[IMAGE]

Temperate nemoral deciduous forest with beech, oaks and hornbeam (Zonobiome VI) in the Eifel, Germany (photo: E. Fischer)

[IMAGE]

The New Zealand Edelweiss (*Leucogenes leontopodium*) in the alpine elevational zone of the New Zealand Alps (Orobiom V) between rocks densely covered with lichens (photo: Breckle).

II Special part

Part I - ZB VI: Zonobiome of winter bare deciduous forests or temperate nemoral climate

1 Leaf shedding as an adaptation to the winter cold

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[IMAGE]

Old beech trees near Lemgo (Teutoburg Forest) in a nemoral mixed oak forest (zonobiome VI) with tree fungi on the left trunk in winter; the tree roots are partly exposed by soil erosion over the decades (photo: Breckle)

1 **Leaf shedding as an adaptation to the winter cold**

A temperate climate zone, zonobiome VI, with a distinct but not too long cold season (◘ Fig. I-1) is clearly developed only in the northern hemisphere. It is absent from the southern hemisphere except for certain mountainous areas of the southernmost Andes and New Zealand. We had already become acquainted with facultatively deciduous tree species in the tropics, whose leaves fall when the water balance is disturbed during a prolonged drought, thus reducing the water losses of the trees.

The triggering factor that causes yellowing of the foliage in autumn before the first frosts is usually not known more precisely. It is probably partly the shortening of the day length. Strikingly, the foliage discoloration of the various tree species takes place in a relatively short period of time. According to the phenological calendar in the twentieth century, yellowing in Central Europe occurs between October 10 and 20, with no sharp difference between places in the west and in the east, nor between low and high mountainous areas. Trees near street lamps remain green longer. In recent years one observes an extension of the vegetation period in Central Europe from the 20th to the 30th of October.

The evergreen foliage is neither resistant to cold nor to frost-dryness, i.e. prolonged temperatures below 0 °C. In Central Europe, the evergreen cherry laurel (Prunus laurocerasus) always freezes back in gardens and parks during severe frost (► Fig. H-10 c,f). Several subspecies of these have perhaps also become widely established in central European front gardens, forest edges, etc. in the course of Climate Change, which is now noticeable after all.

Even with moderate frost, the leaves show CO2 releasein the light, which means that respiration continues, but photosynthesis is blocked. Ilex aquifolium (holly) has an Atlantic distribution. Hedera helix (ivy) is a sub-Atlantic evergreen species that avoids eastern continental areas with cold winters. The same is true of the broom species Ulex and Sarothamnus. The evergreen alpine roses (Rhododendron) and the cranberry (Vaccinium vitis-idaea) can only withstand the winter cold in Central Europe under snow protection.

The shedding of the thin, deciduous leaves in winter and the protection of the buds from water loss mean a saving of substance compared to the freezing of thick evergreen leaves. The prerequisite, however, is that the newly formed leaves in spring have a sufficiently long and warm summer period of at least four months to ensure the growth and maturation of the lignifying axial organs and the accumulation of substance reserves for fruiting and for budding in the following year. But even in the leafless state, the branches lose water in winter, and to varying degrees in the different hardwood species. The Central European beech therefore avoids the zone of cold Eastern European winters. The oak, on the other hand, even reaches the Urals. In extremely continental Siberia, deciduous trees are absent except for the small-leaved tree species birch (Betula) and trembling poplar (Populus tremula) as well as mountain ash (Sorbus aucuparia) with its small leaflets.

◘ **Fig. I-1** Climate diagrams from the sub-Mediterranean zone (without cool winters: Valence), from the warm and humid deciduous forest zone (Lugano), and from the Central European beech forest zone (Luxembourg).

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| Box I-1 Forms of adaptation of the ZB of deciduous forests  |
| In ZB VI, the zonobiome of temperate deciduous forests, leaf drop is an adaptation to a cold season. However, it is not facultative but obligate, so it occurs even if tree plants are protected from the winter cold in a greenhouse. |

If the summers are too short and too cool, the evergreen conifers take the place of the deciduous trees. Their xeromorphic needles acquire a higher resistance to cold in winter and are ready to produce again when the warm weather arrives in spring. This makes better use of the short growing season. While deciduous trees require a growing season with daily averages above 10 °C of at least 120 days, conifers can manage with as little as 30 days. However, the resistance of the individual species also varies. The yew (Taxus baccata) does not go further east in Europe than the ivy. Pinus sylvestris (pine) and Picea abies (spruce) are very resistant. Abies sibirica and Pinus sibirica (P. cembra) hold out in Siberia, but farthest into the continental Arctic (to 72° 40' N) advances the deciduous conifer, the larch (Larix dahurica), which has a very high productive power in the short summer. We thus see that, depending on the external conditions and the ecophysiological properties of the species, those with evergreen assimilation organs soon outperform those with short-lived deciduous ones in competition and achieve dominance (► compare ZB II, 2).

2 **Importance of winter cold for species of the nemoral zone**

In Zonobiome VI, as we have seen, winter frost, even if usually brief, plays an important role in species adaptation. The damage that occurs in cold winters can have two causes:

1. These are direct cold damages, which are related to the freezing of water in the tissues; they are then called frost damages.
2. There is a drying out of the above-ground organs, which have a certain transpiration even at low temperatures and are not able to cover the water losses from the frozen soil due to blockage of the conductive vessels by ice. In this case, therefore, we are dealing with frost drought or frost desiccation.

Plants have no protection against the effects of low temperatures. Their temperature adapts to the prevailing air temperature. The only adaptation to prevent the damage caused by low temperatures is to become hardened, the hardening process. If one tests the cold resistance of plant parts in summer by exposing them to various temperatures below 0 °C in the freezer, for example for two hours, it is found that even low freezing temperatures are sufficient to cause irreversible damage. The same plant parts, on the other hand, can withstand exposure to much lower temperatures in winter without damage because they are hardened off. Hardening is a physiological process that takes place in autumn when the first cold nights begin. It is replaced in the warm spring by the opposite process of “softening”, dehardening.

Hardening is associated with certain physicochemical changes in the protoplasm. The stability of the membranes (for example due to additional sulphur bridges -S-S-) increases, as does the viscosity of the plasma. It can be recognised by the fact that during plasmolysis (shrinkage of the protoplast of a plant cell) a concave plasmolysis occurs instead of a convex one. This change is accompanied by a sudden increase in cell sap concentration due to an increase in sugar concentration and other osmotica. In the hardened state, the protoplasm is largely inactivated. Cold resistance can increase in overwintering buds of our deciduous trees from -5 °C in autumn to over -25 °C, even -35 °C in January to February. The increase in cold resistance is greater in cold winters than in mild ones, and in related species of a genus the greater the further a species advances into the continental region.

Hardening is a very complicated process that occurs in several stages. The first, which leads to a certain state of dormancy, is initiated in autumn by the shorter length of the day. Further hardening takes place when the temperature drops to a few degrees above 0 °C. The strongest hardening off is observed in species that have already been exposed to very low temperatures, i.e. after the first heavy frosts have occurred. If hardened plant parts are suddenly cooled extremely strongly so that vitrification of the protoplasm occurs (without ice crystal formation), freezing in liquid nitrogen (at -190 °C), even at -238 °C, is possible. However, it is necessary to carry out the heating slowly in several steps until thawing, so that subsequently no plasma-damaging ice crystal formation occurs. Then the hardy species of the cold climate zones remain alive. In eastern Siberia around the cold pole, forest vegetation is normally exposed to winter temperatures of -60 °C or lower. Tropical species and even those of ZB IV or ZB V cannot be hardened off.

Hardening generally prevents frost damage to native trees even in severe winters, whereas planted exotics from warmer home areas without hardening- ability often suffer such damage. Frost damage, on the other hand, often occurs when early frosts set in before plants have been hardened, or a late frost sets in after dehardening has already occurred. It is especially common to see late frost damage to young foliage that has sprouted and is very sensitive to frosts. Cambium damage due to late frost also occurs when the trees are already "in sap", i.e. the plasma is already in an active state.

The eastern limit of the beech area is probably due to frequent late frost damage, which reduces competitiveness. For the herbs of the forest, an increase in cold resistance can also be observed in winter due to hardening. However, they are not exposed to such low temperatures under a litter and snow cover. In line with this, cold resistance (for example of Hepatica triloba) increases even in the evergreen leaves only down to -15 °C, in the better protected flower buds down to -10 °C and in the rhizomes only down to -7.5 °C.

It is more difficult to detect damage caused by frost-drought. The shedding of the strongly transpiring leaves, the protection of the buds by hard bud scales, and of the twigs by layers of cork, prevent greater losses of water in deciduous trees in winter. Nevertheless, some transpiration of the leafless branches in winter can be detected; it is higher than in the evergreen conifers, and higher in the hardwood species with a southern distribution than in those occurring farther north. These transpiration losses become critical when the intensity of insolation increases in spring and the air temperature rises, but the ground is still frozen solid. Buds and twigs may then dry out. Particularly sensitive in this respect are evergreen species, such as the holly (Ilex) or rod shrubs such as the broom species.

In general, frost damage occurs during the coldest part of the year, while frost drought damage occurs in the transitional period to spring and on warm southern slopes (in the northern hemisphere). They should not be confused with late frost damage.

3 **Distribution of the zonobiome VI**

The climate of ZB VI, with a warm growing season of four to six months with sufficient rainfall and a winter season of three to four months that is not too long or extremely cold, is particularly suitable for the deciduous tree species of the temperate climate zone (Ellenberg & Leuschner 2010). These trees avoid the extreme maritime, as well as the extreme continental areas. We speak of the nemoral zone. Such a climate with a precipitation maximum in summer is found in the Northern Hemisphere in eastern N America and in E Asia between the warm temperate and the cold or arid temperate zones. In Western and Central Europe, it is the region north of the Mediterranean zone where, under the influence of the Gulf Stream, winter rains are replaced by evenly distributed precipitation or those with a summer maximum, and the cold season is relatively short.

The Mediterranean winter rainfall area with sclerophyllous vegetation extends south of it very far from west to east and passes northwards into very different vegetation zones. In the very maritime area in SW and S Spain (for example near Gibraltar) one finds, as already mentioned, elements of the evergreen warm temperate laurel forests. In Portugal, however, this vegetation merges into the Atlantic heaths, which extend into the coastal area as far as Scandinavia (► Fig. I-2). They are replaced by birch forests in the far north. True laurel forests are found only on the humid windward side of the Canary Islands (e.g., Tenerife) as fog forests (► Fig. G-48) or in the very similar ZE IV/V in northern Anatolia (Colchis). A sub-Mediterranean zone is interposed between the Mediterranean and nemoral zones. In it, winter rains still prevail, but summer drought is no longer pronounced and mild frosts occur regularly in all winter months (► Fig. I-1, Valence).

Northeast of the sub-Mediterranean zone in SE Europe is the steppe zone, which is replaced further N by forests of various types. Finally, in the Near East, the Mediterranean sclerophyllous zone gradually leads to the Mediterranean steppes and semi-deserts.

4 **Atlantic heaths**

The Atlantic heaths (► Fig. I-1, ◘ Fig. I-2) are almost always degradation stages of deciduous forests. The destruction of woodland in this area dates back to prehistoric times; it is now so complete that heathland was long thought to be zonal vegetation. The historical development can be easily traced in pollen diagrams (◘ Fig. I-3). Along with the clearing, the bogging initially increased, and very soon Calluna appeared over large areas, in parallel with charcoal remnants.

