4.1

Historic-Genetic Development of Phytocenoses and Their Dynamics

The species-rich segetal flora in an annual crop of lentils and in a perennial crop of olive trees demonstrates the typical anthropogenic replacement of communities in an area of the European Mediterranean region which is still little influenced by herbicides. Photo K. Müller-Hohenstein

Recommended Literature

To understand the development of the plant cover on earth and provide detailed explanations on individual temporal periods, as well as on the general basic aspects of vegetation dynamics, the following books are recommended in addition to those mentioned at the beginning of Chapter 4:

- Burrows CJ (1990) Processes of vegetation change. Unwin, London
- Ellenberg H (1988) Vegetation ecology of central Europe, 4th ed. Cambridge Univ Press, Cambridge
- Graham LA (1993) Origin of land plants. Wiley, New York
- Lovett Doust J, Lovett Doust L (eds) (1988) Plant reproductive ecology. Patterns and strategies. Oxford Univ Press, Oxford
- Solomon AM, Shugart HH (eds) (1993) Vegetation dynamics and global change. Chapman & Hall, New York London
- Sukopp H, Hejny S (eds) (1990) Urban ecology. SPB Acad Publ, The Hague
- Thompson JN (1995) The coevolutionary process. Univ of Chicago Press, Chicago

Recent ecological interactions between living organisms and their environment are the basis of the present structure and distribution of vegetation. Thus, present-day conditions can only be understood on the basis of abiotic and biotic interactions, i.e. ecologically. However, the existence of species and communities may only be explained historically on the basis of knowledge of evolution and distribution.

Three important geological events have contributed significantly to the formation of present-day patterns of distribution:

- continuous **migration of the continents in relation to the poles** (Fig. 4.1.1, see also Table 4.1.1). According to measurements of palaeomagnetism, the magnetic North Pole in the Cambrium was in the Pacific, not far from

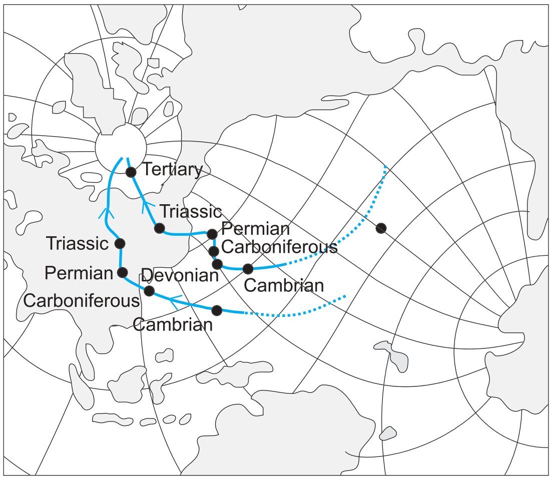

Fig. 4.1.1. Changes in the position of the magnetic North Pole during geological time (determined from palaeomagnetic measurements of North American (upper curve) and British (lower curve) rocks. (Kreeb 1983)

the Japanese island group, but in the Trias it was in north-east Asia.

- formation of continents arising from the **permanent changes in position of parts of the earth's crust** (Fig. 4.1.2). Despite controversy (plate tectonics) the theory of continental shift formulated by Wegener is valid and confirmed in its basic features.
- **solar effects** (different radiation conditions) arising from the composition of the atmosphere, and from the changing distances between earth and sun.

These events are linked to two influences directly affecting plants and their evolution. Firstly, climatic conditions have changed drastically, and secondly the possibility for expansion of plants by the opening or closing of land bridges or by the rise of mountain barriers was limited or enhanced. In this context events related to catastrophic **asteroid impacts** which greatly reduced biodiversity at the end of the Permian (Barbault and Sastrapradja 1995) and the Mesozoic should be mentioned.

In the recent past, the development of vegetation has been changed worldwide to a much greater extent and within a much shorter time span by the continuously growing **influence of human settlement and land use.** This shows clearly that palaeo-ecological links and historical development must be known to understand the present-day vegetation and its structure, composition and spatial distribution.

