conditions, fungi predominate over bacteria. Earthworm populations are low in mor forest floors, which results in little fragmentation and mixing with the underlying soil (Phillipson et al. 1978).

Mull forest floors are typically found under deciduous forests in warm temperate climates. Most of the characteristics of mulls are in contrast to those of mors. Decomposition is more rapid, residues are less acidic, and earthworms are more abundant. Bacteria play a greater role in decomposition processes in mull forest floor, and the pH is higher. Fragmentation and mixing often make differentiation of the forest floor difficult and obscure sharp boundaries between the mineral horizons. Under pH 5.0-7.0, which are typical of these soils, Si is relatively soluble. Thus Si, Fe, and AI are removed in relatively equal proportions from the A horizon minerals, and there is no sharply defined A3 horizon (Pedro et al. 1978).

Soil Organic Matter: a source of plant nutrients

Soil organic matter and humus are terms which refer to the partially decomposed residue of plants, animals, and other organisms. Organic matter refers to all organic material including fresh crop residues. Humus is the more stable decomposed organic residue. Organic matter has long been recognized as having many beneficial effects on physical and chemical properties of the soil. Some of the more important effects of organic matter are:

- Improves Soil Structure. Organic matter acts as a bonding agent which holds soil particles together in aggregates. Without organic matter, aggregates are less stable and are easily broken apart. Good soil structure promotes water movement and root penetration while reducing soil crusting, clod formation, and erosion.
- Contributes to Cation Exchange Capacity (CEC). Soil organic matter has great ability to attract and hold cations (Fig. 6.5).
- Provides Plant Nutrients. One of the most important attributes of organic matter is its contribution to soil fertility.
  - Approximately 90% to 98% of the total N and S and 30% to 50% of the P exist in the soil in organic forms.

- Soil organic matter is approximately 5% N and 0.5% P or S.
- Organic matter is also the primary reservoir for available forms of most of the micronutrients.
- Potassium is an important exception and does not exist in organic forms.

Even though plants are not able to utilize nutrients in organic matter directly, decomposition of humus releases ionic forms of nutrients which are available to plants.

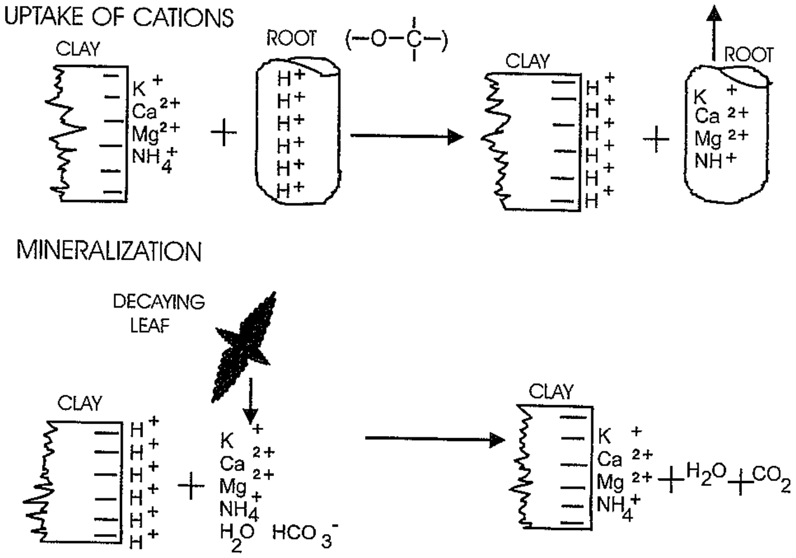


Figure 6.5. The cation cycle begins with positively nutrient ions held on negatively charged clay particles. The cations are excharged for hydrogen ions released as organic acids by plants. Roots take up the nutrients and leaf litter returns them annually to the soil. Through decomposition, nutrient cations are released to return again to the soil exchange sites. (From Glatzel 1991, Warring, Running 1998).

Forest composition and nutrient availability

Forest composition and nutrient availability are often closely interlinked, as we inferred from the earlier discussion on nutrient use efficiency. In the case of nitrogen, tree species with extremely low requirements are adapted to soils where DON is the major form present (Northrup et al. 1995); most conifers are adapted to intermediate conditions where NH_4^+ is the dominant form, whereas riparian zone species are particularly suited to high levels of NO_3^- through their ability to induce the formation of nitrate-reducing enzymes in their foliage (Smirnoff et al. 1984; Smirnoff and Stewart 1985). Ecosystem retention of N, as we shall see, is also progressively reduced with increasing availability, so that high losses of NO_3^- usually indicate an excess availability while a dominance of DON in leachate reflects extreme scarcity of N.

The following summarizes some key points and implications from the last three sections (Waring, Runnig 1998):

- Fragmentation and mixing are essential steps that a host of small soil animals perform on litter before it is subjected to microbial decomposition. The introduction of pesticides or other toxic chemicals may reduce the efficiency of various groups of animals and could substantially alter the normal rates of decomposition and mineralization,

- Decomposition of woody debris, leaf litter, and belowground components of detritus proceeds at significantly different rates. For this reason, it is generally recommended that these organic pools be separately recognized.
- Moisture and temperature conditions strongly affect decomposition and mineralization rates. The hydrologic and energy balance models introduced in earlier chapters provide a means of defining these environmental variables without requiring direct measurements in the litter and soil.
- The chemical quality of the organic substrate, which can be quantified by C:N ratios and other related indices, strongly affects the mineralization and immobilization processes.
- As a scaling principle, a decreasing amount of detail is required to estimate process rates at progressively longer time intervals. Thus, on an annual basis, decomposition rates can be relatively easily assessed, on the basis of decomposition constants acquired from litterbag studies, forest floor/litterfall mass comparisons, and even from satellites by monitoring the annual transfer of leaf litter from the canopy to the ground. The general reliability of these annual estimates, however, rests on an understanding of key variables and interactions acquired at much shorter time steps.

6.7. The main biogeochemical cycles

The Nitrogen Cycle

The Nitrogen Cycle is the biogeochemical cycle that describes the transformation and translocation of nitrogen (N) in soil, water, and living and dead organic material. The biogeochemical cycling of N is highly dependent on the activities of microorganisms. Nitrogen fixation generally refers to the process in which atmospheric nitrogen (N_2) is converted into ammonia (NH_3). Conversion of atmospheric N to ammonia requires the enzyme nitrogenase. The conversion of organic nitrogen to NH_3 is called ammonification. In the presence of water, NH_3 becomes ionized and forms ammonium (NH_4^+). Ammonium in the soil is the starting point for a series of processes and reac-tions including: uptake by plants; fixation by clay minerals and organic matter; immobilization by microorganisms; transformation into ammonia gas and exported to the atmosphere by volitalization; and nitrification. Nitrification is a two-step process. In the first step of this process, nitrite (NO_2^-) is formed when NH_3 or ammonium (NH_4^+) is oxidized by nitrifying bacteria. Nitrifying bacteria are also responsible for the second step of the nitrification process which involves the oxidation of NO_2^- to nitrate (NO_3^-). Plants readily take up NO_3^- ions through their roots and assimilate them into organic compounds. Denitrification is the microbially mediated process of NO_3^- reduction. In the absence of oxygen, NO_3^- ions can act as terminal electron acceptors and can result in the production of molecular nitrogen (N_2) through a series of intermediate gaseous nitrogen oxide products including nitrous oxide (N_2O). Immobilization occurs when inorganic N, as NH_4^+ and NO_3^-, are assimilated by microorganisms. As microorganisms decompose carbonaceous organic residues they may require more N than is contained in the residue. Subsequently they assimilate inorganic N into their cellular components which becomes unavailable for plant uptake. The conversion of organic N compounds to inorganic

N ions is known as mineralization. In nitrogen mineralization, organic nitrogen from decaying plant and animal residues (proteins, nucleic acids, amino sugars, urea) is converted back to NH_4^+ and NO_3^-. Leaching refers to the export of N as NO_3^- from the soil which makes it unavailable for plant uptake. In contrast to NH_4^+ ions, which are attracted to negatively charged soil particles, the net negative charge of NO_3^- ions means that they are repelled by negatively charges soil particles. Consequently, under wet conditions, NO_3^- ions move downward with drainage water and are readily leached from the soil (Fig. 6.6).

