

Vegetation of the Czech Republic: diversity, ecology, history and dynamics

Vegetace České republiky: diverzita, ekologie, historie a dynamika

Dedicated to the centenary of the Czech Botanical Society (1912–2012)

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This review summarizes basic information on the diversity of vegetation in the Czech Republic. It describes basic environmental factors affecting vegetation, vegetation history since the last glacial, biomes occurring in the Czech Republic (zonal biomes of broad-leaved deciduous forest and forest-steppe, and azonal biomes of taiga and tundra), altitudinal zonation of vegetation and landscapes with an exceptionally high diversity of vegetation types (deep river valleys in the Bohemian Massif, karst areas, sandstone pseudokarst areas, solitary volcanic hills, glacial cirques, lowland riverine landscapes and serpentine areas). Vegetation types, delimited according to the monograph *Vegetation of the Czech Republic*, are described with emphasis on their diversity, ecology, history and dynamics.

Key words: alpine, aquatic, central Europe, forest, grassland, phytosociology, plant communities, ruderal, vegetation change, vegetation classification, vegetation history, weed, wetland

Introduction

The Czech Republic is a land-locked country in central Europe occupying an area of 78,867 km². It is situated in the zone of temperate broad-leaved deciduous forest, which in the south-east borders on the forest-steppe zone. Its current vegetation is affected by abiotic conditions such as geology, soil and climate, historical biogeographical processes and human activity.

This paper provides a review of the diversity of Czech vegetation. Previous reviews were published in Czech as introductory chapters to major national botanical monographs (Neuhäusl 1988, Neuhäuslová et al. 1998b, Sádlo 2007), but there is no comprehensive review in another language. Specific information on individual vegetation types is summarized in recent phytosociological overviews, in particular four volumes of the unfinished series *Vegetation survey of the Czech Republic*, which focused on forest vegetation (Moravec 1998, Moravec et al. 2000, Husová et al. 2002, Neuhäuslová 2003), in the monograph *Vegetation of the Czech Republic* (Chytrý 2007, 2009, 2011; www.sci.muni.cz/botany/vegsci/vegetace.php) and *Habitat catalogue of the Czech Republic* (Chytrý et al. 2010b). Czech vegetation was mapped as reconstructed natural vegetation at a scale 1 : 200,000 (Mikyška et al. 1968–1972), potential natural vegetation at 1 : 500,000 (map: Neuhäuslová et al. 1997; Czech explanatory text: Neuhäuslová et al. 1998a; English explanatory text: Neuhäuslová et al. 2001) and actual vegetation as part of

habitat mapping at 1 : 10,000 (Härtel et al. 2009, Chytrý et al. 2010b; mapy.nature.cz). Brief regional accounts of major vegetation types within biogeographical regions of the Czech Republic are provided by Culek (1996). History of the research on vegetation in the Czech Republic is summarized by Krahulec (2012). The taxonomy and nomenclature of species in this paper follow Danihelka et al. (2012) and Kučera et al. (2012).

Abiotic factors

Altitudinal range of the Czech Republic is 115–1602 m a.s.l. (Fig. 1). There are two major geological units in the country (Chlupáč et al. 2011): the Bohemian Massif in the western and central part (Bohemia and western and north-western Moravia) and Western Carpathians in the eastern part (eastern and southern Moravia). The Bohemian Massif is an old mountain system created by Variscan (Hercynian) orogeny in the Late Palaeozoic and is formed mainly of igneous and metamorphic rocks of pre-Permian age such as granite, granodiorite, gneiss and schist, which in places are covered by younger sedimentary or volcanic rocks (Fig. 2). In the Cretaceous the northern half of Bohemia was flooded by a marine transgression. Cretaceous sediments, occurring mainly in the lowlands of northern, central and eastern Bohemia, include two bedrock types: (i) acidic siliceous sandstones, which locally form sandstone pseudokarst with deep gorges and rock towers (Fig. 3), and (ii) calcareous claystones and marlstones. Cretaceous freshwater sediments occur in two large basins in southern Bohemia: Českokubějovická Basin and Třeboňská Basin. By the Tertiary the Bohemian Massif had been weathered to a gently undulating peneplain, but during the Alpine orogeny in the Tertiary it was broken into smaller tectonic units, some of which were elevated, forming mountain ranges especially along what are now the national borders with Austria, Germany and Poland. The highest of these mountain ranges are the Sudetes along the Czech-Polish border, consisting of several more or less isolated mountain groups, most notably the Krkonoše (Giant Mts; 1602 m), Králický Sněžník (1424 m) and Hrubý Jeseník (1492 m). Other prominent mountain ranges are the Krušné Mts (Ore Mts; 1244 m) on the border with Saxony and the Šumava (Bohemian Forest; 1456 m) on the border with Bavaria and Upper Austria. In the Pleistocene local glaciers developed on the highest mountain ranges, forming cirques, some with lakes. However, flat or gently undulating terrain was preserved in large areas of these mountain ranges. In other areas of the Bohemian Massif, most notably those in the southern foothills of the Krušné Mts, large land masses sank during the Alpine orogeny to form basins, which were subsequently filled with Upper Tertiary sediments. Alpine orogeny also caused volcanic activity in the north-western and northern part of the Bohemian Massif, which gave rise to a large area of basalt bedrock in the Doupovské Mts and a number of isolated volcanic hills in the České středohoří Mts, which are formed of both base-rich (e.g. basalt) and acidic (e.g. phonolite) rocks. Since the Upper Tertiary v-shaped river valleys deeply cut in hard, poorly weathering rocks of the Bohemian Massif, forming landscapes of high geodiversity with a broad variety of contrasting vegetation types (e.g. the Vltava, Otava, Lužnice, Berounka, Sázava, Dyje and Jihlava valleys; Fig. 4).

Western Carpathians are separated from the Bohemian Massif by broad elongated depressions, running in a SW–NE direction across Moravia, which are filled with Upper Tertiary and Quaternary sediments. The Czech part of the Western Carpathians is formed

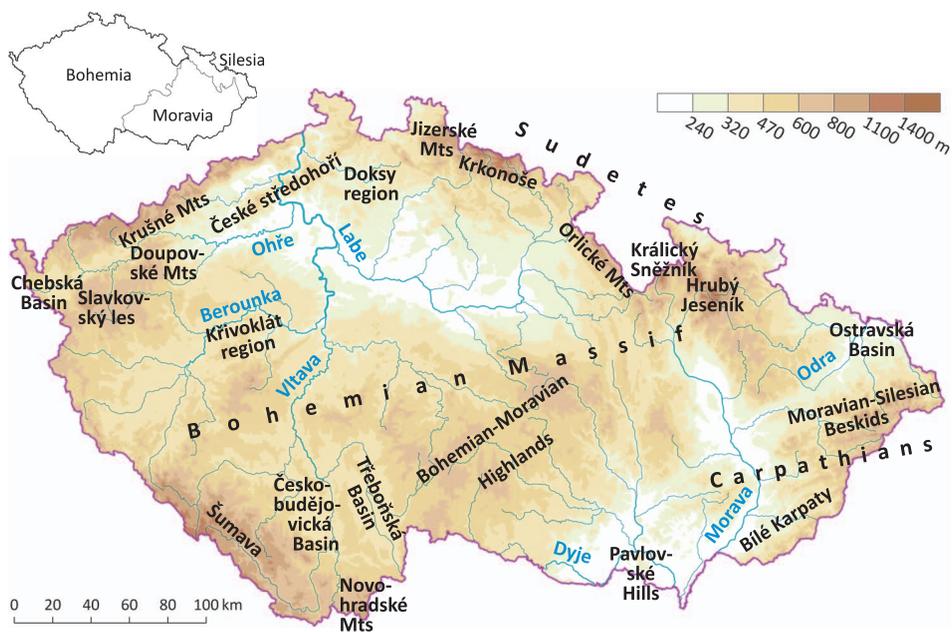


Fig. 1. – Basic topographic map and historical lands of the Czech Republic. See Appendix 1 for a guide to Czech toponyms. All the maps in this paper were prepared by O. Hájek.

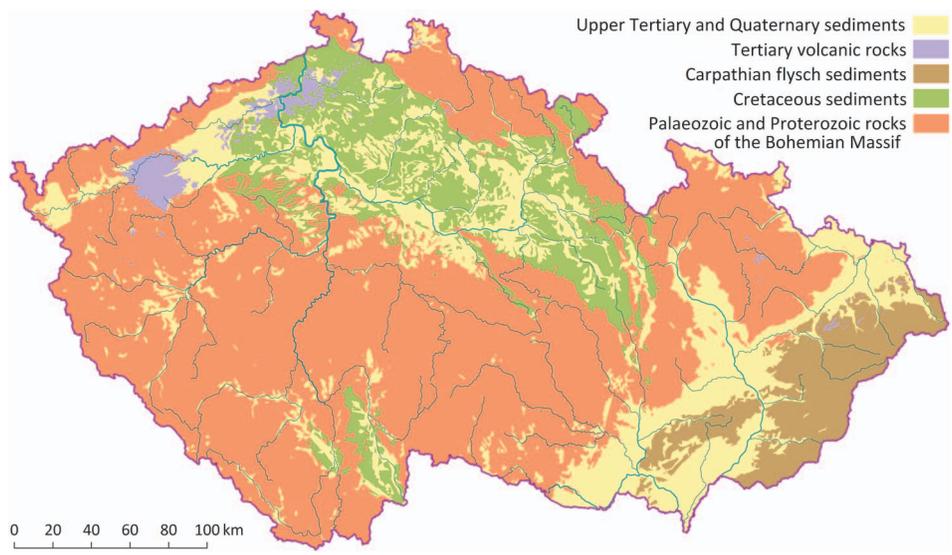


Fig. 2. – Simplified geological map of the Czech Republic (based on the digital geological map 1 : 500,000 – GEOČR500 by Czech Geological Survey 1998).

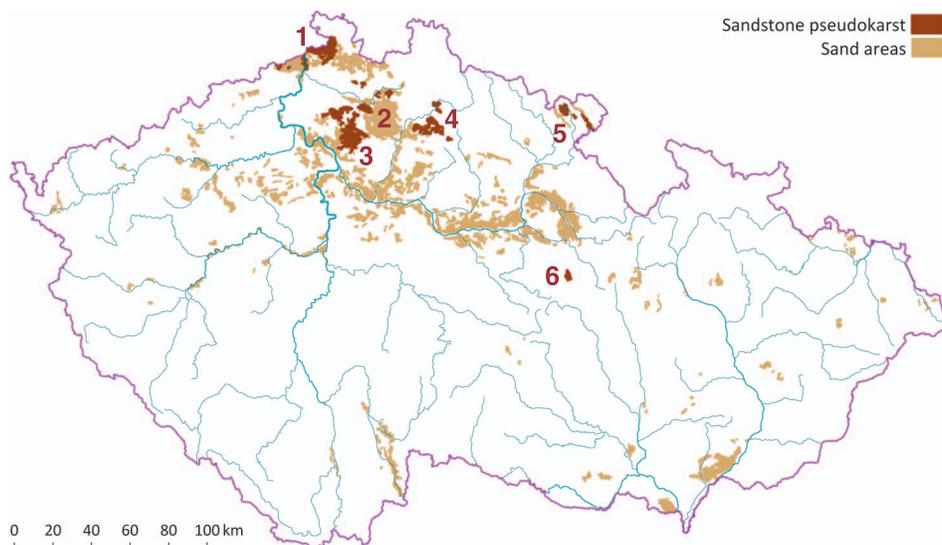


Fig. 3. – Areas of sandstone pseudokarst (based on topographic maps 1 : 50,000) and sand deposits (based on interpretation of the soil map of the Czech Republic provided by Czech University of Life Sciences to the Czech National Geoportal at <http://geoportal.cenia.cz>). (1) Labské pískovce, (2) Hradčanské Cliffs, (3) Kokořín region, (4) Český ráj, (5) Broumov region, (6) Toulovcovy Maštale site.

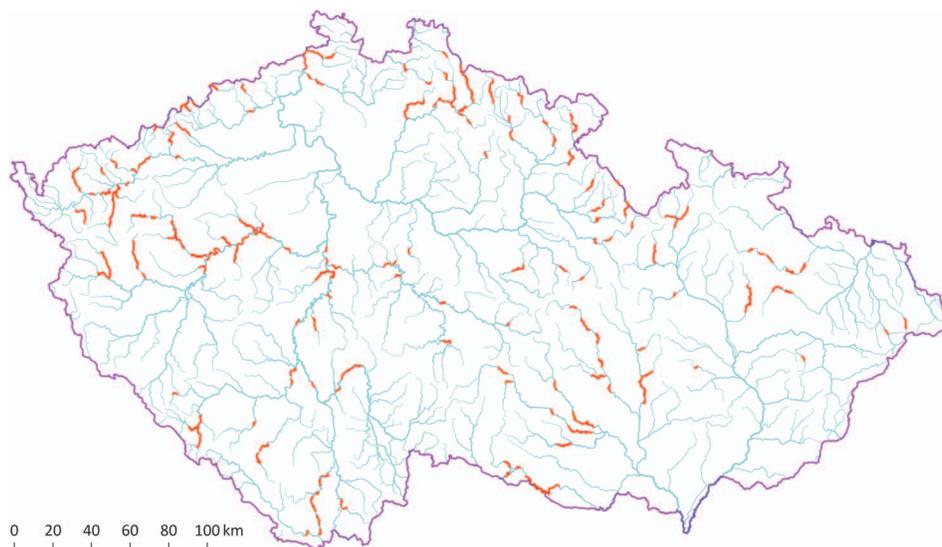


Fig. 4. – Deep river valleys, defined as areas with elevation range larger than 60 m within 300 m on both sides of the river.

of flysch, a bedrock type composed of alternating layers of water-permeable sandstone and impervious claystone of Cretaceous to Lower Tertiary age. These rocks are rather soft and prone to erosion, forming landscapes with broad valleys and gentle slopes. Flysch sediments can be both calcareous (especially in the southern Moravian lowlands and upland fringes) and acidic (especially in the Moravian-Silesian Beskids of north-eastern Moravia). Flysch landscapes are rich in springs and small-scale landslides, and on the calcareous sediments there is a combination of calcareous and relatively wet soils, which is otherwise rare in the Czech Republic. The highest part of the Carpathians in the Czech Republic is the Moravian-Silesian Beskids, which reach an altitude of 1424 m.

Acidic bedrock with cambisol, and less frequently, podzol soils prevails throughout the Czech Republic, especially in the submontane and montane areas of the Bohemian Massif, but also in some lowland areas. Therefore, local occurrences of limestone or other calcareous rocks (Fig. 5) markedly increase local diversity of flora and vegetation. Areas of poorly weathering, hard limestone of Silurian, Devonian or Jurassic age, with well-developed karst features and rendzina soils occur especially in the Bohemian Karst of central Bohemia, and Moravian Karst and the Pavlovské Hills of southern Moravia. Small patches of metamorphic limestone (marble), occurring in association with siliceous metamorphic rocks, are found especially in south-western Bohemia (Šumava foothills), north-eastern Bohemia and western Moravia. Other calcareous rocks include soft sedimentary limestone, calcareous claystone and marl of Cretaceous to Tertiary age, which occur mainly in the lowlands of northern, central and eastern Bohemia and broad valleys and adjacent hilly landscapes fringing the Carpathians. Many areas below 300 m a.s.l. (or below 400 m in the driest regions) are covered by loess, a wind-blown calcareous sediment of Pleistocene age, which supports development of chernozem soil. Another bedrock type with a strong effect on local vegetation diversity is serpentine, a metamorphic rock rich in magnesium and heavy metals, which is toxic for many plant species. Small patches of serpentine occur in various areas of the Bohemian Massif, especially in the Slavkovský les Mts of western Bohemia, south-western Bohemia and the Bohemian-Moravian Highlands. Specific flora and vegetation is confined to sandy areas with dunes, which develop especially along the Labe (Elbe) river in eastern and northern Bohemia, lower Vltava in central Bohemia, Lužnice in southern Bohemia and on the terraces of the Morava and Dyje in southern Moravia (Fig. 3).

The climate in the Czech Republic is temperate oceanic to temperate continental (Rivas-Martínez et al. 2004), with continentality increasing from west to east and from mountains to lowlands. Generally, temperature decreases and precipitation increases with altitude, summer and winter temperatures are positively correlated and so is summer and winter precipitation. Both temperature and precipitation peak in July. Lowlands are warm and dry, with a mean annual temperature of 8–9.5 °C (January mean –2 to 0 °C, July mean 18–20 °C) and annual precipitation of 400–600 mm (Tolasz et al. 2007; Figs 6 & 7). The driest area in the Czech Republic is the middle Ohře valley in northern Bohemia, located in the lee of the Krušné Mts, which receives less than 450 mm of precipitation per year. An exception from the general correlation between high temperature and low precipitation in the Czech lowlands occurs in the Ostravská Basin in north-eastern Moravia, which is warm, but because of its location at the foot of the windward front ridge of the Moravian-Silesian Beskids, it receives 650–800 mm of precipitation annually. The highest areas in the mountains have a mean annual temperature of about 1–2 °C (January mean about –7 to –6 °C, July mean about 8–10 °C) and annual precipitation of 1200–1400 mm.

Vegetation history since the last glacial

During the Pleistocene glaciations the area of the Czech Republic was in a non-glaciated corridor between the continental ice sheet in the north and the extensive mountain glacier in the Alps in the south (Lang 1994). Mollusc fossils in loess sediments suggest that in the coldest and driest periods, lowland areas were covered by continental loess steppe (Ložek 2001). Nevertheless, palaeobotanical data for the last (Weichselian) full glacial provide evidence for refugia of boreal and even some temperate trees. Both charcoal analyses from Upper Palaeolithic sites in southern Moravia (Musil 2003, Willis & van Andel 2004) and pollen analyses of fossil peat deposits from southern and eastern Moravia (Rybníčková & Rybníček 1991, Jankovská & Pokorný 2008), dated to the period of ca 48,000–28,000 cal. yr BP¹, i.e. before the last glacial maximum, indicate common occurrence of boreal coniferous trees such as *Larix*, *Picea*, *Pinus cembra* and *P. sylvestris*, and cold-adapted deciduous trees such as *Alnus* and *Betula*. Rare occurrence of broad-leaved temperate woody species such as *Acer*, *Corylus*, *Fagus*, *Fraxinus*, *Quercus*, *Tilia* and *Ulmus* is also recorded. This indicates that the vegetation and landscape in the Moravian lowlands and Carpathian foothills at that time may have been similar to the modern forest-steppe in the southern Siberian mountain ranges (Kuneš et al. 2008a). In contrast, most landscapes in the Bohemian Massif were probably open at that time, although forest occurred at sites with locally favourable mesoclimate, such as river valleys, as indicated by a fossil record from the Vltava valley in Prague (Jankovská & Pokorný 2008). *Pinus* cf. *mugo*, *P. cembra*, *Picea*, *Alnus*, *Betula* and *Corylus* probably occurred in the valleys of the Krkonoše Mts as high as ca 1000–1100 m a.s.l. before the last glacial maximum (ca 30,000 cal. yr BP; Engel et al. 2010).

Whether these trees and forests survived the last glacial maximum (ca 22,000–16,500 cal. yr BP) is unknown due to the scarce fossil record, however, pollen of *Pinus* cf. *mugo*, *Picea*, *Alnus* and *Betula* is recorded from this period even at a high-altitude site in the Krkonoše Mts (Engel et al. 2010). Late-glacial (ca 16,500–11,500 cal. yr BP) climatic amelioration was marked by the spread of *Pinus sylvestris* and *Betula pendula* to the lowland steppe-tundra landscape with *Betula nana*, *Juniperus* and steppe plants such as *Artemisia*, *Chenopodiaceae* and *Ephedra*; on the floodplains there were fens and tall-herb vegetation with *Cyperaceae*, *Filipendula*, *Polemonium*, *Trollius* and *Veratrum* (Rybníčková & Rybníček 1972, Pokorný 2002a, Jankovská 2006, Kuneš et al. 2008a). There was a large increase in the area covered by forest during the warmer period of Bølling and Allerød, which probably occurred as a single late-glacial interstadial rather than two distinct warm periods in the area of the present Czech Republic (Pokorný 2002a).

The Holocene started with rapid climate warming 11,500 cal. yr BP (Ralska-Jasiewiczowa et al. 2003). Holocene stratigraphy used in the Czech Republic follows either the classical scheme based on pollen zones, detailed for central Europe by Firbas (1949, see also Rybníčková & Rybníček 1996), or a modified scheme proposed by Ložek (1973) based on the study of sediments and fossil molluscs. These stratigraphies recognize periods of the Preboreal, Boreal, Atlantic, Subboreal and Subatlantic (and the Epitlantic as an additional period between the Atlantic and Subboreal in Ložek's stratigraphy), however, their dating differs considerably among authors (Dreslerová in Pokorný 2011: 116).

¹ cal. yr BP = calendar years before present, i.e. before 1950. Dates indicated in radiocarbon years only in the original publications were transformed to calendar years throughout this paper, based on calibration curves published by Reimer et al. (2004, 2009).

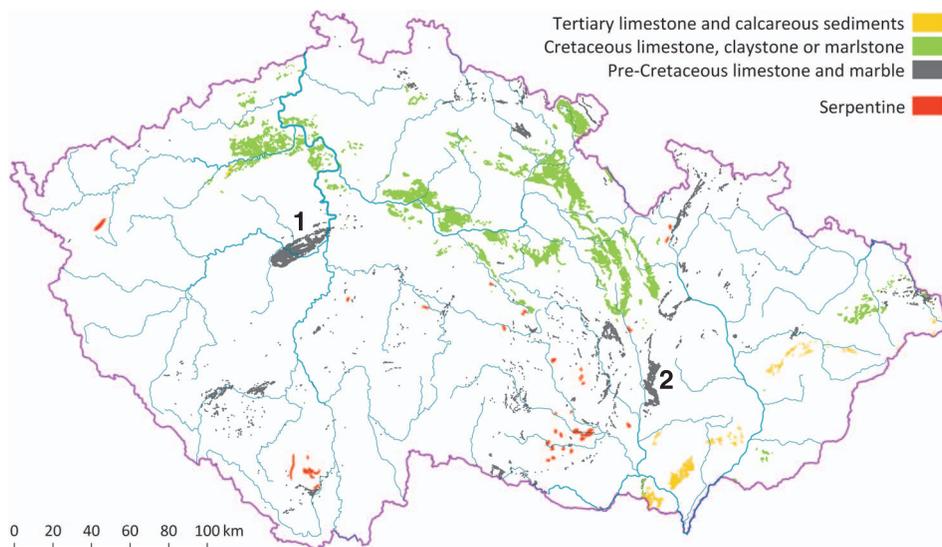


Fig. 5. Areas of limestone, related calcareous bedrock and serpentine (based on digital geological map of the Czech Republic 1 : 50,000 by Czech Geological Survey 2004). The map shows all limestone and serpentine occurrences, including those covered by superficial deposits. (1) Bohemian Karst, (2) Moravian Karst.