In the following, older periods of the history of life on earth, including selected aspects of the phylogeny and the coevolution of organisms (eophyticum, palaeophyticum, mesophyticum), will only be briefly outlined. The neophyticum will be discussed in more detail with two of its most important periods:

1. Late and postglacial development of vegetation. The links between climate and vegetation in the most recent geological past will be central.
2. Direct and indirect influence of humans on plant cover. These influences dominate partic-

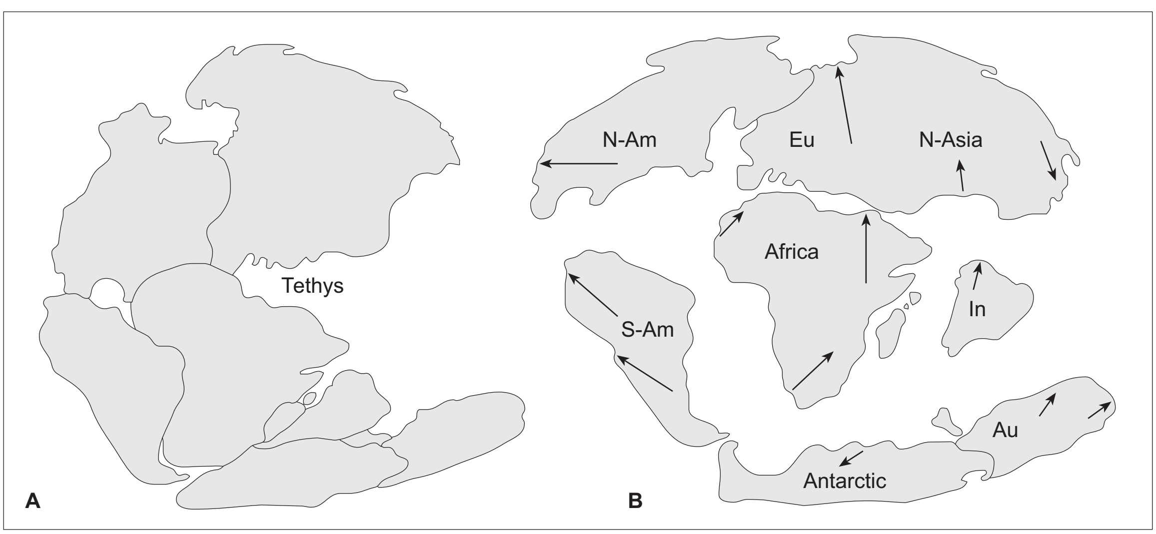

Fig. 4.1.2. Stages in development of the present distribution of the continents. A Joined landmass of Pangaea in the Triassic. B Distribution of continents at the end of the Cretaceous. (After Bick 1993)

Table 4.1.1. The putative evolution of life forms and ecosystems during the history of the earth. (After Kreeb 1983)

	Time in millions of years	Geological formation	Plant	Animal	Ecosystem type
Neophyticum (Angiosperm time)	0	Present	Agricultural techniques	*Homo faber*	Anthropogenic ecosystem disruption
	0.005	Holocene	Cultivated plants	Domestication of animals	Anthropogenic changes in ecosystems
	0.5	Pleistocene		*Homo sapiens*	All land ecosystems, deserts, halophytic communities, cold areas
	30	Tertiary	Deciduous trees	Freshwater fish, humanisation	
	95	Cretaceous	Angiosperms		
Mesophyticum (Gymnosperm time)	150	Jurassic	Pine trees, first flowering and seed plants	Early birds	Plant adaptation to different climate zones
	200	Triassic		Dinosaurs, early mammals	
Palaeophyticum (Pteridophyte time)	230	Permian			Species diversity decreases slightly
	280	Carboniferous	First tree-like ferns: Lycopods Calamites Horsetails Ferns	Reptiles and dinosaurs	Swamp forests (dry land not colonised)
	340	Devonian		Lung fish, amphibians, insects	First highly developed land ecosystems in moist places
	450	Silurian	First land plants: early ferns	First vertebrates	Simple ecosystems without consumers on land near coasts
Eophyticum (algal time)	500	Cambrian	Algae	All animal types except vertebrates	Higher developed aquatic ecosystems
	2000	Algoncium	Photosynthesis, respiration using oxygen		(Oxygen atmosphere) simple aquatic ecosystems
	3000	Archaean	First chemosynthetically active organisms		(Anaerobic aquatic ecosystems?) thermophilic organisms
	4000	Early ocean/early atmosphere	Start of biological evolution: first cells		(Oxygen-free environment) (Salt-free ocean?)

ularly in old, cultural landscapes developed by man and in regions of intensive agriculture and forestry.

The main focus of the following subchapters is Europe. More recent developments in other continents will be mentioned briefly. Problems of global change will be discussed comprehensively in Chapter 5.