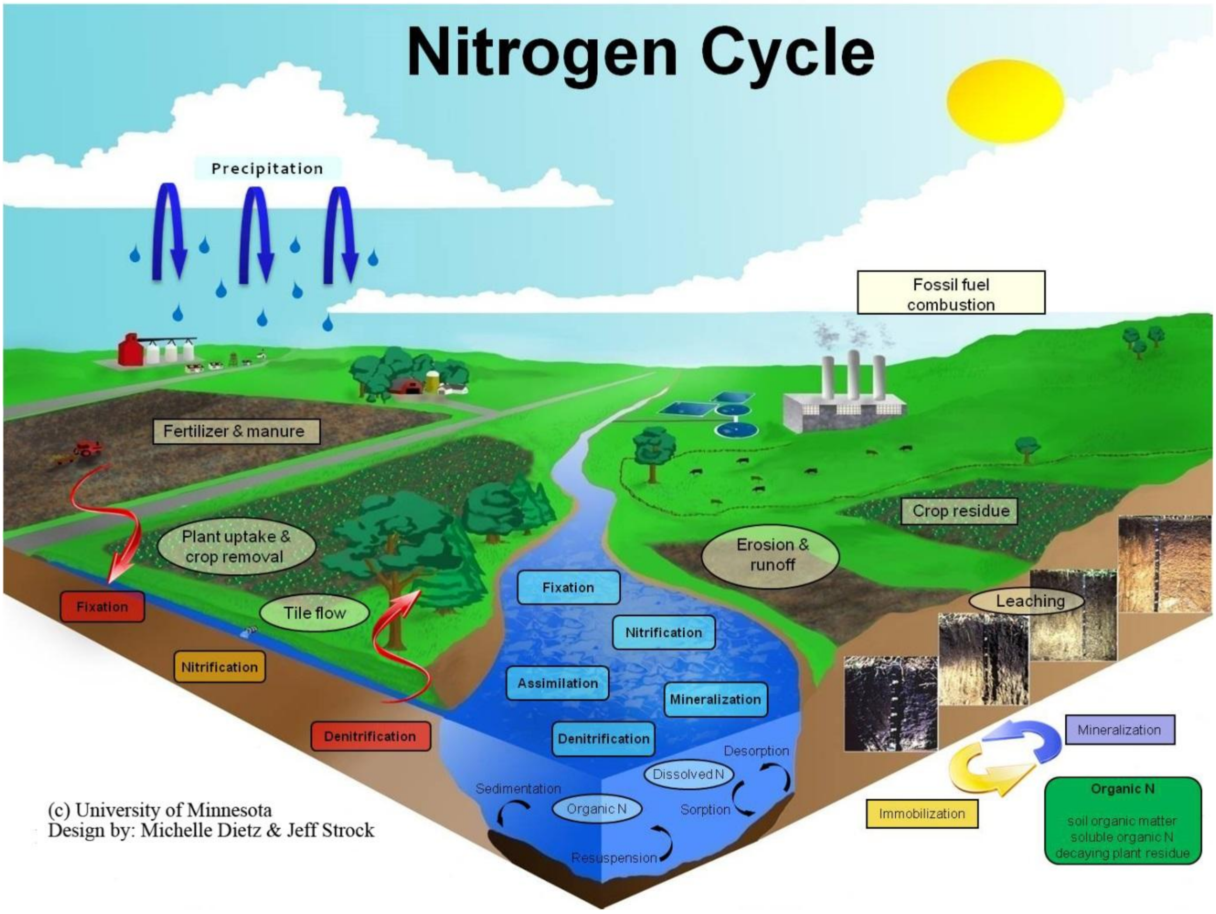


Figure 6.6. The Nitrogen Cycle.
(Source: http://swroc.cfans.umn.edu/ResearchandOutreach/SoilManagement/SoilResearch/NitrogenCycle/index.htm)

The Phosphorus Cycle

Phosphorus (P) is an essential element for all life forms and is stored primarily in soil and sediment. Phosphorus is an essential component of adenosine triphosphate (ATP) which transports chemical energy within cells for metabolism (i.e. uptake and transport of nutrients); deoxyribonucleic acid (DNA) which is a nucleic acid that contains the genetic instructions used in the development and functioning of all known living organisms; and ribonucleic acid (RNA) which is important for protein synthesis in plants and animals (Fig. 6.7).

Phosphorus occurs in soil as inorganic and organic P compounds. Most soils contain a relatively low amount of total P, and only a small fraction of the total P is available to plants. Most P compounds in soils have low water solubility. One in the soil solution, soluble P moves mainly by diffusion. Phosphorus in soils generally occurs as the anions $H_2PO_4^-$ or HPO_4^{2-}. Phosphorus reacts with calcium (Ca^{2+}), magnesium (Mg^{2+}), iron (Fe^{3+}), and aluminum (Al^{3+}). Phosphorus reactions in soil are pH dependent. In acid soils, soluble phosphorus in the soil solution reacts with Fe and Al to form low solubility Fe and Al phosphates. In calcareous soils, soluble phosphorus in the soil solution reacts with Ca to form low solubility Ca phosphates.

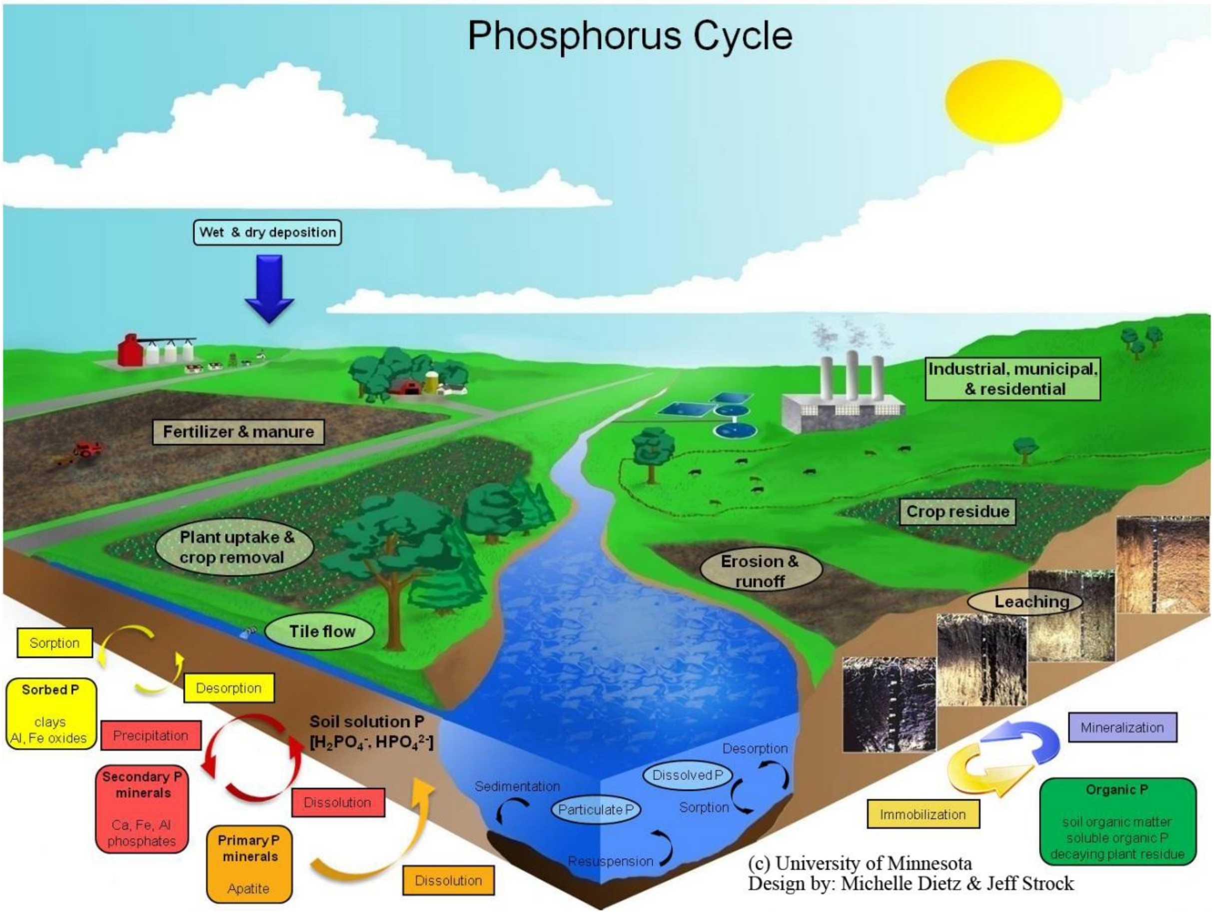


Figure 6.7. The Phosphorus Cycle.
(Source:
http://swroc.cfans.umn.edu/prod/groups/cfans/@pub/@cfans/@swroc/documents/asset/cfans_asset_290225.jpg)

The Phosphorus Cycle is the biogeochemical cycle that describes the transformation and translocation of phosphorus in soil, water, and living and dead organic material. Phosphorus additions to soil occur due to additions of inorganic and organic (manure) fertilizer and the degradation and decomposition of organic (plant and animal) material. Export of P from soil occurs mainly through plant uptake. Phosphorus may also exported from soil via surface runoff and erosion or subsurface loss through leaching. Sorption and desorption reactions of P occurs on the surfaces and edges of hydrous oxides, clay minerals, and carbonates. Sorption generally occurs by covalent bonds of P with Fe and Al in acidic soils and calcium carbonate ($CaCO_3$) in alkaline soils. Precipitation and dissolution reactions greatly influence the availability of P in the soil. Dissolution of P minerals occurs when P minerals dissolve over time and replenish the P in the soil solution. This reaction increases the availability of P. On the other hand, precipitation occurs when P minerals form by removing P from soil solution. This reaction decreases the availability of P. Precipitation and dissolution are very slow processes. Dissolution and precipitation of P can also occur due to changes in redox potential caused by seasonal or periodic waterlogging and draining soil. The microbial cycling of P from inorganic soluble forms to insoluble organic forms is known as immobilization. The reverse is known as mineralization. Mineralization of P is catalyzed by the phosphatase enzyme.

6.8. Review questions

6. Main definition and principles of cycling of elements.
7. Identify and describe the flow of nutrients in each biogeochemical cycle.
8. N-cycle in forest ecosystems, main parts and evaluation.
9. Cycling of other mineral elements, mineral nutrition.
10. Explain the impact that humans have on the biogeochemical cycles.

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Chapter 7. Ecological stability and ecosystem interaction

7.1. Introduction

Humans are dependent upon natural systems for the necessities of life such as air and water, as well as resources that are essential for modern societies (Odum 1993). As humans have imposed greater and greater demands upon natural systems, Arrow et al. (1995) and many others have raised concerns about the sustainability of the resource flows from these systems.

Ecological stability defined as the ability of an ecosystem to resist changes in the presence of perturbations leads to consideration of the effective choice of the pathways for energy flow. The roles of diversity and complexity (i.e. interdependence) in determining stability arise naturally in the development of an index from the qualitative concepts of information theory. As a tool for ecosystem analysis, the stability measure developed in this paper is applied to two example systems (Ludwig et al. 1997).

7.2. Principles and definitions

Stress is changes in physiology that occur when species are exposed to extraordinary unfavourable conditions that need not represent a threat to life but will induce an alarm response.

Equilibrium - a mechanical system is at equilibrium if the forces acting on it are in balance.

Resilience - has been defined in two different ways in the ecological literature, each reflecting different aspects of stability. One definition focuses on efficiency, constancy and predictability – all attributes of engineers' desire for failsafe design. The other focuses on persistence, change and unpredictability – all attributes embraced and celebrated by evolutionary biologists and by those who search for safe fail designs.

Ecological stability - can refer to types of stability in a continuum ranging from resilience (returning quickly to a previous state) to constancy to persistence. The precise definition depends on the ecosystem in question, the variable or variables of interest, and the overall context. In the context of conservation ecology, stable populations are often defined as ones that do not go extinct.