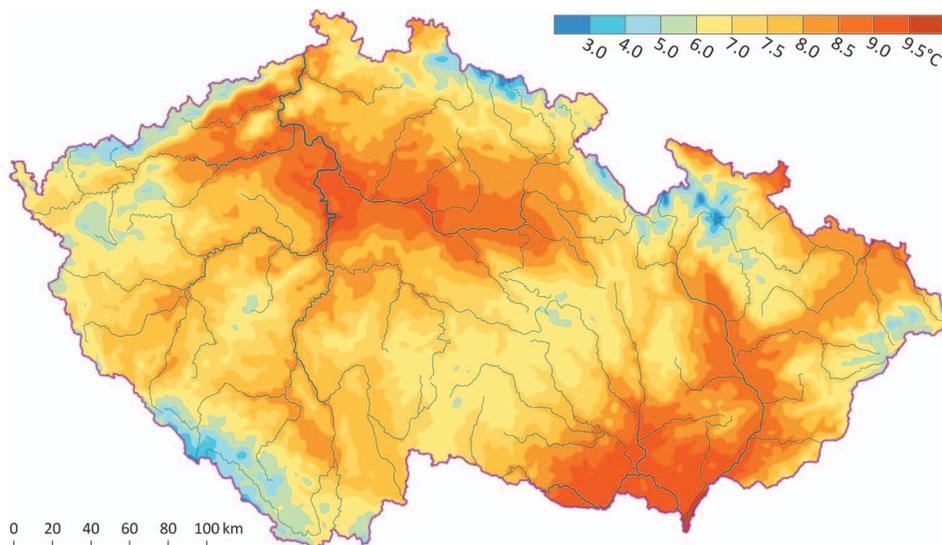


Fig. 6. – Mean annual temperature (based on the source data for the Climate atlas of Czechia, Tolasz et al. 2007, provided by Czech Hydrometeorological Institute).

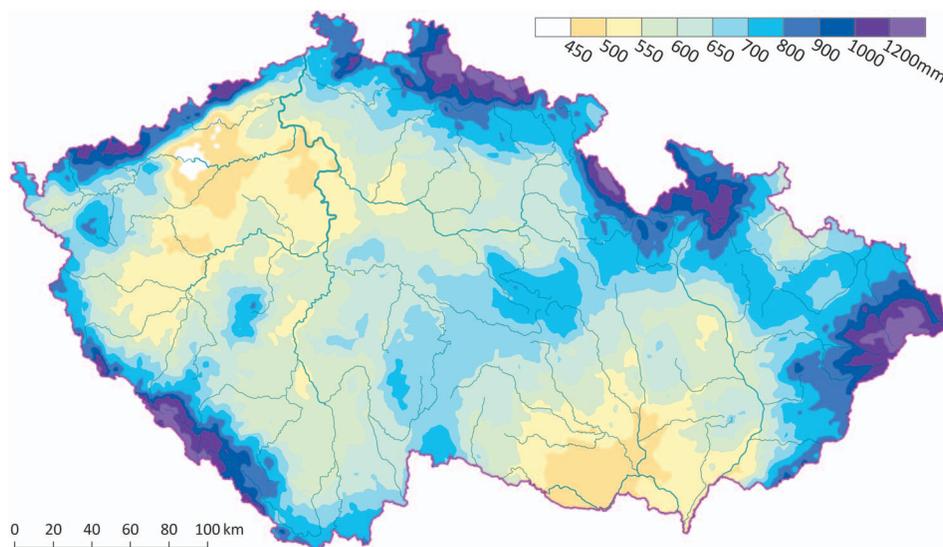


Fig. 7. – Annual precipitation (data source as for Fig. 6).

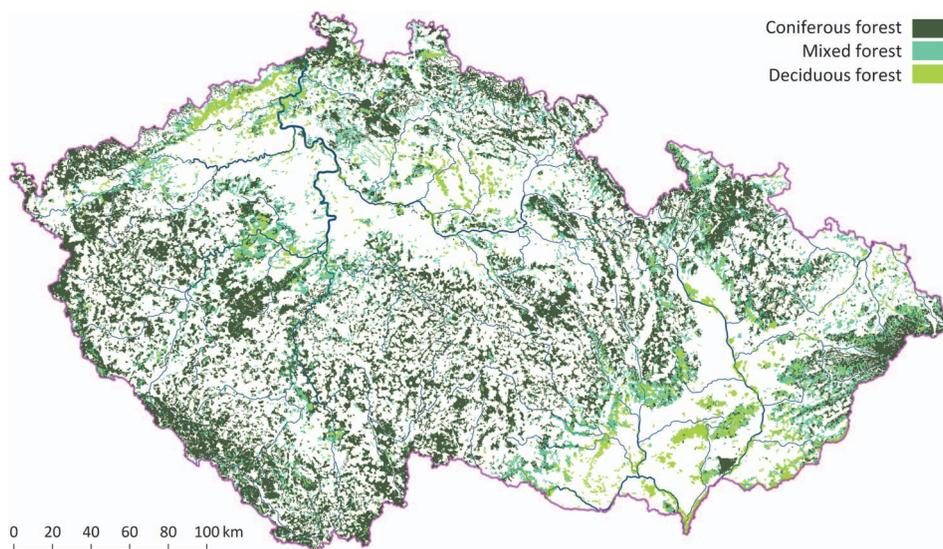


Fig. 8. – Forest cover (based on CORINE Land Cover 2000 data set; Bossard et al. 2000).

Preboreal and Boreal (ca 11,500–8000 cal. yr BP) correspond to the Mesolithic in archaeological stratigraphy. These periods are characterized by a continuous spread of forest in response to climate warming at the Pleistocene/Holocene boundary. Open forests of *Betula pendula* and *Pinus sylvestris* extended their area at the expense of late-glacial open steppe and tundra. Subsequently, *Corylus avellana* and *Ulmus* started to spread to mesic sites (the former may have been partly influenced by the activities of Mesolithic hunter-gatherers; Kuneš et al. 2008b) and *Alnus* on the floodplains. Expansion of *Corylus* and *Alnus* was followed by the spread of broad-leaved temperate trees such as *Acer*, *Fraxinus*, *Quercus* and *Tilia* at low altitudes and *Picea abies* at mid-altitudes and in the mountains. The dense canopy of broad-leaved trees decreased the light available to the herb layer, leading to a decline in light demanding species typical of the herb layer of birch-pine forests and probably also to a decline in overall herb-layer species richness (Chytrý et al. 2010a). Steppe-tundra with *Pinus mugo* and local occurrence of *P. cembra* probably still persisted in the Krkonoše Mts (Tremel et al. 2008).

Atlantic (ca 8000–4500 cal. yr BP) is considered as the Holocene climatic optimum, with mean temperature estimated to have been 2–3 °C higher than today (Ložek 2007). Evidence from fossil tufa formation (Žák et al. 2002) and precipitation of calcareous foam sinter in caves (Ložek 2007) indicates high precipitation. Low-altitude areas were dominated by forests of *Quercus* and noble hardwoods (*Acer*, *Fraxinus*, *Tilia* and *Ulmus*), often referred to by palynologists as a mixed oak forest (*Quercetum mixtum*; Firbas 1949). However, mixed oak forest should not be understood as a single climax community containing both oak and noble hardwoods, because long-term coexistence of light-demanding oak and noble hardwoods, which have high shading capacity at maturity, coupled with shade tolerance when young, is hardly possible in the same undisturbed stands. Most probably oak tended to dominate at dry or disturbed sites while noble hardwoods dominated at mesic sites. The Atlantic was a period of maximum extent of forest at the expense of open land, and consequently it was a bottleneck for survival of late-glacial and early Holocene steppe flora and vegetation in the Czech lowlands. Both floristic evidence and continuous fossil record of steppe snails throughout the Holocene climatic optimum in dry lowland areas (e.g. the western part of the České středohoří and Pavlovské Hills; Ložek 2007) support the view that steppe vegetation was continuously present throughout the Holocene at least in dry areas in northern and central Bohemia and southern Moravia (Sádlo et al. 2005). The floristic evidence includes the large species pool of Czech steppe flora, joint occurrence of many steppe species at the same sites and isolated localities of steppe species far to the west from their continuous range, e.g. *Carex obtusata*, *Helictotrichon desertorum* subsp. *basalticum* and *Stipa dasyphylla*. In the Boreal and early Atlantic, areas of open land may have been maintained by Mesolithic hunter-gatherers (Kuneš et al. 2008b), large herbivores (Vera 2000) or a natural water deficit in dry areas and habitats; however direct evidence for any of these factors is missing. At about 7500 cal. yr BP Neolithic farming began in Moravian and Bohemian lowlands, especially in loess areas, and crop planting and livestock grazing led to significant extension of the area of open land at the expense of forest. However, forest dominated the landscape until the Bronze Age and only in the Iron Age did the open cultural landscape become established in the Czech lowlands (Kaplan et al. 2009, Pokorný 2011). Since the Atlantic, areas at high altitudes followed a sharply different trajectory of landscape and vegetation development than the lowlands because they were not permanently settled by farmers and forest

therefore covered the landscape continuously except for cliffs, mires and the highest mountains. Mid-altitudes were covered by forests of *Acer*, *Fraxinus excelsior* and *Ulmus glabra*, in which an admixture of *Abies alba* and *Fagus sylvatica* started to appear, while areas above 800 m a.s.l. were covered by forests of *Picea abies*. It is possible that due to the favourable climate the timberline was at about 1400 m, i.e. higher than today. Both in the Krkonoše and Hrubý Jeseník Mts *Corylus avellana* was common at high altitudes (Engel et al. 2010, Dudová et al. 2012). A belt of *Pinus mugo* krummholz occurred above the timberline in the Krkonoše (Rybníček & Rybníčková 1994). However, some areas of alpine grassland possibly remained on the highest summits of the Sudetes (Jeník & Lokvenc 1962, Jeník & Hampel 1992, Soukupová et al. 1995, Treml et al. 2010).

Subboreal (ca 4500–2500 cal. yr BP) was probably cooler than the Atlantic and during the later stage after 3400 cal. yr BP, it was also drier (Jäger & Ložek 1968). It corresponds to the latest stage of the Late Neolithic (Copper Age, Eneolithic), Bronze Age and early Iron Age. Density of prehistoric human habitation peaked in the Bronze Age, when new areas were settled in basins and river valleys in western and southern Bohemia (Číšecký & Dreslerová in Pokorný 2011). The Subboreal was characterized by the spread at low altitudes of *Carpinus betulus* from the north-east (Pokorný & Kuneš 2005, Pokorný 2011: 97) and of *Fagus sylvatica* and *Abies alba* at mid-altitudes (Rybníčková & Rybníček 1988). The latter two species gradually outcompeted noble hardwoods (*Acer*, *Fraxinus*, *Tilia* and *Ulmus*) at most sites except on scree slopes and in ravines. At higher altitudes they spread into forests of *Picea abies*, forming mixed spruce-fir-beech forests. Considerable changes in vegetation associated with landscape acidification and retreat of noble hardwoods occurred in the Bronze Age, especially on acidification-prone substrates such as Cretaceous sandstones and sandy-gravelly river terraces in the northern half of Bohemia (Ložek 1998, Pokorný 2005, Pokorný & Kuneš 2005). In some areas this change may have been due to human activity such as logging and forest grazing, but in scarcely populated regions, such as Labské pískovce or the Broumov region it may have been due to suppression of noble hardwoods by competitively stronger, spontaneously spreading *Fagus* and *Abies*. Unlike other trees, *Acer*, *Fraxinus*, *Tilia* and *Ulmus* produce leaf litter rich in calcium citrate, which provides easily accessible calcium to the ecosystem. When these trees retreat, calcium cycling in ecosystem is reduced (Wäreborn 1969) and acidophilous forest replaces previous nutrient-rich forest.

Subatlantic (ca 2500 cal. yr BP to present) is a period with a climate roughly corresponding to the present, although with some fluctuations such as the cold period of the Little Ice Age (16–19th century AD). It corresponds to the late Iron Age, Roman, Migration, Medieval and Modern Periods. Around 2000 cal. yr BP, lowland areas in Bohemia and Moravia were dominated by forests of *Quercus* and *Carpinus betulus*, with a significant presence of *Abies alba* and *Fagus sylvatica* (Pokorný 2002b). Mid-altitudes were covered by forests of *Fagus sylvatica* and *Abies alba* (Rybníček & Rybníčková 1978, Kozáková et al. 2011). *Picea abies* was common in mixed forests in the mountains, but it also occurred in locally suitable habitats at mid-altitudes and rarely also in the lowlands (Pokorný 2002b). The spread in the Subatlantic of some trees, especially hornbeam, fir and pine, and to some extent also beech, was probably influenced by humans (Pokorný 2005). Hornbeam easily regenerates by resprouting and therefore was favoured by coppicing and other forest disturbances. Fir establishes from seed on mineral soil and it is probably less preferred than broad-leaved trees by domestic livestock, therefore it may have been favoured

by litter raking and grazing in forests (Málek 1983, Vrška et al. 2009). Human population density was high in the Iron Age, which resulted in a large-scale deforestation in low-altitude areas (Pokorný 2011). However, the human population decreased in the Roman Period and especially in the Migration Period (5–6th century AD). Until the 12th century AD human settlements were concentrated in the lowlands and upland fringes, however, localized human activity is supposed even in areas above 1000 m in some of the periods between the Iron Age and Early Medieval (Speranza et al. 2000, Novák et al. 2010). Nevertheless, large-scale colonization of mid-altitude areas occurred only in the High Medieval, mainly in the 13–14th centuries (Klápště 2006). The settlement and associated deforestation of upland areas proceeded more or less continuously, with the exception of the flat summits of the flysch Carpathians, which were colonized at the same time as the valleys and used as communal pasture lands. Unlike in the Bohemian Massif, the forest belt between the deforested valleys and mountain summits was usually preserved in the Carpathians. Higher mountain areas were colonized only in the 16–17th centuries, when chalets were built in the Krkonoše Mts (Lokvenc 1978) and deforested areas on the Carpathian summits were extended by the Wallachian colonists (Rybníček & Rybníčková 2008). Today forests cover 34.9% of the area of the Czech Republic; however, most of them are coniferous plantations (ÚHÚL 2007; Fig. 8).

Biomes

The most widespread biome in the Czech Republic is broad-leaved deciduous forest, which is predominant over most of western and central Europe. Other biomes occupy restricted areas, including continental forest-steppe, which is at the western edge of its Eurasian distribution, and extrazonal occurrences of boreal coniferous forest (taiga) and tundra (Fig. 9).

Broad-leaved deciduous forest biome occurs from the lowlands up to 1000–1200 m a.s.l., but is absent from dry and warm lowlands. Dominant zonal types of natural vegetation are forests of *Fagus sylvatica* with an admixture of *Abies alba* at middle and higher altitudes and of *Carpinus betulus* at low altitudes. Other broad-leaved trees (*Acer platanoides*, *A. pseudoplatanus*, *Alnus glutinosa*, *A. incana*, *Fraxinus excelsior*, *Quercus petraea*, *Q. robur*, *Tilia cordata*, *T. platyphyllos*, *Ulmus glabra* and *U. laevis*) occur especially at sites where the composition of tree species has changed as a result of past forest management or natural disturbances, or at azonal sites such as floodplains, scree slopes, ravines, rock outcrops and dry slopes with shallow soil. Natural treeless vegetation is very rare and spatially restricted, e.g. on cliffs. Large areas of potential broad-leaved forest are now covered by coniferous plantations, arable land and different types semi-dry, mesic and wet grasslands.

Forest-steppe biome is found in two lowland areas of the Czech Republic that are characterized by a dry and warm climate. Forest-steppe of northern and central Bohemia, which occurs in the rain shadow of the Krušné Mts, is an isolated extrazonal occurrence of this biome. In contrast, forest-steppe in southern Moravia, which occurs in the less pronounced rain shadow of the Bohemian-Moravian Highlands, is a part of the continuous forest-steppe area that extends from the Pannonian Basin through eastern Austria and south-western Slovakia to southern Moravia. These two forest-steppe areas in the Czech

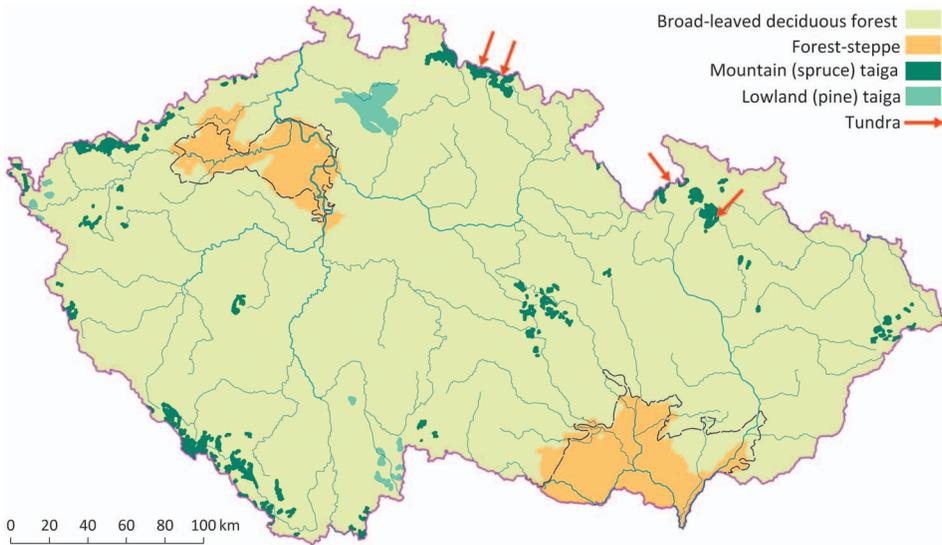


Fig. 9. – Approximate distribution of Czech biomes. Forest-steppe biome is delimited in two ways: (1) areas with annual precipitation lower than 525 mm and mean annual temperature higher than 8.25 °C (following Tolasz et al. 2007; yellow area) or (2) as grouped phytogeographical districts with predominance of forest-steppe vegetation (following Skalický 1988; black broken line). The taiga areas are partly delimited based on the interpretation of mapping units corresponding to this biome in the Map of potential natural vegetation (Neuhäuslová et al. 1997). Tundra biome is delimited as areas above the natural timberline; because of their small size, they are indicated by red arrows.

Republic are generally characterized by an annual precipitation lower than approx. 525 mm and a mean annual temperature higher than 8.25 °C. The temperature regime of the Bohemian forest-steppe is less continental than that of the Moravian forest-steppe: the former has a warmer winter and cooler spring, summer and autumn, but these differences do not exceed 1 °C of mean monthly temperature values (Tolasz et al. 2007). Forest-steppe is characterized by a mosaic of forest and open land. Forests include *Quercus pubescens* and *Q. petraea* forests on dry soils, *Carpinus betulus* forests on mesic soils and floodplain forests along rivers. Treeless vegetation includes various types of steppe, ranging from rock-outcrop steppe through short-grass steppe with *Festuca* and *Stipa* (on shallow rendzina/ranker or deep chernozem over loess) to semi-dry tall-grass steppe with *Brachypodium pinnatum*. There are intermittently wet meadows on the floodplains and different types of dry to mesic scrub are common at various sites. This biome also includes inland saline vegetation around mineral springs and shallow lakes, which was nearly destroyed by draining except for the few remaining fragments. Vegetation of forest-steppe landscapes has been continuously managed by humans since the onset of the Neolithic. Large areas of chernozem steppes were converted into arable land and the area of forest reduced. Therefore, the relative extent of forest and non-forest areas under natural conditions is unknown.

Taiga biome occurs in extrazonal patches of natural coniferous forest in the belt between the broad-leaved forests and timberline in the mountains, and in some lowland basins. Mountain taiga, dominated by *Picea abies* (dark taiga), occurs on high mountain ranges. In flat areas, especially on the summit plateau of the Šumava Mts, spruce forests are associated with bogs, either open or covered with shrubby *Pinus mugo* or arboreal *Pinus uncinata* subsp. *uliginosa*. The replacement vegetation of the mountain taiga includes low-productive grasslands. Lowland taiga occurs in the basins in the Doksy region in northern Bohemia, Chebská Basin in western Bohemia and Třeboňská Basin in southern Bohemia. The mean altitude of the bottoms of these basins is around 290 m in the former and around 450 m in the latter two. All of these basins are characterized by nutrient-poor acidic bedrock (siliceous sand, sandstone, but also less acidic clay), frequent accumulations of cold air resulting in temperature inversions and a high water table, which is currently maintained by the system of fishponds built in the Medieval and early Modern Period. Dominant vegetation in the lowland taiga is acidophilous forest of *Pinus sylvestris* with *Vaccinium* spp. (light taiga) and local admixtures of *Picea abies* and broad-leaved deciduous trees, especially *Quercus petraea* or *Q. robur*. These areas of lowland taiga also contain bogs, most of which are forested with *Pinus uncinata* subsp. *uliginosa* or *P. sylvestris*, and minerotrophic mires. Although the persistence of lowland taiga may be partly due to human activity (nutrient depletion by litter raking and forest grazing, replacement of broad-leaved trees by pine), it can be a natural vegetation type especially in the Doksy region, which was poorly inhabited because of its infertile soils (predominantly lowland podzols). Analyses of fossil charcoal and pollen records from the Doksy region indicate that pine forests dominated this area throughout the Holocene, possibly maintained by recurrent wildfires (Jankovská 1992, Novák et al. 2012).

Tundra biome occurs as alpine tundra only on the highest summits of the Sudetes (Krkonoše, Králický Sněžník and Hrubý Jeseník Mts), being a remnant of a presumably larger area of this biome at middle to high altitudes in the full glacial. The hypothesis of continuous occurrence of the tundra biome on the Krkonoše summits throughout the Holocene is supported by the occurrence of patterned grounds (Tremel et al. 2010), which would probably be destroyed if overgrown by forest. Further support for this hypothesis is the occurrence of presumably relict tundra species (e.g. *Carex bigelowii*, *Pedicularis sudetica* and *Rubus chamaemorus*) and of neoendemics of the genus *Hieracium* confined to open tundra habitats (Soukupová et al. 1995). The alpine tundra includes mainly grasslands consisting of *Avenella flexuosa*, *Festuca supina* and *Nardus stricta*, and heathlands of *Calluna vulgaris*. The surface microtopography of the mires on the summit plateaus of the Krkonoše Mts is similar to the string-and-flark pattern of Scandinavian aapa mires (Jeník & Soukupová 1992).