The soils in this region are usually extremely poor and acid, and it was supposed that, in consequence of the humid climate, they were naturally exhausted, and could support only a poor heath vegetation. But the same is true in this case as we have stated with regard to the tropical rain-forest, which is also very humid. As long as the natural forest vegetation is not touched, there is no leaching of nutrients from the biogeocoen; the nutrient stock remains for the most part stored in the above-ground phytomass. However, once the woodland is cleared and burnt, most of the now mineralised nutrients are lost and only the poor soil remains. If the heath vegetation is subsequently exploited or repeatedly burned, the reforestation, already difficult here, cannot take place. One knows of uninhabited very extreme oceanic climates with similar temperature conditions and even double to four times the amount of precipitation on the Pacific coast of NW North America, in the SW of S America, on Tasmania and on New Zealand, where the virgin forests grow in great luxuriance and show no signs of degradation by a leaching of the nutrients.

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| Box I-2 Nearly all plants of the sub-Mediterranean zone are not sclerophyllous species  |
| In the sub-Mediterranean zone, the evergreen woody species are absent except for Buxus. Tree species such as downy oak (Quercus pubescens), manna ash (Fraxinus ornus), French maple (Acer monspessulanum), hop hornbeam (Ostrya carpinifolia) or the frequently cultivated chestnut (Castanea sativa) are all deciduous, which is why this zone is classified as a temperate deciduous forest zone and not as a Mediterranean zone. It can be called ZE IV/VI. |

Fig. I-2 Distribution of Atlantic heaths in W Europe (modified after Hüppe 1993).

◘ Fig. I-3 Atlantic heaths in the fog coasts of NW Norway near Bergen (photo: D. Killmann).

How the original forests in W Europe were composed is not easy to say. Oaks (Quercus petraea and Qu. robur) probably played the main role, in the N also birches (Betula); in addition, Ilex aquifolium was an evergreen species. The heath (Calluna) was formerly present as an undergrowth in these forests and formed independent communities only in sparse places on shallow or peaty soils. After the destruction of the forests, it then took possession of the entire area (◘ Fig. I-4). The regeneration of forest formations after the cessation of grazing and ploughing (in which the upper 10 cm of the raw humus layer is cut off in square pieces, used as litter in the stable and then brought to the field as stable manure for fertilization) proceeds differently depending on the land endowment. This has been pointed out by Leuschner (1993) (◘ Fig. I-5) and he has reconstructed the corresponding regeneration stages with those originally decisive before heath formation (◘ Fig. I-6). Also indicated are the factors responsible for the regeneration of woodland on heathland and, conversely, for the maintenance of heathland.

In the S part of this coastal zone (► Fig. I-2), broom species (Ulex, Sarothamnus, and Genista species) play the main role, along with various Erica species. In the central part, the broom species recede more; Ulex europaeus, Sarothamnus scoparius and Genista anglica remain as the most important representatives; in return, the Ericaceae become more prominent in terms of quantity, besides Erica cinerea and E. tetralix especially the heather (Calluna vulgaris). In the N, Empetrum, Vaccinium, Phyllodoce and Cassiope dominate.

Calluna heaths account for  to of the total area in Scotland (► Fig. I-3); the soil type is iron podsole with a hard cemented B horizon often formed as a hardpan (“Ortstein”, a subsoil cemented horizon = eluviated soil). The heath is periodically burnt. Calluna vulgaris is the absolutely dominant species. It is a dwarf shrub, growing to about 50 cm high, forming a dense web of roots in the upper 10 cm of the soil, with individual roots going down 75 to 80 cm to the cementation horizon. Calluna's very small leaves are densely attached to short shoots, a large proportion of which are shed in autumn, reducing the risk of frost-dryness during cold spells. The annual litter production in a dense stand is 421 kg per hectare.

If burning occurs every 30 years, three phases (each 10-year) of stock development can be distinguished:

1. the **build-up phase** (reconstructive pahse) of the dwarf shrub layer after the fire; some of the nutrients are fixed in the litter,
2. the **ripening phase** (phase of maturity) with increasing litter production but a decreasing increase in phytomass,
3. the **degeneration phase**, in which litter production remains constant and litter decomposition increases until a state of equilibrium is reached. After 35 years, the standing phytomass is 24,000 kg/ha and the litter quantity is 17,000 kg/ha.

**Fig. I-4** Development of heathland in the postglacial period as shown by a simplified pollen diagram from the raised bog (modified after Hüppe 1993).

◘ **Fig. I-5** Hypothetical scheme of present-day regeneration stages and forest dynamics of the Lüneburg Heath on nutrient-poor sands under different human interventions (after Leuschner 1993). Processes inhibited by high game densities are drawn with dashed lines, those with fragmented forest cover are dotted dashed lines (modified after Leuschner 1993).

◘ **Fig. I-6** Hypothetical scheme of regeneration stages and forest dynamics of the Lüneburg Heath under natural conditions before forest destruction (ca. 800 BC) (modified after Leuschner 1993).

Most often, people do not wait for the degeneration phase, but burn down the heath already after 8-15 years. In this humid area the fires are caused only by man. Natural fires caused by lightning hardly ever occurred in the original forests, so without human intervention there is no degradation of the forest. From heath to moor there are all transitions. We list four stages of increasing waterlogging, in each of which the species are named according to the decreasing abundance:

**1.** *Erica cinerea - Calluna vulgaris - Deschampsia flexuosa - Vaccinium myrtillus*,

**2.** *Calluna vulgaris - Erica tetralix - Juncus squarrosus*,

**3.** *Erica tetralix - Molinia coerulea - Nardus stricta - Calluna vulgaris - Narthecium ossifragum,*

**4.** *Erica tetralix - Trichophorum caespitosum - Eriophorum vaginatum - Myrica gale - Carex echinata*.

In Scotland, heathland is used for hunting and as extensive sheep grazing, with 1.2 to 2.8 ha of grazing area calculated for one sheep. Due to grazing and the anthropogenic nitrogen input coming from the atmosphere today, the growth of the grasses is more promoted. But even in earlier times, there was a cycle in the heathlands between a *Calluna* and an *Avenella* phase(◘ Fig. I-7).

◘ **Fig. I-7** Possible cyclic change in dominance between Calluna and Avenella on Dutch heathland (modified after Kaagman & Fanta 1993).

In the Lüneburg Heath (◘ Fig. I-8a), which is also of purely anthropogenic origin, arable farming was formerly practised on sandy podsol soils (◘ Fig. I-8b) often with buckwheat (◘ Fig. I-9); in the process, the heath was ploughed off for peat. This “plaggenhieb” prevented the reforestation. Today, after the heath is no longer used, it becomes wooded through the growth of birch and pine seeds, or it is systematically reforested.

In the extremely maritime area, besides the heath, blanket bogs play a major role. The climate is very balanced; on Ireland, for example, the temperature in January is 3.5 to 3.7 °C, whereas in July it is 14 to 16 °C. Frost may occur, but snow is only from 3 to 10 days a year. Precipitation ranges from 350 to 1,000 mm per year and is very regular throughout the year. It also varies from year to year by no more than 25%. With the heavy cloud cover, the sunshine duration is only 31% of the maximum possible. Under these circumstances, the risk of swamp formation (paludifikation) after forest destruction is very high. The forest releases more water than low herbaceous vegetation due to the transpiration of the tree layer. Therefore, after clear-cutting in the humid area, one can notice a rise in the water table, which favours the growth of *Sphagnum* mosses. In addition to Sphagnum species, Racomitrium lanuginosum plays a major role. In areas with more than 235 rainy days, the bogs can cover the entire area even in an undulating terrain. Such blanket bogs are found in W Ireland, Wales and Scotland, where the largest bog covers 2,500 km2.

In areas farther away from the Atlantic coast, the heath is not a danger because all heath species have a low resistance to frost-drought, although the leaves of Calluna are very small and have a thick cuticle; the stomata lie in a groove lined with hairs. Calluna is distinguished from the true xeromorphic leaves by the very loose structure of the mesophyll. Transpiration may be relatively brisk in summer when water supply is good, and in shady locations it equals that of wood sorrel (Oxalis acetosella) when calculated on fresh weight; it may be greatly reduced when water is scarce. But these characteristics are not sufficient to prevent water loss during prolonged frosts. Even in the mild winters of the Upper Rhine Valley, Calluna very often dries up without snow protection. Even in the north it is only found where there is a snow cover every year.

◘ **Fig. I-8** Landscape of the Lüneburg Heath in Lower Saxony (**a**) on the nutrient-poor sandy podsol soils (**b**) (photos: Breckle).

◘ Fig. I-9 Buckwheat (Fagopyrum esculentum, Polygonaceae) was once one of the most important foods in Central Europe. Today, it has been largely replaced by wheat, but above all by potatoes (photo a: Breckle; b: http://bit.do/6nfR).

Heath occurs inland on the western slopes of the low mountain ranges with oceanic climate, also island-like (Ardennes, Hohes Venn, Eifel, Vosges and even in the Black Forest at the Feldberg). It also extends as a narrow strip to the Baltic Sea.

5 **The deciduous forest as an ecosystem**

5.1 **General**

The deciduous forest is a multi-layered plant community. It often consists of one or two tree layers, a shrub and a herb layer. In the latter, one finds hemicryptophytes, but also many geophytes that develop only in spring. For therophytes, i.e. annual plants, the development conditions are too unfavourable in the poor light conditions on the forest floor. A missing ground layer of mosses would be covered by the falling leaves. Mosses therefore only grow on boulders, tree stumps etc. that protrude above the ground surface. (◘ Fig. I-10) These plant groups each form synusia.

◘ **Fig. I-10** Primeval forest of Bialowiez (Poland). The mosses grow on tree bark and hardly on the forest floor. In the mixed forest area, numerous ash, hornbeam and oak trees grow densely high (photo: E. Fischer).

In the European deciduous forest area, we do not know of any primeval forest stands on euclimatopes, on flat areas with normal soils (perhaps apart from the area near Bialowieca in eastern Poland), where, however, beech already no longer occurs (► Fig. I-10, ◘ Fig. I-11, ◘ Fig. I-12).

Fig. I-11 Primeval forest of Bialowiez (Poland). An open forest area with very old oaks (Quercus robur) and younger hornbeams (Carpinus betulus). In the background a forest gap with numerous young trees (photo: Breckle).

◘ Fig. I-12 Primeval forest of Bialowiez (Poland). In winter, the bison "kept semi-wild" there are together in large herds. In gathering places, the shrub and herb layer of the tall, old oak forest is considerably degraded (photo: Breckle).

The structure of forests in Central Europe is entirely determined by the type of management. For forestry, the wood species are of importance; the herb layer is only indirectly influenced by it. In the case of forest grazing, on the other hand, it is precisely the herb layer that is exposed to selective cattle browsing, from which the young tree growth also suffers (► Fig. I-12). Rationally managed high forests come close to virgin forests, but differ essentially in the low number of species in the tree layer, their uniformity, the absence of dead wood rotting on the ground, and the homogeneous structure. Primeval forests, on the other hand, usually show a mosaic-like structure.

Managed beech forests are pure stands with only a herb layer. Oak forests are often mixed stands of different hardwood species and have a shrub layer (► Fig. I-10, ► Fig. I-11). Of the various deciduous forest biogeocoenoses, a western mixed forest in Belgium, beech forests and spruce forests in the Solling, and oak forests in the east on the forest-steppe border were studied in more detail, among others, during the IBC-programm (see below).

In deciduous forests, the canopy is the active layer in which most of the direct solar radiation (including diffuse radiation) is converted into heat. Only a small fraction of the daylight penetrates the forest stand.