4.1.1 History of Vegetation to the End of the Tertiary

In the **Precambrium** two large separate landmasses (first continents) had formed, each near the poles: in the northern hemisphere **Laurasia,** in the southern hemisphere **Gondwana** (Table 4.1.1). These two landmasses merged over time forming one large landmass, the **Pangaea,**

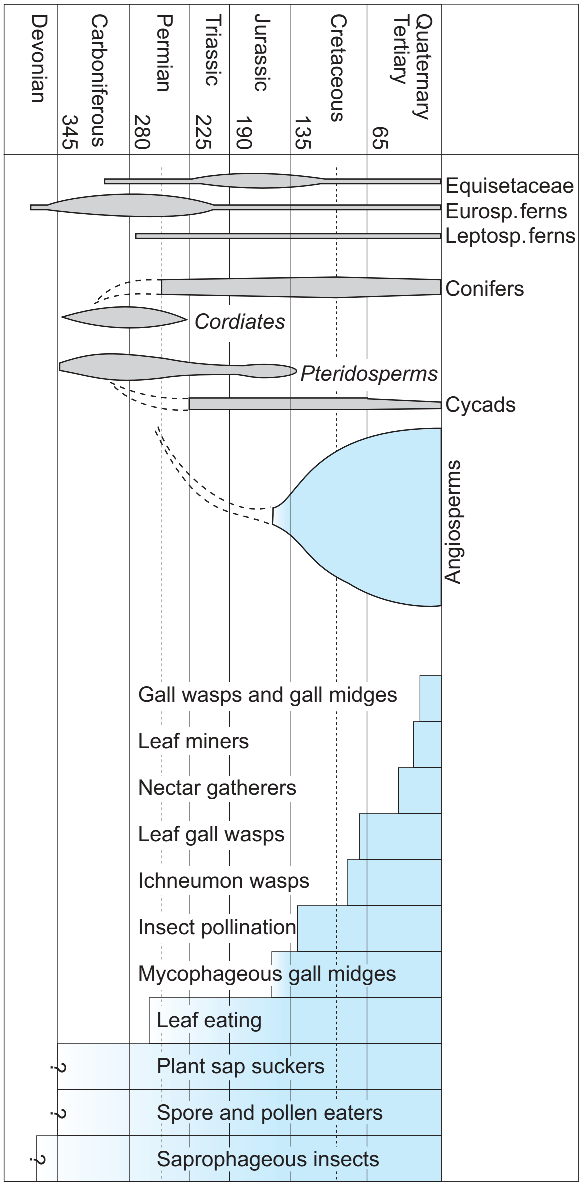

Fig. 4.1.3. Age and development of important groups of vascular plants, and of phyto- and entomophageous insects, as well as evidence of pollination and herbivory. (After Zwölfer 1978)

which remained until the Palaeozoic (about 220 million years ago; see Fig. 4.1.1) with changing positions towards poles and equator.

Traces of life and the first single-cell prokaryotes (bacteria, cyanobacteria) existed for about 3 billion years in an oxygen-poor atmosphere. Eukaryotes and multicellular forms could only develop with increasing oxygen content. This period, extending into the **Silurian** (about 400 million years ago), is called the **eophytic** (proterophytic) or the algal period.

The most important developmental step occurred with the settling of the land at the change from the eophytic to the **palaeophytic** during the Silurian period. The first land plants possessed cells with large vacuoles, already had stomata and had developed supporting tissues. These autotrophic producers lived together with fungi and bacteria as decomposers and formed the first bioscenoses.

Evolution of animal and plant species and communities progressed in parallel (see Table 4.1.1 and Fig. 4.1.3). Psilophytes (archetypal ferns) are regarded as precursors of the Pteridophyta (ferns and their allies), to which Filicinae (ferns proper), Equisitinae (horsetails) and Lycopodiniae (club mosses) belong. At that time Bryophyta (mosses) split off and remained at this developmental stage, but the other groups in the warm and humid climate of the **Carboniferous** formed luxurious forests with tree-like horsetails, club mosses and Cordiates, which later became extinct, on the swampy and boggy sites. Analyses of deposits of bituminous coal allow exact reconstruction of this very structured vegetation, including indications of symbiotic interactions (mycorrhiza) and the animal kingdom linked to it.

At the transition from the Carboniferous to the **Permian** climatic conditions became dryer. Many species did not survive and many land plants were unable to adapt their water relations. Thus the transition from the palaeophytic to the mesophytic is characterised by a decrease in species diversity. At the beginning of the **Triassic**, the Tethys Ocean separated off the eastern part of Pangaea (Fig. 4.1.2). During the **Jurassic**, the North Atlantic developed, and during the Cretaceous period the South Atlantic formed; in the early **Tertiary** the Antarctic and Australia seperated. The continents moved into their present position only in the **Pliocene**.