Altitudinal vegetation belts

In general, altitude is correlated with both temperature (negatively) and precipitation (positively) in the Czech Republic: low altitudes are usually warm and dry, whereas high altitudes are cool and wet. However, there are some anomalies, especially at low altitudes, most notably in the low-altitude region in north-eastern Moravia. Therefore, altitudes of individual vegetation belts can vary among regions and altitudinal ranges of individual

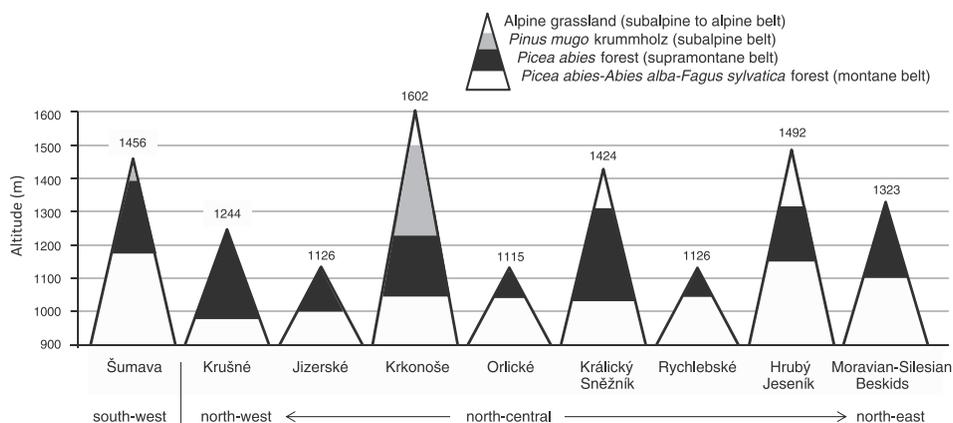


Fig. 10. – Altitudinal belts and timberline in the summit areas of the highest Czech mountain ranges. Altitudes of the highest peak of each range are given. The scheme represents entire mountain ranges including the parts outside the borders of the Czech Republic (based on data from Jirásek 1996a, Neuhäuslová et al. 1997, Tremel & Banaš 2000 and Neuhäuslová 2001).

belts can broadly overlap if compared across the country. Consequently, there are different classifications of vegetation belts in Czech botanical and geographical literature (Holub & Jirásek 1967, Kučera 2000). Currently the most widely accepted classification is the one proposed by Skalický (1988) with eight vegetation belts:

Lowland belt includes areas adjacent to large lowland rivers at altitudes below 210 m, locally below 240 m, with floodplain forests, wetlands, inundated meadows, sandy grasslands and saline habitats. Main crops include wheat, oil-seed rape, maize, sugar beet, vegetables, barley, grapes, hop and thermophilous fruit trees such as apricots and peaches.

Colline belt includes upland areas at altitudes below 500 m, although on some hills in dry and warm areas this belt occurs locally at higher altitudes. Typical vegetation is thermophilous oak forests, oak-hornbeam forests, steppe grasslands and dry scrub. The lowland and colline belts include the entire area of the forest-steppe biome and also some low-altitude areas of the broad-leaved deciduous forest biome. The spectrum of planted crops is similar to that in the lowland belt.

Supracolline belt overlaps the colline belt in its altitudinal range, but occurs in cooler and wetter areas, especially in basins or on upland plateaus. It is characterized by oak-hornbeam, acidophilous oak, fir and beech forests, and in basins also by mires. Deforested areas were converted not only into arable land but also different types of wet, mesic or dry grasslands. Main crops include oil-seed rape, wheat, barley, rye and potatoes. Fruit trees are mainly apples, pears, cherries and plums.

Submontane belt occurs mainly between 450 and 800 m a.s.l., although it can locally occur at higher or lower altitudes. It is dominated by beech or fir-beech forests, in deforested areas also by mesic and wet meadows and pastures. Main crops are wheat, barley, oats, rye, potatoes and oil-seed rape; fruit trees are the same as in the supracolline belt.

Montane belt includes mainly areas at altitudes of 750–1100 m. It is characterized by fir-spruce-beech forests and spruce forests at water-logged sites in association with minerotrophic mires and bogs. Replacement vegetation includes mesotrophic and oligotrophic grasslands used for grazing or hay making. In the past potato fields occurred in this belt mainly at lower altitudes, but they were converted to grasslands in the 1990s.

Supramontane belt at altitudes 1000–1370 m is dominated by natural spruce forests. In the northern mountain ranges the altitude of this belt increases with climate continentality from the west (Krušné Mts) to the east (Moravian-Silesian Beskids), and the belt also occurs at higher altitudes in the Šumava (Fig. 10). Deforested areas are used as low-productive meadows and pastures.

Subalpine belt ranges from 1200 to 1500 m. In the Krkonoše Mts it consists of a nearly continuous belt of *Pinus mugo* krummholz, but it also includes birch-willow scrub, tall-forb vegetation and grasslands in the cirques, open park-like woodland at the timberline and closed grasslands of *Avenella flexuosa*, *Calamagrostis villosa*, *Deschampsia cespitosa*, *Molinia caerulea* and *Nardus stricta* above the timberline.

Alpine belt is not a continuous vegetation belt in the Czech mountains, although alpine vegetation types occur on the highest summits, especially in the Krkonoše. They include open lichen-rich grasslands of *Festuca supina* or heathlands of *Calluna vulgaris*, as well as boulder fields with predominantly cryptogamic vegetation.

Landscapes with a high diversity of vegetation types

About 60% of the landscape of the Czech Republic is flat or gently undulating at altitudes of 200–600 m and covered with a mosaic of forests, arable land, meadows and pastures. The mountain areas characteristically have rounded ridges and extensive plateaus very different from the rugged landscapes in the Alps and Inner Carpathians. Gently undulating landscapes in the Czech Republic are characterized by a low diversity of vegetation types. However, there are some restricted areas of high topographic heterogeneity, geological diversity or occurrence of bedrock types with sharply different effects on vegetation than the bedrock types predominating in the wider landscape (Kučera 2005, Ložek 2011; Fig. 11). In particular, they include:

Deep river valleys of the Bohemian Massif are incised in a gently undulating landscape formed of metamorphic and igneous rocks, mainly gneiss or granite. They are up to 200 m deep, with a v-shaped cross-section and numerous deeply entrenched meanders. They have a narrow, discontinuous floodplain, which only occurs on the inner banks of meanders or along some straight sections, being replaced by steep slopes adjacent directly to the river above the outer banks of meanders. Vegetation in these valleys is diverse and relatively well preserved in a natural or semi-natural state as this rugged terrain is unsuitable for agriculture. Best examples of the natural/semi-natural vegetation in these valleys are found in the Vltava valley in southern and central Bohemia (Jeník & Slavíková 1964, Zelený 2008) and adjacent lower sections in the Otava and Lužnice valleys, Berounka valley in western and central Bohemia (Sofron 1967, Kolbek et al. 1997, 1999, 2001, 2003), Sázava valley in central Bohemia, and valleys in south-western Moravia, especially of the Jihlava and Dyje rivers (Chytrý & Vicherek 1995, 1996, 2003, Tichý 1997; Fig. 4). These valleys are generally warmer than the surrounding landscape, but there are relatively cool

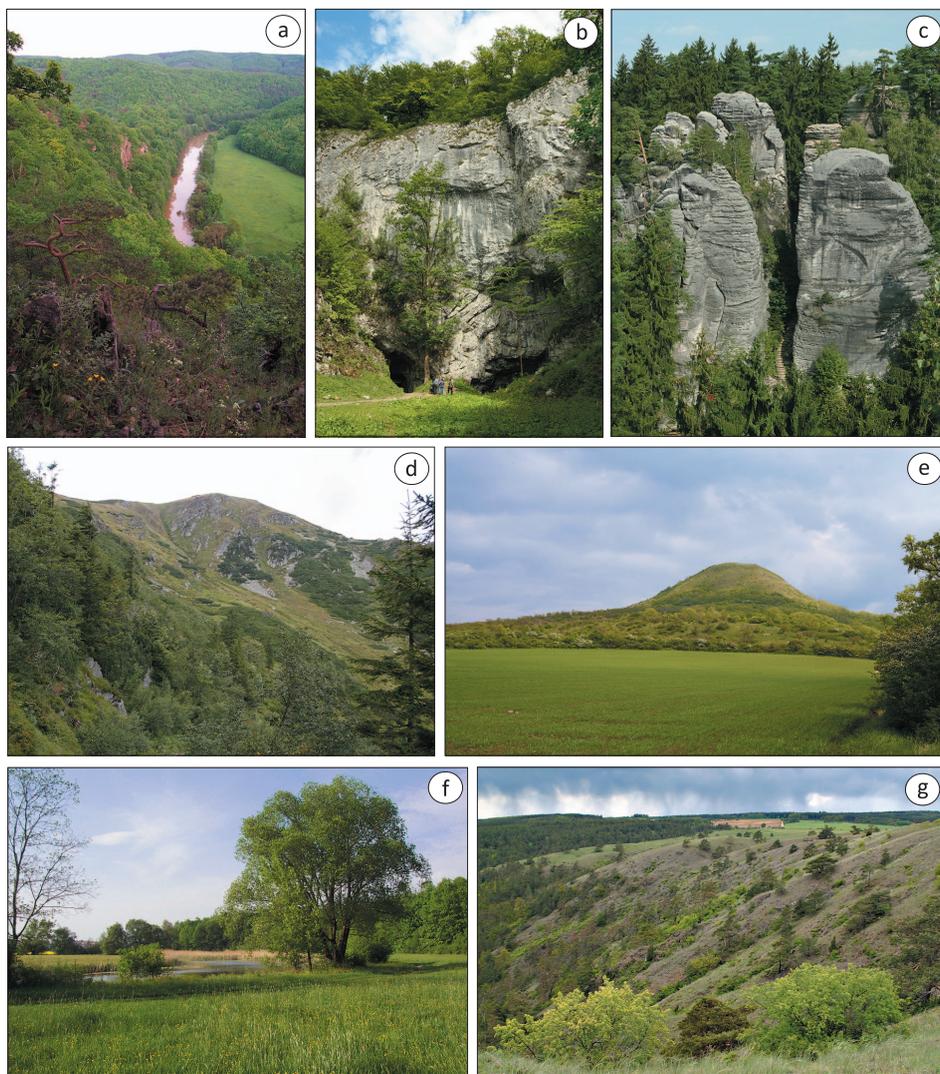


Fig. 11. – Examples of landscapes with a high diversity of vegetation types: (a) deep valley of the Dyje river, southern Moravia; (b) Moravian Karst, southern Moravia; (c) sandstone pseudokarst in the Prachovské Rocks, eastern Bohemia; (d) Kotelní jámy cirque in the Krkonoše Mts, eastern Bohemia; (e) Oblík volcanic hill in the České středohoří Mts, northern Bohemia; (f) floodplain of the lower Morava river, southern Moravia; (g) Mohelno serpentine steppe, southern Moravia.

sites on the north-facing lower slopes (Chytrý & Tichý 1998). Distribution of forest vegetation in the valleys is strongly determined by topography, namely slope, aspect and position on the upper or lower slopes or at the bottom (Jeník & Slavíková 1964, Chytrý & Vicherek 1996, Tichý 1999, Zelený & Chytrý 2007). Heterogeneous mosaics of vegetation types occur especially along meandering sections of rivers. South-facing upper slopes

support thermophilous oak forests, whereas the opposite north-facing slopes are covered by beech or acidophilous oak forests. Lower parts of the valleys contain ravine forests on steeper slopes or oak-hornbeam forests on moderate slopes. Higher river terraces on the floors of the valleys are covered with oak-hornbeam forests, while there are riverine alder forests on the lower terraces. Open patches of grassland and scrub vegetation occur in some places at the upper edges of valley slopes, especially those with a southern aspect (Kučera & Mannová 1998). The diversity of flora and vegetation is locally enriched in places where there are outcrops of base-rich rocks such as metamorphic limestone, serpentine, amphibolite or spilite. In many places river terraces have been deforested and converted into mesic meadows.

Karst areas occur locally in the colline and supracolline belts in the Czech Republic. They are formed mainly of limestone of Silurian to Jurassic age, whereas dolomites are nearly absent in the country. The largest areas with well-developed karst features include the Bohemian Karst in central Bohemia, the Moravian Karst in central Moravia and the Pavlovské Hills in southern Moravia. These three areas differ in terms of precipitation, which is highest in the Moravian Karst and lowest in the Pavlovské Hills (Fig. 5). Vegetation reflects the differences in humidity. Moravian Karst is dominated by beech forests and contains small areas of oak-hornbeam forests, ravine forests and patches of thermophilous oak forests associated with dry grasslands on some south-facing upper slopes (Šmarda 1967). It is a plateau dissected by deep karst valleys that because of topographic shading contain patches of submontane-montane vegetation. In contrast, the Pavlovské Hills is an isolated limestone ridge in the middle of a dry and warm forest-steppe landscape. In this area there are extensive steppes (Unar 2004), some of them probably natural, thermophilous oak forests, oak-hornbeam forests and ravine forests; however, beech forests are absent (Horák 1969). The Bohemian Karst is intermediate between these two extremes, with a mosaic of different vegetation types ranging from steppes to beech forests (Skalický & Jeník 1974). The typical vegetation in all karst areas is *Sesleria caerulea* grassland with thermophilous or steppe species, occurring mainly on north-facing cliffs and limestone outcrops (Zlatník 1928).

Sandstone pseudokarst occurs at several sites at the margins of the area of Cretaceous sediments in northern, central and eastern Bohemia (Fig. 3). Most notable examples are in (i) Labské pískovce (Elbe Sandstone Mts), including the České Švýcarsko (Bohemian Switzerland) National Park, in northern Bohemia, (ii) Hradčanské Cliffs in northern Bohemia (Sýkora 1970, Sádlo et al. 2011), (iii) Kokořín region in central Bohemia (Kučera & Špryňar 1996, Sádlo 1996), (iv) Český ráj (Bohemian Paradise) region in central and eastern Bohemia (Slavík 1977), (v) Broumov site in eastern Bohemia (Sýkora & Hadač 1984) and (vi) Toulouvcovy Maštale site in eastern Bohemia (Neuhäusl & Neuhäuslová-Novotná 1972). The altitude of these landscapes ranges from about 140 m (Labské pískovce) to about 600 m (Broumov region). Cretaceous sandstones are predominantly siliceous, acidic and nutrient-poor; only in a few places do they contain spatially restricted layers enriched with calcium carbonate, especially in the area of the Hradčanské Cliffs (Sádlo et al. 2011). Sandstone pseudokarst landscapes in their mature developmental phase, called 'rock cities', are made up of 100 m deep, narrow canyons and dry gorges, which dissect sandstone plateaus, and isolated sandstone towers, protected from weathering by surface hardening caused by silica impregnation (Čílek & Kopecký 1998, Härtel et al. 2007). These landscapes contain a broad variety of different vegetation types occurring on

different landforms, although most of them are rather poor in species, a feature typical of acidic bedrock (Härtel et al. 2007). Sandstone plateaus at lower altitudes may be locally covered with loess (e.g. in the Kokořín region) and such places support oak-hornbeam or thermophilous oak forests. However, the predominant vegetation in sandstone pseudokarst landscapes are acidophilous oak, beech or pine forests (*Quercion roboris*, *Luzulo-Fagion sylvaticae* or *Dicrano-Pinion sylvestris*). Sandstone gorges are dominated by acidophilous beech forest. Growing locally at the bottom of the gorges are alder galleries along the creeks and, in shaded deep gorges, wet spruce forests with montane plant species or small mires (Kuneš & Jankovská 2000), especially in the Broumov region. Patches of naturally open vegetation are found on the upper edges of sandstone cliffs, steep rock faces and shaded bottoms of deep gorges, where moss litter from polsters falling from the weathering cliffs accumulates (Zittová-Kurková 1984, Herben 1992, Sádlo 1996) or accumulations of sand from the weathering of the cliffs form cones that are subject to erosion and support a primary succession of bryophytes, dwarf shrubs and herbs (Gutzerová & Herben 2001).

Solitary volcanic hills occur scattered across northern Bohemia, with the highest concentration in the České středohoří Mts. They are formed of either base-rich basalt or base-poor phonolite (or related trachytic rocks), both of Tertiary origin. Cretaceous sandstones or marlstones are usually found at their bases. Relative elevation of these hills above the surrounding landscape is often higher than 250 m and altitudes of the summits are mostly between 400 and 700 m (the highest hill is Milešovka; 837 m a.s.l.). Vegetation on volcanic hills depends on slope, aspect, position on lower or upper slope, bedrock (basalt versus phonolite) and local occurrence of cliffs or boulder screes. Upper parts of the south-facing slopes of many hills are naturally treeless, especially in the precipitation-poor forest-steppe landscape in the south-western part of the České středohoří, where south-facing slopes are covered by short-grass steppe (*Festucion valesiacae*) and north-facing slopes by woodland (Slavíková et al. 1983). In areas with a higher precipitation, located more to the east, especially in the highest part of the České středohoří (Milešovka hill) and east of the Labe river, the natural vegetation of the volcanic hills is mainly beech, oak-hornbeam or ravine forest (*Fagion sylvaticae*, *Carpinion betuli* and *Tilio platyphylli-Acerion*), while treeless areas are small, usually restricted to south-facing cliffs near the tops of the hills (Kolbek 1978) with boulder screes below them (Cílek 1998). There are several light-demanding species with isolated occurrences in these treeless areas (Kolbek & Petříček 1972, 1979, Petříček & Sýkora 1973, Sýkora 1979), which suggests a continuous existence of patches of open vegetation throughout the Holocene.

Glacial cirques occur at altitudes of 1000–1500 m in the highest mountain ranges in the Czech Republic: the Šumava and Sudetes (Krkonoše, Králický Sněžník and Hrubý Jeseník). They occur on massifs of siliceous rocks (phyllite, mica schist, gneiss and granite), on north-eastern to south-eastern slopes of the highest ridges or plateaus, i.e. in leeward positions where snow accumulated in the colder periods of the Pleistocene and resulted in the formation of small glaciers. Cirques in the Šumava Mts occur below the timberline and are covered mainly by spruce and beech forest and small patches of treeless vegetation, especially stands of the tall fern *Athyrium distentifolium* (Sofron & Štěpán 1971). At the bottoms of these cirques there are mesotrophic lakes, two of them with occurrence of quillworts (*Isoetes echinospora* and *I. lacustris*; Husák et al. 2000). Cirques in the Sudetes occur from the beech forest zone near their bottoms to the areas above the

timberline. They are treeless in the central part due to periodical disturbances by avalanches. There are a great variety of landforms in the cirques with slopes of different aspect and inclination, cliffs, boulder screes and bottom areas with accumulation of fine soil. Soft-water springs are scattered on the slopes of the cirques and there are small outcrops of base-rich rocks such as porphyry or metamorphic limestone in some of them. Due to their leeward position cirques are protected from strong wind and have a warmer mesoclimate than the adjacent mountain slopes and summits (Jeník 1961). In winter there is deep snow cover, which protects the plants from frost; however, there are few areas where the snow covers the ground until summer (Jeník 1958, Hejcman et al. 2006a). Snow-bed vegetation is nearly absent except for some fragmentary stands with *Gnaphalium supinum* in open *Nardus stricta* grassland. Vegetation in the cirques in the Sudetes, especially in the Krkonoše and Hrubý Jeseník, is very diverse (Jeník 1961, Jeník et al. 1980). There are various types of tall-herb subalpine vegetation dominated by forbs (alliance *Adenostylin alliariae*), grasses (*Calamagrostion villosae* and *Calamagrostion arundinaceae*) and ferns (*Dryopterido filicis-maris-Athyrium distentifolii*), *Vaccinium myrtillus* heaths (*Genisto pilosae-Vaccinion*), deciduous scrub of *Betula carpatica* and *Salix silesiaca* adapted to avalanche disturbance (*Salicion silesiaca*), *Pinus mugo* krummholz (*Pinion mugo*), rock-outcrop grasslands (*Agrostion alpinae*), shallow mires (*Caricion canescenti-nigrae*) and spring vegetation (*Swertio perennis-Dichodontion palustris*). Spruce and beech forests (*Piceion abietis*, *Fagion sylvaticae* and *Luzulo-Fagion sylvaticae*) grow on milder slopes of the cirques and on the moraines at the bottom. Lakes are absent in the cirques in the Sudetes, however, there are lakes in those on the Polish side of the Krkonoše Mts and there used to be a lake in the Labský důl valley in the Krkonoše that disappeared as a result of a natural in-filling during the Atlantic period (Jankovská 2004, Engel et al. 2010). There are a remarkable number of thermophilous species typical of low altitudes and peculiar plant communities of alpine, subalpine and lowland species in the cirques in the Sudetes. *Calamagrostis arundinacea* grasslands on the warm slopes of cirques (*Calamagrostion arundinaceae*), which are particularly rich in these species, contain higher numbers of species than any other vegetation type in the Czech mountains. Jeník (1959, 1961) suggests that propagules of thermophilous species were transported to the cirques from the western foothills of the mountain ranges by topographically modified wind currents ('theory of anemo-orographic systems'; see also Jeník 1997).

Lowland riverine landscapes occur especially along the middle Labe river and lower courses of its tributaries the Vltava and Ohře (Neuhäuslová-Novotná 1965) and along the middle and lower Morava and lower courses of other rivers in southern Moravia (Dyje, Jihlava and Svatka; Vicherek 1962b, Vicherek et al. 2000). Floodplains of these rivers have been strongly modified by floods and associated accumulation of loamy sediments. The incidence of floods increased after the deforestation of submontane and montane areas that occurred in the Medieval (Opravil 1983, Štěrbá et al. 2008, Ložek 2011). Typically the rivers flood after snowmelt in March–April and occasionally after heavy rainfall in summer or other periods of the year. The incidence of floods has declined during the last decades as a result of regulating the rivers. Lowland alluvial landscapes contain a rich mosaic of aquatic vegetation in oxbows and pools (*Lemnetea* and *Potametea*), reed and tall-sedge marshes (*Phragmito-Magno-Caricetea*), productive meadows (*Deschampsion cespitosae*) that are inundated in spring but may dry out in late summer when the water table is more than 1 m below ground level (Balátová-Tuláčková 1968), softwood

floodplain forests with *Salix alba* or, very rarely, also with *Populus nigra* (*Salicion albae*), and hardwood floodplain forests with *Fraxinus excelsior*, *Quercus robur* and *Ulmus laevis*, and in southern Moravia also with *Fraxinus angustifolia* (*Alnion incanae*). Some terraces of the Labe river and lower Morava river (near Hodonín and Bzenec) are covered by acidic siliceous sand originating either from Tertiary fluvial sedimentation or Pleistocene aeolian sedimentation. Nowadays these sandy landscapes are covered mainly by pine forests, many of which are recent plantations, but there are also local remnants of acidophilous or thermophilous oak forests (Šmarda 1961, Chytrý & Horák 1997). There are sandy grasslands (*Corynephorion canescentis*, *Armerion elongatae* and *Festucion vaginatae*) in deforested areas (Klika 1931, Šmarda 1961). Besides lowland riverine landscapes, well-preserved complexes of floodplain vegetation also occur at mid-altitudes. Fast-running streams are rare in the Czech Republic and most rivers at mid-altitudes either flow in deep v-shaped valleys or, locally, in broad floodplains with numerous oxbows and alluvial pools with accumulations of organic sediment. Best examples of mid-altitude broad floodplains occur along the upper Lužnice river in the Třeboň basin (Prach et al. 1996) and upper Vltava river in the Šumava Mts (Sádlo & Buřková 2002, Buřková et al. 2005).