In ZB VI of Central Europe, beech is the dominant forest tree (◘ Fig. I-13). In ZB VI of East Asia and North America, beech species also occur, but there the number of tree species is several times higher, (again due to the glacial refugial history), so that the number of forest types is much greater (Peters 1997). There, Fagus species often occur only as relicts in very small areas (► Fig. I-7). Fagus sylvatica has the largest range of all twelve beech species, extending from Scandinavia to N Spain and from England to Turkey (◘ Fig. I-14), forming a number of different beech forests.

◘ Fig. I-13 The autumn aspect of a deciduous forest of the Middle Moselle (Germany), in which Fagus is the dominant element and is distinguished by yellow-red foliage colouration (photo: Rafiqpoor).

Fig. I-14 The ranges of beech forests in Europe (modified after Ozenda 1994).

In addition to beech forests, several other forest types occur in Central Europe, although they are often very strongly influenced by humans. The very soil-acidic oak-birch forests (*Quercus-Betula* forests) or the continental oak-hornbeam forests (*Quercus-Carpinus* forests) (◘ Fig. I-15) can be cited as examples. However, conifers in particular have been very strongly promoted by forestry in the last century (◘ Fig. I-16), so that today pine forests (◘ Fig. I-17), into which, however, beech and oak are gradually migrating again, are the rule on poor sandy soils.

**◘ Fig. I-15** Tall oak-hornbeam forest on basic soils of shell limestone in the Wölmisse National Park in the Thuringian Forest near Jena (photo: Rafiqpoor).

**◘ Fig. I-16** Forest management in a Picea abies forest near Ulm, southern Germany (photo: Barthlott).

**◘ Fig. I-17** Open pine forest with invading birch and oak in the Senne, south of Bielefeld, in the Augustdorf dune field with late glacial fossil dunes. The seedlings initially have a hard time against the competition of the dense Avenella flexuosa carpet (photo: Breckle).

While in the years after 1980 considerable dieback of spruce forests was observed in particular, in the Ore Mountains and the Sudetes entire slopes also died earlier, in the Harz Mountains later (◘ Fig. I-18), significant damage to deciduous trees has also been detected, especially since 1990. However, the causes of this forest damage are very complex and can certainly not be attributed to air pollution and altered inputs of pollutants (SO2, O3) or excessive nitrogen loads (NOx) alone. The additional acceleration of the leaching of nutrients from the leaves and the upper soil layers (cryptopodsolisation) also amplified the effects, as did soil fatigue caused by silviculturally one-sided crops (monocultures). One can only speculate about the effects of Climate change (Breckle 2005).

Recently, forest dieback in Germany became a new dimension. In 2020, about 80.4 million m3 of wood were felled in German forests. This means that logging reached a new record: never before since German reunification has more wood been felled in Germany than in 2020. As the Federal Statistical Office (Destatis) also reports, logging rose again by 16.8% compared to the previous high of 68.9 million m3 in 2019. This development is due to increased forest damage as a result of insect infestation, which is also favored by drought and heat of preceding years: For example, damaged wood felling due to insect damage accounted for more than half (53.8%) of the total logging in 2020. The increased amount of damaged wood in coniferous wood caused by insects underscores a problematic development that has often been discussed in recent years: the bark beetle spreads rapidly in local forests and primarily attacks spruce. Common bark breeders in Central Europe and their preferred tree species are:

Letterpress (*Ips typographus*) (spruce)

Engraver (*Pityogenes chalcographus*) (spruce)

Large and Small Forest Gardener (*Tomicus piniperda, T. minor*) (Pine)

Oak bark beetle (*Scolytus intricatus*) (oak)

Frequent wood breeders (xylomycetophagous, or ambrosia beetles) in Central Europe and preferred tree species:

Striped timber bark beetle (*Trypodendron lineatum*) (on lying softwood)

Black timber bark beetle (*Xyleborus germanus*) (native to East Asia, introduced to North America and Central Europe. On a large number of deciduous and coniferous trees).

**Fig. I-18** Montane, almost dead spruce forest in the western Hochharz (highest forest damage class). In the background the Brocken (photo: Breckle).

5.2 **The beech forest in the Solling as an ecosystem**

Within the framework of the IBP (International Biological Programme and subsequently), three beech forest and three spruce forest plots with differently fertilised meadows and one arable field were studied and compared in great detail in the Solling from 1966 to 1986. Characteristic vegetation types were also studied in other countries over many years. As an example of the main structures and processes in a nemoral forest of ZB VI, we choose results from the Solling and occasionally give comparative figures from studies of a continental oak forest on the Worskla, the left tributary of the middle Dnieper (IBP project of the then Leningrad University). The mixed oak forest is a 1,000 ha forest area for planed experiments, of which 160 ha is a protected primeval forest-like 300-year-old stand.

The beech forest in the Solling (Ellenberg et al. 1986) is a soil acidic beech forest (Luzulo-Fagetum) at about 500 m asl. The soils are predominantly slightly podsolic brown earths, formed from loess layers overlying the red sandstone.

The climate in the Solling beech forest is characterised by a high degree of oceanity, although there are significant differences between the individual years. The mean precipitation (1967 to 1981, IBP-period) amounts to 1,045 mm per year, resp. 1,013 (1960-2018) which corresponds to the typical German rainy low mountain range climate (◘ Fig. I-19 a, b). However, the driest year 1976 brought only 686 mm, the wettest more than double, namely 1,647 (2007). To illustrate the long-term trend it is necessary to have long observation periods. From the Solling there is a sequence of data from 1960 until 2018 (Climatogram Fig. I-19 a, and Climate-diagramm Fig. I-19 b), which we take as an example to demonstrate the changes from year to year. Rather seldomly there is a month which is dry or even arid (indicated by red, Fig. I-19 a), more often there are months, which are hyperhumid with more than 100m rain per month.

Such long-term data enabling us also to see general trends. The increase of the mean annual temperature is considerable and reaches about 1.5 K from 1960 to 2018 (Fig. I-19 c). The trend with the mean annual precipitation is less clear, but it seems that it is also increasing from about 1070 mm to 1150 mm per year.

As indicated above, drier periods occur again and again, but they cannot be assigned to any particular season in Central Europe. Accordingly, days with relatively dense cloud cover and correspondingly low irradiation occur at all times of the year. Some typical diurnal variations of global radiation (◘ Fig. I-20) illustrate this. When the sky is overcast (► Fig. I-20, 3.7.1972), the global radiation can often hardly reach ⅒ of the radiation of a clear day (► Fig. I-20, 13.7.1972).

This then also acts as a limiting factor for the photosynthesis of the beech trees.

The weather conditions are predominantly determined by W and SW winds, as illustrated by the wind roses (◘ Fig. I-21). E winds occur occasionally during high-pressure weather in winter, N winds are practically non-existent.

5.3 **Ecophysiology of the tree layer**

A tree is not a favorable object for experimentation because of its size. Its shape depends very much on the stand. A free-standing tree has a dome-shaped to spherical crown, while this is very small in a dense stand. However, since the leaves are arranged in several layers, the outer ones are exposed to full daylight, while the inner ones develop in the shade. A distinction is therefore made between sun leaves and shade leaves, which are connected by transitions. The anatomical-morphological and ecophysiological characteristics are different for both.

**Fig. I-19** Climate diagram and climatograms (1960-2018) from the Solling, the number of days in the year with temperature averages above 10 °C is indicated in the middle (partly from Ellenberg et al. 1986, with courtesy from Markus Wagner, Nordwestdeutsche Forstliche Versuchsanstalt/Göttingen).

**Fig. I-20** Diurnal variations of insolation (global radiation) in early summer and summer 1972 for three clear and three cloudy days each (modified after Ellenberg et al. 1986)**.**

**Fig. I-21** Daily and hourly mean values of the percentage frequency of prevailing wind directions in the Solling (modified after Ellenberg et al. 1986)**.**

Sun leaves are smaller, thicker, have a denser venation and more stomata on the lower side of the leaf per square millimeter, that is, they are more xeromorphic than the large and thin shade leaves.

The structural differences are controlled by the less favourable water balance in the establishment of buds sprouting next spring as a result of the greater transpiration of the sun branches, indicated by the increased cell sap concentration; the latter is, for example, 1.6 MPa for sun leaves and 1.2 MPa for shade leaves in beech. Differences are also noticeable with respect to CO2 assimilation.In laboratory experiments, it was found that in the dark, shade leaves respire less intensively per square decimetre of surface area than sun leaves; for example, shade leaves of beech excrete only 0.2 mg of CO2 per dm2/h compared with 1.0 mg of sun leaves. Therefore, in spring, the light compensation point (where respiration = gross photosynthesis) of shade leaves is already at 350 lux, whereas that of sun leaves is at 1,000 lux. With increasing illumination, photosynthesis increases proportionally with light intensity until a maximum is reached (◘ Fig. I-22). In shade leaves and shade plants, this is already less than 20% of the maximum daylight, whereas in sun leaves it is only about 40%. Shade leaves thus make better use of low light intensities, whereas sun leaves make better use of higher light intensities.

In the case of the sun leaves, it strangely appears that they do not make sufficient use of the full daylight. But these figures only apply to leaves oriented perpendicular to the light, while the sun leaves at the crown of the tree are always quite steeply erect. This prevents them from overheating too much in the sun, i.e. suffering too much water loss, but at the same time allows more light to pass through the outer crown, which benefits the lower leaves. In addition, thus the morning (from the east) and evening (from the west) sunlight is better utilised.

**◘ Fig. I-22** Light saturation curve of photosynthesis (left: leaf area-related; right: weight-related) of some species of the beech forest in Solling (juv. = young growth) (from Ellenberg et al. 1986).

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| Box I-3 Sun and shade leaves |
| Sun leaves usually are oriented vertically, parallel to the incoming rays of light, whilst shade leaves often stand horizontal, perpendicular to the incoming rays.  |

The leaves standing in deep shade are oriented perpendicular to the incident light, allowing an average positive mass balance even with a LAI = 5 or more.

A detailed production analysis by direct measurements of CO2 assimilationof beech at the site was carried out by Schulze (1970). A single day measurements are shown in ◘ Fig. I-23. It could be deduced that the production of sun and shade leaves per dry weight is the same during the entire vegetation period because the shade leaves remain active longer in autumn (◘ Fig. I-24).

**Fig. I-23** Diurnal course of important microclimatic and ecophysiological parameters of sun and shade leaves of beech in the Solling on a fair-weather day (modified after Ellenberg et al. 1986)**.**

If the illumination falls permanently below a certain light minimum, the respiration of the leaf is no longer compensated by photosynthesis, substance losses occur, the leaf turns yellow and is shed. This light minimum, expressed in % of full daylight, varies from one tree species to the other. A distinction can be made between shade woods with a very dense crown and low light minimum (1.2% for beech) and light woods with a light crown and high light minimum [birch (Betula) and aspen (Populus tremula) 11%]. In between are maple (Acer) and oak (Quercus). This light minimum in the canopy need not coincide exactly with the light minimum that must be exceeded for tree seedlings to grow on the forest floor, but the values do go in parallel. Beech seedlings manage with little light, birch seedlings need at least 12 to 15% of daylight.

**◘ Fig. I-24** Annual patterns of diurnal balances of CO2 gas exchange ofbeech and spruce (modified after Ellenberg et al. 1986).

An oak forest reflects 17% of the incident radiation when it is leafy, and only about 11% when it is leafless, i.e. significantly less than meadows and crops (25%). Halfway up the stand or on the ground, only 1.2% and 0.6% of the daylight is measured in the fully leafy state in young stands, and about 20% and 2% in very old stands.