7.3. Ecological stress

The environment affects an organism in many ways, at any time. To understand the reactions of a particular organism in a certain situation, individual external influences, so-called environmental factors, are usually considered separately, if at all possible. Environmental factors can be of abiotic and biotic nature. Biotic environmental factors, resulting from interactions with other organisms, are, for example, infection or mechanical damage by herbivory or trampling, as well as effects of symbiosis or parasitism. Abiotic environmental factors include temperature, humidity, light intensity, the supply of water and minerals, and CO_2; these are the parameters and resources than determine the growth of a plant (Fig. 7.1).

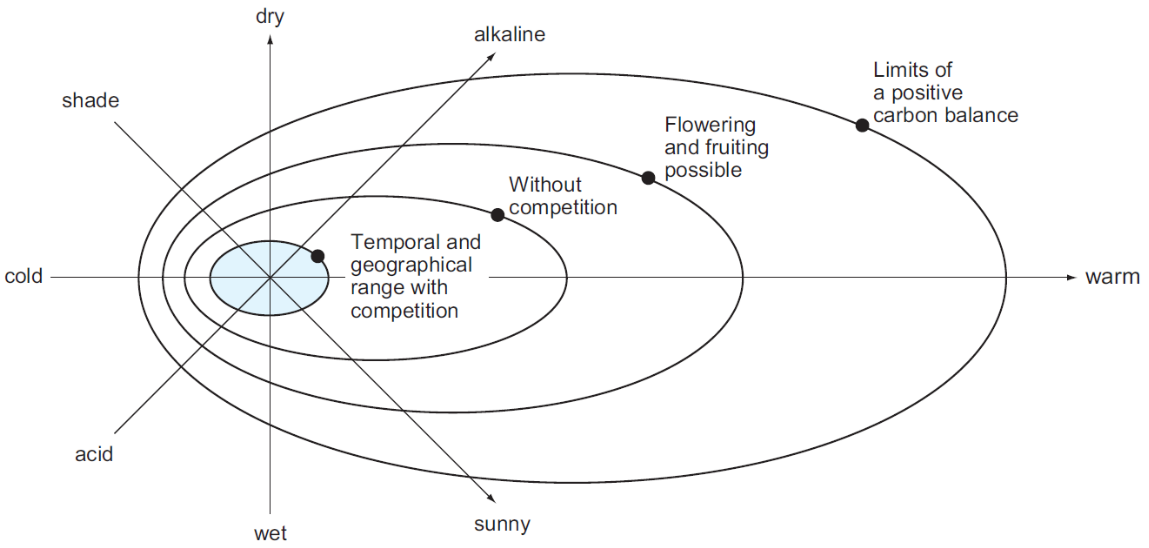


Figure 7.1. Distribution of a species depends on different environmental factors. The actual distribution area is significantly smaller than the potential areas of distribution witch are reached without competition at the extreme limits of flowering or at the boundaries of a positive material balance. In the example shown, temperature is the dominant factor, but this may differ in other cases. According to the species, the limits of distribution change (Schulze et al. 2005).

A commonly accepted stress concept in the biomedical sciences is the ‘General Adaptation Syndrome’ (GAS) of the endocrinologist Hans Selye (1936), who defined it *as “the non-specific response of the body to any demand for change”*. The GAS comprises three phases (Fig. 7.3).

Plant stress has been defined by Lichtenthaler (1996) as “any unfavourable condition or substance that affects or blocks a plant’s metabolism, growth or development”, by Strasser as “a condition caused by factors that tend to alter an equilibrium”, and by Larcher as “changes in physiology that occur when species are exposed to extraordinary unfavourable conditions that need not represent a threat to life but will induce an alarm response” (reviewed in Gaspar et al. 2002).

Environmental stress refers to physical, chemical, and biological constraints on the productivity of species and on the development of ecosystems. When the exposure to environmental stressors increases or decreases in intensity, ecological responses result. Stressors can be natural environmental factors, or they may result from the activities of humans. Some environmental stressors exert a relatively local influence, while others are regional or global in their scope. Stressors are challenges to the integrity of ecosystems and to the quality of the environment.

Species and ecosystems have some capacity to tolerate changes in the intensity of environmental stressors. This is known as resistance, but there are limits to this attribute, which represent thresholds of tolerance. When these thresholds are exceeded by further increases in the intensity of environmental stress, substantial ecological changes are caused.

Environmental stressors can be grouped into the following categories:

- Physical stress refers to brief but intense exposures to kinetic energy. This is a type of ecological disturbance because of its acute, episodic nature. Examples include volcanic eruptions, windstorms, and explosions.
- Wildfire is also a disturbance, during which much of the biomass of an ecosystem is combusted, and the dominant species may be killed.
- Pollution occurs when chemicals are present in concentrations large enough to affect organisms and thereby cause ecological changes. Toxic pollution can be caused by gases such as sulphur dioxide and ozone, by elements such as arsenic, lead, and mercury, and by pesticides such as DDT. Inputs of nutrients such as phosphate and nitrate can influence productivity and other ecological processes, causing a type of pollution known as eutrophication.
- Thermal stress occurs when releases of heat influence ecosystems, as happens in the vicinity of natural hot-water vents on the ocean floor, and near industrial discharges of heated water.
- Radiation stress is associated with excessive loads of ionizing energy. This can occur on mountain tops where there are intense exposures to ultraviolet radiation, and in places where there are exposures to radioactive materials.
- Climatic stress is associated with excessive or insufficient regimes of temperature, moisture, solar radiation, and combinations of these. Tundra and deserts are examples of climatically stressed ecosystems, while tropical rainforests occur under a relatively benign climatic regime.
- Biological stresses are associated with the diverse interactions that occur among organisms of the same or different species. Biological stresses can result from competition, herbivory, predation, parasitism, and disease. The harvesting and management of species and ecosystems by humans is a type of biological stress. The introduction of invasive, non-native species may be regarded as a type of biological pollution.

Various types of ecological responses occur when the intensity of environmental stress causes significant changes. For example, disruption of an ecosystem by an intense disturbance causes mortality of organisms and other ecological damage, followed by recovery through succession.

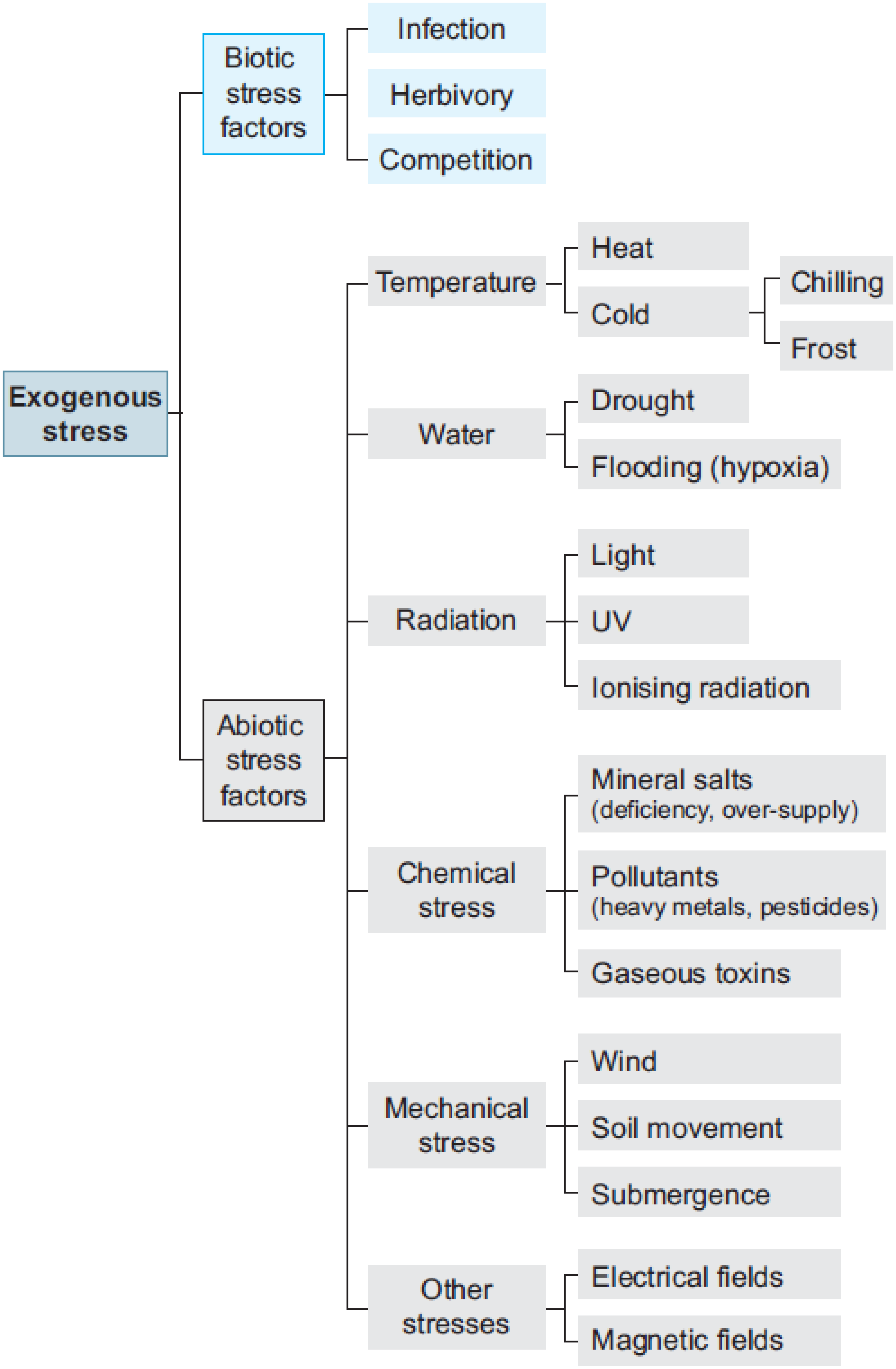


Figure 7.2. Biotic and abiotic environmental factors creating stress for plants (Schulze et al. 2005).

More permanent ecological adjustments occur in response to longer-term increases in the intensity of environmental stress, associated perhaps with chronic pollution or climate change. The resulting effects can include reductions in the abundance of vulnerable species, their elimination from sites stressed over the longer term, and replacement by species that are more tolerant of the changed environmental conditions. Other commonly observed responses to longer-term increases in stress include a simplification of species richness and decreased rates of productivity, decomposition, and nutrient cycling. In total, these changes represent a longer-term change in the character of the ecosystem, or an ecological conversion.