Serpentine areas occur in small patches in various areas of the Bohemian Massif, namely in western and south-western Bohemia, the Bohemian-Moravian Highlands and northern Moravia (Fig. 5). Serpentines are metamorphic rocks occurring in association with other types of metamorphic rocks, particularly granulite. They have no causal links with specific topographic features, however, they affect vegetation through their extraordinary chemistry, namely a high content of magnesium and occurrence of heavy metals such as nickel, chromium and cobalt, which are toxic to many plant species (Proctor & Woodell 1975). Serpentines occurring in flat or gently undulating landscapes with deep soil may have weak or no effect on the vegetation. However, when crossed by stream valleys or occurring on the tops of hills, serpentine bedrock is exposed to erosion and covered by thin soil. In such situations the vegetation is markedly different from that in the surroundings. In particular, *Fagus sylvatica* and *Carpinus betulus* are replaced by *Pinus sylvestris*, and locally also by *Quercus petraea*. Therefore serpentine forests are rather open and it is possible that various light-demanding species have survived in them since the Holocene. In addition, the plant populations in these forests are isolated, which may have resulted in speciation of neoendemics such as *Cerastium alsinifolium* and *Minuartia smejkalii*. Best examples of specific serpentine vegetation are found in the Slavkovský les Mts in western Bohemia, near Křemže in southern Bohemia, near the Želivka water reservoir in central Bohemia, in the middle Jihlava valley near Mohelno in south-western Moravia and near Raškov in northern Moravia. The serpentine area near Mohelno (Suza 1928, Chytrý & Vicherek 1996) is the warmest and driest of all the serpentine areas in the Czech Republic. Here the north-facing slopes are covered by forests of *Pinus sylvestris* with *Sesleria caerulea* and other montane basiphilous species (*Erico carnae-Pinion*), whereas there are thermophilous oak forests (*Quercion petraeae*) on the south-facing slopes, however, the deforestation of the south-facing slopes and livestock grazing has resulted in the development of *Festuca-Stipa* steppe (*Alyso-Festucion pallentis*, *Festucion valesiacae*). Other serpentine areas are covered mainly by pine forests (*Dicrano-Pinion sylvestris* and partly also *Erico carnae-Pinion* at Želivka), although some have been deforested and transformed into low-productive pastures. The coolest and wettest of these are in the

Slavkovský les Mts (Hejtmánek 1954, Jeník 1994), where *Picea abies* frequently occurs in the understorey of species-poor *Pinus sylvestris* forest. Rock outcrops in all serpentine areas are characterized by the occurrence of small ferns that are serpentine specialists: *Asplenium adulterinum*, *A. cuneifolium* (Tájek et al. 2011) and at Mohelno, also *Notholaena marantae* (*Asplenion cuneifolii*; Vicherek 1970).

Vegetation types

Detailed phytosociological classification and description of vegetation types is available in the monograph *Vegetation of the Czech Republic* (Volumes 1–3: Chytrý 2007, 2009, 2011; Volume 4: in press). The brief overview presented here follows this classification at the levels of class and alliance (Appendix 2). Orders are omitted in order to keep the classification hierarchy simple. References cited here include particularly important studies of ecology, history and dynamics, but also recent papers presenting comprehensive classifications of selected vegetation types. More information, including classification to the level of associations and details on ecology, history and dynamics of particular vegetation types can be found in *Vegetation of the Czech Republic*, as well as in more specialized, local or older studies cited therein.

Forests

Forest history

Hypothetical distribution of forest vegetation in the Czech Republic is presented in the maps of reconstructed and potential natural vegetation (Mikyška et al. 1968–1972, Neuhäuslová et al. 1997; Fig. 12). According to these maps, lowlands of Moravia and northern half of Bohemia would be dominated by oak-hornbeam forests, driest areas of northern and central Bohemia and southern Moravia by a mosaic of oak-hornbeam and thermophilous oak forest, mid-altitudes of western and southern Bohemia by acidophilous oak (partly also pine or fir) forests, submontane and montane areas by beech forests, the highest mountain areas by spruce forests and subalpine and alpine vegetation, and floodplains by alluvial forests. However, there is much uncertainty about actual species composition and distribution of potential natural vegetation types, especially in the lowlands and at mid-altitudes, where forests have long been exploited by humans (Nožička 1957).

Forests in lowland areas settled by prehistoric farmers were used as either coppices or wooded pastures. Comparative studies of ancient woods in southern Moravia indicate that coppices (including coppices with standards) were probably more common on nutrient-rich soils and on steeper slopes, whereas wooded pastures prevailed on less fertile soils and on flat terrain, although this pattern may have been modified by socio-economic factors (Szabó & Hédl 2012). Coppicing was a single-purpose use, aimed at firewood production (or combined firewood and timber production in coppices with standards). Rotation cycles shorter than ten years were common in southern Moravian coppices in the Medieval (Szabó 2010). In contrast, wooded pastures served multiple purposes, including grazing, hay making and obtaining firewood, timber, leaf fodder from pollarded trees and acorns and beech mast for pigs. Litter for animal bedding also used to be collected from the

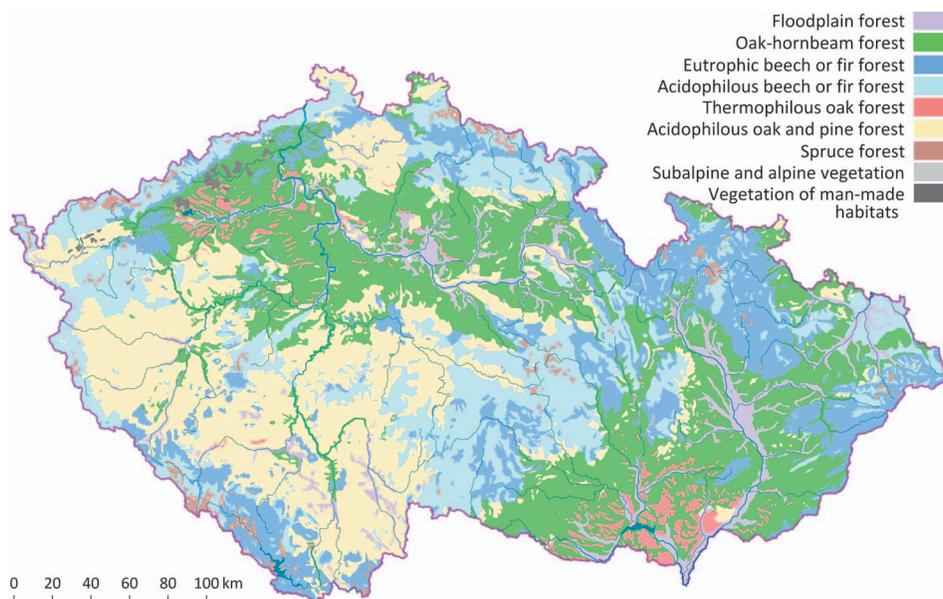


Fig. 12. – Potential natural vegetation according to Neuhäuslová et al. (1997).

forests (Nožička 1957). Coppicing favoured those trees that were good at regenerating vegetatively, especially *Carpinus betulus*. Light-demanding oak regenerated especially in wooded pastures, but it was also selectively favoured by humans in coppices with standards (Vera 2000). Although these historical management practices were ultimately abandoned by the mid-20th century (Poleno 1999, Machar 2009), they are still strongly reflected in the structure and composition of the present high forests in the lowlands, which probably contain more oak and less beech than would be present in non-managed natural forests.

Mid-altitude and montane forests followed a different trajectory of historical development than lowland forests. Negative archaeological evidence suggests that these areas were scarcely populated before the medieval colonization, which implies that many forests in these areas were probably in near-natural or climax state until the High Medieval. Those forests that were not clearcut to obtain agricultural land were used for selective timber logging and charcoal production from beech wood (Nožička 1957). The increasing interest of the state in controlling forest resources led the Empress Maria Theresa to issue forest regulation orders for Bohemia (1754), Moravia (1756) and Silesia (1769). State control of forest management led to a gradual exclusion of domestic livestock from forests and reduction in litter raking (Nožička 1957). The decline in the area of natural forests led some land owners to declare selected areas of mountain old-growth forests as nature reserves: two sites in the Novohradské Mts of southern Bohemia, Hojná Voda and

Žofínský prales, protected by Count Buquoy since 1838, are among the oldest nature reserves in Europe. Clear-cutting and establishing extensive even-aged plantations of *Picea abies* and *Pinus sylvestris*, and to some extent also of *Larix decidua*, occurred throughout the country in the first half of the 19th century. Of the total area of present forests, 47.7% are of *Picea abies*, 13.9% of *Pinus sylvestris* and 3.8% of *Larix decidua* (ÚHÚL 2007).

Main tree species

Most Czech forests are dominated by a single species or co-dominated by 2–3 tree species (Svoboda 1953–1957, Neuhäuslová et al. 1998a). Superior competitors in zonal habitats include *Carpinus betulus* in the lowlands, *Fagus sylvatica* (and to some extent also *Abies alba*) at mid-altitudes and on mountains, and *Picea abies* at the highest altitudes. Other tree species are either confined to azonal (too wet or too dry) habitats or supported by forest management (Fig. 13).

Beech (*Fagus sylvatica*) is the most common deciduous tree in the country, occupying 7.2% of the total forested area (ÚHÚL 2007). It is a superior competitor on zonal, fertile soils because of its tall stature (it can be more than 40 m tall), dense canopy, life span of 200–300 years in undisturbed stands, shade tolerance when young (Svoboda 1953–1957) and intense root competition (Slavíková 1958). It does not tolerate flooded or waterlogged sites, dry soils and areas where there is a risk of late frosts during the period of leaf flushing in spring (Ellenberg & Leuschner 2010), but it can grow on both acidic and base-

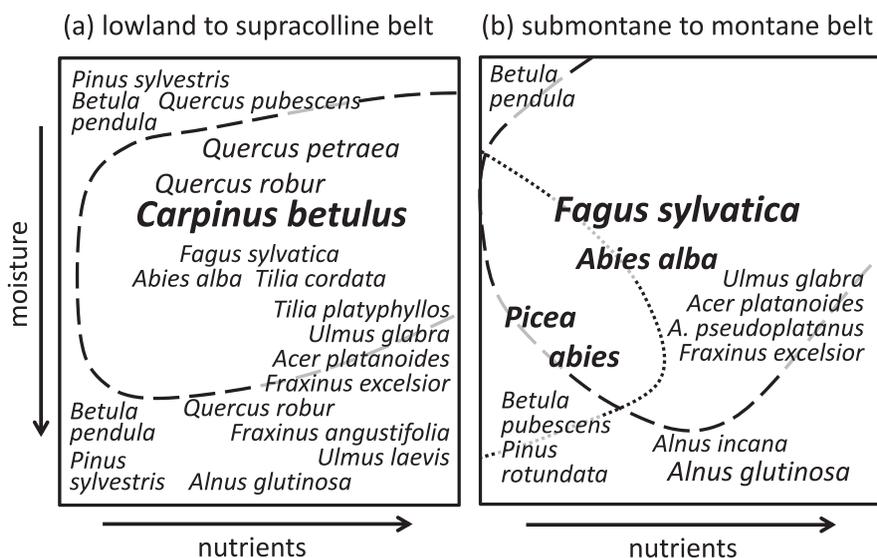


Fig. 13. – Schematic representation of realized niches of the main forest trees of the Czech Republic, with respect to soil moisture and nutrient availability (Ellenberg-type ecograms): (a) lowland to supracolline belt and (b) submontane to montane belt. Superior competitors are in larger bold letters and their realized niches are bounded by broken or dotted lines.

rich soils. Beech forests or mixed forests of beech with fir and/or spruce are common in mid-altitude areas and the mountains but very rare in dry lowlands. However, beech forests can occasionally occur at altitudes of about 200 m. Rarity of beech in the lowlands may be partly due to historical management, e.g. its decline in coppiced forests in which hornbeam and other deciduous trees were favoured. Interestingly, former beech coppices are rare in the Czech Republic, although rather common in other countries in central Europe.

Hornbeam (*Carpinus betulus*) is widespread from the lowlands to the supracolline belt. Because of its shorter life span and shorter stature, it is a weaker competitor than beech. Nevertheless, it also has a dense canopy like beech, which negatively affects recruitment of the light-demanding trees and makes it a superior competitor in areas where beech suffers from seasonal droughts or is injured by late frosts. It is most common on mesic nutrient-rich soils, but also grows on acidic or intermittently wet soils. Hornbeam was locally present in the lowlands of the south-eastern Czech Republic already in the early Atlantic (Doláková et al. 2010), however, it was the last species to expand its range in the Czech territory during the Holocene. Its spread in the Czech lowlands occurred only in the Subatlantic and it was probably aided by forest management such as coppicing, because hornbeam easily resprouts from stumps. It migrated from the north-east (Pokorný 2002b) and it is still absent from some parts of south-western Bohemia, where there are suitable habitats.

Oaks (*Quercus* spp.) are long-living but light-demanding deciduous trees unable to reproduce generatively under the canopy of other broad-leaved trees. In undisturbed, non-managed forests oaks would probably be confined to south-facing slopes with shallow soil, which are too dry for other broad-leaved trees. In spite of this, oaks are currently quite common in Czech forests, covering 7.4% of the forested land (ÚHÚL 2007), which is for most part a heritage of historical forest management. Oaks were preserved as standards in coppiced woodlands, planted for acorns or regenerated spontaneously from seed in wooded pastures. In today's forest reserves that are left to spontaneous succession, old individuals of oak that die are often replaced by other species, e.g., hornbeam on mesic soils in the lowlands, beech at mid-altitudes and ash on floodplains but also on slopes with mesic soils (Hofmeister et al. 2004). *Q. petraea* is drought-resistant and often occurs on slopes with shallow soil, both on acidic and base-rich bedrocks. *Q. robur* occurs not only in floodplain forests along lowland rivers, but also on dry slopes, especially in south-western Bohemia. *Q. pubescens* is a rare thermophilous species in the Czech Republic, occurring on dry, base-rich soils in the driest parts of northern and central Bohemia and southern Moravia. *Q. cerris* is a rare admixture in thermophilous oak forests on heavy soils over loess in southern Moravia and is locally planted. Other species of oak reported from the Czech Republic have unclear taxonomic status, or are not native, or their status as native is questionable. The most frequently planted and spontaneously spreading alien oak species is *Q. rubra*.

Noble hardwoods (*Acer platanoides*, *A. pseudoplatanus*, *Fraxinus excelsior*, *Tilia cordata*, *T. platyphyllos* and *Ulmus glabra*) are confined to nutrient-rich soils that are well supplied with water and aerated. Leaf litter of these trees is rich in nutrients and decomposes rather fast (1–2 years), therefore the base status and nutrient availability in the topsoil is rather high (Ellenberg & Leuschner 2010). Canopy shading by these trees is less intense than that by beech, hornbeam or fir, but stronger than by oak, and shade tolerance

of their seedlings and saplings is positively correlated with the shading capacity of adult trees. Therefore these trees were superior competitors in the Atlantic, when they dominated landscapes at low and mid-altitudes, but were largely outcompeted from zonal habitats by beech, fir and hornbeam in the Subboreal and the Subatlantic. Currently noble hardwoods are confined to ravines and lower slopes with scree accumulation, where they grow quickly, favoured by abundant moisture and nutrients, as opposed to beech and hornbeam, which fail to develop monodominant stands in such habitats. Within the group of noble hardwoods, *Tilia cordata* and *T. platyphyllos* are more thermophilous, having their optimum at lower altitudes, while *Ulmus glabra* and especially *Acer pseudoplatanus* are more tolerant of cold conditions and commonly occur in montane ravine forests. *A. pseudoplatanus* locally grows in mixed stands with beech on precipitation-rich slopes in the mountains. *Fraxinus excelsior* is common not only in ravines and on talus slopes but also in floodplain forests along the middle and lower courses of rivers.

Alders (*Alnus* spp.) are typical trees of wet habitats. *Alnus glutinosa* is the most common tree in riverine forests at mid-altitudes and also dominates carrs in water-logged depressions. In contrast, *A. incana* only occurs naturally on coarse well-aerated fluvial sediments (stones, gravel and sand) along mountain streams with fast running water.

Birches (*Betula* spp.) are competitively weak, light-demanding but stress-tolerant trees. *Betula pendula* is common as an early successional species at deforested sites, including abandoned agricultural land, but it also grows in nutrient-poor, dry or wet habitats that are too stressful for broad-leaved species. *Betula pubescens* is typical of nutrient-poor, wet or water-logged sites, typically marginal parts of mires or drained mires. *Betula carpatica* occurs on high mountains, where it forms stands near avalanche tracks in cirques in the subalpine belt.

Poplars (*Populus* spp.) are represented by *Populus tremula*, a stress-tolerant pioneer species ecologically similar to *Betula pendula*, but with extensive clonal growth, and two species that occur in lowland floodplain forests, *Populus nigra* and *P. alba*. The former is now very rare and the latter is considered as native only in southern Moravia. Several species or hybrids of alien poplars are planted: in particular, *P. ×canadensis* is used in forestry plantations established in the potential habitats of floodplain hardwood forests.

Willows (*Salix* spp.) are represented mainly by shrubby species. Species with predominant arboreal growth include *Salix alba*, typical of lowland softwood floodplain forests, *S. euxina*, which is common in riverine woodland and scrub at mid-altitudes, and *S. caprea*, a species of early successional stages in disturbed forests or abandoned grasslands, especially on slightly wet mineral soils.

Black locust (*Robinia pseudoacacia*), a tree of North American origin, is the most common alien woody species in the Czech Republic, dominating in 0.6% of the total forested land (ÚHÚL 2007). It has been extensively planted since the 1860s in warm areas as a honey plant, a source of hard, resistant wood and to stabilize erosion-prone soils (Kolbek et al. 2004).

Other deciduous tree species in the Czech Republic include *Fraxinus angustifolia*, a dominant tree in floodplain hardwood forests in southern Moravia, *Ulmus laevis*, a common species in floodplain hardwood forests, *Acer campestre* and *Ulmus minor*, subcanopy trees in lowland forests, *Sorbus* species (*S. aucuparia*, *S. aria* and related hybridogenes and apomictic taxa, *S. torminalis* and *S. domestica*), which are admixed in different types of forest, usually as subcanopy trees, and fruit trees or their native wild ancestors (especially

Malus domestica, *M. sylvestris*, *Prunus avium*, *Pyrus communis* and *P. pyraeaster*), which are found as solitary specimens in lowland forests that were formerly managed as wooded pastures or coppices with standards.

Fir (*Abies alba*) grows in similar habitats as beech, especially on deep and not too dry soils; these two species often form mixed stands. Unlike beech, however, fir also occurs on heavy and wet mineral soils such as planosols or stagno-gleyic luvisols (Mráz 1959), but not organic soils or dry soils in sandstone pseudokarst areas. Like beech, fir is sensitive to late spring frosts (Ellenberg & Leuschner 2010). Fir canopy is dense and there is limited light available to the understorey, however, fir saplings tolerate deep shade. Small fir individuals with thin stem can persist for dozens of years in the understorey and grow rapidly when a canopy gap appears above them. This enables fir to compete successfully with fast-growing beech seedlings. Fir was very common in Czech forests between the Bronze Age and the Medieval Period. Its expansion in forests at the expense of beech was probably aided by forest management, namely livestock grazing and litter raking (Málek 1983, Vrška et al. 2009). While deer frequently browse fir saplings, domestic livestock prefer saplings of broad-leaved trees. Raking removes the thick layer of slowly decomposing beech litter, which fir seedlings have difficulty penetrating. However, as a result of the forest regulations of 1754–1756, livestock was gradually removed from forest and replaced by deer. Deer densities in the 19th–20th centuries considerably exceeded those typical of the Middle Ages, because large predators (wolf, bear and lynx) had been eradicated. Incidence of litter raking also steadily decreased. These changes led to a decline in the abundance of fir early in the 19th century, which may have been accelerated by air pollution in the 20th century (Málek 1983, Vrška et al. 2009).

Spruce (*Picea abies*) is tolerant of cool and long winters, but it requires moist conditions and occurs naturally either in areas of high-precipitation or in wet depressions. It is adapted to acidic, nutrient-poor soils such as podzol or ranker on boulder scree, but it also grows on organic soils. Due to its shallow root system spruce is vulnerable to uprooting by wind. It dominates forests in the supramontane belt (Fig. 10) and regularly occurs in mixed stands with beech and fir in the montane belt. In the warmer climate at lower altitudes it is competitively inferior to broad-leaved deciduous trees, therefore its natural occurrence is restricted to wet organic soils, depressions where cold air accumulates or shaded bottoms of deep valleys; in such habitats spruce occurs even at altitudes below 200 m (Mráz 1959). Spruce has been favoured since the Middle Ages by selective logging of beech for charcoal production in montane and submontane forests. In the 16–18th centuries, it was rather common from the supracolline belt to higher altitudes, although it rarely dominated forests at mid-altitudes (Mráz 1959). Since the early 19th century it was extensively planted for timber, also at low altitudes. Large areas of spruce forests declined in the 1980s, especially in the Krušné and Jizerské Mts, and to a notable extent also in the Krkonoše and Moravian-Silesian Beskids, as a result of atmospheric emissions of sulphur dioxide (Kubíková 1991). Periodical decline of spruce stands at a more local scale is caused by outbreaks of bark beetle (*Ips typographus*), especially in plantations and forests weakened by air pollution or wind disturbance, but also in natural spruce forests in the mountains (Šantrůčková et al. 2010).

Pine (*Pinus sylvestris*) has a very broad ecological niche, similar to that of birch. It occurs on soils that range from very wet to very dry, from acidic to basic, and from nutrient-poor to nutrient-rich. However, it is unable to regenerate when shaded by other trees.

Therefore it is one of the weakest competitors among the trees native to the Czech Republic. It is a pioneer species in disturbed habitats or on abandoned agricultural land, but it can also occur as a dominant tree species in successional stable vegetation on forested peatlands, rock outcrops or serpentine soils. In some lowland areas pine forests may have existed for millenia, probably supported or maintained by wild fires (Novák et al. 2012). In some of its habitats, especially in sandstone pseudokarst areas such as Labské pískovce, *Pinus sylvestris* has been recently outcompeted by *Pinus strobus*, an invasive species of North American origin (Hadincová et al. 1997).