Light conditions are crucial for the competitiveness of tree species. In a clearing, the light woods can grow in a few years. Under their canopy, the shade woods germinate and only very slowly grow higher and higher. Their canopy is so dense that the lightwoods underneath do not gain any material and do not rejuvenate. In time, the most shade-tolerant species becomes dominant, if the other site conditions suit it.

In Central Europe this is the beech (Fagus sylvatica), it is the species of the zonal forests. Only on very poor soils or at high groundwater levels, or in the driest basin landscapes it is not competitive. In the W part of Eastern Europe, the climate is too continental for the beech, which there is replaced by the hornbeam (Carpinus betulus) as a shade wood species, and even further east by the oak (Quercus).

The mean daily temperature is 2 °C higher at the canopy in summer than at ground level, the mean daily maximum even up to 11 °C higher, while the mean daily minimum is about 2 to 3 °C lower. The mean humidity is 98% at ground level and decreases with increased height to 77%. The wind speed is low in the forest. Since the forest floor is protected from direct radiation, it remains noticeably cooler in the forest during the day than in open stands.

The leaf area index (**LAI**), i.e. the ratio of the total leaf area of the tree stand to the ground area it covers, is very important for forest productivity. It can only reach a certain maximum, because otherwise the lower shaded leaves would not show a positive mass balance. But this maximum does not only depend on the daylight intensity, but becomes smaller with insufficient water supply and with nutrient deficiency. In pure oak stands the LAI = 5 to 6 (higher in wet years), in fresh mixed stands it can exceed 8, including all wood species and shrubs.

Dry matter production (t · ha-1· a-1) of a 40-year-old beech stand in Denmark:

* Gross production of assimilating leaves = 23.5
* Respiratory losses (leaves 4.6; stems 4.5 and roots 0.9) = 10.0
* Annual production (leaves 2.7; stems 1.0; litter and roots 0.2) = 3.9
* Wood production (aboveground 8.0; belowground 1.6) = 9.6

Of the maximum 8 t/ha of stemwood, an average of 6 t/ha can be exploited for forestry, which corresponds to 11 m3.In the case of spruce, the timber yield is equally large in terms of weight, but volume-wise approx. 17 m3.

How the production figures change with the age of the beech stand is shown ◘ Fig. I-25.

The mass of dead wood going off is hardly less than the wood increment in the same period, which means that the net phytomass increment here is practically zero, as it must be in a virgin forest in the optimum phase.

The beech forest areas in the Solling also reach about 10 t·ha-1·a-1 annual production, of which about 3 t are leaves, the blossoms and fruits account for very varying shares from year to year (mast years). The production of twigs and branches comprises about 10% of the annual production, the production of roots about 10% of the aboveground production.

**Fig. I-25** Production curves of the beech forest (modified after Walter 1990)**.**

Primary production per year is reported as 8.9 t·ha-1, including herb layer 9.6 t·ha-1. The underground production was not determined.

In accordance with the semi-arid climate, primary production is somewhat lower than in western deciduous forests.

The leaf mass and leaf area formed each year increases rapidly in the first 20 years. However, once a dense canopy is reached, leaf mass and LAI remain almost constant. The canopy is only raised more and more above the ground by the height increase of the stems. The leaves with the falling branches form the litter and together with the dying roots the total litter.

Only the wood mass produced is stored, so that the standing phytomass of the forest increases constantly but ever more slowly until old age, and can exceed 200 t·ha-1 for 50-year-old stands and 400 t·ha-1 for 200-year-old stands.

For the oak forest the following mean wood increment was found depending on the age of the stand (in brackets): 3.8 t·ha-1 (13), 3.6 t·ha-1 (22), 4.3 t·ha-1 (42), 4.7 t·ha-1 (56), 0.4 t·ha-1 (135), 0.0 t·ha-1 (220). The increasing log diameter (DBH: diameter at breast height) means a corresponding increasing wood supply in the log. This relationship is shown in ◘ Fig. I-26.

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| Box I-4 Phytomass in a mixed *Quercus* forest |
| For phytomass of mixed oak forest in Russia, Goryschina (1974) gives the following values: Aboveground 306.7 t·ha-1 (leaves 3.7, twigs and branches 71.2 and stems 230.8); belowground 124.9 t·ha-1; total 431.6 t·ha-1; plus herb layer 0.7 t·ha-1. |

**Fig. I-26** The dependence of aboveground biomass (marked belowground with open squares) on stem diameter (DBH) in beech from different sites (modified after Ellenberg et al. 1986)**.**

The amount of litter also accumulates in the forest until an equilibrium is reached, i.e. as much of the litter is mineralised each year as is newly added. A part of the most important nutrient elements (N, P, K, Ca) is fixed in the litter. Thick layers of raw humus are therefore unfavourable. However, litter use is particularly harmful; it removes nutrients altogether, especially lime, which rapidly depletes and acidifies forest soils, reducing timber yields. Nitrogen compounds are mineralized during litter decomposition. Most of the nutrients are available to tree roots in the lower decomposing humus layer; this is therefore always very densely rooted. Soil life is of particular importance for the forest stand, in addition to the water supply. In contrast, the proportion of animal organisms above the soil is very small; even insect feeding normally accounts for only a few percent.

The litterfall itself occurs very periodically in the deciduous trees and shows only slight differences from year to year. More than 90% of beech leaves fall in October (◘ Fig. I-27, top). In spruce, on the other hand, dry or yellowed needles fall almost all year round, although there is also a small maximum of needle fall here, a little later than in beech (► Fig. I-27, bottom).

**Fig. I-27** Course (in %) of annual leaf fall of beech (top, 1967-1975) and needle fall of spruce (bottom) (fine litter from three spruce plots 1968-1971) over the course of the year in the Solling shown as a plot of curves (after Ellenberg et al. 1986)**.**

5.4 **Ecophysiology of the herb layer (synusiae)**

The microclimate on the forest floor is very different from that on open sites: After the foliage of the forest, the illuminance on the forest floor is lower, the temperature conditions are more balanced, the humidity of the air as well as of the upper soil layers is higher than outside the forest. Therefore, the herbs in the forest are shade plants and hygrophytes with very low cell sap concentration, i.e. favourable hydrature of the plasma.

The light conditions at the bottom of a deciduous forest can be very heterogeneous on clear days, because individual rays of sunlight falling through the treetops create light spots on the ground. As the sun moves across the sky and the tree branches are bent back and forth by the wind, the light spots change their position and intensity within seconds.

If a leaf is hit by a spot of light, the illuminance can increase more than 30 times, which is of great importance for the photosynthesis of the herbs. Therefore, to determine the light enjoyment of herbaceous plants as a percentage of full daylight, comparative measurements are most appropriately made on bright, uniformly cloudy days. But they can only give a certain indication. It is better to have the daylight totals automatically recorded for specific locations on the forest floor. The amount of light absorbed by the herbaceous layer before the trees are in leaf, is very great, and then falls rapidly as the tree foliage develops completely.

The **spring geophytes** (Galanthus, Leucojum, Scilla, Ficaria, Corydalis, Anemone, etc.) take advantage of the favourable light conditions before leafing of the trees (◘ Fig. I-28). They benefit from the fact that the little weakened solar radiation warms the litter and humus layer in which the geophytes are rooted to 25 to 30 °C already in April. The aerial litter layer has a low heat capacity and consequently a very good temperature conductivity. The tree root in deeper layers that hardly warm up at all, which delays foliage growth.

**◘ Fig. I-28** The spring geophytes (e.g. wood anemone, Anemone nemorosa) or, as here, the liverwort (Anemone hepatica) take advantage of the light phase before the forest greening and complete their entire generative cycle until seed maturity (photo: Breckle).

During the short early spring period, geophytes flower and fruit, replenish their reserves in underground storage organs for the next year. When tree foliage sets in, the leaves of the geophytes turn yellow and a period of dormancy starts. This yellowing is not only due to increasing shade, but corresponds to an endogenous developmental rhythm. In the light, the geophyte leaves die even sonner. It is thus a plant group that was able to fill an existing ecological gap (niche) in the developmental process of deciduous forests.

The spring geophytes are also called **ephemeroids**; for they are characterised by a vegetation period as short as that of the annual ephemerals, but are perennial species with underground storage organs. They behave ecologically similarly and have almost the same developmental rhythm, thus forming a "working group", a functional unit which is called a **synusia.**

In the Russian mixed oak forest (Goryschina 1974, Walter 1976), the following representatives of five deciduous forest synusia were distinguished:

1. Ephemeroids: Scilla sibirica, Ficaria verna, Corydalis solida, Anemone *ranunculoides*.
2. Hemi-ephemeroids: Dentaria *bulbifera*.
3. Early summer species: Aegopodium podagraria, Pulmonaria obscura, Asperula (Galium) odorata, Stellaria holostea.
4. Late summer species: Scrophularia nodosa, Stachys sylvatica, Campanula trachelium, Dactylis glomerata, Festuca gigantea.
5. Evergreen species: Asarum europaeum, Carex pilosa.

The individual synusia take advantage of the different light phases on the forest floor through morphological/physiological adaptations. Thus, Aegopodium first forms small light leaves, then large shade leaves in summer and finally very small xeromorphic, cold-resistant leaves in autumn at lower temperatures, which overwinter (Aegopodium has no winter dormancy phase). The same takes place in Stellaria and Asperula, only the different leaves form successively on the same vertical shoot axis.

Very different in the individual synusia is the assimilate budget, that is, the way they use the assimilates:

Scilla uses up all the assimilates stored in the bulb to build up the flowering shoot and leaves; it is only towards the end of the short growing season that the newly formed assimilates are channelled into the young bulb for use the following year.

Dentaria, on the other hand, starts to fill up the reserves in the rhizome early and therefore needs more time for flowering and fruiting. Aegopodium uses up the sparse reserves to form the light leaves, which assimilate CO2 intensively and replenish the reserves as early as the beginning of May, while at the same time providing the assimilates for building up the shade leaves.

The late summer plant Scrophularia has only a few reserves in the large tuber for the formation of the first leaves. Their assimilate yield is low in the shade, so that it takes until autumn until the shoot is fully grown and the fruits ripen.

In the assimilate household of Asarum it is characteristic that the previous year's (evergreen) leaves assimilate again immediately after winter, they die only in the course of early summer, long after photosynthesis of the young leaves has fully started.

The total phytomass of the herbaceous layer is not large, but its significance for the ecosystem is that it is rapidly decomposed and, in this way, promotes the turnover of matter throughout the ecosystem, while tree leaf litter decomposes slowly; the nutrients contained in the latter are not available until the following year.

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| Box I-5 Synusia in certain ecosystems  |
| Synusia are only subsystems within certain ecosystems. They do not have an own material cycle.  |

Most species of the herbaceous layer are hemicryptophytes, i.e. their renewal buds are laid at the base of the shoots and overwinter just below the soil surface, protected by the leaves that fall in autumn and any snow cover. However, very many representatives are clonally constructed, that is, they reproduce in a variety of ways by division, that is, vegetatively. The division of the mother plant, the formation of stolons, shoot or root tubers always serve to preserve the species and its distribution. Van Groenendael et al. (1996) have compiled a comparative list of the large number of clonal types; examples of species from the Central European deciduous forest are also given in ◘ Fig. I-29.

**◘ Fig. I-29** Various clonal structures with information on the spread and life span of crown connections (modified after Van Groenendael et al. 1996).