7.4. Stress phase

In ecological terms, stress may therefore be defined as any internal state in an organism resulting from placing it outside its fundamental ecological niche, whereby the niche may be defined in terms of gene expression profiles under normal or ideal operating conditions (van Straalen 2003). Selye (1936) showed that a stress response includes three different phases: the bipartite alarm phase, the resistance phase, and the exhaustion phase (Fig. 7.3).

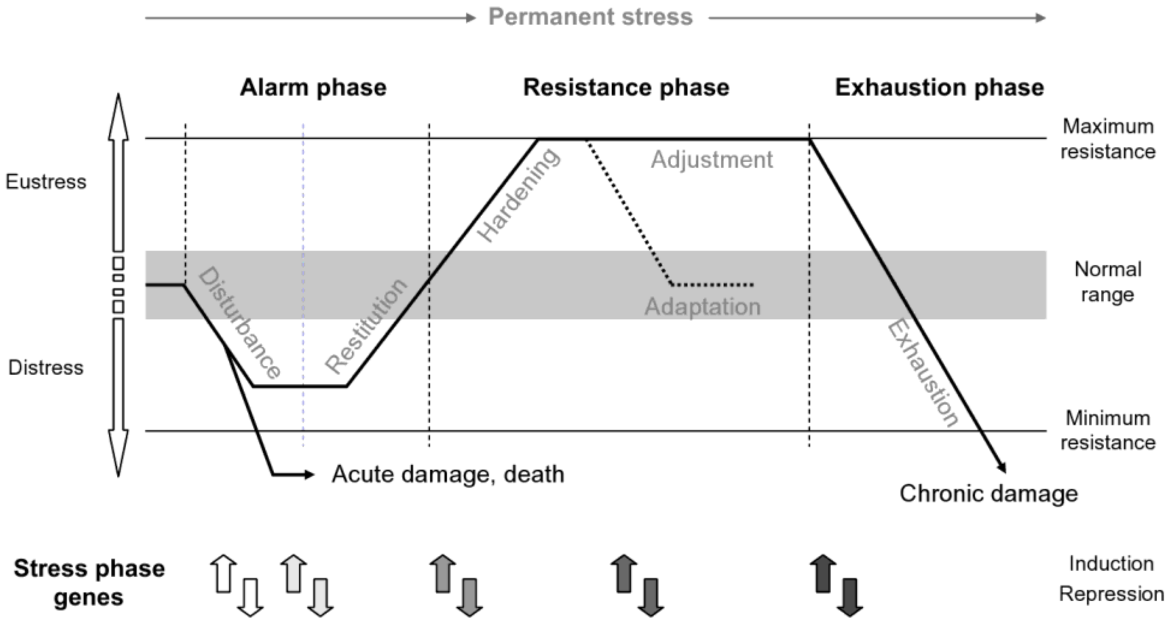


Figure 7.3. Stress phase model based on Selye (1936) and amended by several authors. Shades of grey of arrows represent different genes specifically expressed during the individual stress phases. Note, the gene profiles in the various stress phases are unique, even when exposed to the same stressor at a different intensity (Steinberg et al. 2008, Steinberg 2012).

The alarm phase corresponds to modifications of biochemical and genetic parameters in the absence of reduced vita] activities and growth. These physiological reactions terminate a primary disturbance and enable restitution. An exposure that is too strong or fast will result in acute damage and cell death. The resistance phase is characterized by the activation of defense mechanisms (e.g., antioxidant defense, protein repair, biotransformation) that are concomitant with first signs of reduced vital activity and growth. The exhaustion phase becomes apparent by a collapse of vital cellular functions (e.g. photosynthesis, membrane integrity, reproduction), leading to chronic damage and ultimately to death.

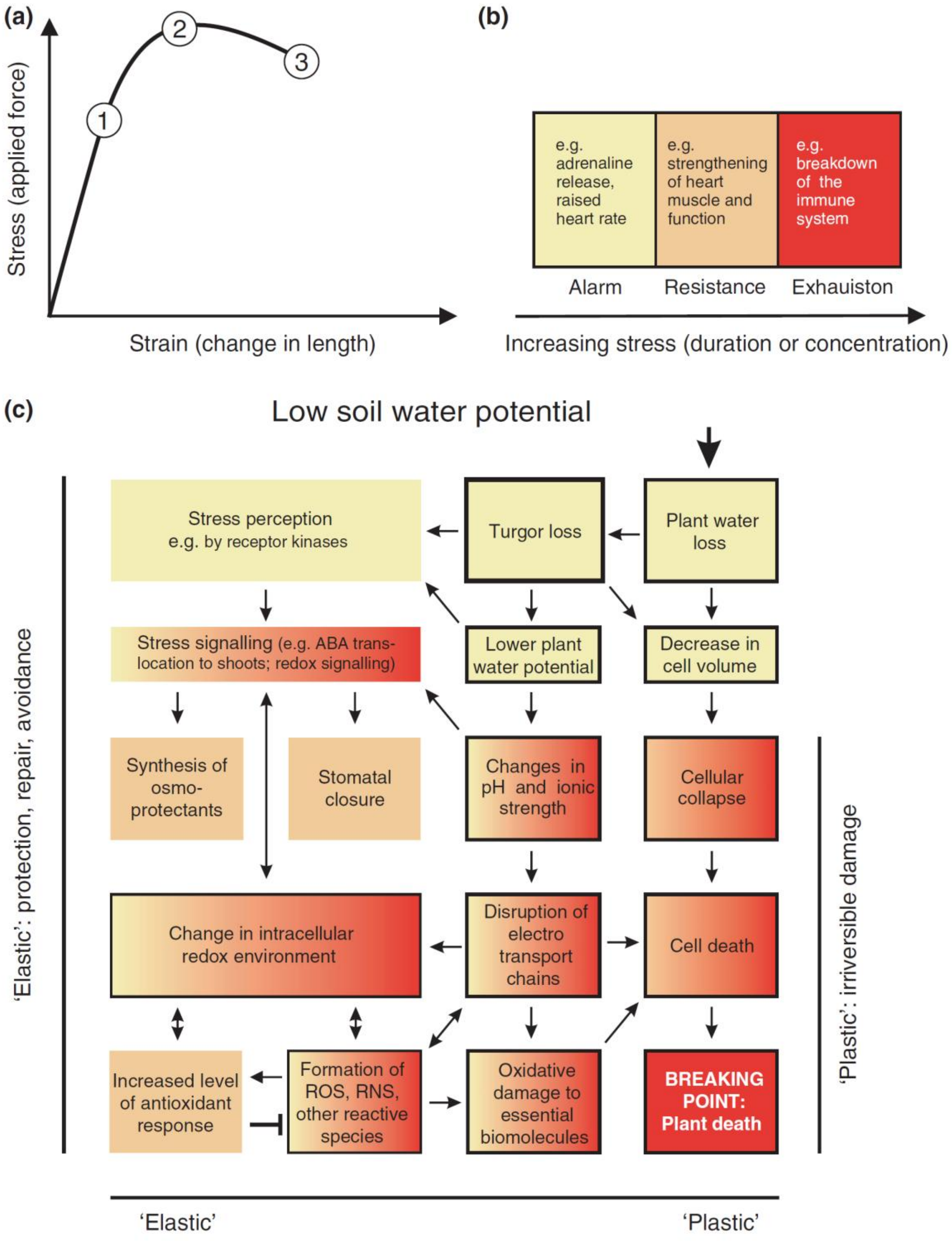


Fig. 7.4. Can stress concepts from physics and medicine be applied to plants? (a) Simplified scheme of material stress following the law r = F/A, where r is 'stress' and F is the force acting over an area A. The change in length in response to the applied pressure is termed 'strain'. Plotting stress against strain shows an initial linear relationship in which the slope is equivalent to the modulus of elasticity, until the proportionality limit (1), and thereafter the relationship is nonlinear. When the elastic limit (2) is exceeded, the material deforms plastically until the rupture point (3) is reached. (b) Selye's 'General Adaptation Syndrome' defines human stress for medical purposes. Three phases of stress response include alarm (yellow), resistance (orange) and exhaustion (red); see text for details. (c) In

biological systems, the term 'stress' is often used to describe what would correspond to a 'strain' according to the definition used in materials science. The flow chart is an extremely simplified example of the intricately linked effects of a 'stress', water deprivation, to give examples of strains (bold lines around boxes) that evoke responses of the plant (no lines) and intermediate processes that have elements of strain and response (thin lines). The responses of the plant can feed back downstream and upstream into the system, leading to resistance based on protection and repair. The individual processes are also assigned the colours yellow, orange and red according to 'alarm', 'resistance' and 'exhaustion'. Two or three colours within one box indicate that the process corresponds to more than one of the phases in Selye's stress concept (Kranner et al. 2010).

7.5. Ecological stability

Ecosystems are open thermodynamic systems characterized by input and output of energy and matter. Stability may be defined as the ability of a system to remain near an equilibrium point or to return to it after a disturbance (Orians, 1975; Harrison, 1979). Hence, ecosystem stability is characterized by a dynamic equilibrium (steady state) achieved through interactions among functional groups of organisms and the physical environment. For example, the nutrient cycling results from the functional synchrony of autotrophs, heterotrophs, the atmosphere, and the soil compartment (Larsen 2005).

Ecological stability can refer to types of stability in a continuum ranging from resilience (returning quickly to a previous state) to constancy to persistence. The precise definition depends on the ecosystem in question, the variable or variables of interest, and the overall context. In the context of conservation ecology, stable populations are often defined as ones that do not go extinct. Researchers applying mathematical models from system dynamics usually use Lyapunov stability (Justus 2008).

Ecologists have proposed several incompatible definitions of ecological stability. Emulating physicists, mathematical ecologists commonly define it as Lyapunov stability. This formalizes the problematic concept by integrating it into a well-developed mathematical theory. The formalization also seems to capture the intuition that ecological stability depends on how ecological systems respond to perturbation. Despite these advantages, this definition is flawed. Although Lyapunov stability adequately characterizes perturbation responses of many systems studied in physics, it does not for ecological systems. This failure reveals a limitation of its underlying mathematical theory, and an important difference between dynamic systems modeling in physics and ecology (Justus 2008).