Bog pine (*Pinus uncinata* subsp. *uliginosa*) is an endemic to central Europe. It occurs on bogs in the supracolline to montane belt especially in western and southern Bohemia (Businský 2009).

Larch (*Larix decidua*) is often used in forestry plantations. It was present in the Czech Republic in the last glacial (Willis & van Andel 2004, Jankovská & Pokorný 2008) but disappeared in the Holocene. However, a native population of larch may have survived throughout the Holocene in the Hrubý Jeseník Mts and its foothills, although larch does not form any distinct type of natural forest in this area. This hypothesis is supported by a find of a larch pollen grain in this area dated to 2500 cal. yr BP (Dudová et al. 2012) and written reports of the local use of larch wood in the 16th century (Nožička 1962).

Yew (*Taxus baccata*) is a small tree occurring locally in the subcanopy of deciduous forests on steep slopes.

Main types of forest vegetation

Alder carrs (class *Alnetea glutinosae*, alliance *Alnion glutinosae*; Fig. 14a) are forested wetlands dominated by *Alnus glutinosa* with a species-poor herb layer with tall sedges, especially *Carex acutiformis*, *C. elongata* and *C. riparia*. They occur on organic or gleyic soils in water-logged depressions, often near fishponds and in terrestrialized oxbows, from the lowlands to submontane areas (Douda 2008). Many current stands have developed from wet meadows and other types of abandoned wetland (Douda et al. 2009). Jeník (1980) proposed a model of natural autogenic cyclic succession of alder carrs with alternating forest and treeless stages. The pattern found in fossil pollen data from eastern Bohemia was interpreted as alternations of these two stages (Pokorný et al. 2000), however, it may have other causes than natural dynamics, e.g. human activities or changes in hydrological regime caused by external factors (Douda et al. 2009).

Riparian willow-poplar forests (class *Salicetea purpureae*, alliance *Salicion albae*) occur mainly along lowland rivers, where they are dominated by *Salix alba* or, rarely, by *Populus nigra*, and in southern Moravia *P. alba* is also present. Some stands can further be found along streams at mid-altitudes, where the dominant tree species is usually *Salix euxina* (Neuhäuslová 1987). These forests occur on fluvisols or gleyic soils on lower river terraces, which are flooded annually (Mezera 1956–1958). Because the rivers are now regulated and the ground-water table is lower, these softwood floodplain forests are changing into more mesic forest types such as hardwood floodplain forests (Vrška et al. 2006).

Riparian alder forests (class *Carpino-Fagetea*, alliance *Alnion incanae*; Fig. 14b) occur along medium-sized streams, brooks and around springs from the lowlands to the montane belt. Forests dominated by *Alnus incana* form narrow galleries along strong-flowing mountain brooks with fluctuating water discharge. More extensive stands of

A. incana occur on the montane floodplain of the upper Vltava river in the Šumava Mts (Sádlo & Buřková 2002). Forests of *Alnus glutinosa*, in places with an admixture of *Fraxinus excelsior* or other trees, occur on fluvisols or gleyic soils along streams from the mountains to the lowlands. Their herb layer is usually richer than that of upland forests in the same areas; it contains a mixture of species of alluvial habitats and mesophilous species that occur in adjacent forests (Douda 2008).

Hardwood floodplain forests (Fig. 14c) replace riparian alder forests on the floodplains of large lowland rivers. They are dominated by *Fraxinus excelsior*, *Quercus robur*, *Ulmus laevis* and in southern Moravia also by *Fraxinus angustifolia* (Mezera 1956–1958). Presence of oak in these forests may be a result of past management. In the past they were flooded almost every year in spring, but floods are now rarer because the rivers are regulated; therefore, these forests are currently becoming more mesic (Vrška et al. 2006, Janik et al. 2011). As the species composition of the herb layer is similar to that of riparian alder forests (Douda 2008), they are assigned to the same alliance (*Alnion incanae*).

Oak-hornbeam forests (class *Carpino-Fagetea*, alliance *Carpinion betuli*; Figs 14d & 15a) are widespread from the lowlands to the supracolline belt. Dominant trees usually include *Carpinus betulus* and/or *Quercus petraea*, in some areas also *Q. robur*, and frequently there is a small admixture of *Tilia cordata*. These forests have developed as a result of intensive management since the Iron Age and although no longer managed in this way the tree species composition still reflects this influence. In the absence of management, oak would be probably outcompeted by hornbeam (or noble hardwoods), and at higher altitudes, hornbeam by beech. Hornbeam did not reach some areas of southern and western Bohemia during its postglacial migration, where habitats suitable for oak-hornbeam forests are currently dominated by *Quercus robur* (Moravec 1964). Herb-layer species composition of oak-hornbeam forests is slightly different in the Bohemian Massif, Pannonian part of southern Moravia and Carpathian part of Moravia due to different phytogeographical influences (Neuhäuslová-Novotná 1964, Knollová & Chytrý 2004).

Beech and fir forests (Figs 14e & 15b) are the predominant type of natural forests in the supracolline to montane belt. At most sites there are currently monodominant stands of beech, but in the past mixed fir-beech or pure fir forests were common at mid-altitudes (Rybníček & Rybníčková 1978, Kozáková et al. 2011). Nowadays fir-dominated forests occur mainly in south-western Bohemia and in northern and north-eastern Moravia (Boublík 2010). Although mixed spruce-fir-beech forests are typical of the montane belt, many of these stands are currently composed of only beech and spruce. In many areas beech forests were replaced by spruce plantations. The dynamics of old-growth beech or mixed beech forests have been studied in several nature reserves, e.g. Boubín, Milešice and Stožec in the Šumava Mts, Žofín and Hojná voda in the Novohradské Mts, Polom and Žákova hora in the Bohemian-Moravian Highlands and Razula, Salajka and Mionší in the Moravian-Silesian Beskids (Průša 1985, Vrška et al. 2002, 2012, Šamonil & Vrška 2007, 2008, Král et al. 2010). The results of these studies indicate that these forests partly follow the classical model of cyclic changes in the climax forest driven by canopy gap dynamics, with stages of growth, optimum and disintegration ('small developmental cycle'; Leibundgut 1993, Korpeř 1995, Fischer 1997). However, some of the observed changes rather indicate the trends in forest development due to abandonment of livestock grazing, increases in the population density of game since the 18th century or air pollution

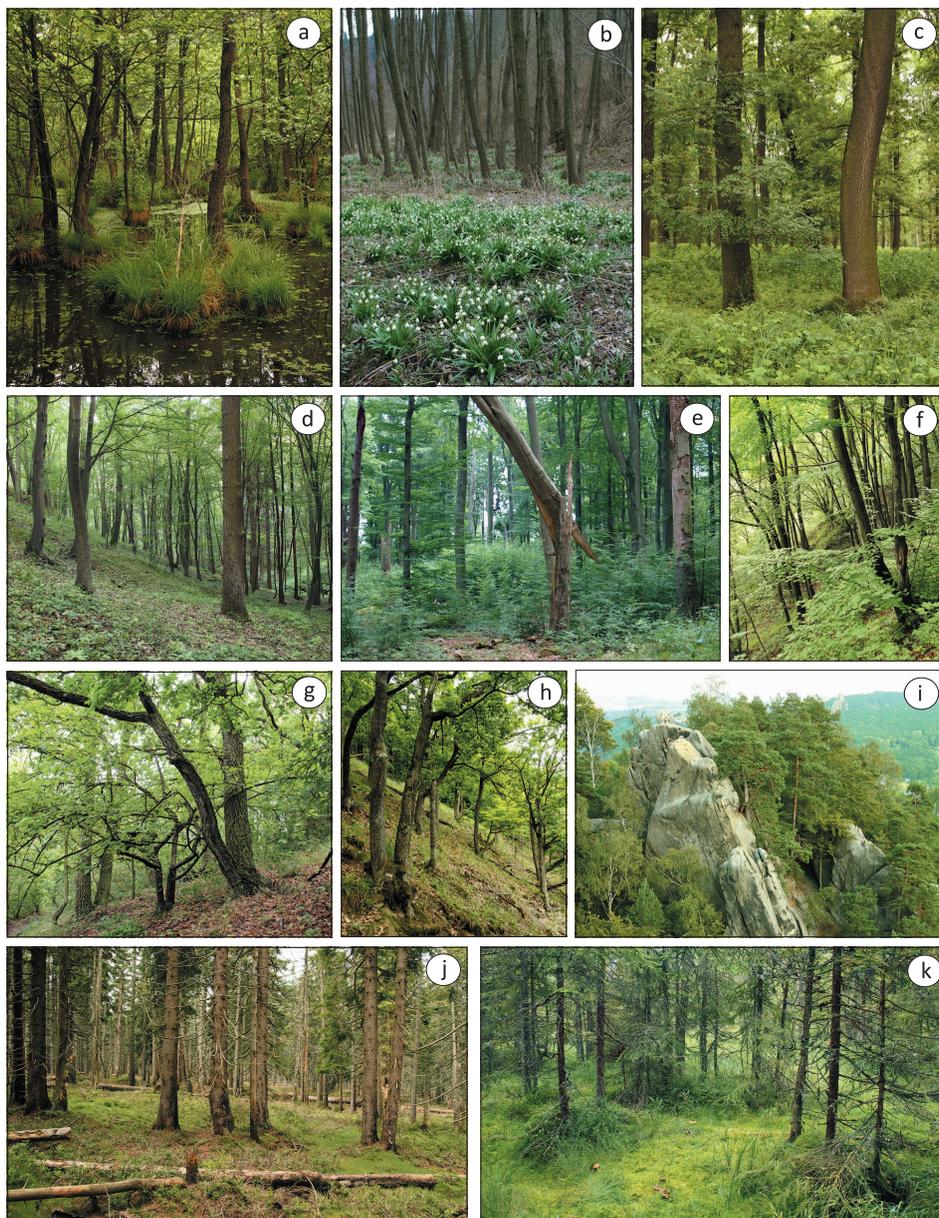


Fig. 14. – Examples of different types of forest vegetation in the Czech Republic: (a) *Alnus glutinosa* carr with *Carex elongata* near Polanka nad Odrou, north-eastern Moravia; (b) floodplain forest with *Alnus glutinosa* and *Leucojum vernum* near Chlébské, Bohemian-Moravian Highlands; (c) floodplain forest with *Fraxinus angustifolia* near Rohatec, south-eastern Moravia; (d) oak-hornbeam forest near Podmokly, Křivoklátsko region, central Bohemia; (e) beech forest near Roštejn castle, Bohemian-Moravian Highlands; (f) ravine forest with *Tilia cordata* near Svatý Jan pod Skalou, Bohemian Karst, central Bohemia; (g) thermophilous oak forest with *Quercus pubescens* near Svatý Jan pod Skalou, Bohemian Karst, central Bohemia; (h) acidophilous oak forest with *Quercus petraea* near Rozdrojovice, southern Moravia; (i) pine forest on a sandstone outcrop near Malá Skála, northern Bohemia; (j) supramontane spruce forest on Mt Černá, Krkonoše Mts; (k) bog woodland with *Picea abies* near Nová Hůrka, Šumava Mts.

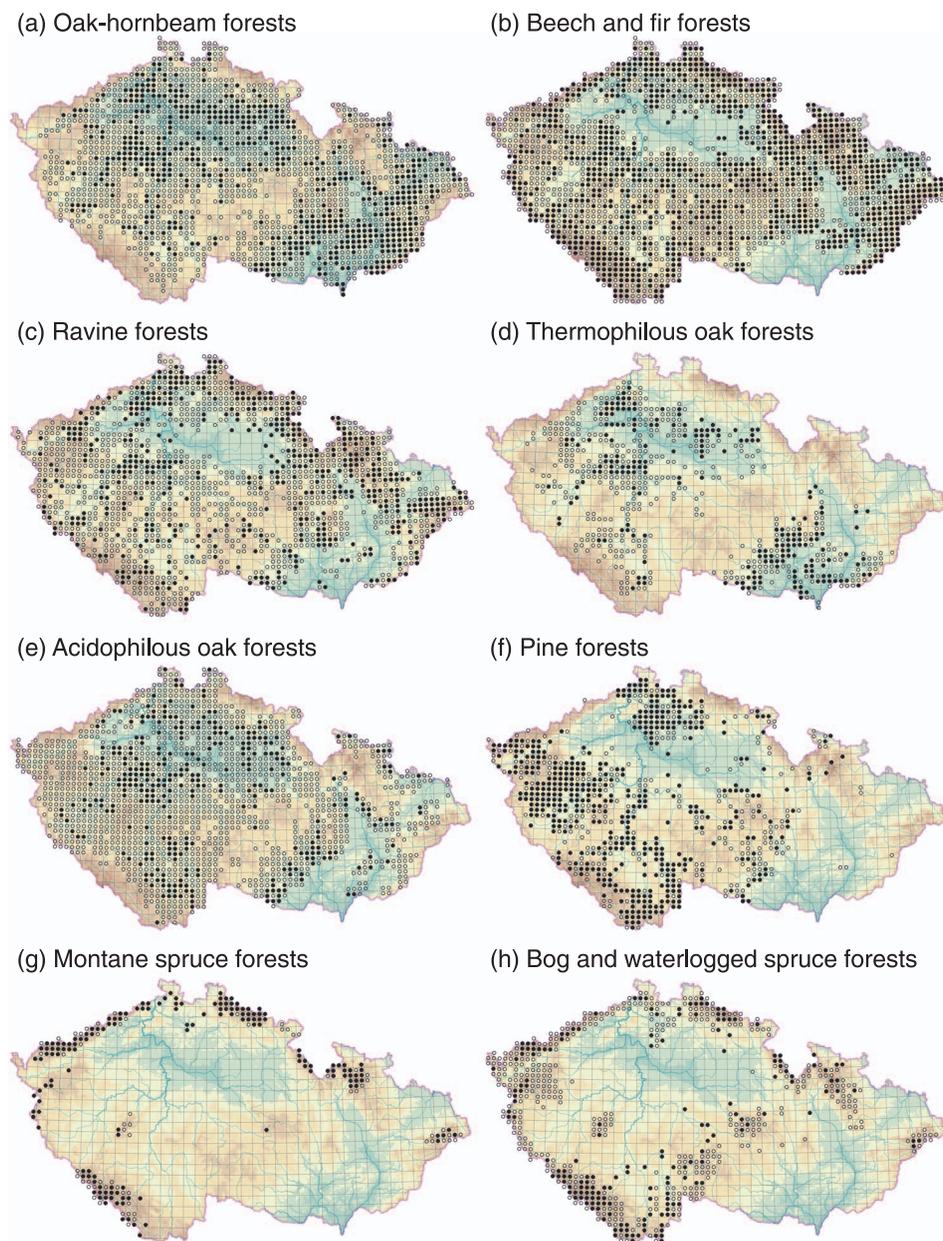


Fig. 15. – Distribution of selected types of forest vegetation. Black circles indicate sites of relevés from the Czech National Phytosociological Database (Chytrý & Rafajová 2003) and Database of Forest Typology of the Forest Management Institute (ÚHÚL) which represent typical examples of particular vegetation types, although in the case of pine and spruce forests some sites may be plantations that resemble natural vegetation. Open circles indicate observations based on habitat mapping in 2001–2008 (Härtel et al. 2009), revised by Chytrý et al. (2010b), which include fragmentary or transitional occurrences of individual vegetation types. Phytosociological units: (a) *Carpinion betuli*; (b) *Fagion sylvaticae*, *Sorbo torminalis-Fagion sylvaticae* and *Luzulo-Fagion sylvaticae*; (c) *Tilio platyphylli-Acerion*; (d) *Quercetea pubescentis*; (e) *Quercetea robori-petraeae*; (f) *Erico carnea-Pinion*, *Festuco-Pinion sylvestris* and *Dicrano-Pinion sylvestris*; (g) *Piceion abietis*, associations *Calamagrostio villosae-Piceetum abietis* and *Athyrio distentifolii-Piceetum abietis*; (h) *Piceion abietis*, associations *Equisetio sylvatici-Piceetum abietis*, *Soldanello montanae-Piceetum abietis* and *Sphagno-Piceetum*.

(Šamonil & Vrška 2007, 2008). Species composition of the herb layer in beech and fir forests varies mainly in response to soil nutrient and base status. These forests are assigned to the class *Carpino-Fagetea* and alliances *Fagion sylvaticae* (on eutrophic soils), *Sorbo torminalis-Fagion sylvaticae* (on calcareous soils; Boublík et al. 2007) and *Luzulo-Fagion sylvaticae* (on acidic soils). However, there is some evidence that atmospheric pollution in the second half of the 20th century caused soil acidification and decline of nutrient-demanding species in the herb layer of mountain beech forests, which resulted in the *Fagion sylvaticae* forests changing into *Luzulo-Fagion sylvaticae* forests (Hédl 2004, Hédl et al. 2011).

Ravine forests (class *Carpino-Fagetea*, alliance *Tilio platyphyllo-Acerion*; Figs 14f & 15c) occur in ravines and on steep slopes, most commonly in deep river valleys. *Tilia cordata* and *T. platyphyllos*, with an admixture of *Carpinus betulus*, are more common in drier and warmer habitats at lower altitudes or on upper slopes, whereas *Acer pseudo-platanus*, *Ulmus glabra* and *Fraxinus excelsior* with an admixture of *Fagus sylvatica* and *Abies alba* are typical of wetter and cooler habitats at higher altitudes, on lower slopes or mountain-tops where is high precipitation. Ravine forests are capable of vegetative regeneration after disturbances caused by soil erosion or rock fall on steep slopes.

Thermophilous oak forests (Figs 14g & 15d) are dominated by *Quercus pubescens* in the driest and warmest habitats with base-rich soils, or *Q. petraea* in cooler habitats or on more acidic bedrock, or *Q. robur* on more mesic soils (Chytrý 1997, Roleček 2007). Natural stands are typically confined to the upper parts of south-facing slopes; they have an open canopy, well-developed shrub layer and species-rich herb layer. However, there are thermophilous oak forests that developed as a result of historical management such as forest grazing (Mráz 1958). Abandonment of historical management by the mid-20th century caused the spread of trees with a denser canopy than oaks (e.g. *Fraxinus excelsior*; Hofmeister et al. 2004), decline of light-demanding, thermophilous species in the herb layer and the spread of species typical of mesic forests (Hédl et al. 2010). Thermophilous oak forests are assigned to the class *Quercetea pubescentis* and alliances *Quercion pubescenti-petraeae* (on slopes with shallow, base-rich soils, especially those on limestone, with some sub-Mediterranean species and frequent occurrence of *Quercus pubescens*), *Aceri tatarici-Quercion* (on loess and sandy soils in southern Moravian forest-steppe area, often on flat land, with continental floristic influence) and *Quercion petraeae* (on slopes of acidic rocks or on luvisols with a decalcified upper soil horizon, with dominance of *Quercus petraea* or *Q. robur*).

Acidophilous oak forests (class *Quercetea robori-petraeae*, alliance *Quercion roboris*; Figs 14h & 15e) are dominated by *Quercus petraea* or *Q. robur*. In places *Betula pendula* or *Pinus sylvestris* occur in mixed stands with oaks. Their herb layer is species-poor, consisting of a few acidophilous species. These forests are confined to low-pH soils, which are usually mesic but can also be slightly dry or slightly wet (Neuhäusl & Neuhäuslová-Novotná 1967). In the Map of potential natural vegetation (Neuhäuslová et al. 1997), acidophilous oak forests, together with mixed acidophilous forests with pine, fir and birch, are mapped over large areas at mid-altitudes of western and southern Bohemia, however, few such forests currently occur in that area, which is largely covered by a mosaic of arable land and conifer plantations. Pollen diagrams from the early Subatlantic (around 2000 cal. yr BP) indicate that these areas were mainly covered by fir forests with an admixture of beech and spruce while oak was rare there (Pokorný 2002b).

Pine forests (Fig. 15f) are common at low and middle altitudes in the Czech Republic, but most of them are forestry plantations of native *Pinus sylvestris*. Pine forests were common in the Late Glacial. Their area was strongly reduced due to the spread of deciduous trees by the mid-Holocene, but they spread again with the increase in human activity since the Subboreal (Pokorný 2002b, 2005, 2011, Kuneš et al. 2008a). In some areas they may have been maintained for millenia by periodical wild fires (Novák et al. 2012). Because of the weak competitive ability of *Pinus sylvestris*, pine forest can persist in undisturbed conditions only in small patches of stressful habitats that are unsuitable for broad-leaved trees, especially on rock outcrops, serpentine soils and bogs. There are several types of *Pinus sylvestris* forests in the Czech Republic with the diversity of the herb and moss layers depending on soil chemistry and moisture. Basiphilous pine forests of the class *Vaccinio-Piceetea*, alliance *Festuco ovinae-Pinion sylvestris*, occur on calcareous sandstone and marlstone, especially in northern Bohemia; in their herb layer there are several continental species typical of forest-steppe. Acidophilous pine forests (class *Vaccinio-Piceetea*, alliance *Dicrano-Pinion sylvestris*; Fig. 14i) occur in sandstone pseudokarst areas, on outcrops of igneous or metamorphic rocks in river valleys of the Bohemian Massif, and on sand dunes, however, in many cases they may have developed as a result of historical management. They are characterized by frequent occurrence of dwarf shrubs (*Vaccinium myrtillus* and *V. vitis-idaea*) and bryophytes of boreo-continental distribution. Pine forests on serpentines at higher altitudes are similar to this boreo-continental type of pine forest, therefore they are also assigned to the alliance *Dicrano-Pinion sylvestris*. However, in pine forests on serpentine slopes at lower altitudes (near Želivka water reservoir in central Bohemia and in the Jihlava river valley near Mohelno in south-western Moravia) there is *Sesleria caerulea* and some species typical of basiphilous montane pine forests in the Alps and Carpathians; therefore they are assigned to the class *Erico-Pinetea* and alliance *Erico carneae-Pinion*.

Spruce forests (class *Vaccinio-Piceetea*, alliance *Piceion abietis*; Figs 14j, 15g & 15h) are very common throughout the country, but most of them are plantations of native *Picea abies*. Natural spruce forests occur in the supramontane belt of higher mountain ranges (Fig. 10) or at lower altitudes at the margins of bogs or in broad valleys where cold air accumulates and soil paludification occurs. They are characterized by occurrence of dwarf shrubs and bryophytes of boreo-continental distribution, but central-European mountain species, such as *Calamagrostis villosa*, are also common (Sofron 1981, Jirásek 1996a). Tree-ring analyses from natural spruce forests in the Šumava Mts suggest that the dynamics of mountain spruce forests over periods of centuries are affected by infrequent but severe large-scale disturbances, most probably caused by windstorms and subsequent bark beetle outbreaks (Svoboda et al. 2012). Such disturbances are followed by rapid secondary succession of roughly even-aged spruce forests (Jonášová & Prach 2004).