The total biomass of the herb layer is usually very low (◘ Fig. I-30), but it converts rapidly. Shoots and roots do not react in the same way every year, depending on the water and nutrient supply, as ◘ Fig. I-31 shows. The number of shoots also varies greatly from year to year (► Fig. I-31). The herb layer can adapt very quickly to changing conditions.

In mast years, such as 1971, however, the number of beech seedlings is also very high, but then declines very sharply over the next few years. The few (from one million beech nuts perhaps 0.1 to 1 seedlings and young plants grow) that remain, however, are sufficient to ensure a new generation of trees.

For many species of the herbaceous layer in the forest, illumination values have been determined. They have a illumination**maximum** (Lmax) because they are not found in full daylight, and a illumination**minimum** (Lmin) because they avoid the deepest forest shade. Example of the two limits in % of daylight are: Lamium maculatum 67 to 12%, Lathyrus vernus 33 to 20%, Geranium robertianum 74 to 4%, Prenanthes purpurea 10 to 5% (sterile to 3%).

**Fig. I-30** Changes in above- and belowground biomass of the herb layer in the beech forest in Solling, in 1969 and 1970. In 1970, the growing season started later and the year was rainier (modified after Ellenberg et al. 1986)**.**

**◘ Fig. I-31** Different numbers of shoots of some species of the beech forest in four consecutive summer half-years from 1968 onwards. Avenella was not yet counted in 1968 (modified after Ellenberg et al 1986).

Lmax is dependant upon the water balance; for the hygrophilous species require a moist soil and do not tolerate high saturation deficits of the air, such as occuring at full illumination.

Lmin is a starvation threshold for the plants. The light intensity is just sufficient to enable the production of the substances necessary for development. In general, the **dead forest shade** begins in the forest at 1% of daylight, in which not only the fruiting bodies of heterotrophic fungi can be found but also holosaprophytes among the flowering plants, for example the bird's nest orchid (Neottia nidus-avis) (◘ Fig. I-32).

**◘ Fig. I-32** Neottia nidus-avis (Orchidaceae) is a holosaprophyte that lives in dead forest shade, e.g. in the beech forests of Saguramo-Sedaseni in Georgia, but also in many beech forests in Germany, and manages without daylight, has no chlorophyll and does not assimilate (photo: E. Fischer).

Another very important factor for the herbaceous layer is the competition of tree roots. In the dry forest areas bordering the forest steppes, the water factor is of great importance. The trees, whose cell sap concentration is higher than that of the herbs, are able to develop high suction tensions in suction roots and thus to extract water from the soil better than the herbs. As a result, the soil in such beech forests (Fagetum nudum) is "bare" (► Fig. I-15). If, on the other hand, the tree roots are cut through, thus eliminating their competition, herbs establish themselves on the forest floor, a sign that the limiting factor was not the light conditions but the water.

In very shallow soils, the tree roots also take the nutrients for themselves, especially the nitrogen. The herbs have to make do with what is left by the tree roots. As a result, only herbs with low nutrient requirements such as Luzula luzuloides, Avenella flexuosa, Potentilla sterilis, Vaccinium myrtillus, etc. are found in such forests.

5.5 **Water balance**

In the Solling, the sum of precipitation is the input variable for water turnover. The output consists of evaporation and runoff, each of which consists of partial variables (◘ Fig. I-33A). In the water balance equation, internal water fluxes can also be taken into account in the forest, such as crown runoff and stem runoff, which plays a role in beech but is negligible in spruce (◘ Fig. I-34).

**◘ Fig. I-33 A** Compartment model of the water balance in the ecosystem with a level location in the Solling (Rs = subsurface runoff; E = evaporation; I = interception; P = precipitation; Pd = crown runoff; Ps = stem runoff; dS = storage size; T = transpiration). The width of the arrows indicates the magnitude (modified after Ellenberg et al. 1986).

**◘ Fig. I-33 B** Dependence of the annual values of the stand precipitation (Nb), the interception (I) and the deep infiltration (Au) on the amount of the total precipitation (N) for the beech (B) and spruce (F) old wood stocks in the Solling for the Years 1969 to 1975 (after Ellenberg et al. 1986, Lozan & Breckle 2021).

Interception is the proportion of water that is retained in the canopy. In the beech forest, the walker gets really wet if rain exceeds 3 mm , in the spruce forest it is only from more than 5 mm of precipitation.

Of the precipitation falling on the forest, the crowns of the beech trees retain an average of 17% (summer half-year, as deciduous), and the spruce trees retain about 27% (all year round, as evergreen). The rest either drips through or runs off the trunks. In dry years, interception ratio is significantly higher than in wet years (Fig. I-33 B).

The snow that accumulates on the forest floor in winter thaws slowly in spring and the meltwater seeps almost completely into the litter layer. It is part of the varying term dS. The transpiration of the tree layer is so strong that in summer, under forest no water is supplied to the groundwater. The water release of the herb layer is five to six times less. A well-developed deciduous forest in the forest-steppe region uses practically all the water supplied by precipitation, whereas a beech forest in Central Europe uses only 50 to 60% of the precipitation, with no surplus in the summer months either.

**Fig. I-34** Interception, crown emergence and stem run-off in the months of full foliage in beech and spruce as a function of outdoor precipitation. In spruce, stem run-off is negligible (modified after Ellenberg et al. 1986).

In the Solling, in accordance with the water turnover model shown in ► Fig. I-33, the flows through individual soil layers were also measured using tensiometers (soil suction tension), lysimeters (with suction devices) and with tritium water. The infiltration water in the soil, as far as it is not taken up by the plant roots, penetrates 1.65 m into the depth under beech trees and 1.20 m under spruce trees in the course of one year.

If one sets the chemical energy determined during production in relation to the energy irradiated onto a hectare of forest, one obtains about 2% for gross production and 1% for primary production. One third of the irradiated energy is used for transpiration, a total of about 80% for the evaporation of water (evaporation, interception), the rest is converted into heat.

The coupling of CO2 assimilationwith transpiration, both processes being regulated by one and the same factors controlling stomatal aperture, can be expressed quantitatively with the transpiration coefficient. Herbaceous plants (for example wheat) consume 540 kg of water to produce 1 kg of plant matter. The beech in the Solling has an average transpiration coefficient of only 180, the spruce of 220. The way in which the beech achieves its so particularly rational performance can be seen in part from the gas exchange measurements (► Fig. I-24). Depending on illuminance, humidity, and CO2 concentration, the leaves regulate stomatal width so rapidly that they adapt immediately to any change. Moreover, photosynthesis of the thin, shade leaves of beech is as effective relative to their dry weight as that of the sun leaves. As a result, the beech is able to make much better use of sunlight than the oak, which forms only about three layers of sun leaves, while in the beech there are an additional three to four layers of shade leaves. Below this, due to the lack of light, the substance production of the herb and moss layer is insignificant on acid soils, while it can be considerable in mixed oak forests.

The overall result is that in the Solling there has been hardly ever a lack of water for the beech.

5.6 **The long cycle (consumers)**

The role of animals in an ecosystem is primarily determined by their feeding relationships. The diversity of food chains with their interconnections is so great that they have not yet been fully recorded for any ecosystem.

Plants are attacked by various parasites, mainly fungi, and a large number of insect pests. Their individual organs serve as food for various phytophages, and these in turn form the food of 1st order predators, namely large (birds, mammals) and small invertebrate predators. These are eaten by 2nd order predators, for example birds or shrews that catch predatory insects.

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| Box I-6 Relation between precipitation and infiltration in a spruce and a beech forest  |
| The spruce forest in Solling lets through up to 880 mm into the groundwater in wet years (1970), in dry years (1971) only 232 mm. The corresponding values for the beech forest are: 1970: 973 mm; 1971: 304 mm. These are the values that ultimately contribute to groundwater recharge in each case. |

Some quantitatively significant feeding relationships in the Solling beech forest are shown in ◘ Fig. I-35. However, it should be kept in mind that many of the relationships indicated are not unambiguous, but often only facultative or even episodic. Overall, two main pathways can be identified: a phytophage food chain that depends on living plant matter, mainly beech foliage, and a saprophage food chain that starts from the dead organic matter mainly stored on the ground.

Only a very small part of the chemical energy in the food of animal organisms is converted into secondary production, i.e. animal body substance. For the most part, it is excreted with the excrement or breathed.

If you look closely at the leaves or other organs of plants, you will see how frequently they are damaged. In the case of the oak alone, one will easily find more than 20 species of insects that live on the leaves or the buds, the bark or the wood; already the number of gall-producing insects is very large in the case of the oak or the beech.

In the Solling region, many years of detailed work have gone into compiling an overview of the animal groups that occur and their food sources. In ◘ Fig. I-36 the most important groups are shown according to their numerical occurrence of individuals. It is understandable that the microscopic groups can occur in huge numbers of individuals in the process. In ◘ Fig. I-37, the biomass of the individual groups of organisms is contrasted in area terms as a frame of reference. Many of these species are soil or old-growth wood dwellers.

An investigation of old trees in Bavaria revealed the following for the beetle fauna: of about 8,000 native beetle species, about 2,000 are inhabitants of old wood. The beetle communities change considerably in the course of an oak's life, as shown in ◘ Fig. I-38. Many of these old wood inhabitants are relict forest species that were once widespread (six or eight tree generations ago, reckoned in evolutionary timescales a few moments ago), i.e. about 2000 years ago, and are now relegated to a few sites. At that time, dead wood and old trees were probably the most common organic substrates, which is why so many small animal species have taken over this habitat (Leicht 1996). The diversity of habitat structures in an old-growth tree is indicated in ◘ Fig. I-39. But there are hardly any old trees left in the managed forests of today..

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| Box I-7 Important factors in forest management  |
| The preservation of old trees needs a lot of time and requires turning away from unnecessary "maintenance measures" and "exaggerated tree renovation". Understanding for natural processes, but also sensible handling of nature, and no insistence on the "duty of care" (Leicht 1996) is required. |

**Fig. I-35** Essential foraging relationships in the Solling beech forest (modified after Ellenberg et al. 1986).

**Fig. I-36** The individual densities of individual animal groups in the Solling beech forest, indicating the predominant diet (logarithmic ordinate in individuals per m2; nematodes and aphidines with supplementary data) (modified after Ellenberg et al. 1986).

**Fig. I-37** Zoomass of individual animal groups in the Solling beech forest (logarithmic ordinate in per m2) (modified after Ellenberg et al. 1986)**.**

**◘ Fig. I-38** The beetle communities occurring during the long natural life cycle of an oak (modified after Leicht 1996).

**Fig. I-39** Overview of habitat structures in old-growth and dead wood thatare significant on an old tree (modified after Leicht 1996).

5.7 **Decomposers in litter and soil**

Most of the annual litter in a deciduous forest consists of dead, yellowed leaves from the litter layer above the ground. It is immediately crushed by soil organisms and then attacked and broken down by microorganisms, fungi and bacteria. The small fauna of saprophages feed on the litter, and by crushing it they make it easier for microorganisms to enter. In addition to insect larvae and countless other arthropods, however, it is primarily earthworms, as explained above, in whose faecal clots the bacteria develop a lively activity.

The activity of these animals in deciduous forest stands has been studied more precisely, including quantitative relations (Edwards et al. 1970).

Leaf fall in autumn is completed by the end of October, often within a few days. Sugars, organic acids and tannins are first leached from the litter by rain.

The smaller the C/N ratio of the litter, the faster the further decomposition takes place. By the following June, birch litter loses about ⅘ of its dry weight, linden litter half and oak litter, which is difficult to decompose, only about a quarter.