Up to the **Cretaceous** period the flora was very similar worldwide. The oceans forming between the drifting continents were no obstacles to the exchange of flora. The history of vegetation up to the **mesophytic** is also called the period of the gymnosperms. After the extinction of the larger club mosses and horsetails, gymnosperms gained space, particularly conifers and the Ginkgoaceae. The only present-day representative of the Ginkgoaceae is *Ginkgo biloba*, regarded as a “living fossil”. In the northern regions the first representatives of the Pinaceae and the genus *Juniperus* have been found. Cupressaceae, as well as the genus *Araucaria*, which today is limited to the tropics of the southern hemisphere, occurred worldwide.

The boundary between the Jurassic and Cretaceous periods also divides the mesophytic from the neophytic and the period of gymnosperms from that of the angiosperms. The first angiosperms occurred at the end of the Jurassic period. In a relatively short period, 25 million years of the Cretaceous period, flowering plants developed very rapidly and suppressed many of the gymnosperms which had dominated until then. Almost at a stroke all main angiosperm groups developed; all available sites which could be occupied were filled with adapted species and the intercontinental flora exchange was still not too difficult. A much stronger floristic separation occurred during the upper Cretaceous period. The so-called **plant kingdoms** developed and – corresponding to the slightly earlier division in the south – distinction is made between the three floristic realms in the southern hemisphere (**Antarctic, Australis and Capensis**), two tropical equatorial floristic realms (**Neotropics** and **Palaeotropics**) and only one northern hemisphere floristic realm (**Holoarctic**).

Zwölfer (1978) has given an overview of the geological occurrence of vascular plants as well as phytophageous and entomophageous insects, and thus of the development of communities. There is proof that pollen and dead plant material were eaten as early as the Devonian period and in the Permian leaves were consumed. In the Triassic period insect pollination of flowers occurred and there were entomophageous parasites (ichneumon wasps) and plant galls. From the Tertiary period onwards all present-day phytophages are represented: herbivores, nectar collectors, leaf miners, gall flies and gall gnats. Figure 4.1.3 shows that development of phytophageous and entomophageous forms is geologically fairly recent and occurred at the same time as the development of angiosperms.

Mutual adaptations of floristic and faunistic partners is a consequence of the **selection pressure** linked to this development. Plants developed thorns, spines or chemical defence substances, animals responded with adaptive changes to their mouth parts or resistance against plant toxins. Some flowering plants were, however, particularly successful as they were able to protect themselves against herbivory; e.g. gentians (defence by indoalkaloids) or deadly nightshades (defence by tropanalkaloids). During this evolution, some insects used secondary plant metabolites for their own defence, e.g. against entomophagous enemies.

The most important groups of flowering plants were present at the beginning of the Tertiary period and, therefore, the period of the history of vegetation from then to the present day is called the **neophytic** or angiosperm period. Amongst the flowering plants, specialists adjusted to stress environments such as deserts and saline soils developed. Along with the formation of mountain ranges, in the northern hemisphere, including the central Asiatic and European Mediterranean mountains, young mountain floras developed (**oreophytes**, closely related to flora in plains). Often individual altitudinal steps are characterised by vicarious species and genera.

Holoartic flora has been found in Palaeozoic to Eocene lignite deposits in Spitzbergen, where not only remains of plants (e.g. *Acer*, *Betula*, *Fagus*, *Quercus*, *Salix*, *Tilia*, *Pinus* and *Picea*) growing today in central Europe under conditions of a temperate climate were found, but also those which now grow only in humid, subtropical conditions (e.g. *Taxodium*, *Magnolia*, *Liriodendron*), as well as species which survived in Ice Age refuges in North America and east Asia. Comparable plants (e.g. *Aesculus*, *Castanea*, *Plantanus*, *Vitis*) found in Greenland represent the so-called **arcto-tertiary flora**, the basis of the Holoarctic flora.

From the Eocene flora from southern England and the "flora from the Geiseltal" near Merseburg, Germany, plant lists were compiled containing families of plants (e.g. species of Annonaceae, Pandanaceae, Sterculiaceae) which now occur in seasonally moist tropical regions. At that time the vegetation in Europe was similar to that in mountain regions of Southeast Asia. Europe only took its current position during the Tertiary, evidenced by fossiles from the early Tertiary (Miocene and Pliocene).

In plant remains of **Pliocene** in central Europe, tropical species could no longer be found, but representatives of present-day genera (*Fagus*, *Quercus*, *Salix*, *Fraxinus*, *Populus*, *Pinus*), and also species of genera which are at present extinct in this region (*Liriodendron*, *Sequoia*). Comparable fossiles from north-east Asia and North America indicate **worldwide progressive cooling.** In Europe, climate and vegetation zones shifted to the south. The west-east extension of the Alps and the Mediterranean made it difficult