Types of ecological stability

- **Constancy and persistence** - Observational studies of ecosystems use constancy to describe living systems that can remain unchanged.
- **Resistance and inertia (persistence)** - deal with a system's inherent response to some perturbation. A perturbation is any externally imposed change in conditions, usually happening in a short time period. Resistance is a measure of how little the variable of interest changes in response to external pressures. Inertia (or persistence) implies that the living system is able to resist external fluctuations.
- **Resilience, elasticity and amplitude** - resilience is the tendency of a system to return to a previous state after a perturbation. Elasticity and amplitude are measures of

resilience. Elasticity is the speed with which a system returns. Amplitude is a measure of how far a system can be moved from the previous state and still return. Ecology borrows the idea of neighborhood stability and a domain of attraction from dynamical systems theory.

7.6. Resilience

In ecology, resilience is the capacity of an ecosystem to respond to a perturbation or disturbance by resisting damage and recovering quickly. Such perturbations and disturbances can include stochastic events such as fires, flooding, windstorms, insect population explosions, and human activities such as deforestation and the introduction of exotic plant or animal species. Disturbances of sufficient magnitude or duration can profoundly affect an ecosystem and may force an ecosystem to reach a threshold beyond which a different regime of processes and structures predominates (Folke et al. 2004). Human activities that adversely affect ecosystem resilience such as reduction of biodiversity, exploitation of natural resources, pollution, land-use, and anthropogenic climate change are increasingly causing regime shifts in ecosystems, often to less desirable and degraded conditions (Folke et al. 2004; Peterson et al. 1998) Interdisciplinary discourse on resilience now includes consideration of the interactions of humans and ecosystems via socio-ecological systems, and the need for shift from the maximum sustainable yield paradigm to environmental management which aims to build ecological resilience through "resilience analysis, adaptive resource management, and adaptive governance" (Walker et al. 2004).

The concept of resilience in ecological systems was first introduced by the Canadian ecologist C.S. Holling (1973) in order to describe the persistence of natural systems in the face of changes in ecosystem variables due to natural or anthropogenic causes. Resilience has been defined in two ways in ecological literature:

- as the time required for an ecosystem to return to an equilibrium or steady-state following a perturbation (which is also defined as stability by some authors). This definition of resilience is used in other fields such as physics and engineering, and hence has been termed “engineering resilience” by Holling (Holling 1973, Gunderson 2000).
- as "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks" (Walker et al. 2004).

The second definition has been termed ‘ecological resilience’, and it presumes the existence of multiple stable states or regimes (Gunderson 2000, 2002).

Human impacts on resilience

Resilience refers to ecosystem's stability and capability of tolerating disturbance and restoring itself. If the disturbance is of sufficient magnitude or duration, a threshold may be reached where the ecosystem undergoes a regime shift, possibly permanently. Sustainable use of environmental goods and services requires understanding and consideration of the resilience of the ecosystem and its limits. However, the elements which influence ecosystem resilience are complicated. For example various elements such as the water cycle, fertility, biodiversity, plant diversity and climate, interact fiercely and affect different systems. There are many areas where human activity impacts upon and is also dependent upon the resilience of terrestrial, aquatic and marine ecosystems. These include agriculture, deforestation, pollution, mining, recreation, overfishing, dumping of waste into the sea and climate change.

7.7. Territorial system of ecological stability (TSES)

The TSES is a mutually interconnected complex of both natural and semi-naturalmodified ecosystems, which maintains natural balance. There are three levels of the TSES, namely
local, regional and supra-regional TSES (Sec.5 of the Act No. 114/1992 Gazette); generally, we speak about the Territorial Systems of Ecological Stability. A local Territorial System of Ecological Stability is a part of the regional and supra-regional systems. The whole complex of Territorial Systems of Ecological Stability consists of biocentres, which are core areas, mutually connected with biocorridors. The latter form linear elements in the landscape. The spatial and functional parameters of the individual TSES components depend on the biotic, hydrological, soil and relief conditions.

Sec. 4 of the Act No.114/1992 Gazette (par. l) states: . . . the protection of the System of Ecological Stability is a duty of all owners and users of the land plots which form its basis; its formation is public interest, shared by the land owners, communities and the State (Pekárek et al. 1995). The Territorial System of Ecological Stability consists of both the existing and proposed elements. The whole system is the network of ecologically significant segments of landscape, efficiently distributed on the basis of functional and spatial criteria (Low et al. 1995).

The aims of establishing the Territorial System of Ecological Stability in the landscape are the following (Plesník 1996):

- conservation and support of the development of the natural genetic diversity of organisms inhabiting the landscape,
- providing favourable influences on the surrounding, ecologically less stable parts of the landscape,
- support of polyfunctional utilization of the landscape,
- conservation of significant landscape elements.

TSES elements

Biocentre

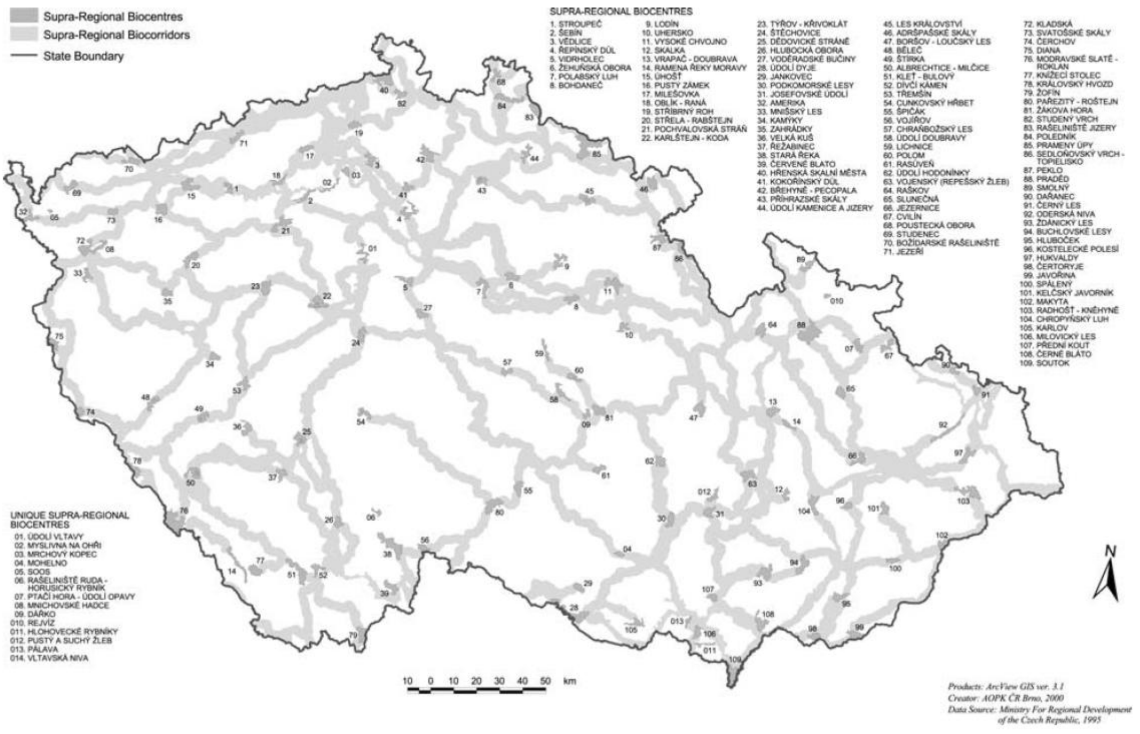
This is defined as a biotope or centre of biotopes in a landscape, which, due to its condition and scope, facilitates the existence of a natural or near-natural, altered ecosystem.

Ecological corridor

This is a territory that does not facilitate permanent or long-term existence of a significant number of organisms, but does provide for their migration between different biocentres, creating a network of isolated biocentres.

Interaction element

This is defined as a landscape segment, which, on a local level, mediates the favourable effect of basic TSES elements (biocentres and biological corridors) on surrounding less stable landscape. Besides this, interaction elements often enable the permanent existence of certain species with limited territorial requirements (besides a range of plant species, these include some species of insects, small rodents, insectivores, birds, amphibians etc.).



Products: ArcView GIS ver. 3.1
Creator: AOPK ČR Brno, 2000
Data Source: Ministry For Regional Development of the Czech Republic, 1995

Figure 7.5. The Territorial System of Ecological Stability of the Czech Republic. Supra-Regional Biocentres, Supra- Regional Biocorridors According to the Territorial Technical Document (B΄ınova et al., 1997). Legend: supra-regional biocorridors supra-regional biocentres (Mackovčin et al. 2000).

TSES categories according to significance

Supraregional TSES

These are vast (at least 1000 ha) landscape units and areas of ecological significance, forming a network providing conditions for the existence of characteristic coenosis together with complete biota biodiversity in the context of a certain biogeographical region.

Regional TSES

These are landscape units and areas of ecological significance (minimum area of 10 - 50 ha). A network of these units must represent a diversity of biochore types in the context of a certain biogeographical region.

Local TSES

These are small landscape units of ecological significance (area about 5 - 10 ha). A network of these represents biogeocoenosis type groups in the context of a certain biochore.

TSES plans

TSES are established by plans that should include in particular the following:

a) a draft map of existing and proposed biocentres and ecological corridors with marked protected areas to a minimum scale of 1:50 000 (supraregional and regional TSES) or 1:10 000 (local TSES).

b) a table and a theoretical section describing functional and spatial factors

c) detailed rationale including outline measures for its conservation or regeneration.

The TSES plan serves as documentation for TSES projects, land consolidations and land replotting, processing of territorial planning documentation, forest management plans, water management documents and other documents regarding protection and restoration of the landscape.

TSES elements are being established in 2005 in almost all PLA territory with a few exceptions.

7.8. Review questions

1. Ecological stress.
2. Stress phase.
3. Ecological stability.
4. Resilience, resistence.
5. Territorial system of ecological stability

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Chapter 8. The Role of Forests in Global Ecology

8. 1. Global forest distribution

Forest definition (FAO 1998) - forest is a land spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10 percent, or trees able to reach *in situ* these thresholds.