The mineralisation of the litter is not complete, but humus substances are also formed, which, when saturated with Ca, result in the mull horizon, which is rich in lumbricids (earthworms), and in the case of an acid reaction, the mould horizon with oribatids (horn mites) and collembolae (springtails). In extreme cases, a highly acidic reaction results in a difficult-to-decompose layer of raw humus almost devoid of animal organisms but rich in fungal hyphae. The fine structure of the uppermost organic humus layer and litter reveals certain differences between beech forest and spruce forest in the Solling (◘ Fig. I-40). In the spruce humus, the structure is looser, with fewer fine roots, fungal mycelia and animals present. Litter decomposition to the Fm (the decay horizon of medium decomposition) takes about , in the spruce forest only years.

Satchell (from Duvigneaud 1974) gives the activity, i.e. respiration in kilocalories per square metre per year, for the individual soil organism groups of an English oak forest on calcareous soil:

* Invertebrates (dipterans, collembolae, oribatids, molluscs, enchytraeids, lumbricids, nematodes, protozoa) together 361 kcal/m2/year.
* Bacteria and actinomycetes: 77 kcal/m2/year.

**Fig. I-40** Schematic drawings of the humus profiles in the beech forest and spruce forest of the Solling (modified after Ellenberg et al. 1986)**.**

**Fig. I-41** Variations in DW (dry weight in g/ha) of fruiting bodies of mycorrhizal fungi and all higher fungi between June and November in the wet year 1970 in the Solling beech forest (modified after Ellenberg et al. 1986)**.**

The most significant activity is that of fungi: in the litter layer 543, in humus 220 and in the A and B horizons 380, i.e. a total of 1,143 kcal/m2/year. The mass of microorganisms is very low compared to that of invertebrates.

The dead wood lying on the ground is 90% destroyed by microorganisms, especially fungi. The fungi also have a great importance as mycorrhiza partners for the trees. In the Solling, almost half of the higher fungi can be classified as mycorrhizal fungi. The maximum of fruiting body formation is in September (◘ Fig. I-41); however, the other fungi also form fruiting bodies mainly in summer. This is explained by a different balance of growth substances between the fungal root and the tree during mycorrhizal symbiosis.

5.8 **Solling ecosystem**

In conclusion to the somewhat more detailed discussion of some phenomena of the nemoral beech forest, reference should be made briefly to a comparison of the productivity of the various areas studied and to the energy flow. In ◘ Fig. I-42, the annual net primary production of the sample plots investigated in the Solling is shown.

**Fig. I-42** Annual net primary production on the sample plots investigated in the Solling (beech forest, spruce forest, golden oat meadow, ryegrass meadow) given in 1,000 MJ per ha (open columns: estimated values) (modified after Ellenberg et al. 1986)**.**

Surprisingly, the productivity of the fertilized meadows and that of an arable field is about the same magnitude as that of the forests. Under the climatic and soil conditions given in the Solling, the different plant stands have approximately the same productivity (► Fig. I-42). Productivity is expressed in ◘ Fig. I-43 as a measure of energy retention. This energy flux through the major compartments (► Fig. I-43) suggests that among the heterotrophs, decomposers have the greatest energy turnover. This characterises the short cycle of organic matter, while vanishingly little is converted through the long cycle (0.5%, via herbivores and carnivores) as is also known from other terrestrial ecosystems. Interestingly, the proportion of zoophages is even greater than that of herbivores; the food pyramid is "distorted" here by a high proportion of saprophagous animals.

**◘ Fig. I-43** Energy flux in the Solling beech forest (partly calculated according to respiration values (figures in kJ per m2 and a; in parentheses assuming that 5 % of the organic matter is converted into permanent humus; carnivores are assumed to eat about 10% of the saprophagous and herbivorous animals) (modified after Ellenberg et al. 1986).

The Solling as a low mountain range shows in a certain way already montane features, the precipitation is clearly increased compared to the lower lying surrounding area, there are more clouds and the temperature is somewhat lower. In the other low mountain ranges and even more so in the northern Alps, however, the third dimension, the orozonal sequence, becomes clearer.

**6 Orobiome VI -the Northern Alps and the alpine forest and tree line**

The Alps separate Central Europe (ZB VI) from Southern Europe (ZB IV) like a crossbar. Geologically, the Alps are characterised by the "crystalline" Central Alps and by limestone in the marginal Alpine chains of both the northern and southern Alps (◘ Fig. I-44). This has implications for flora and vegetation.

**Fig. I-44** Schematic of the geological situation of mountains in Central Europe (modified after Ozenda 1994)**.**

6.1 **The elevational belts**

The elevational belts of orobiome VI are well developed on the northern regions of the Alps. With increasing elevation, the mean annual temperature in the mountains decreases and the vegetation period shortens. Direct solar radiation increases with elevation, but diffuse radiation decreases; as a result, thermal differences between S and N slopes become sharper. Due to the wind congestion at the northern edge of the Alps, precipitation increases rapidly with elevation, for example Munich (569 m asl) 866 mm, Wendelstein (1,727 m asl) 2,869 mm. The vegetation of the individual elevational levels on the northern parts of the Alps changes accordingly:

|  |  |
| --- | --- |
| Elevationalinal belt | Vegetation |
| Nivale | Cushion plants, mosses and lichens |
| **Climatic snow line at about 2600m asl** |
| Alpine | Alpine mats and meadows |
| Subalpine | Krummholz and dwarf shrubs |
| **Timberline at about 1800m asl** |
| High **Montane** | Spruce forest |
| **Montane** | Beech and fir forest |
| Submontane | Buchenwald |
| Colline | Mixed oak forest |

As the Alps are an interzonal mountain range, we have to do with an elevational succession of Orobiom IV at the S edge of the Alps and the tree line is formed by the beech. The succession of elevational belts in the continental inner Alpine valleys is also different; the deciduous forest belts are absent, below the spruce belt there is a pine belt, above the spruce belt a larch (*Larix)* - pine (Pinus cembra) belt follows up to the timberline. Here, the timberline and the snowline are 400 to 600 m higher due to the stronger insolation with less cloud cover. We distinguish a Helvetic (northern edge), Penninic (central Alps) and Insubrian (southern edge) sequence of elevational belts:

|  |  |  |
| --- | --- | --- |
| Helvetic | Penninic | Insubric |
|  |  |  |
| (Central European) | (Continental) | (Submediterranean) |
| Alpine belt | Alpine belt | Alpine belt |
| Spruce forest | Larch-Arpine Forest | Beech forest |
| Beech forest | Spruce forest | Downy Oak Forest |
| Oak Forest | Pine forest | Sclerophyllic scrub (partly) |

6.2 **The forest belts**

The uppermost forest belt in the Central Alps is formed by the European larch (Larix decidua) and the Swiss stone pine (Pinus cembra), which is closely related to the Siberian subspecies. Larix decidua is the light-loving pioneer species, which is gradually displaced by the more shade-tolerant five-needled stone pine. On avalanche tracks the larch descends to low elevations.

Above the timberline, the two-needled Scots pine (Pinus mugo) or mountain pine (Pinus montana) can be found as krummholz, which is replaced by the shrubby green alder (Alnus viridis) in damp locations.

On the ecology of spruce biogeocoenes (see below).

The question was presented whether the short summer or the long winter was responsible for the cessation of tree growth. It was found that both are of importance. When the growing season is less than three months, the young needles cannot mature properly; their cuticle does not reach its final thickness. As a consequence, during the long winter and especially in spring, when the sun is already strong but the soil is still frozen, high water losses occur, indicated by the increase of cell sap concentration up to more than 6.5 MPa. Damage due to frost-drought becomes noticeable and the needles fall off. This does not occur under a blanket of snow; therefore, the stunted forms protected by snow in winter still extend somewhat above the forest line. It is through the combined effect of both factors, the shortening vegetation period and the simultaneous aggravation of the danger of frost-drought, that the sharp boundary at a certain altitude comes about. The mountain pines growing above the spruce forest line endure a somewhat shorter growing season, but a few hundred metres higher up the same phenomenon repeats itself for them, the needles no longer ripen and suffer damage from frost-drought, the upper mountain pine tree line therefore stands out just as sharply as the forest line.

At the N part of the Alps, the causes determining the spruce forest line (◘ Fig. I-45) have been studied. The vegetation period shortens with elevation, summers become cooler, winters colder and longer. These climatic changes proceed steadily. In contrast, the timberline in the high mountains forms a rather sharp line. The vigour of the trees suddenly diminishes and a very narrow zone of low stunted forms (◘ Fig. I-46) forms the transition to the forestfree alpine belt.

**◘ Fig. I-45** The forest and tree line in Vorarlberg near Bludenz (Austria). View from the Saladina-peak (Freiburg hut) southwards to the opposite northern slopes (photo: Breckle).

The causes of the polar **spruce forest line** could be of a similar nature, with the difference that solar radiation plays no role in frost-drought damage there during the polar night in winter. It is replaced by the strong and cold drying winds. Accordingly, the timberline advances in the wind-sheltered valleys farther north than on the watersheds. In the Alps it is the other way round, because in the valleys, due to lakes of cold air, the temperatures reach lower degrees than on the mountain ridge from which the cold air flows.

**◘ Fig. I-46** The spruce forest boundary with wind-swept stunted spruce, on the Tegelberg near Füssen (1,600 m asl). The lower branches under winter snow cover are green, above them wind and snow blowing causes the branches to die (photo: Breckle).

The forest line is highest in the central Alps at 2,000 to 2,150 metres. Here, as we have mentioned, it is not formed by the spruce, but by the needle-throwing larch and the evergreen, relatively tender-needled stone pine (Pinus cembra). Here, continuous measurements of climatic factors and photosynthesis were carried out over the course of an entire year, including the entire winter. This makes it possible to accurately compare the substance production of the larch with that of the stone pine.

In the cold winter photosynthesis is also dormant in the evergreen Swiss stone pine, but in spring the needles quickly become active, whereas the larch at this elevation does not green up until mid-June and already turns yellow at the end of September. While the Swiss stone pine has 181 days available for substance production, the larch has only 107 days. However, the needle mass of young larches is three to six times greater than that of young stone pines; moreover, despite the shorter growing season, they assimilate 47% more CO2 per gram of needle mass per year. Therefore, the total production of a 4-year-old larch is 4.5 times and that of a 12-year-old 8.5 times greater than that of pines of the same age. It is only from the 25th year onwards that the amount of needles of larches is lower compared to that of stone pines, so that they lag behind in growth, especially on raw humus soils. With time, therefore, the Swiss stone pine also establishes itself as a shade wood species. The ratio of larch to stone pine is thus reminiscent of that of pine to spruce.

All boundaries were up to 400 m higher during the postglacial warm period in the Alps, as evidenced by wood finds in subfossil peat deposits in the subalpine belt. The dwarf shrubs that overwinter under snow are therefore partly remnants of the former forestation. The forest and snow line in the course of the postglacial is given in ◘ Fig. I-47.

As a result of the high precipitation, which falls as snow in winter, the snow cover in the alpine belt is very thick, so that for the low alpine vegetation not the air temperature plays the main role, but the [snow-free](https://dict.leo.org/englisch-deutsch/snow-free) period.

**◘ Fig. I-47** The fluctuations of the tree and snow line in the Late and Postglacial in the Swiss Central Alps (modified after Ozenda 1994). Due to human activities, the current timberline is lower today than the potential timberline, which corresponds to the tree line.