Bog woodland (class *Vaccinio-Piceetea*, alliance *Vaccinio uliginosi-Pinion sylvestris*; Fig. 14k & 15h) occurs on the drier parts of bogs and at their margins. Their dominant trees are *Betula pubescens*, *Picea abies*, *Pinus sylvestris* and *P. uncinata* subsp. *uliginosa*, and their herb and moss layers consist of a mixture of dwarf shrubs, herbs and bryophytes typical of either organic or mineral soils. *Betula pubescens* occurs especially in moist habitats at lower altitudes, *Pinus sylvestris* in habitats in which the water table is regularly deeper than 30 cm below the soil surface and *Picea abies* in wet habitats in the mountains. *Pinus uncinata* subsp. *uliginosa* is typical of wet sites in the central parts of some bogs in the

mountains and basins, especially in western and southern Bohemia (Neuhäusl 1972, Bastl et al. 2008), but it can also dominate bog woodlands in places where the water table is occasionally deeper than 30 cm.

Black locust groves are common in warm areas. For the most part, they are established plantations, but *Robinia pseudoacacia* has also spread spontaneously in abandoned grasslands and open oak or pine forests. Being a legume, *Robinia* increases soil nitrogen availability through symbiotic fixation, which results in a dramatic change in the herb layer after *Robinia* is planted or invades. Therefore, *Robinia* is a significant threat especially to abandoned species-rich dry grassland and open forests. In some schemes of vegetation classification, *Robinia* groves are included in the separate class *Robinietea pseudoacaciae* (Hadač & Sofron 1980, Vítková & Kolbek 2010), but they also have features in common with the class of mesic to xeric scrub, *Rhamno-Prunetea*. In spite of large changes in the herb layer that occur after invasion by *Robinia* the groves are distinctly differentiated according to habitat. Vítková & Kolbek (2010) distinguish three alliances: *Chelidonio majoris-Robinion pseudoacaciae* includes mesic stands in potential habitats of hornbeam or ravine forests, *Balloto nigrae-Robinion pseudoacaciae* includes high *Robinia* groves in dry lowland sandy habitats, and *Euphorbio cyparissiae-Robinion pseudoacaciae* is an alliance comprising *Robinia* woodlands or scrub on south-facing slopes with shallow soil in the potential habitats of thermophilous oak forests.

Scrub

Scrub vegetation is widespread and common in the intensively managed landscape of the Czech Republic, especially in successional habitats on abandoned grasslands and ex-arable land (Osbornová et al. 1990, Jírová et al. 2012). However, there is also scrub vegetation that is dependent on natural disturbance, such as riparian willow stands.

Willow carrs (class *Alnetea glutinosae*, alliance *Salicion cinereae*), in most cases dominated by *Salix cinerea* or *S. aurita*, occur in similar habitats as alder carrs, i.e. in water-logged depressions, often on organic soils. They are also spreading in abandoned wet meadows. At many sites, alder and willow carrs are linked both spatially and in terms of succession.

Riparian willow scrub commonly occurs along rivers from the upper to lower reaches. This vegetation is maintained by periodic disturbances due to changes in the flow of the river, including damage by floating ice. The sandy or loamy sediments that accumulate on the banks of most Czech rivers create a suitable habitat for *Salix viminalis* and *S. triandra*, and shrubs or trees of *S. euxina*. In gravelly places *S. purpurea* is more abundant. There are very few braided streams with extensive gravel beds in the Czech Republic, with the most notable exceptions of the Ostravice and Morávka rivers in the northern part of the Moravian-Silesian Beskids and their foothills in north-eastern Moravia. These rivers support scrub of *Salix elaeagnos* and *S. purpurea*, rarely also *S. daphnoides* and *Myricaria germanica*. Riparian willow scrub is assigned to the same class as the riparian willow-poplar forests, *Salicetea purpureae*. Within this class, vegetation on sandy and loamy sediments is assigned to the alliance *Salicion triandrae* (Neuhäuslová 1985) and that on gravelly sediments to the alliance *Salicion elaeagno-daphnoidis*.

Mesic and xeric scrub is represented by several vegetation types in the Czech Republic. Low-growing scrub of the *Prunion fruticosae* alliance, dominated by the continental species *Prunus fruticosa* and *P. tenella*, is usually associated with dry grasslands in forest-steppe landscapes; the latter species only occurs at three sites in southern Moravia. Tall dry to mesic scrub of the *Berberidion vulgaris* alliance occurs commonly on abandoned dry or mesic grasslands and at forest fringes. Dominant species include *Cornus mas*, *C. sanguinea*, *Corylus avellana*, *Cotoneaster integerrimus*, *Crataegus levigata*, *C. monogyna*, *Euonymus europaeus*, *E. verrucosus*, *Ligustrum vulgare*, *Prunus mahaleb*, *P. spinosa*, *Rhamnus cathartica* and some species of *Rubus fruticosus* agg. A specific type of scrub, assigned to the alliance *Sambuco-Salicion capreae*, occurs in forest clearings, windthrow areas and where there are gaps in the canopy. Typical dominant species of this type of scrub include *Corylus avellana*, *Populus tremula*, *Rosa pendulina*, *Rubus idaeus* and some other *Rubus* species, *Salix caprea*, *Sambucus racemosa* and *Sorbus aucuparia*. Another type of tall scrub, assigned to the alliance *Aegopodio podagrariae-Sambucion nigrae*, occurs on nutrient-rich sites in warm areas, often in human settlements or agricultural landscapes. It is frequently dominated by *Sambucus nigra*, but alien shrub species are also common, including *Acer negundo*, *Lycium barbarum* and *Syringa vulgaris*.

Subalpine and alpine vegetation

Only three mountain groups, all located in the Sudetes Mts in the north of the Czech Republic, reach above the alpine timberline: Krkonoše, Králický Sněžník and Hrubý Jeseník (Fig. 10). There are two treeless areas above the timberline in the Krkonoše Mts, one at the headwaters of the Labe in the western Krkonoše (ca 23 km²) and the other in the headwaters of the Úpa in the eastern Krkonoše (ca 32 km²). In the Králický Sněžník there is one small area above the timberline (ca 0.7 km²) and in the Hrubý Jeseník seven small areas above the timberline with a total area of ca 10.5 km² (Tremel & Banaš 2000). The altitude of the timberline in the Sudetes increases from west to east (Fig. 10), which may be partly due to the increasing continentality of the climate towards the east and partly due to competition with krummholz (*Pinus mugo*), which is present in the Krkonoše but absent in the two eastern ranges. Currently the mean timberline altitude is 1207 m in the western Krkonoše, 1245 in the eastern Krkonoše, 1305 m in the Králický Sněžník and 1310 m in the Hrubý Jeseník Mts, with maxima of 1340 m in the Krkonoše (Mt Růžová) and 1405 m in the Hrubý Jeseník (Mt Praděd; Tremel & Banaš 2000). Besides the Sudetes, timberline is also reached by Mt Großer Arber on the Bavarian side of the Šumava Mts (Bayerischer Wald), which has a small treeless area above ca 1400 m, however, there is no area on the Czech side of the Šumava above the timberline (Neuhäuslová 2001).

At the timberline there is almost exclusively spruce, with a very rare occurrence of beech (Jeník & Lokvenc 1962). Beech is present at the timberline on the south-west-facing slope of the Krkonoš ridge in the western Krkonoše, which is the northernmost timberline formed by beech in Europe (Vacek & Hejcman 2012). Scattered groups of stunted individuals or solitary trees or shrubs of spruce occur above the timberline and their occurrence above an altitude of 1400 m is not exceptional. Often they form polycorms reproducing vegetatively by layering on the leeward side (Vacek et al. 2012). On the Krkonoš

ridge, beech trees and shrubs also occurs above the timberline; they also reproduce by layering and occur up to an altitude of 1370 m (Vacek & Hejcman 2012).

The continuous existence of a timberline and treeless summit areas in the Sudetes throughout the Holocene is supported especially by the occurrence of well-developed patterned grounds and other periglacial landforms that could not develop or remain preserved in forest (Sekyra et al. 2002, Treml et al. 2010), by the isolated localities of several light-demanding species of arctic or alpine grasslands and occurrence of several neoendemic species of *Hieracium* that could not survive on forested summits (Soukupová et al. 1995). However, human activity influenced the extent of the naturally treeless summit areas. Chalets were built at high altitudes in the Krkonoše from the 15th century onwards and the demand for firewood and pastures caused deforestation. However, Jeník & Lokvenc (1962) estimated that the Krkonoše timberline was lowered on average only by 20–30 m as a result of human activities. In the Hrubý Jeseník, the pollen and charcoal data and written sources indicate a significant effect of human activity on the summits already in the High Medieval and local effects even earlier (Jeník & Hampel 1992, Rybníček & Rybníčková 2004, Novák et al. 2010). Before human activity had an effect the timberline in this mountain range was probably at 1400–1450 m a.s.l. and only restricted areas on the highest summits and exposed edges of summit plateaus were treeless (Rybníček & Rybníčková 2004, Treml et al. 2008, Novák et al. 2010). The artificial lowering of the timberline in the Krkonoše and Hrubý Jeseník was partly reversed by afforestation with *Picea abies* in the 19th and the first half of the 20th century.

Krummholz with *Pinus mugo* on mineral soils (class *Roso pendulinae-Pinetea mugo*, alliance *Pinion mugo*; Fig. 16a) occurs only in the Krkonoše and Šumava Mts. It is absent in the Králický Sněžník and Hrubý Jeseník Mts, except for the recent plantations, and is not recorded there even in the fossil charcoal from the last 2000 years (Novák et al. 2010) or in written historical sources (Jeník & Hampel 1992). On the Czech side of the Šumava *Pinus mugo* occurs in small patches on boulder screes and rock outcrops below the timberline at altitudes of 1080–1360 m, but on the Bavarian side it is also found at the timberline on Mt Großer Arber at about 1400 m. In the Krkonoše krummholz is widespread at the timberline and above it, being most common at altitudes of 1230–1500 m. On boulder screes and avalanche tracks it descends as low as 1050 m. It declined slightly in abundance in the past as it was cut for firewood and removed in order to enlarge the grassland areas for grazing and haymaking, but was planted in some areas in the late 19th and 20th century. Krummholz vegetation occurs on acidic soils in the Czech mountains and accordingly it is rather poor in species, with frequent occurrence of *Avenella flexuosa*, *Vaccinium myrtillus* and *V. vitis-idaea* (Jirásek 1996b, Šibík et al. 2010).

Subalpine deciduous scrub or woodland (class *Mulgedio-Aconitetea*, alliance *Salicion silesiaca*) occurs in cirques of the Krkonoše and Hrubý Jeseník Mts at the edges of avalanche tracks and on slopes where there are thick snowpacks. It is dominated by *Betula carpatica*, *Salix silesiaca* and *Sorbus aucuparia* and locally also *Prunus padus* subsp. *borealis* and the Krkonoše endemic *Sorbus sudetica*. Subalpine tall forbs and tall ferns are common in the herb layer of this scrub or woodland.

Alpine and subalpine grasslands and heathlands above the timberline in the Sudetes are dominated by oligotrophic grasses adapted to acidic soils (Jeník 1961, Krahulec 1990a, Soukupová et al. 1995). Exposed wind-swept summit areas are covered by open grasslands of *Festuca supina* or heathlands of *Calluna vulgaris* (Fig. 16b), both with the boreo-alpine

species *Carex bigelowii* and *Juncus trifidus*, endemic *Hieracium* species and arcto-alpine lichens. These grasslands belong to the class *Juncetea trifidi*, alliance *Juncion trifidi* and heathlands to class *Loiseleurio-Vaccinietae*, alliance *Loiseleurio procumbentis-Vaccinion*. At less exposed sites protected by deep snow cover there are species-poor closed grasslands dominated by *Nardus stricta* (more common in the Krkonoše) or *Avenella flexuosa* (more common in the Hrubý Jeseník) and with occurrence of *Carex bigelowii* (class *Juncetea trifidi*, alliance *Nardo strictae-Caricion bigelowii*). These are the most common types of grassland on the summits of the Sudetes (Krahulec et al. 1997). The widespread distribution of *Nardus stricta* on the Krkonoše summits may have resulted from long-term cutting, grazing and the resulting nutrient depletion; after cessation of management, tall grasses such as *Calamagrostis villosa* and *Molinia caerulea* spread in these grasslands (Hejcman et al. 2006b, 2007, 2009). Locally at the timberline and on the slopes of cirques species-rich *Nardus stricta* grasslands occur (class *Calluno-Ulicetea*, alliance *Nardion strictae*). *Vaccinium myrtillus* heathlands extend over large areas at sites with deep snowpacks on the leeward slopes, around the timberline and in open spaces among *Pinus mugo* bushes (class *Calluno-Ulicetea*, alliance *Genisto pilosae-Vaccinion*; Fig. 16c). On restricted outcrops of base-rich rocks (e.g. marble or porphyry) in the cirques of the Krkonoše and Hrubý Jeseník Mts, patches of species-rich basiphilous grassland with *Agrostis alpina* and *Festuca versicolor* occur (class *Elyno-Seslerietea*, alliance *Agrostion alpinae*).

Subalpine tall-forb vegetation (class *Mulgedio-Aconitetea*) occurs on treeless slopes and at the bottoms of the cirques, especially on avalanche tracks, along mountain streams and in wet and nutrient-rich sites in canopy openings around the timberline. Tall grasslands with *Calamagrostis villosa*, *Deschampsia cespitosa* and *Molinia caerulea* (alliance *Calamagrostion villosae*) occur on mesic soils on plateaus or gentle slopes. Grasslands of *Calamagrostis arundinacea* (alliance *Calamagrostion arundinaceae*) are typical of leeward steep slopes on avalanche tracks in the Krkonoše and Hrubý Jeseník Mts, which are protected by distinct snow cover in winter but exposed to the sun and relatively warm in summer. In these moderate mesoclimatic conditions there are the most species-rich communities of the montane to alpine belt in the Czech Republic, which contain several thermophilous species typical of low-altitude grasslands and deciduous forests (Jeník 1961, Kočí 2001). Vegetation of tall broad-leaved dicots, such as *Adenostyles alliariae*, *Cicerbita alpina* and *Veratrum album* subsp. *lobelianum*, occurs at moist nutrient-rich sites in the subalpine belt, e.g. at seepage sites, along creeks and bottoms of cirques (alliance *Adenostylon alliariae*; Fig. 16d). Stands of tall ferns, mainly *Athyrium distentifolium* and locally also *Dryopteris filix-mas*, are common on boulder scree in the cirques (alliance *Dryopterido filicis-maris-Athyrium distentifolii*).

Rock and scree vegetation

Treeless rock outcrops, cliffs and scree occur mainly in river valleys of the Bohemian Massif, karst and sandstone pseudokarst areas, on volcanic hills and in mountain cirques. However, they are generally rare, small-sized and isolated in a forested landscape (Kubešová & Chytrý 2005). Therefore, there are very few specialized or endemic species confined to these habitats in the Czech Republic (Kaplan 2012), which sharply contrasts with a high level of habitat specialization and endemism on rock outcrops and scree in the

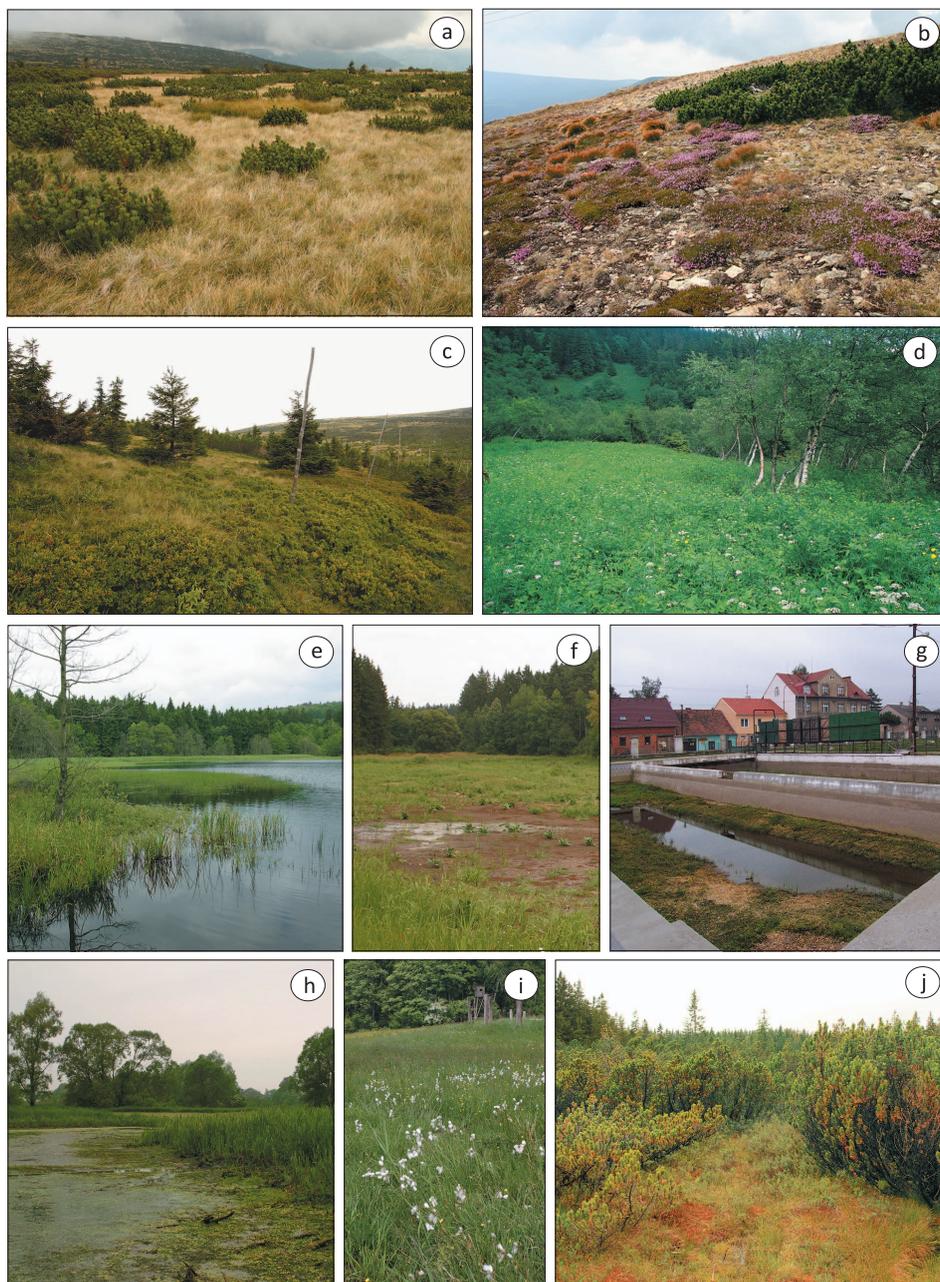


Fig. 16. – Examples of alpine, subalpine, aquatic and wetland vegetation types in the Czech Republic: (a) a mosaic of *Pinus mugo* scrub and *Nardus stricta* grassland above the timberline in the western Krkonoše Mts; (b) alpine heathland with *Calluna vulgaris* on Mt Sněžka, Krkonoše Mts; (c) subalpine heathland with *Vaccinium myrtillus* above the timberline in the western Krkonoše Mts; (d) tall-forb vegetation at the end of an avalanche track in the Velká kotlina cirque, Hrubý Jeseník Mts; (e) fishpond Horní Mrzatec near Mrákočin, Bohemian-Moravian Highlands; (f) exposed bottom of drained fishpond U Skřipu near Kraselov, Bohemian-Moravian Highlands; (g) fish-storage ponds in Vodňany, southern Bohemia; (h) oxbow lake with *Glyceria maxima* marsh on the Odra river floodplain near Studénka, north-eastern Moravia; (i) fen meadow with *Eriophorum angustifolium* near Velké Meziříčí, Bohemian-Moravian Highlands; (j) montane bog with *Pinus mugo* at the Tříjezerní slať mire, Šumava Mts.

Alps, Carpathians or mountain ranges of southern Europe (Valachovič et al. 1997). Specialist species of rock habitats and stable boulder screes in the Czech Republic include small ferns such as *Asplenium* spp., *Cryptogramma crista*, *Cystopteris fragilis*, *Gymnocarpium robertianum*, *Polypodium interjectum*, *P. vulgare*, *Trichomanes speciosum* (only gametophytes; Vogel et al. 1993) and *Woodsia ilvensis*, and some dicots such as *Saxifraga rosacea*. Some of these species also occur in man-made habitats such as stone quarries or walls; however, wall vegetation is poorer in species and contains a higher proportion of alien, annual, nutrient-demanding and ant-dispersed species than vegetation on natural rocks (Láníková & Lososová 2009, Lososová & Láníková 2010). Habitat specialists of mobile screes include *Epilobium dodonaei*, *Galeopsis angustifolia*, *G. ladanum*, *Gymnocarpium robertianum* and *Teucrium botrys* (Sádlo & Kolbek 1994).

Mobile screes composed of fine rock debris are mainly found in stone quarries in the Czech Republic and are rapidly stabilized by succession of perennial vegetation after the rock material has ceased to accumulate. The most common type of natural screes are stabilized talus slopes consisting of large boulders, which occur in river valleys of the Bohemian Massif and on volcanic hills in northern Bohemia. Some basalt talus slopes in the České středohoří Mts are characterized by an internal air circulation system (ventaroles) with winter exhalations of warm air at the top of the talus slope and summer outflows of cold and humid air at their foot, at some sites even with summer ice holes (Kubát 1999). Consequently, the upper parts of these talus slopes locally support frost-sensitive species such as the Mediterranean or subtropical-suboceanic liverworts *Riccia ciliifera* and *Targionia hypophylla* on Boreč hill, while lower parts are often characterized by natural occurrence of spruce at low altitudes and a high diversity of bryophytes, many of them typical of boreal forests (Pilous 1959).

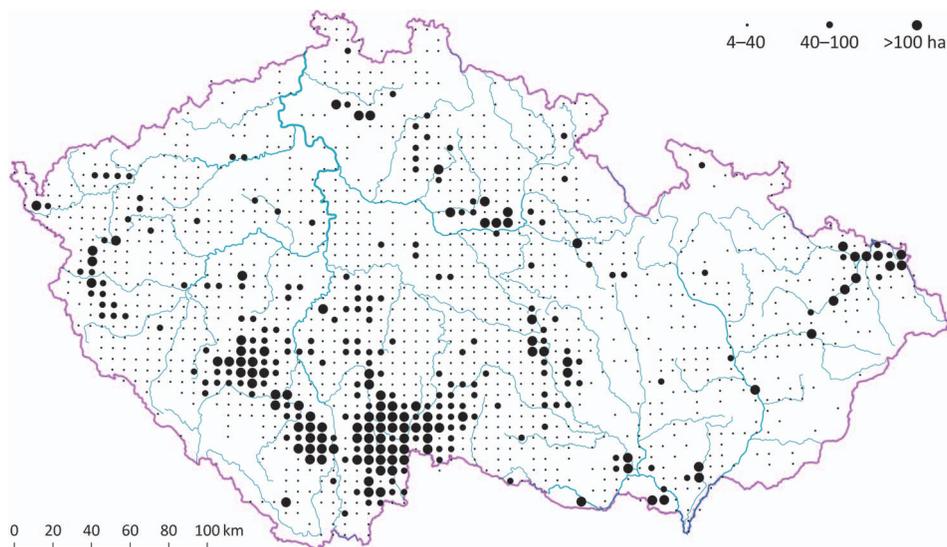


Fig. 17. – Fishpond areas. Dot size indicates summed hectareage of fishponds per grid square of 3×5 geographical minutes.