Forests cover 31 percent of total land area (fig. 1). The world's total forest area in 2010 is estimated to be just over 4 billion hectares, corresponding to an average of 0.6 ha of forest per capita. However, the area of forest is unevenly distributed. The five most forest-rich countries (the Russian Federation, Brazil, Canada, the United States of America and China) account for more than half of the total forest area (53 percent), while 64 countries with a combined population of 2 billion people have forest on no more than 10 percent of their land area. These include a number of fairly large countries in arid zones, as well as many small island developing states (SIDS) and dependent territories. Ten of these have no forests at all. The total area of other wooded land is estimated to be at least 1.1 billion hectares, equivalent to 9 percent of the total land area. The total area of other land with tree cover was reported to be 79 million hectares, but is undoubtedly much higher as information availability was limited.

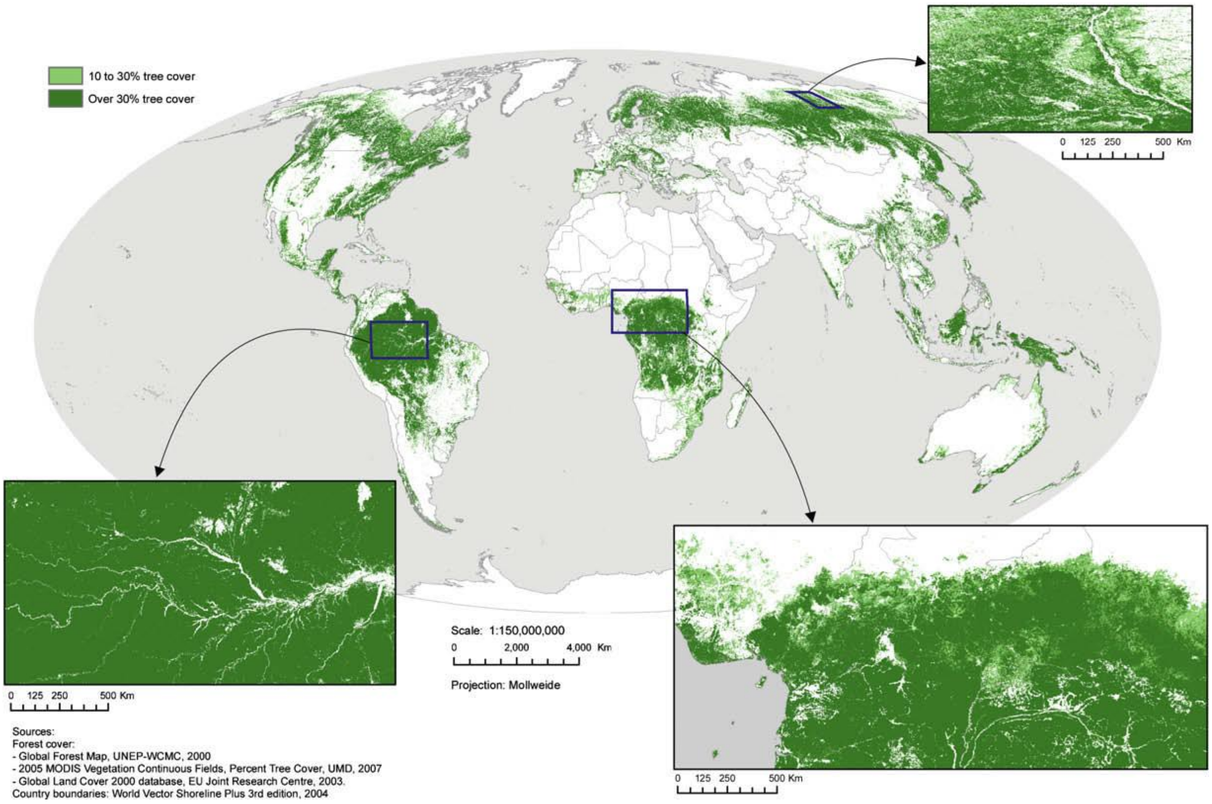
The **rate of deforestation** shows signs of decreasing, but is still alarmingly high. Deforestation – mainly the conversion of tropical forest to agricultural land – shows signs of decreasing in several countries but continues at a high rate in others. Around 13 million hectares of forest were converted to other uses or lost through natural causes each year in the last decade compared with 16 million hectares per year in the 1990s. Both Brazil and Indonesia, which had the highest net loss of forest in the 1990s, have significantly reduced their rate of loss, while in Australia, severe drought and forest fires have exacerbated the loss of forest since 2000.

Afforestation and **natural expansion** of forests in some countries have significantly reduced the net loss of forest area at the global level The net change in forest area in the period 2000–2010 is estimated at -5.2 million hectares per year at the global level (an area about the size of Costa Rica). This is down from -8.3 million hectares per year in the period 1990–2000. This substantial reduction is due to both a decrease in the deforestation rate and an increase in the area of new forest established through planting or seeding and the natural expansion of existing forests.

More than 90 percent of the total forest area consists of naturally regenerated forests. Primary forests – forests of native species in which there are no clearly visible signs of past or present human activity – are estimated to occupy 36 percent of the total forest area. Other naturally regenerated forests make up some 57 percent, while planted forests account for an estimated 7 percent, of the total forest area.

Primary forests account for 36 percent of forest area – but have decreased by more than 40 million hectares since 2000. On a global average, more than one-third of all forest is primary forest, i.e. forest of native species where there are no clearly visible indications of human activities and the ecological processes have not been significantly disturbed. Primary forests, in particular tropical moist forests, include the most species-rich, diverse terrestrial ecosystems. The decrease of primary forest area, 0.4 percent annually over a ten-year period, is largely due to reclassification of primary forest to ‘other naturally regenerated forest’ because of selective logging and other human interventions.

The area of **planted forest is increasing** and now accounts for **7 percent of total forest area.** Forests and trees are planted for many purposes and make up an estimated 7 percent of the total forest area, or 264 million hectares. Between 2000 and 2010, the area of planted forest increased by about 5 million hectares per year (Fig. 8). Most of this was established through afforestation (i.e. planting of areas not forested in recent times) particularly in China. Three-quarters of all planted forests consist of native species while one-quarter comprises introduced species.



Sources:
Forest cover:
- Global Forest Map, UNEP-WCMC, 2000
- 2005 MODIS Vegetation Continuous Fields, Percent Tree Cover, UMD, 2007
- Global Land Cover 2000 database, EU Joint Research Centre, 2003.

Country boundaries: World Vector Shoreline Plus 3rd edition, 2004

Figure 8. 1. Global forest cover (Schmitt et al. 2009)

Forest fires are severely underreported at the global level. While some forest ecosystems depend on fire for their regeneration, in others forest fires can be devastating and also frequently cause loss of property and human life. On average, 1 percent of all forests were reported to be significantly affected each year by forest fires. However, the area of forest affected by fires was severely underreported, with information missing from many countries, especially in Africa. Less than 10 percent of all forest fires are prescribed burning; the rest are classified as wildfires.

Insect pests and diseases, natural disasters and invasive species are causing severe damage in some countries. Outbreaks of forest insect pests damage some 35 million hectares of forest annually, primarily in the temperate and boreal zone. The mountain pine beetle has devastated more than 11 million hectares of forest in Canada and the western United States of America since the late 1990s – an unprecedented outbreak exacerbated by higher winter temperatures. Severe storms, blizzards and earthquakes have also damaged large areas of forest since 2000. Woody invasive species are of particular concern in small island developing states, where they threaten the habitat of endemic species. Information availability and quality continues to be poor for most of these disturbances.

8. 2. Forests in global carbon cycle and global climatic changes

Forests, like other ecosystems, are affected by climate change. In some places, impacts may be negative, while in others they may be positive. Forests also influence climate and the climate change process. They absorb carbon in wood, leaves and soil and release it into the atmosphere when burned, for example during forest fires or when forest land is cleared.

Quantifying the substantial roles of forests as carbon stores, as sources of carbon emissions and as carbon sinks has become one of the keys to understanding and influencing the global carbon cycle. Global forest resources assessments have the potential to contribute to, or substantiate, the estimates of the magnitude of carbon stocks and flows made by scientific bodies such as IPCC. At the same time, they complement and facilitate international reporting by countries on greenhouse gas emissions and removals under the UNFCCC.

Status

In total, 180 countries and areas, representing 94 percent of the world's forests, reported on carbon in biomass for 2010. For carbon in dead wood the corresponding figures are 72 countries (61 percent), for carbon in litter 124 countries (78 percent) and for soil carbon 121 countries (78 percent). For the remaining countries and areas, FAO estimated the carbon stocks by taking subregional averages per hectare and multiplying these by the forest area for the respective years. In 2010, the total carbon stock in the biomass of the world's forests is estimated at 289 Gt. For most countries, carbon in biomass merely reflects the biomass stock as the default carbon fraction from the IPCC guidelines has been used. In FRA 2010, most countries used a carbon fraction of 0.47 (as in the 2006 IPCC Guidelines), while some countries used the carbon fraction of 0.5 suggested in the IPCC 2003 Good Practice Guidance. A few countries have used country-specific carbon fractions for their estimates. Globally, the average carbon fraction used is 0.48 with minor variations between subregions.

The total carbon stock in dead wood and litter in 2010 amounts to 72 billion tonnes or 17.8 tonnes per hectare. This is slightly more than reported in FRA 2005. However, data on carbon stock in dead wood and litter are still very weak. Most countries do not have national data on these carbon pools, so until the IPCC provides better default values, estimates of these carbon pools will continue to be weak. ***The total stock of carbon in soil*** is estimated at 292 billion tonnes or 72.3 tonnes per hectare. This is slightly more than the total carbon stock in forest biomass. Taking together all carbon in biomass, dead wood, litter and soils, the estimated total carbon stock in forests in 2010 is 652 billion tonnes, corresponding to 161.8 tonnes per hectare.

Trends

In total, 174 countries and areas (representing 93 percent of the total forest area) have reported a complete time series on carbon stock in forest biomass (above-ground and below ground). For the remaining countries and areas, FAO estimated carbon stock in forest biomass by taking the subregional averages of carbon stock per hectare and multiplying them by the forest area for the respective years.

The total carbon stock in the biomass of the world's forests shows a decrease of about 10 Gt for the period 1990–2010 or -0.5 Gt per year on average, mainly due to a reduction in the world's forest area. As for biomass, the carbon stock per hectare does not show any significant change at the global level.