This is very much determined by the relief, the wind direction and the exposure: The snow is deposited in hollows and as snow cornices on the leeward side of a ridge, whereas it is blown away on its windward side. If the windward side is also on the sunny side, the snow also thaws, so that the site is open all year round. There the plants (Loiseleurietum association) are exposed to extreme frost-drought as in the mountain tundra and are also accompanied by the same lichens. On a shady windward slope there is no warming by insolation. In the case of heavy snow deposits at the foot of a slope exposed to the north, the [snow-free](https://dict.leo.org/englisch-deutsch/snow-free) period is reduced to a minimum (snow valleys) or is absent altogether where the snow remains throughout the summer. Depending on the snowfall in the individual years at the same location, the [snow-free](https://dict.leo.org/englisch-deutsch/snow-free) period (Aper-time) may be longer or shorter. The average [snow-free](https://dict.leo.org/englisch-deutsch/snow-free) period decreases with elevation and is theoretically zero when the climatic snow line is reached (mountain glaciation). In individual cases, however, it can still be very long high above the snow line on steep faces. This is why flowering plants in the Alps on favoured sites occur in the nival belt, i.e. above the climatic snow line.

In any case, the microclimate on sunny days is characterised by favorable temperature conditions, even at high elevation. The temperature of the leaves in the sunshine can be up to 22 K above the air temperature. There are warm niches everywhere, known to the climber, and these are exploited especially by the low-growing plants near the ground. In cloudy weather the differences balance out.

From what has been said it is clear that in the steep alpine belt there is no standard climate with regard to vegetation, but that there is a subdivision into the smallest climatic spaces; these can differ sharply at the shortest distance, for example on the sunny and shady side of a rock. Of paramount importance is the snow deposition in winter, which one must know in order to be able to judge the [snow-free](https://dict.leo.org/englisch-deutsch/snow-free) period; otherwise the vegetation division remains incomprehensible to one.

A major role is played by temperature inversions and cold air lakes, which lead to a reversal of the sequence of the altitudinal belts (beech over spruce). Even in midsummer, night frosts occur in sinkholes (dolines) when there is outgoping radiation, so that no tree growth is possible at the bottom of the sinkhole.

In addition, the elevationalbelts are disturbed by avalanche tracks; on these, the alpine vegetation descends deep into the forest belt, because there it is not exposed to the competition of the forest vegetation. Alpine exclaves can also be found in the middle of the forest on heavily weathered dolomite with very shallow, nutrient-poor soils. Also known are the relict sites of alpine species on moors in the foothills of the Alps. At such sites the undemanding but slow-growing alpine species are less exposed to competition from others.

6.3 **Alpine and nival belts**

The vegetation of the Alps has been well studied ecologically. In the evergreen species, the same annual cycle of frost hardiness with hardening in late autumn and dehardening in spring can be observed as in the deciduous forests. While spruce needles are killed by frosts as low as -7 °C in summer, they can still withstand -40 °C in winter. Although the alpine species grow much higher than the spruce, their maximum frost hardiness is usually lower (below -30 °C), because they overwinter under snow and are therefore not exposed to the low winter temperatures. Only Loiseleuria, which grows on wind-exposed sites that are impermeable in winter, has greater frost hardiness. In strong winds, the lowest temperatures are usually not reached in such locations, but the risk of frost-drought is increased. Loiseleuria, notwithstanding its xeromorphic leaf structure, dries out within 15 days in winter if left to hang freely. However, as it grows close to the ground in its natural snow-free habitat, even in winter sunlight thaws the snow held between its shoots, allowing water uptake in between. The dwarf shrubs hibernating under snow are not exposed to frost drought.

In summer, with frequent precipitation, the water balance is fairly equalised. The plants are only exposed to high evapotranspiration for hours when there is strong radiation or strong wind. The latter is slowed down near the ground. The water supply of the soil is always good, even at superficially dry looking scree slopes or rocky sites. At such sites, plants have extensive root systems or taproots that penetrate deep into moist rock crevices, whereas normally the root system is spread very shallowly in the upper soil layers. The favorable water balance is reflected in the low cell sap concentrations of 0.8 to 1.2 MPa. Even in xeromorphic species such as Dryas octopetala, Carex firma and Androsace helvetica, it never reaches 2.0 MPa. It is perhaps more correct to speak of peinomorphs caused by nitrogen (N) deficiency, since N uptake is more difficult at low soil temperatures. Lush hygromorphic herbs grow on nitrogen-rich sites, such as cattle paddocks. If one calculates the total water release of the plant cover of alpine grass communities, one arrives at 200 mm per year. The evaporation size depends mainly on the wind, it is therefore conditioned by the relief, but in the opposite sense as the snow deposition.

In the alpine belt, the short vegetation period raises the question of sufficient substance production just as it does in the Arctic. The day length is shorter than in the Arctic, but radiation is stronger and the night temperature lower. Under favorable lighting conditions, 100 to 300 mg/dm2 of CO2 is assimilated per day. One month of good weather would be enough to accumulate sufficient reserves for the next year and for the seeds to mature. Since the growing season lasts three months, sufficient production is assured in any case. The primary production of the plant communities depends very much on the vegetation density.

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| --- |
| Box I-8 What does the [snow-free](https://dict.leo.org/englisch-deutsch/snow-free) period (Apertime) mean?  |
| Apertime (lat. apertus = open) is the time without snow cover.  |

The following were found:

* closed mats 50-276 g/m2
* Dryadeto-firmetum (cushion sedge lawn) 91 g/m2
* Salicetum herbaceae (herbaceous willow lawn) 85g/m2
* Oxyrietum (acid grassland) 15 g/m2
* on limestone scree 1 g/m2

Photosynthesis in dwarf shrubs is less intense than in herbaceous species; however, because their total leaf area is larger and the growing season is longer at lower alpine belts, higher primary production occurs.

The most unfavourable conditions are found in the so called “snow hollows (Schneetälchen)” with chionophytes, i.e. where in the area of silicate rocks the snow on the northern slope thaws very slowly and gradually releases the surface from the edge. Therefore, a zonation with decreasing [snow-free](https://dict.leo.org/englisch-deutsch/snow-free) period can be distinguished in a very small area. The soil at such sites is rich in humus and slightly acidic, always well moistened with meltwater, but therefore also relatively cool. With a [snow-free](https://dict.leo.org/englisch-deutsch/snow-free) period of three months a normal Carex curvula lawn develops. If the growing season is shortened to two months, Salix herbacea becomes predominant, a species of willow that only sticks the shoot tips out of the ground, so that its leaves form a dense lawn or flat espalier. This willow, however, only fruits when the [snow-free](https://dict.leo.org/englisch-deutsch/snow-free) period is three months after winters with little snow. A number of very small species, such as Gnaphalium supinum, Alchemilla pentaphylla, Arenaria biflora, Soldanella pusilla, Sibbaldia procumbens, and others, join it. With an even shorter vegetation period, mosses can grow that do not need to form flowers and fruits, namely Polytrichum sexangulare (P. norvegicum). If the snow-free period is also too short for these green mosses, only Anthelia juratzkana, a liverwort that looks like a mouldy coating, will grow because the moss grows in symbiosis with a fungus and feeds partly saprophytically. After snowy winters, this zone does not aperture at all.

On firn surfaces in the nival belt, the last living organism to be found is the alga Chlamydomonas nivalis, which gives the snow surface a pink sheen or rosy hue (◘ Fig. I-48).

Since bare rock soils predominate in the Alpine belt, the chemical composition of the rock plays a major role for the vegetation, it determines the soil reaction. The floristic differences between the “Limestone Alps” and the Central Alps with siliceous rocks are very striking. Accordingly, a distinction is made between calcareous or basophilic species and limestone-avoiding or acidophilic species. Often, there are vicariant species, as in the well-known example of alpine roses: Rhododendron hirsutum on limestone, Rh. ferrugineum on silicate rock or acid humus soil. Other examples are: *Achillea atrata, Carex firma, Gentiana clusii, Sesleria coerulea* on limestone and *Achillea moschata, Carex curvula, G. kochiana, Sesleria disticha* on silicate soils.

**◘ Fig. I-48** Chlamydomonas nivalis as the highest-occurring organisms in snowfields at 5,000 m altitude on the northern slope of Shah Fuladi, Kohe Baba, Afghanistan. They are found in old snowfields in all mountains (photo: Breckle).

From 1969 to 1976, within the framework of the International Biological Programme (IBP) on the Patscherkofel near Innsbruck, the ecosystems of the alpine dwarf shrub heaths were investigated on the following three sample areas above the present forest line (Larcher 1980):

1. Vaccinium heath (1,980 m asl), in a wind-protected hollow with winter snow protection: *Vaccinium myrtillus* 3, V*. uliginosum* 2, *V. vitis-idaea* 1, *Loiseleuria procumbens* 1, *Calluna vulgaris* 1, *Melampyrum alpestre* 1, mosses 1, lichens 1.
2. Loiseleuria heath (2,000 m asl), dense stand often free of snow in wind-exposed position: Loiseleuria 5, Vaccinium uliginosum 1, V. vitis-idaea 1, others only +, lichens (Cetraria islandica 1, Alectoria ochroleuca 1, others only +).
3. Open, trellis-like and lichen-rich Loiseleuria stand (2,175 m asl) in extremely wind-exposed location: Loiseleuria 3, stunted Vaccinium uliginosum 2, V. vitis-idaea 1, Calluna 1, others +, mosses +, lichens (Cetraria islandica 2, C. cuculata 1, Alectoria ochroleuca 1, Cladonia rangiferina 1, C. pyxidata 1, Thamnolia vermicularis and others +).

The climate is cold with an annual temperature slightly above 0 °C, frosts can occur in any month (abs. minimum around -20 °C, but daily maxima reach +20 °C in the summer months). Snow lasts for about six months in sample plot A, about four to six months in sample plot B, whereas in sample plot C it is only sporadic and temporary. The microclimate in stands A and B is slightly warmer, while in C there are very sharp temperature differences. The CO2 assimilation periodis about 100 days for deciduous species and about 140 days for evergreens. ◘ Figure I-49 shows the structure of the stands and the photosynthetically active radiation (PhAR) in them, as well as the cumulative leaf area index (LAI). For further data on production ecology, see ◘ Table I-1. Wind is strongly slowed down in dwarf shrub heath stands, even during storms, so that humidity remains high in the same. Precipitation in the area, is about 900 mm per year, with each summer month receiving an average of over 100 mm.

**◘ Fig. I-49** Middle: Phytomass stratification of Vaccinium and Loiseleuria heath (assimilating parts on the left, non-assimilating and dead parts on the right). Left half: Cumulative leaf area index (LAI, **red curve**) and attenuation of light (PhAR) in the stand under clear (**blue curve**) and overcast (**grey curve)** skies (modified after Cernusca 1976; from Larcher 1977).

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| --- |
| ◘ **Table I-1** Production ecological parameters of alpine vegetation units; living standing phytomass, dead parts, and litter in grams of dry matter per m² from the dwarf shrub heath (A), the dense Loiseleuria heath (B), and the open Loiseleuria stand (C). |
| Sample area | A | B | C |
| Living above-ground phytomass (max.) | 983 | 1105 | 748 |
| Adhering dead parts | 263 | 123 | 72 |
| Living underground phytomass | 2443 | 2200 | 803 |
| Dead underground parts | 1549 | 608 | 56 |
| Total living phytomass | 3426 | 3305 | 1551 |
| Together with dead parts | 5238 | 4036 | 4036 |
| Litter on the ground | 819 | 1080 | 931 |
| Shoot/root ratio | 1:2,5 | 1:2,0 | 1:1,1 |
| Percentage of assimilating parts of living phytomass | 55 % | 68 % | -?- |
| Above-ground net primary production (t·ha-1·a-1) | 4.8 | 3.2 | 1.,1 |

The soils above schistous biotite gneisses are sandy, acidic iron podsols with a thick layer of raw humus, which is only weakly developed in stand C. The soils have developed from former stone pine forest soils. The humus is mineralized very slowly (supply of nitrogen about 3 to 4 kg/ha, at C only ⅓ of it).