Vegetation of limestone and other calcareous rock outcrops is characterized by ferns *Asplenium ruta-muraria*, *A. trichomanes* subsp. *quadrialeans*, *Cystopteris fragilis*, *Gymnocarpium robertianum* and *Polypodium interjectum* (class *Asplenieta trichomanis*, alliance *Cystopteridion*), and very similar vegetation also occurs on walls in which mortar was used as a binding material (Kolbek 1997, Duchoslav 2002). Serpentine rocks host specialist ferns *Asplenium adulterinum* and *A. cuneifolium*. On the serpentine outcrops in the Jihlava valley near Mohelno (south-western Moravia), also the southern European-western Asian fern *Notholaena marantae* occurs at an isolated site (Vicherek 1970; class *Asplenieta trichomanis*, alliance *Cystopteridion*). The vegetation on siliceous rocks and stabilized talus slopes includes *Asplenium septentrionale*, *A. trichomanes* subsp. *trichomanes*, *Polypodium vulgare*, and at some sites also *Saxifraga rosacea* subsp. *sponhemica*, *S. r.* subsp. *steinmannii* and *Woodsia ilvensis* (class *Asplenieta trichomanis*, alliance *Asplenion septentrionalis*). Locally there are stands of the boreo-alpine fern *Cryptogramma crispa* (class *Asplenieta trichomanis*, alliance *Androsacion alpinae*) on screes of siliceous rocks in mountain cirques and on summit areas. On some walls, especially in lowland areas, there is vegetation dominated by *Cymbalaria muralis* and *Pseudofumaria lutea*, both neophytes of Mediterranean origin (class *Cymbalario muralis-Parietarietea judaicae*, alliance *Cymbalario muralis-Asplenion*). Mobile limestone screes occurring in karst areas, often in quarries, are characterized by *Galeopsis angustifolia*, *Gymnocarpium robertianum*, *Melica ciliata* and *Teucrium botrys* (class *Thlaspietea rotundifolii*, alliance *Stipion calamagrostis*). On mobile screes of siliceous rocks there is locally species-poor vegetation with *Galeopsis ladanum* (class *Thlaspietea rotundifolii*, alliance *Galeopsion*).

Aquatic vegetation

Natural lakes are rare in the Czech Republic, as most of the territory was not glaciated. Some natural lakes, especially in the lowlands, vanished as a result of natural terrestrialization in the Holocene or were drained by humans, mainly in the 19th century (Břízová 2009). However, a typical feature of the Czech landscape is fishponds, shallow water reservoirs built from the 11th century onwards for fish farming (Fig 16e). The main species farmed has always been common carp (*Cyprinus carpio*), which requires warm and shallow water. Therefore, most of the fishponds are in lowlands or mid-altitude basins and are on average about 2 m deep. In the heydays of fish farming at the turn of the 17th century there were about 70,000 fishponds in the Czech lands. Later on, many of them, especially those in the lowlands, were drained to obtain arable land or grasslands, and currently there are about 25,000 fishponds, the largest with an area of almost 500 ha (Čítek et al. 1998). They are concentrated mainly in the basins of southern Bohemia around Blatná, České Budějovice and Třeboň, in the Ostravská Basin in north-eastern Moravia and other, smaller basins, as well as in flat areas in the Bohemian-Moravian Highlands (Fig. 17). Various types of aquatic and wetland vegetation occur in fishponds (Dykyjová & Květ 1978) and many of them are of high conservation importance (Chytil et al. 1999). Other types of wetland habitats are small oxbow lakes on floodplains and water bodies in abandoned quarries or loam, sand or gravel pits.

Aquatic vegetation of eutrophic water is best developed in small fishponds which are not used for intensive fish farming, alluvial pools or channels. The vegetation of free-floating aquatic plants (class *Lemnetea*) is composed of lemnids, such as *Lemna gibba*, *L. minor*, *L. trisulca* and *Spirodela polyrhiza*, or the aquatic liverworts *Riccia fluitans*, *R. rhenana* and *Ricciocarpos natans*. The rare species *Salvinia natans* and *Wolffia arrhiza* occur in this vegetation in the lowlands of north-eastern and southern Moravia, respectively (alliance *Lemnion minoris*). Bladderwort vegetation of eutrophic to mesotrophic water bodies is mostly composed of *Utricularia australis*, while the rare species *U. vulgaris* occurs only in the middle Labe valley (alliance *Utricularion vulgaris*). Larger free-floating aquatic plants include *Ceratophyllum demersum*, *C. submersum*, *Hydrocharis morsus-ranae* and *Stratiotes aloides* (alliance *Hydrocharition morsus-ranae*). Aquatic plants rooted in the bottom with leaves floating on the water surface include *Nuphar lutea*, *N. pumila*, *Nymphaea alba*, *N. candida*, *Nymphoides peltata*, *Persicaria amphibia* and *Trapa natans* (class *Potametea*, alliance *Nymphaeion albae*). Submerged aquatic plants occurring in still or slowly moving water include various species of *Potamogeton*, *Myriophyllum spicatum*, *M. verticillatum*, *Najas marina*, *N. minor*, *Zannichellia palustris*, the neophyte *Elodea canadensis* (class *Potametea*, alliance *Potamion*) and stoneworts (*Chara* spp., *Nitella* spp. and *Tolypella* spp.; class *Charetea*, alliances *Charion globularis* and *Nitellion flexilis*). A few aquatic species may occur in monodominant stands in streams with a current of high or medium velocity: most commonly it is *Batrachium fluitans*, *B. peltatum*, *Callitriche hamulata* or the moss *Fontinalis antipyretica* and less frequently *Batrachium penicillatum* or *Myriophyllum alterniflorum* (class *Potametea*, alliance *Batrachion fluitantis*). *Batrachium aquatile*, *B. circinatum* and other species of this genus and in some places also *Callitriche hermaphroditica* and *Hottonia palustris* (class *Potametea*, alliance *Ranunculion aquatilis*) occur in still water bodies where the water level fluctuates and can occasionally be below the level of the bottom.

Vegetation of oligotrophic and mesotrophic water (class *Littorelletea uniflorae*) is rare in the Czech Republic, partly due to anthropogenic eutrophication of water bodies and partly because of the marginal position of this country with respect to the oceanic distribution range of this vegetation. Two natural lakes in the Šumava Mts (Plešné, 1087 m a.s.l., and Černé, 1008 m a.s.l.) contain sparse low-productive monodominant stands of *Isoetes echinospora* and *I. lacustris*, respectively (alliance *Littorellion uniflorae*; Husák et al. 2000, Čtvrtlíková et al. 2009). In some fishponds on acidic bedrock in submontane areas there is a rare type of amphibious vegetation consisting of perennial plants with *Juncus bulbosus*, *Littorella uniflora* and *Pilularia globulifera* and more commonly vegetation with *Eleocharis acicularis* (alliance *Eleocharition acicularis*). Mire pools locally contain vegetation consisting of *Sparganium natans*, *Utricularia intermedia*, *U. minor* and *U. ochroleuca* (alliance *Sphagno-Utricularion*; Dítě et al. 2006).

Wetland vegetation

Like aquatic vegetation, the wetlands are mainly associated with fishponds and lowland river floodplains in the Czech Republic. There are two basic types of wetland: those with annual wetland herbs and marshes with tall perennials.

Vegetation of annual wetland herbs occurs mainly on the exposed bottoms of fishponds, although it can also be found on fluvial muddy deposits along lowland rivers and in other habitats including man-made ones. Traditional fishpond management included periodical summer draining at intervals of a few years, aimed at increasing pond productivity, suppressing fish parasites and reducing productive pond vegetation (Fig. 16f). Specialized annual wetland species germinate in the mud at the bottoms of drained fishponds which remain saturated with water or very shallowly flooded for a period of several days or a few weeks after draining. In addition to the type of substrate in the bottom of the pond and climate, the species composition of this vegetation depends on timing and for how long the pond is drained (Šumberová et al. 2005). Since the 19th century fertilizers and lime were increasingly applied and the fish fed in some fishponds, and the period when the ponds were drained was reduced to maximize fish production. From the mid 20th century such intensive management was applied in most fishponds (Čítek et al. 1998, Šumberová 2003). Fishponds are rarely drained nowadays, but there is suitable habitat for annual wetland herbs in fish-storage ponds (Šumberová et al. 2006). These are small ponds, often bounded by concrete walls, which are used for short-term storage of marketable fish and then drained (Fig. 16g). There are usually more species per unit area in fish-storage ponds than ordinary fishponds, but due to a stronger human impact, the former also contain more alien species (Šumberová et al. 2006). Vegetation of fishponds in submontane areas and basins with acidic bedrocks, but with nutrient-rich mud, includes *Carex bohemica*, *Coleanthus subtilis*, *Elatine triandra* and *Eleocharis ovata*, and that of fishponds in warmer areas or on more calcareous substrates additionally includes *Cyperus fuscus* (class *Isoëto-Nano-Juncetea*, alliance *Eleocharition ovatae*). On the exposed nutrient-poor sandy bottoms of fishpond margins or fish-storage ponds, or on wet sandy arable land in the southern Bohemian basins, a few last remnants can be found of vegetation with the rare species *Centunculus minimus*, *Hypericum humifusum*, *Illecebrum verticillatum*, *Juncus capitatus*, *J. tenageia*, *Pseudognaphalium luteoalbum*, *Radiola linoides* and *Tillea aquatica* (class *Isoëto-Nano-Juncetea*, alliance *Radiolion linoidis*). Disturbed wet soils in warm lowlands, especially in southern Moravia, which are more base-rich than those at higher altitudes, are characterized by another group of rare species, including *Centaurium pulchellum*, *Cerastium dubium*, *Juncus ranarius*, *Lythrum hyssopifolia*, *Mentha pulegium*, *Pulicaria vulgaris*, *Ranunculus sardous*, *Veronica anagalloides* and *V. catenata* (class *Isoëto-Nano-Juncetea*, alliance *Verbenion supinae*). In addition to this low-growing vegetation stands of tall annual herbs (e.g. *Bidens cernuus*, *B. radiatus*, *B. tripartitus*, *Persicaria hydropiper*, *P. lapathifolia*, *Ranunculus sceleratus* and *Rumex maritimus*) also grow on the initially bare or frequently disturbed wet soils, which are rich in nutrients. If the bottom of the pond is exposed for a few months these stands of tall-herbs constitute the next successional stage, which displaces the short-growing annual vegetation (class *Bidentetea tripartitae*; alliance *Bidention tripartitae*). On ammonium-rich and slightly saline wet soils, both in natural and man-made habitats, the vegetation includes nutrient-demanding *Chenopodiaceae* such as *Atriplex prostrata* subsp. *latifolia*, *Chenopodium ficifolium*, *C. glaucum* and *C. rubrum* (class *Bidentetea tripartitae*; alliance *Chenopodion rubri*).

Marsh vegetation (class *Phragmito-Magno-Caricetea*) occurs mainly in fishpond littoral zones (Dykyjová & Květ 1978) and river floodplains. Stands of *Phragmites australis* are the most common type of marsh vegetation. *Phragmites* is the strongest competitor among wetland herbs and has a broad ecological range, growing both in oligotrophic and

eutrophic water bodies, and in water as deep as 2 m and at sites that are drained for a significant part of the growing season. Other wetland herbs dominate the vegetation only in habitats that are, for different reasons, unsuitable for *Phragmites* (Ellenberg & Leuschner 2010). For example, *Schoenoplectus lacustris* dominates in deeper water, *Typha angustifolia* and *T. latifolia* in nutrient-rich habitats the bottoms of which are frequently exposed so that they can quickly regenerate from seed, *Glyceria maxima* in hypertrophic wetlands (Fig. 16h), *Acorus calamus* (alien to the Czech Republic) and *Sparganium erectum* in frequently disturbed littoral habitats, and shorter stands of *Equisetum fluviatile* occur in places where there is a deep layer of organic sediment on the bottom. Dominance stands of the above-mentioned species are included in the alliance *Phragmition australis*. In the littoral zone of brackish water bodies or around mineral springs in lowland areas, marshes are dominated by halophilous species of *Bolboschoenus* (*B. maritimus* and *B. planiculmis*; Hroudová et al. 2009) or *Schoenoplectus tabernaemontani* (alliance *Meliloto dentati-Bolboschoenion maritimi*), but nowadays this vegetation is rather rare in the Czech Republic. In wetlands with a fluctuating water table such as shallow littoral zones of fishponds, or fishponds in the years following draining, the vegetation consists of perennial or biennial herbs, e.g. *Alisma plantago-aquatica*, *Bolboschoenus yagara*, *Butomus umbellatus*, *Eleocharis palustris*, *Hippuris vulgaris*, *Oenanthe aquatica*, *Rorippa amphibia*, *Sagittaria sagittifolia*, *Scirpus radicans* and *Sparganium emersum* (alliance *Eleocharito palustris-Sagittarion sagittifoliae*). Riverine reeds are mostly dominated by *Phalaris arundinacea*, but in places that are less frequently flooded tall-sedge stands of *Carex buekii* also occur. *Calamagrostis pseudophragmites* is typical of fluvial gravel beds, mainly in north-eastern Moravia (Kopecký 1969; alliance *Phalaridion arundinaceae*). Short-growing small-sized marshes or carpet-like stands of *Berula erecta*, *Glyceria fluitans*, *G. notata*, *Leersia oryzoides* and *Nasturtium officinale* occur in small streams or ditches and on their banks, in fish-storage ponds and in fishpond littoral zones (alliance *Glycerio-Sparganion*). Another type of wetland vegetation develops in mesotrophic to dystrophic water bodies and wetlands in an advanced successional stage of terrestrialization, where organic sediment mixed with mud has accumulated. These stands may be dominated by *Calla palustris*, *Carex pseudocyperus* and *Cicuta virosa* (alliance *Carici-Rumicion hydrolapathi*). Tall-sedge stands generally develop in the later stages of wetland succession, in places where the accumulation of undecomposed litter of reed plants has raised the ground level and, as a consequence, flooding is shallower or shorter. There are two major types of tall-sedge marshes, mesotrophic (alliance *Magno-Caricion elatae*) and eutrophic (*Magno-Caricion gracilis*). The former includes especially stands dominated by *Carex rostrata* and less commonly *C. appropinquata*, *C. diandra*, *C. elata* and *C. lasiocarpa*. Marshes with *Cladium mariscus*, which occur in a few calcium-rich fens in the lowland along the middle Labe river, are also mesotrophic. The latter, eutrophic type, includes especially the common stands with *Carex acuta* in fishpond littoral zones and on floodplains of large rivers, and also stands of *Carex acutiformis*, *C. disticha*, *C. paniculata*, *C. riparia*, *C. vesicaria* and *C. vulpina*.

Spring and mire vegetation

Spring and mire vegetation occurs mainly in mid- to high-altitude areas in the Czech Republic, with the exception of calcareous fens, which are also found in the lowlands, especially in areas of central and eastern Bohemia with Cretaceous marlstone. Another exception is the basins around Doksy, Cheb and Třeboň (see the Taiga biome description above), which contain different types of acidic fens and bogs (Fig. 18).

Spring vegetation (class *Montio-Cardaminetea*; Fig. 18a) with specialized short-growing vascular plants and abundant bryophytes occurs in small patches at seepage sites. Main factors determining its species composition are altitude, site insolation and calcium carbonate precipitation resulting in tufa formation. The most common type of spring vegetation occurs at soft-water seepage sites without tufa formation that are shaded by trees. Typical species of these forest springs include *Cardamine amara* subsp. *amara*, *C. a.* subsp. *austriaca*, *Carex remota*, *Chrysosplenium alternifolium* and *C. oppositifolium* (alliance *Caricion remotae*). Forest springs with tufa formation are mainly confined to the Bohemian Karst (Rivola 1982) and the Carpathian flysch zone in eastern Moravia. Their vegetation has a sparse herb layer, but the moss layer is well-developed and includes specialized bryophytes such as *Eucladium verticillatum*, *Palustriella commutata* and *Pellia endiviifolia* (alliance *Lycopodo europaei-Cratoneurion commutati*). Soft-water springs at open sites locally support specialized light-demanding vegetation with *Montia fontana* subsp. *amportitana* or *M. f.* subsp. *fontana*, occurring especially in the montane belt of higher mountain ranges (alliance *Epilobio nutantis-Montion fontanae*). Springs with tufa formation at open sites are found especially in the Carpathian flysch zone. They are characterized by the accumulation of organic sediment and their vegetation consequently corresponds to calcareous fens rather than to specialized spring vegetation. Special types of spring vegetation occur around seepages in the subalpine belt of the Krkonoše and Hrubý Jeseník Mts; dominant species include *Allium schoenoprasum*, *Cardamine amara* subsp. *opicii*, *Swertia perennis* and mosses *Dichodontium palustre*, *Philonotis seriata* and *Pohlia wahlenbergii* (alliance *Swertio perennis-Dichodontion palustris*).

Vegetation of fens and transitional mires (class *Scheuchzerio palustris-Caricetea nigrae*) occurs in habitats that are permanently saturated with water and poor in available nitrogen and phosphorus, in which undecomposed litter of sedges, other herbs and mosses accumulates to form a peat layer. Although some fens and transitional mires existed on the territory of the present Czech Republic already in the Late Glacial and remained in the landscape throughout the Holocene (Sádlo 2000), most of them developed at sites of former forested seepages or carrs after deforestation, especially during the medieval colonization of mid-altitude areas (Rybníček & Rybníčková 1974, Rybníčková 1974, Rybníčková et al. 2005, Hájek et al. 2011). This vegetation varies along a 'poor-rich gradient', i.e. from acidic, base-poor and species-poor types to species-rich calcareous fens (Hájek et al. 2002, 2006). Calcareous fens with short sedges (*Carex davalliana*, *C. flacca*, *C. flava*, *C. nigra* and *C. panicea*) and several species of specialist herbs and mosses such as *Bryum pseudotriquetrum* and *Campylium stellatum* (alliance *Caricion davallianae*) occur mainly in the Carpathian flysch zone and in the lowland areas with Cretaceous marlstone in eastern Bohemia (Fig. 18b), however, in the latter area many sites have been drained. Other fen types occur mostly at higher altitudes (Fig. 18c). At some mid-altitude sites, especially in the Bohemian-Moravian Highlands, fen vegetation contains a mixture

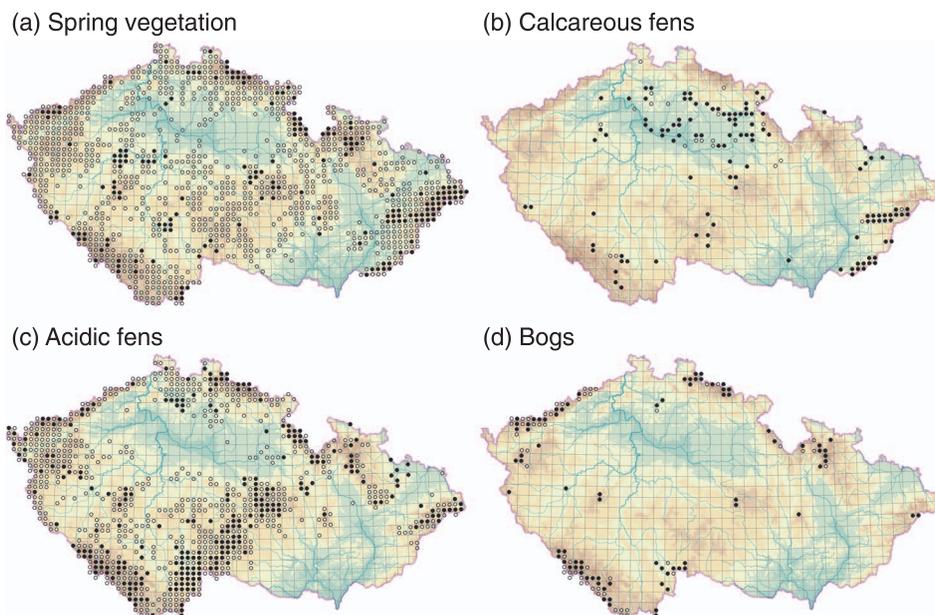


Fig. 18. – Distribution of spring and mire vegetation types. Black circles indicate sites of relevés from the Czech National Phytosociological Database that correspond to formal definitions of vegetation types published in Volume 3 of *Vegetation of the Czech Republic* (Chytrý 2011). Open circles as in Fig. 15. Phytosociological units: (a) *Montio-Cardaminetea*; (b) *Caricion davallianae*; (c) *Sphagno warnstorffii-Tomentypnion nitentis*, *Caricion canescenti-nigrae*, *Sphagno recurvi-Caricion canescentis*; (d) *Oxycocco-Sphagnetea*.

of calcicolous and acidophilous species, including calcium-tolerant peat mosses (e.g. *Sphagnum contortum*, *S. teres* and *S. warnstorffii*; alliance *Sphagno warnstorffii-Tomentypnion nitentis*). The most common type of Czech fen vegetation is moderately rich in bases, with a substrate of pH 5–6, and is usually rather rich in species. It consists of short sedges, grasses, dicots and a rich moss layer with *Aulacomnium palustre*, *Sarmentypnum exannulatum*, *Straminergon stramineum* and peat mosses, e.g. *Sphagnum palustre* and *S. subsecundum* (alliance *Caricion canescenti-nigrae*; Fig. 16i). Acidic fens (transitional mires) at mid-altitude sites, which are very poor in calcium despite being fed by ground water rather than rain water, support species-poor vegetation of sedges (*Carex canescens*, *C. echinata*, *C. lasiocarpa*, *C. nigra* and *C. rostrata*) and mosses (*Polytrichum commune*, *Sphagnum fallax*, *S. flexuosum* and *S. palustre*; alliance *Sphagno-Caricion canescentis*). In the course of mire succession they develop from the above-mentioned fen types. Bog hollows with continuous or nearly continuous moss layer (mainly *Sphagnum cuspidatum* and *Warnstorffia fluitans*) and sparse herb layer with *Carex limosa*, *C. rostrata*, *Eriophorum angustifolium* and *Scheuchzeria palustris* are extremely poor in nutrients and bases, nevertheless, their structure is similar to fens (alliance *Sphagnion cuspidati*).