For dead wood carbon the response rate for FRA 2010 was lower than in FRA 2005, mainly because of the IPCC's decision to omit default conversion factors from the latest version of their guidelines. A complete time series on carbon in dead wood was reported by 66 countries and areas (representing 61 percent of the world's forest area). For carbon in litter the response rate was much higher than in FRA 2005 when only 54 countries reported. For FRA 2010, 119 countries (accounting for 77 percent of the world's forest area) reported on carbon in litter. For the remaining countries and areas, FAO estimated carbon stocks by taking the subregional average carbon stocks per hectare and multiplying them by the forest area for the respective years.

A complete time series on soil carbon was reported by 117 countries and areas (representing 78 percent of the world's forest area). This is a substantially larger response rate than in FRA 2005 when only 43 countries reported. For the remaining countries and areas, FAO made estimates by taking the subregional average soil carbon stocks per hectare and multiplying these by the forest area for the respective years. Most countries have used IPCC default values of stocks per hectare which relate to a soil depth of 30 cm. In this analysis, no adjustment has been made for countries reporting soil carbon to non-standard soil depths.

The declining trend in the total stock of carbon in the soil for the period 1990–2010 is attributed to the loss of forest area during this period as the stocks per hectare show almost no change.

The estimated total carbon stock in forests in 2010 is 652 billion tonnes, which equates to 161.8 tonnes per hectare. The total carbon stock has decreased during the period 1990–2010, mainly as a result of the loss of forest area during the period. Carbon stocks per hectare show a slight increase, but it is unlikely to be significant in statistical terms. FRA 2010 shows slightly higher carbon stocks than those estimated for FRA 2005. This is mostly because forest area is estimated to be higher in FRA 2010 compared with FRA 2005. The stocks per hectare are almost the same, but while FRA 2005 presented a decreasing trend in stocks per hectare, FRA 2010 shows almost no change over time.

Forests store a vast amount of carbon. Estimates made for FRA 2010 show that the world's forests store 289 gigatonnes (Gt) of carbon in their biomass alone. While sustainable management, planting and rehabilitation of forests can conserve or increase forest carbon stocks, deforestation, degradation and poor forest management reduce them. **Forests contain more carbon than the entire atmosphere.** The world's forests store more than 650 billion tonnes of carbon, 44 percent in the biomass, 11 percent in dead wood and litter, and 45 percent in the soil. While sustainable management, planting and rehabilitation of forests can conserve or increase forest carbon stocks, deforestation, degradation and poor forest management reduce them. For the world as a whole, carbon stocks in forest biomass decreased by an estimated 0.5 Gt annually during the period 2005–2010. This was mainly because of a reduction in the global forest area and occurred despite an increase in growing stock per hectare in some regions.

8. 4. Sustainability and global biodiversity conservation

Twelve percent of the world's forests are designated for the conservation of biological diversity. The area of forest where conservation of biological diversity is designated as the primary function has increased by more than 95 million hectares since 1990, of which the largest part (46 percent) was designated between 2000 and 2005. These forests now account for 12 percent of the total forest area or more than 460 million hectares. Most but not all of them are located inside protected areas.

Biological diversity encompasses the variety of existing life forms, the ecological roles they perform and the genetic diversity they contain (FAO, 1989). In forests, biological diversity allows species to evolve and dynamically adapt to changing environmental conditions (including climate), to maintain the potential for tree breeding and improvement (to meet human needs for goods and services, and changing end-use requirements) and to support their ecosystem functions.

In recent years, the Global Forest Resources Assessment has increased its focus on forest biological diversity. For FRA 2000, data were compiled on the proportion of forests in protected areas. Relevant information was compiled at the landscape and species levels for FRA 2005, while some structural and compositional aspects were also addressed. At the ecosystem level, for FRA 2005 countries provided information on the area of forests and, more specifically, on the area of primary forests and on forests designated for the conservation of biological diversity (including protected areas). At the species level, for FRA 2005 FAO focused on the assessment of the number of both native and endangered forest tree species at the country level. In addition, country reports included lists of the ten most common tree species (measured by their share of total growing stock), thus providing important information on the tree species composition of forests.

The variables measured for FRA 2010 with relevance to forest biological diversity include:

- area of primary forests;
- forest area designated primarily for conservation of biological diversity;
- area of forests in protected areas;
- tree species composition of forests.

KEY FINDINGS

Primary forests account for 36 percent of forest area – but have decreased by more than 40 million hectares since 2000. Globally, more than one-third of all forest is classified as primary forest. This is defined as forest of native species where there are no clearly visible indications of human activities and the ecological processes have not been significantly disturbed. Primary forests, in particular tropical moist forests, include some of the world's most speciesrich, diverse terrestrial ecosystems. The area of primary forest decreased by about 0.4 percent annually over the last ten years, largely as a result of the reclassification of primary forest to 'other naturally regenerated forest' because of selective logging and other human interventions.

Twelve percent of the world's forests are designated primarily for the conservation of biological diversity. The area of forest where conservation of biological diversity is designated as the primary function has increased by more than 95 million hectares since 1990, of which the largest part (46 percent) was designated between 2000 and 2005. These forests now account for 12 percent of the total forest area or more than 460 million hectares. Most, but not all, of them are located inside protected areas.

Legally established protected areas cover an estimated 13 percent of the world's forests. National parks, game reserves, wilderness areas and legally established protected areas cover more than 10 percent of the total forest area in most countries and regions. The primary function of these forests may be the conservation of biological diversity, the protection of soil and water resources, or the conservation of cultural heritage. The area of forest within protected area systems has increased by 94 million hectares since 1990. Two-thirds of this increase has been since 2000.

Analysis of data on growing stock composition can provide proxy indicators of forest tree species richness and relative abundance. This is useful for qualitative assessment and monitoring of biological diversity. While the growing stock of the ten most common tree species represents more than 90 percent of the total growing stock in many countries in the temperate and boreal zone, it represents less than 20 percent of total growing stock in tropical countries with high species diversity. The availability and comparability of information remains poor, however.

a) Area of primary forests

Of the 233 countries and areas reporting for FRA 2010, 200 countries, accounting for 94 percent of total forest area, reported on the area of primary forest. Globally, close to 1.4 billion hectares, were classified as primary forest, which represents over one-thir (36 percent) of total forest area of the reporting countries. However, information was missing for many of the smaller islands and territories, as well as for countries such as Cameroon and the Democratic Republic of the Congo (two of the largest countries in the Congo Basin, the second largest expanse of tropical forest) and for the Bolivarian Republic of Venezuela, so the actual area is probably slightly higher. Several countries reported that they had insufficient information on the area of primary forests, so they included it in the category of other naturally regenerated forests. Others used the current area of forests in national parks and other protected areas as a proxy value or provided an expert estimate of the percentage of natural forests that could be considered primary according to the FRA 2010 definition.

At the global level the area of primary forest decreased by around 4.7 million hectares per year in the 1990s, and by 4.2 million hectares per year between 2000 and 2010. This loss, which equates to 0.4 percent of the area of primary forest annually over the ten-year period, is largely due to the reclassification of primary forest to other categories of forest because of selective logging and other human interventions during this period.

While globally more than one-third of total forest area is classified as primary forest, this area has decreased by more than 40 million hectares over the last ten years. Although there have been improvements in the availability of data on primary forests since the last global assessment, many countries still rely on proxies such as the area within national parks and other protected areas. Furthermore, information is still insufficient to determine what proportion of the decrease in primary forest is due to deforestation and what is due to a reclassification to one of the two other categories: 'other naturally regenerated forests' and 'planted forests'.

b) Forest area designated primarily for conservation of biological diversity

Of the 233 countries and areas reporting for FRA 2010, 205 countries and areas, representing 99.9 percent of the total forest area, provided information on forest area designated primarily for the conservation of biological diversity. The availability of information has improved compared with the last assessment (FRA 2005), when only 172 countries reported on this variable. This is particularly noticeable in Western and Central Africa, where all 24 countries provided data (compared with only 15 for FRA 2005). The availability of information for FRA 2010 was low only in the Caribbean. These data show that, globally, 463 million hectares of forest, or 11.5 percent of the total forest area of the reporting countries, are designated for the conservation of biological diversity as the primary function. The largest area of forest designated for conservation of biological diversity is found in South America (116 million hectares), followed by North America and Africa. Central America and South and Southeast Asia have the highest percentage of forests designated primarily for conservation, while Europe (including the Russian Federation), and Western and Central Asia have the lowest.

The area of forest designated for the conservation of biological diversity has increased by more than 95 million hectares, or 30 percent, since 1990, of which the largest part was designated between 2000 and 2005. This trend is apparent in all regions and subregions except Northern Africa and Central America. The highest rates of increase are seen in South America (mainly due to recent conservation measures in Brazil) and Europe.

The period 2005–2010 shows a contrasting trend in some subregions however, with a decrease in South and Southeast Asia (mainly in Myanmar) and Eastern and Southern Africa, possibly correlated to the loss of forest area in these subregions.

c) Area of forests in protected areas

National parks, game reserves, wilderness areas and other legally established protected areas cover approximately 13 percent of the world’s forest area and more than 10 percent of the total forest area in most countries and regions. The primary function of these forests may be the conservation of biological diversity, the protection of soil and water resources or the conservation of cultural heritage. The area of forest within protected area systems has increased by 94 million hectares since 1990. Two-thirds of this increase has been since 2000.

d) Tree species composition of forests.

For FRA 2010 only 79 countries (together representing 61 percent of the total forest area) provided data on the ten most common species (2005 data). The subregions with the highest response rates were East Asia, Europe, North America, Northern Africa and South and Southeast Asia. While the growing stock of the ten most common species represents more than 90 percent of the total growing stock in many countries in the temperate and boreal zone, it represents less than 20 percent of the total growing stock in tropical countries with high species diversity, such as the reporting countries from Western and CentralAfrica. Data comparability is still an issue as indicated by the range of figures for each subregion. Some countries only have data on growing stock of commercial species with a merchantable diameter (e.g. Equatorial Guinea), others have data only for part of the country (e.g. Malaysia and United Republic of Tanzania) or have grouped some species (e.g. Guatemala and Poland). In addition, there is wide natural spread within some subregions – particularly when composed of both large, species-rich countries and small island states (e.g. Eastern and Southern Africa). Comparison of the 1990 and 2005 data did not show significant changes in the relative ranking of the tree species, or in the share of growing stock occupied by the ten main species.