The phytomass should remain constant except for certain fluctuations, i.e. the stands are in ecological equilibrium with their environment, with an increase in phytomass also being prevented by browsing (game, ptarmigan, arthropods) and by certain losses of substance in winter (freezing and drying of parts protruding above the snow).

The photosynthetic capacity per leaf area is the same in deciduous and evergreen dwarf shrub species; in terms of dry leaf weight, it is similar to that of soft-leaved deciduous woody species in deciduous dwarf shrubs and comparable to that of coniferous species in evergreens. The shallow temperature optimum for photosynthesis in the Ericaceae is between 10 °C and 30 °C and corresponds to the usual temperatures in stands on cloudy and clear days; the temperature minimum for CO2 assimilationis -5 °C to -6 °C with super-cooled leaves. Overheating of leaves rarely occurs, as does restriction of photosynthesis due to lack of water. Although water supply is adequate during the growing season and the total transpired water volume is equivalent to 100 to 200 mm, transpiration limitation has been observed during foehn periods. In winter, cuticular transpiration is very low.

Heat damage during the summer is observed at most in individual shoots over loosely lying stones or over vegetation-free raw humus blankets. Cold damage in winter can only occur in the apical state. Hardening protects plants from frost damage; late frosts after dehardening, on the other hand, can be dangerous. Damage caused by frost-drought is difficult to prove; in most cases, the damage is caused by a combination of several factors. Completely frost-hardy are the arctic-alpine species Loiseleuria procumbens and Vaccinium uliginosum.

Respiration is markedly excessive at the time of main growth. Around this time, in the fat-storing Loiseleuria, the respiration coefficient drops to 0.8 to 0.9 and rises again to 1 after completion of intensive growth.

The efficiency of net primary production during the growing season is 0.9% for the dwarf shrub heath, 0.7% for the dense Loiseleuria heath, and 0.3% of photosynthetically active irradiance for the open stand.

The Ericaceae store abundant fat in addition to starch, but the latter is only partially mobilized; the greater part remains in the dead parts. The dwarf shrubs react immediately to the first days of frost by converting a large part of the starch into sugar, Loiseleuria turning a reddish colour due to anthocyanin accumulation.

Further investigations were carried out in the nival belt, i.e. above the climatic snow line, on the high Nebelkogel in the Stubai Alps under particularly difficult conditions (Moser et al. 1977). An experimental hut had to be lowered by helicopter and carefully insulated and grounded, as it was often located in the middle of thunderclouds.

At this elevational belt there is no longer a closed plant cover. On the 0.5 ha experimental plot, at 3184 m asl, a flat ridge section with seven flowering plants and several cryptogam species, a northern slope with very sparse vegetation and a southern slope with eleven phanerogam species on flat steps were selected.

The climatic conditions are by no means those of the high Arctic, but in summer more like those of the Páramos in the tropics. On clear days, the leaf temperature is often over 15 °C, to drop below zero at night, without photosynthetic activity suffering. In contrast, the arctic 24-hour summer day with low sun is characterized by a fairly uniform temperature.

Of the three sites selected, the southern slope has the most favourable light and temperature conditions. The phenology of the most important species is shown in ◘ Fig. I-50. While the flowering period is advanced in Saxifraga oppositifolia (flowering organs frost-resistant), it is postponed furthest in Cerastium uniflorum.

**Fig. I-50** Phenology of nival plants. Flower development and phenological phases at 2,600-3,200 m asl (modified after Moser et al. 1977).

The assimilates are stored as starch in Primula spp. and Ranunculus glacialis, which is converted into sugar in winter, but as fat in the Saxifraga species. The shift in store location is evident from ◘ Fig. I-51. It is striking that in Ranunculus a precautionary translocation from the leaves to the underground storage organs takes place even in the case of a temporary deterioration of the weather, which is reversed when the weather improves. After all, any snow cover in the summer could last until the next spring. In general, the growing season on the south slope is about three months, but as a result of the often poor weather, only 60 to 70 (15 to 100) days are considered for production. At the other locations, the plants may not become snow-free at all during some years.

**◘ Fig. I-51** Energy content of 2 nival species and storage of reserve materials (modified after Moser et al. 1977).

Half of the production in Ranunculus glacialis is generated during the few bright and warm days, the other half during the many cool days with low illumination due to light snow cover or fog. Photosynthesis in this species is possible in the range of -7° to 38 °C. Assimilation efficiency is greatest at the time of full flowering and fruiting. Under optimal conditions, it reaches up to 0.056 g of dry matter per dm2 of leaf area per day in Ranunculus glacialis, and 0.063 g in Primula glutinosa; under unfavourable weather conditions, the values are 0.015 to 0.020 g. During one growing season, the areal extent of Androsace alpina cushions increased by 13.5%; their average net assimilation rate during the growing season was 0.058 g of dry matter per dm2 of cushion surface per day. As a result of low plant cover, primary production in the nival belt is extremely low. Under optimal conditions, at 10% cover, production can be estimated at 0.66 g per m2 per day of dry matter.

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| Box I-9 The scientific investigation of all the Earth's high mountains is very inhomogeneous  |
| Of all the mountain ranges on Earth, none has been studied in as much ecological detail as the complex mountain system of the Alps, located in the centre of western Europe.  |

**7 Zonoecotone VI/VII - Forest-Steppe**

While the deciduous forests of the temperate zone are confined to the oceanic-tinted climatic regions with not too sharp temperature extremes and evenly distributed precipitation, usually with a summer maximum, in the northern hemisphere much more extensive continental parts are occupied by grass steppes and deserts. In the continental climate in Europe from west to east the temperature amplitude increases, the summers become hotter, but the winters colder to a much greater extent, so that the mean annual temperature decreases. At the same time, the annual amount of precipitation becomes less, the summers become increasingly arid.

The ZE VI/VII between the deciduous forests and the grass steppes is the **forest steppe** in Eastern Europe. It is not a homogeneous vegetation formation like the climatic, tropical savannah, but a macromosaic of deciduous forest stands and meadow steppes. At first, the former predominate and the steppes occur in island form. The more arid the climate becomes, however, the more the ratio is reversed, until finally only small islands of forest remain in a sea of steppe. In this transition zone with a climate that favors neither the forest nor the grass steppe unilaterally, the relief or soil type (◘ Fig. I-52) is the deciding factor. The forests are found on well-drained sites, on the slight elevations, on the slopes of river valleys, on permeable soils, while the grass-steppes occupy the poorly drained level sites on relatively heavy soils. This is similar in the savannah. Competition between the sward and tree seedlings also plays a role here. If tree seedlings are protected from grass competition in the early years of afforestation experiments, they may grow in the steppe but not rejuvenate naturally. Steppes used to be favoured by grass fires started by lightning and by grazing by big game. One can only speculate about the real role of big game under natural conditions. However, the grazing density by man's grazing animals (sheep, goats, cows) is certainly much higher than that of the original big game. Nevertheless, in some regions the vegetation composition and mosaic structure are probably very similar to the original one (◘ Fig. I-53). Today, in many places, the steppe has been almost completely converted into arable land.

**◘ Fig. I-52** Relationships between vegetation, soil, and relief in the forest steppe (modified after Walter 1990): 1 deep poorly drained chernosem (black earth) with meadow steppe. 2 degraded chernosem and 3 dark grey forest soils (both well drained); 4 permeable sandy-loamy forest soils; 5 light grey forest soils; 6 solonez on level terraces or around drainless depressions with sodic enrichment; 7 fluvio-glacial sands; 8 moraine deposits or loess-like loams; 9 preglacial strata; 10 alluvium in river valleys. I oak woodland on well-drained elevations or slopes; II floodplain woodland (oaks et al.); III pine woods on poor sands with Sphagnum marsh in wet depressions; IV pine-oak woods on loamy soils; V aspen groves in small depressions (pods) where water stands in spring and slowly percolates (soils depleted in central part); Va the same but willow scrub; VI ravine-oak woods, with steppe scrub at upper margin.

Climatically, one can easily distinguish the forest zone, the forest-steppe zone and the steppe zone in E Europe (Breckle 2021). The climate diagrams of the forest zone do not show a drought period, whereas those of the steppe zone always show a drought period. The diagrams of the forest-steppe zone lack a drought period, but in contrast to the forest zone, a dry period can be recognised (► Fig. K-1).

**◘ Fig. I-53** Steppe and scrub/forest plot mosaic in Dobruja (Romania). Some grazing by goats and sheep keeps larger parts open as steppes and species-rich dry grasslands. The bushes continue to grow outwards only slowly, regeneration is hardly given even without grazing (photo: Breckle).

The boundary between forest and steppe shifted in the postglacial period. In the soil under today's forest stands one can see **Krotovines** (► Fig. K-4), which are the former burrows of steppe rodents (ground squirrel = Spermophilus) that never inhabit forests. Therefore, it must be assumed that the forest was in the process of advancing in the period before human colonization of the forest-steppe, because the climate became somewhat wetter after a warm optimum in the post-glacial. However, due to the strong interventions of man, boundary shifts in the subsequent period can no longer be determined.

The reason for the replacement of the forest zone in the continental area by the steppe zone is the water factor. In the forest-steppe the entire water turnover takes place almost only in the upper 2 m of the soil; a sinking of water to the deep groundwater does not take place. The oak forest consumes all water; the soil always remains dry at greater depths. This is the case on flat surfaces. On S slopes with runoff and high evaporation, the water content of the soil is no longer sufficient for forest, and steppe sets in. In August and September, the grass steppe dries out, because even for it the water supply is not sufficient to cover its transpiration. However, this does not cause any damage to the grass plants, but it does to the trees when the leaves dry out prematurely or entire branches die.

In a SE direction, precipitation decreases and temperatures increase in the forest-steppe. Accordingly, the forest plots become more and more sparse and retreat to the N slopes, until finally, at the S border of the forest-steppe, only oak and sloe scrub (Prunus spinosa) remains in ravines.

Competition in the forest steppe is between grasses and tree seedlings. Clements et al. were able to show in the 1929 partly pristine longgrass prairie of Nebraska (► Fig. K-8), which corresponds to the forest steppe, that planted tree seedlings only persist if all grass roots around them are removed and this tree disk is kept free.

The water consumption of forest stands increases with the age of the stand. Accordingly, reforestation experiments have shown that young, artificially created forest cultures grow relatively well, but in older ones the trees become stunted and then sprout again from below, i.e. they do not develop normally as a result of the lack of water. Good stands, on the other hand, are obtained when additional groundwater is available to the trees. Savannah-like communities are lacking in forest-steppes, because the hardwood species cannot assert themselves individually against the competition of the grasses. Only low shrubs (Spiraea, Caragana, Amygdalus) occur more frequently, but even these more on stony soils, which are less suitable for the steppe grasses with the intensive root system. The steppe component of the forest steppe - the meadow steppe proper - is dealt with in the next chapter (ZB VII).

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Feather grass steppe (Zonobiom VII) in the vicinity of the monastery Dawit Garedscha, Georgia (Photo: E. Fischer)

Iris iberica, an iris endemic to the Caucasus region and one of the many geophytes of the feather grass steppes (Zonobiom VII) of South Georgia on the Azerbeijan border (Photo: Rafiqpoor)