8. 5. Other ecological and societal aspects of forests protection

8. 5. 1. Productive function of forest resources

Thirty percent of the world's forests are primarily used for production of wood and non-wood forest products. Close to 1.2 billion hectares of forest are managed primarily for the production of wood and non-wood forest products. An additional 949 million hectares (24 percent) are designated for multiple use – in most cases including the production of wood and non-wood forest products. The area designated primarily for productive functions has decreased by more than 50 million hectares since 1990, or 0.22 percent annually as forests have been designated for other purposes. The area designated for multiple use has increased by 10 million hectares in the same period.

The area of planted forest is increasing and now accounts for 7 percent of total forest area. Forests and trees are planted for many purposes and make up an estimated 7 percent of the total forest area, or 264 million hectares. Five countries (China, the United States of America, the Russian Federation, Japan and India) account for more than half (53 percent) of this area. Some arid zone countries and the Netherlands report that all their forests are planted. Between 2000 and 2010, the area of planted forest increased by about 5 million hectares per year. Most of this was established through afforestation (i.e. planting of areas not classified as forest) particularly in China. The rate of establishment of planted forests has increased in the past 10 years compared with the 1990s in most regions except for Europe. Given the current trend, a further rise can be anticipated in the area of planted forest to 300 million hectares by 2020.

Three-quarters of all planted forests consist of native species. The remaining quarter comprises introduced species. In sub-Saharan Africa, Oceania and South America a number of countries with a significant area of planted forests report that they almost exclusively plant introduced species. In the temperate and boreal zones of Europe and North America and in arid zone countries introduced species are used to a minor extent.

More than 10 million hectares per year are afforested or reforested each year. In the 10-year period from 1998 to 2007, at the global level, altogether more than 10 million hectares per year were afforested and reforested, mostly with indigenous species. China accounts for a large proportion of this area. Introduced species are used, on average, at a rate of 29 percent in afforestation and 36 percent in reforestation.

Wood removals increased between 2000 and 2005, following a fall in the 1990s. At the global level, reported wood removals in 2005 amounted to 3.4 billion cubic metres annually, similar to the volume recorded for 1990 and equivalent to 0.7 percent of the total growing stock. Considering that informally and illegally removed wood, especially woodfuel, is not usually recorded, the actual amount of wood removals is undoubtedly higher. At the global level, woodfuel accounted for about half of the removed wood. Wood removals from other wooded land amounted to 299 million cubic metres or 9 percent of total wood removals in 2005. The proportions of industrial roundwood and woodfuel did not change significantly between 1990 and 2005.

Food is the largest category of NWFP removals globally. Other important categories include exudates, other plant products, wild honey and beeswax, and ornamental plants. Asia, and in particular China, reported the larges tvolume of NWFP removals, most of which are of plant origin (camellia, oil seeds, nuts and bamboo products). The sheer size of the removals reported by China dwarfs any othercountry’s removals. Europe has the highest reported level of animal based NWF Premovals.

8. 5. 2. Protective functions of forest resources

Eight percent of the world’s forests have protection of soil and water resources as their primary objective. Around 330 million hectares of forest are designated for soil and water conservation, avalanche control, sand dune stabilization, desertification control or coastal protection. The area of forest designated for protective functions increased by 59 million hectares between 1990 and 2010, primarily because of large-scale planting in China aimed at desertification control, conservation of soil and water resources and other protective purposes.

8. 5. 3. Socio-economic functions of forest resources

Eighty percent of the world’s forests are publicly owned, but ownership and management of forests by communities, individuals and private companies is on the rise. Despite changes in forest ownership and tenure in some regions, most of the world’s forests remain under public ownership. Differences among regions are considerable. North and Central America, Europe (other than the Russian Federation), South America and Oceania have a higher proportion of private ownership than other regions. In some regions, there is an increasing trend towards the involvement of communities, individuals and private companies in the management of publicly owned forests.

Governments generally spend more on forestry than they collect in revenue. On average, total forest revenue collection was about US$4.5 per hectare, ranging from under US$1 per hectare in Africa to just over US$6 per hectare in Europe. Public expenditure on forestry was about US$7.5 per hectare on average. Average expenditure was highest in Asia (over US$20 per hectare). In contrast, the average expenditure per hectare was less than US$1 in South America and Oceania.

The value of wood removals is high, but fluctuating. Wood removals were valued at just over US$100 billion annually in the period 2003–2007. Industrial roundwood accounted for most of this value. At the global level the reported value of wood removals showed no change between 1990 and 2000, but increased by about 5 percent annually over the period 2000–2005. This suggests that roundwood prices recovered somewhat from their decline (in real terms) in the decade 1990–2000. However, since 2005 they have fallen sharply.

The value of NWFPs remains underestimated. The reported value of NWFP removals amounts to about US$18.5 billion for 2005. Food products account for the greatest share of this. However, information is still missing from many countries where NWFPs are highly important, and the true value of subsistence use is rarely captured. As a result, the reported statistics probably cover only a fraction of the true total value of harvested NWFPs.

Around 10 million people are employed in forest management and conservation – but many more are directly dependent on forests for their livelihoods. Reported employment in forest establishment, management and use declined by about 10 percent between 1990 and 2005, probably because of gains in labour productivity. Europe, East Asia and North America saw steep declines (15 to 40 percent between 1990 and 2005), while in other regions, employment increased somewhat – probably because roundwood production has increased faster than gains in labour productivity. Most countries reported increased employment in the management of protected areas. Given that much forestry employment is outside the formal sector, forest work is certainly much more important for rural livelihoods and national economies than the reported figures suggest.

The management of forests for social and cultural functions is increasing, but the area is difficult to quantify. Globally, 4 percent of the world's forests are designated for the provision of social services. East Asia and Europe are the only regions with fairly good data on the designation of forests for recreation, tourism, education or conservation of cultural and spiritual heritage. In these two regions, provision of social services was reported as the primary management objective for 3 percent (East Asia) and 2 percent (Europe) of the total forest area. Brazil has designated more than one-fifth of its forest area for the protection of the culture and way of life of forest-dependent peoples.

8. 5. 4. Progress towards sustainable forest management

In addition to reporting on the area of forest designated for specific functions, countries were asked to report on four additional variables to illustrate the status of forest management:

- the area of forest in protected areas;
- the area of permanent forest estate;
- the area of forest with a management plan;
- the area of forest under sustainable forest management.

Area of forest in protected areas (see Biodiversity)

Area of permanent forest estate

The area of permanent forest estate indicates the area of forest designated to be retained as forest. As such, trends in this variable over time are a better indicator of progress towards sustainable forest management than trends in the total forest area in countries where certain forest areas have been set aside for future conversion to other uses (e.g. agriculture, infrastructure or urban expansion) through a transparent and technically sound decision-making process.

FRA 2010 was the first time countries were asked to report on the area of permanent forest estate and some countries clearly had difficulties identifying the equivalent designation in their national classification systems. Nevertheless, a total of 122 countries, together accounting for 84 percent of the total forest area provided information on this variable. At the global level, an estimated 52 percent of the total forest area is designated as permanent forest estate or its equivalent in 2010.

A number of countries were unable to provide a full data series (for 1990, 2000, 2005 and 2010). However, information from 107 countries and areas (representing 77 percent of the world's forests) indicates that the permanent forest estate increased by almost 15 million hectares per year in the 1990s and close to 10 million hectares per year since 2000.

Area of forest with a management plan

The area of forest with a management plan provides another indication of progress towards sustainable forest management, although it must be noted that areas without a plan – including inaccessible areas – may also be conserved and sustainably managed, while the mere existence of a plan does not provide assurance that the plan is sound, is being implemented, or has the intended effect.

A total of 121 countries, representing 79 percent of the global forest area, reported on this variable. These reports indicate that at least 1.6 billion hectares of forest are covered by a management plan with a duration of ten years or more. The true figure is undoubtedly higher as information was missing from many countries. Information on trends over time was more limited with a full data series only available for 94 countries and areas, covering 64 percent of the world's forests. However, there was a clear increasing trend in the area of forest with a management plan in all regions and subregions over the last 20 years. Particularly noteworthy is the rapid increase in this area over the last ten years, primarily in East Asia, sub-Saharan Africa and South America.

Area of forest under sustainable forest management

FRA 2010 is the first time countries have been asked to provide an estimate of the area of forest considered to be under sustainable forest management in the FRA process. Because there is no agreed definition or assessment methodology, this was considered a pilot assessment and countries were also asked to provide the definition, criteria and method used to assess the area under sustainable forest management. The purpose of this pilot was to obtain information on how countries might define and assess this indicator as an input to future discussions on the topic at subregional, regional and global levels, in anticipation of the need for countries to report on it as part of the assessment of progress towards the Global Objectives on Forests by 2015. Where countries did not have established assessment criteria, it was suggested that they might wish to use or adapt those applied by ITTO in its assessment of the Status of Tropical Forest Management (ITTO, 2006), which were as follows:

„Forest areas that fulfil any of the following conditions:
- have been independently certified or in which progress towards certification is being made;
- have fully developed, long-term (ten years or more) forest management plans with firm information that these plans are being implemented effectively;
- are considered as model forest units in their country and information is available on the quality of management;
- are community-based forest management units with secure tenure for which the quality of management is known to be of high standard;
- are protected areas with secure boundaries and a management plan that are generally considered in the country and by other observers to be well managed and that are not under significant threat from destructive agents."

Although this was not an easy task, 104 countries and areas, together accounting for 62 percent of the world's forests provided estimates of the area under sustainable forest management for 2010, and 110 countries covering 81 percent of the global forest area provided an estimate for at least one point in time. Unfortunately, they did not all provide information on the definition, assessment criteria and method used. Due to differences in definitions, it is not possible to compare the results by country or to generate regional or global totals and no attempts have been made to do so. The 82 countries that provided a full data series clearly indicated a positive trend in the total forest area considered to be under sustainable forest management. A separate publication (FAO, 2010c) provides a more detailed analysis of the definitions, assessment criteria and methods applied by countries.

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