Bogs (class *Oxycocco-Sphagnetea*; Fig. 18d) are the most advanced mire type developed through the process of autogenic succession. As bogs are elevated above the adjacent terrain they are entirely fed by rainwater (ombrotrophic mires) and extremely poor in nutrients and bases. They are dominated by specialist peat mosses (e.g. *Sphagnum fallax*,

S. flexuosum, *S. magellanicum*, *S. rubellum* and *S. russowii*) and dwarf shrubs (*Calluna vulgaris*, *Empetrum hermaphroditum*, *E. nigrum*, *Rhododendron tomentosum*, *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea*). Some bogs are characterized by a distinct microtopography with dry hummocks and wet hollows. Continental and subcontinental bogs (alliance *Sphagnion magellanicum*) can be open, especially in precipitation-rich areas, but bogs at the sites where the water level is occasionally lower during dry summer are covered by a sparse tree layer with pine: at low altitudes, namely in the Doksy region and Třeboňská Basin, it is *Pinus sylvestris*, while in the mountain areas (but also in the Třeboňská Basin) it is the central-European endemic *P. uncinata* subsp. *uliginosa*. At higher altitudes of some of the Czech mountain ranges (Novohradské, Šumava, Krušné, Jizerské and Krkonoše Mts), shrubby *Pinus mugo* becomes dominant in bogs (Fig. 16j). A rare type of bog vegetation includes suboceanic mires with *Trichophorum cespitosum* and *Sphagnum papillosum* (alliance *Oxycocco palustris-Ericion tetralicis*); they occur in the Jizerské Mts, the most precipitation-rich area in the Czech Republic. Unlike most other bogs in the Czech Republic, they do not have a hummock-and-hollow microtopography. The boreal type of mires with arctic-boreal species such as *Betula nana*, *Rubus chamaemorus* and *Vaccinium microcarpum* occurs in the supramontane to subalpine belts of the Krkonoše, Šumava and Krušné Mts. Peat mosses typical of this vegetation include *Sphagnum compactum* and *S. fuscum* (alliance *Oxycocco microcarpi-Empetrium hermaphroditum*). In the past large areas of bogs were destroyed by peat extraction, but there has been a tendency for peatland to recover by spontaneous succession at some of these sites (Konvalinková & Prach 2010). Even now undisturbed bogs are endangered by the lowering of the ground-water table and atmospheric nutrient deposition, but the latter has had little effect on species composition even though the levels of nitrogen deposition in the mountain bogs of the northern Czech Republic are among the highest in Europe (Hájková et al. 2011a).

Grasslands and heathlands below the timberline

Most types of grassland and heathland vegetation below the alpine timberline in the Czech Republic, especially in semi-dry, mesic and wet habitats, are secondary, developed in artificially deforested areas. However, some grasslands in such habitats may have locally survived throughout the Holocene due to human management (Hájková et al. 2011b). Large wild herbivores, which lived in central Europe until the Modern Period (auroch, wild horse and European bison), and beaver, may also have contributed to the maintenance of open grassland areas (Vera 2000). In contrast, the driest types of steppe grassland may have existed at some sites throughout the Holocene independently of human influence, especially on south-facing slopes in the forest-steppe areas of northern and central Bohemia and southern Moravia, and on rock outcrops (Ložek 2011). Nevertheless, also dry grasslands are the result of deforestation and livestock grazing at most sites. The extent of grasslands significantly increased with the medieval colonization and deforestation of mid-altitude areas.

Meadows and mesic pastures (class *Molinio-Arrhenatheretea*) are common in the Czech Republic (Havlová et al. 2004). As in other countries of central Europe, the term 'meadow' is reserved for grasslands used for hay making and dependent upon regular

mowing; once abandoned, they are overgrown by shrubs and trees and ultimately replaced by forest. Although meadows and mesic pastures are composed mainly of native species, they are relatively modern vegetation types (Poschlod et al. 2009). Original habitats of meadow and pasture species in the pre-Neolithic period were probably mainly on alluvial accumulations on the floodplains, in open woodlands and in tall-grass steppes. The oldest archaeological finds of scythes are from the 5th century BP (Beranová & Kubačák 2010) and it is therefore assumed that from the Neolithic to the early Iron Age secondary grasslands were maintained almost exclusively by grazing (main source of winter fodder for livestock was not hay but dried twigs with leaves from pollarded trees). Some differentiation between grazed and mown grasslands on less and more productive soils, respectively, may have occurred since the Iron Age, but alternations of these two management types at single sites were probably common. Long-term grazing and hay making led to continuous nutrient depletion of grassland ecosystems, however, fertilizers were not applied until the mid-19th century, except in areas close to some farms (Krahulec et al. 1997, Semelová et al. 2008). Therefore productive grasslands suitable for two or three hay cuts annually were mainly in floodplains, where nutrients were supplied naturally by floods. Non-alluvial grasslands were low-productive, and consequently cut either once a year, often in summer (Jongepierová 2008), or grazed. Continuous shift in animal husbandry from free grazing to livestock enclosure in paddocks and barns since the mid-19th century, motivated by a demand for dung to fertilize arable fields, increased the demand for hay. As a result, clearly differentiated vegetation types of meadows and pastures developed. Since the second half of the 19th century, and more frequently since the 20th century, mineral fertilizers were used to increase grassland productivity. The nutrient status and species composition of fertilized meadows changed from the originally oligotrophic, nutrient depleted grasslands with short grasses such as *Agrostis capillaris* and *Festuca rubra* (Blažková 1979) to mesotrophic or eutrophic types. This change in nutrient status was associated with the spread of tall, nutrient demanding grasses and dicot herbs, most notably *Arrhenatherum elatius*, which is now a very common dominant species in eutrophic meadows, but is considered to be an alien species in central Europe (Poschlod et al. 2009, Pyšek et al. 2012b). Merging small private farms into large cooperative farms enforced by the communist government in the 1950s and increased use of mineral fertilizers led to intensive management of meadows in productive areas and on easily accessible land, whereas grasslands in marginal or less productive areas where hay cutting became unprofitable were abandoned. Large areas of formerly managed grasslands were also abandoned in areas with German-speaking inhabitants who were forced to leave the country after World War II (Kopecký & Vojta 2009, Vojta & Drhovská 2012). Intensive grassland management with plowing and seeding with forage grasses, fertilizer input and several hay cuts per growing season leads to the development of species-poor communities with a few species capable of fast regrowth after cutting, e.g. *Alopecurus pratensis*, *Dactylis glomerata*, *Festuca arundinacea*, *F. pratensis* and *Phleum pratense* (Hejcman et al. 2012). Such high-productive grasslands are currently the most common grassland type in the Czech Republic. On the other hand, abandoned meadows and pastures are overgrown by competitive tall grasses or forbs such as *Aegopodium podagraria*, *Anthriscus sylvestris*, *Arrhenatherum elatius* and *Urtica dioica* in mesic habitats or *Filipendula ulmaria*, *Petasites hybridus* and *Phalaris arundinacea* in wet habitats (Prach 2008). Increasing dominance of single species usually leads to a decrease in species richness. Therefore nature conservation management by



Fig. 19. – Examples of different types of grassland vegetation in the Czech Republic: (a) *Arrhenatherum elatius* meadow near Martinice, Bohemian-Moravian Highlands; (b) lowland flooded meadow near the confluence of the Morava and Dyje rivers, southern Moravia; (c) abandoned wet meadow dominated by *Filipendula ulmaria* near Strašice, south-western Bohemia; (d) a mosaic of submontane *Nardus stricta* grassland and *Calluna vulgaris* heathland near Ražice, southern Bohemia; (e) sand grassland with *Corynephorus canescens* near Bzenec, southern Moravia; (f) short-grass steppe with *Erysimum crepidifolium* on Oblík hill, České středohoří Mts, northern Bohemia; (g) *Sesleria caerulea* grassland on north-facing limestone slopes on Děvín hill, Pavlovské Hills, southern Moravia; (h) species-rich semi dry meadow with scattered oaks at Čertoryje, Bílé Karpaty Mts, south-eastern Moravia; (i) saline grassland with *Puccinellia distans* near Dobré Pole, southern Moravia.

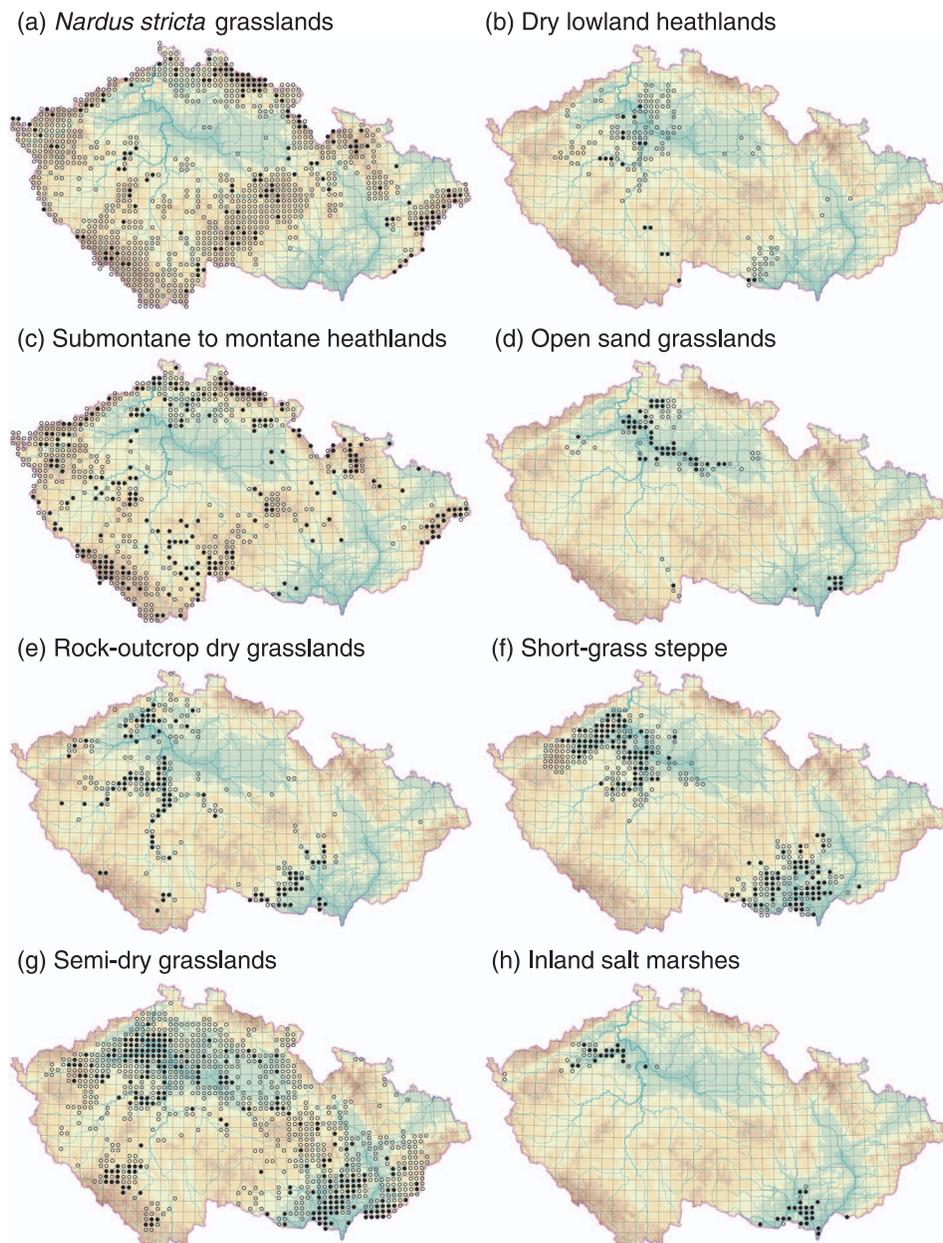


Fig. 20. – Distribution of selected types of grassland and heathland vegetation. Black circles indicate sites of relevés from the Czech National Phytosociological Database that correspond to formal definitions of vegetation types published in Volume 1 of *Vegetation of the Czech Republic* (Chytrý 2007). Open circles as in Fig. 15. Phytosociological units: (a) *Nardion strictae*, *Nardo strictae-Agrostion tenuis*, *Violion caninae*; (b) *Euphorbio cyparissiae-Callunion vulgaris*; (c) *Genisto pilosae-Vaccinion*; (d) *Corynephorion canescentis*; (e) *Alyssso-Festucion pallentis*, *Bromo pannonic-Festucion pallentis* and *Diantho lumnitzeri-Seslerion*; (f) *Festucion valesiaca*; (g) *Cirsio-Brachypodion pinnati* and *Bromion erecti*; (h) *Festuco-Puccinlietea*.

mowing or grazing has been re-introduced to abandoned grasslands at some sites, especially in nature reserves (Krahulec et al. 2001, Pavlů et al. 2007, 2011, Hejcman et al. 2008, Jongepierová 2008). New grasslands were recently restored on ex-arable land, either by seeding commercial seed-mixtures or by spontaneous succession (Lencová & Prach 2011). In some areas, species-rich meadows have been restored using regional seed mixtures (Mitchley et al. 2012) and experimentally also by transplantation of small blocks of meadow turfs (Klimeš et al. 2010).

The most common meadow type in the Czech Republic is mesic meadows dominated by the tall grass *Arrhenatherum elatius* (alliance *Arrhenatherion elatioris*; Fig. 19a), which occur from lowland to montane belt, although at higher altitudes the abundance of *Arrhenatherum* decreases while shorter grasses become dominant, in particular *Agrostis capillaris*, *Festuca rubra* and *Trisetum flavescens*. These meadows are usually cut twice a year with occasional aftermath grazing. At high altitudes, especially in the Krušné, Jizerské, Krkonoše and Orlické Mts, mesic meadows are dominated by the above mentioned short grasses and there are several species there that are absent in low-altitude meadows, e.g. *Arabidopsis halleri*, *Cirsium heterophyllum*, *Geranium sylvaticum*, *Meum athamanticum*, *Poa chaixii* and *Silene dioica* (alliance *Polygono bistortae-Trisetion flavescens*). Because of the shorter growing season and lower productivity in the mountains, these meadows are usually cut only once a year. Mesic pastures with *Lolium perenne*, *Plantago lanceolata*, *P. major*, *Trifolium pratense* and *T. repens* (alliance *Cynosurion cristati*) are also common in this country, especially at mid-altitudes. Many of them are poor in species and their structure and species composition is similar to lawns in city parks, which are mulched several times a year, or to trampled grasslands in human settlements. More species-rich mesic pastures are found especially in the Carpathian flysch zone (Rozbrojová et al. 2010). Meadows on low-productive soils, which are wet in spring but dry in summer, are often dominated by *Molinia arundinacea* or *M. caerulea* (alliance *Molinion caeruleae*; Havlová 2006). Due to their low productivity and the late phenology of the dominant species, they used to be cut once a year, in summer. They occur mainly in the highlands in the central part of the Bohemian Massif (Brdy Mts and Bohemian-Moravian Highlands) and basins of southern Bohemia, but they can also be found on raised areas on the floodplains of large lowland rivers. However, in the last few decades the area of these meadows has been strongly reduced due to eutrophication and abandonment. Wet meadows with natural fertilizer input through spring flooding are divided into the alliances *Deschampsion cespitosae* (Fig. 19b) and *Calthion palustris*. The former includes meadows in broad floodplains, which are flooded in spring but dry out in summer, especially along lowland rivers such as the Labe, lower Dyje and lower Morava (Balátová-Tuláčková 1968). These meadows are dominated by grasses, in particular *Alopecurus pratensis*, and used to be cut three times a year (Honsová et al. 2007). The latter alliance comprises meadows along small streams or at seepage sites, which are usually slightly flooded in spring and where the ground water table remains high in summer and the soil is wet all year round. These meadows are dominated by tall dicot herbs, especially different species of *Cirsium*, depending on soil chemistry (Hájek & Hájková 2004). They used to be cut two times a year. Abandoned meadows of *Calthion palustris* are usually dominated by the tall forb *Filipendula ulmaria* (Fig. 19c).

***Nardus stricta* grasslands** (Figs 19d & 20a) occur on nutrient-poor acidic soils over granite, gneiss, schist and similar hard and nutrient-poor bedrocks. Due to their low

productivity, they were traditionally used for livestock grazing, although occasionally they were mown once a year or every second year in summer. As a result of abandonment since the mid-20th century, coupled with nutrient deposition, many *Nardus* grasslands were replaced by mesic grasslands with a higher biomass (Krahulec et al. 1997). *Nardus stricta* grasslands occur from the submontane belt to areas above the timberline, and their species composition varies with altitude. The most widespread type with some thermophilous species (class *Calluno-Ulicetea*, alliance *Violion caninae*) is found in the submontane to montane belt. In the montane belt of the Krkonoše Mts, *Nardus* grasslands contain a mixture of submontane and subalpine species (class *Calluno-Ulicetea*, alliance *Nardo strictae-Agrostion tenuis*; Krahulec 1990b, Krahulec et al. 1997). *Nardus* grasslands occurring around the timberline in the Krkonoše, Králický Sněžník and Hrubý Jeseník Mts contain subalpine species while submontane species are absent (class *Calluno-Ulicetea*, alliance *Nardion strictae*). *Nardus* grasslands above the timberline in these mountain ranges are species-poor and contain arcto-alpine species such as *Carex bigelowii* (class *Juncetea trifidi*, alliance *Nardo-Caricion bigelowii*; see above). A specific type of species-poor *Nardus* grasslands with *Juncus squarrosus* occurs on wet acidic soils in the montane and submontane areas (class *Calluno-Ulicetea*, alliance *Nardo strictae-Juncion squarrosi*).

Heathlands are dominated by *Calluna vulgaris*, *Vaccinium myrtillus* and *V. vitis-idaea*, and locally also co-dominated by *Arctostaphylos uva-ursi* (northern, central and southern Bohemia), *Erica carnea* (western and southern Bohemia) and *Genista pilosa* (south-western Moravia). Other species of dwarf shrubs that are typical of Atlantic heathlands of western Europe are absent in the Czech Republic because of its more continental climate. Czech heathlands develop on nutrient-poor bedrocks such as granite, gneiss, schist, sandstone or sand, usually on shallow soil. For the most part, they are secondary vegetation that developed in deforested areas that were disturbed and depleted of nutrients by grazing, cutting or burning and locally perhaps also sod-cutting (Sedláková & Chytrý 1999). Small patches of primary heathlands are restricted to rock outcrops and more extensive primary heathlands occur above the timberline. Dry lowland heathlands that occur especially in central Bohemia and south-western Moravia are dominated by *Calluna vulgaris*, while *Vaccinium* species are absent; they are rich in thermophilous continental species typical of dry grasslands (class *Calluno-Ulicetea*, alliance *Euphorbio cyparissiae-Callunion vulgaris*; Fig. 20b). Submontane to montane heathlands are usually co-dominated by *Calluna vulgaris*, *Vaccinium myrtillus* and *V. vitis-idaea*, while thermophilous continental species are absent (Geringhoff & Daniěls 1998). Extensive stands dominated by *Vaccinium myrtillus* occur above the timberline in the Krkonoše, Králický Sněžník and Hrubý Jeseník Mts, in places where thick snow cover provides winter protection to dwarf shrubs (class *Calluno-Ulicetea*; alliance *Genisto pilosae-Vaccinion*; Fig. 20c).

Pioneer vegetation of sandy and shallow soils occurs in lowland sandy areas (Fig. 3) and on outcrops of poorly weathered rocks, especially granite, gneiss and schist of the Bohemian Massif, Cretaceous sandstone and Palaeozoic to Jurassic limestone. Most types of this vegetation occur in habitats of potential forests and are maintained by disturbances. Sand accumulations of both fluvial and aeolian origin in the Czech Republic are siliceous, with a low pH. Species-poor sand grasslands dominated by the subatlantic grass *Corynephorus canescens*, with abundant mosses and lichens, occur mainly in the Doksy region of northern Bohemia, along the Labe river and in the sand area near the town of

Hodonín in south-eastern Moravia (class *Koelerio-Corynephoretea*, alliance *Corynephorion canescentis*; Fig. 19e & 20d). The latter area also hosts species-rich continental (Pannonian) sand-steppe vegetation dominated by *Festuca psammophila* subsp. *dominii* and *Stipa borysthena* and containing several species with a continental distribution (class *Festucetea vaginatae*, alliance *Festucion vaginatae*). In some areas, especially in the lowland and colline belt, small patches of vegetation with the short annual grasses *Aira praecox* (Černý et al. 2007) and *Vulpia myuros* occur in disturbed sandy or gravelly habitats (class *Koelerio-Corynephoretea*, alliance *Thero-Airion*). At less frequently disturbed sites, lowland sand grasslands become more closed and tussocky narrow-leaved fescues (*Festuca brevipila*, *F. ovina* and *F. rubra*) dominate, and sand specialists (e.g. *Armeria elongata* subsp. *elongata*) are also common (class *Koelerio-Corynephoretea*, alliance *Armerion elongatae*). In the colline to submontane belt of the Bohemian Massif, an analogue of the *Festuca*-dominated lowland sand grasslands is the vegetation with *Festuca ovina* and short herbs adapted to nutrient-poor soils with a low pH, e.g. *Jasione montana*, *Pilosella officinarum*, *Rumex acetosella* and *Scleranthus perennis*. These short swards with abundant mosses and lichens (*Ceratodon purpureus*, *Polytrichum piliferum* and *Cladonia* spp.) occur mainly in the southern half of Bohemia and in south-western Moravia (class *Koelerio-Corynephoretea*, alliance *Hyperico perforati-Scleranthion perennis*; Moravec 1967). A specific type of vegetation with short-lived vernal annuals and succulents (especially *Sedum acre*, *S. album* and *S. sexangulare*) occur in dry and warm areas, partly on rock outcrops, partly in disturbed patches within dry grasslands where cover of perennial herbs is reduced. The species composition of this vegetation differs between acidic bedrock and limestone, the former being characterized by *Arabidopsis thaliana*, *Gagea bohemica*, *Myosotis stricta*, *Veronica dillenii* and *V. verna* (class *Koelerio-Corynephoretea*, alliance *Arabidopsion thalianae*) and the latter by *Acinos arvensis*, *Alyssum alyssoides*, *Arabidopsis thaliana*, *Cerastium pumilum*, *Erophila spathulata*, *Medicago minima*, *Poa bulbosa*, *Saxifraga tridactylites*, *Thlaspi perfoliatum* and *Veronica praecox* (class *Koelerio-Corynephoretea*, alliance *Alyssu alyssoidis-Sedion*).

Dry grasslands (class *Festuco-Brometea*) in the Czech Republic have their historical precursor in the vegetation of the Pleistocene cold steppe, which has been reconstructed for both the full and late glacial periods in lowland areas, based on both fossil pollen (e.g. Rybníčková & Rybníček 1972, 1991, Kuneš et al. 2008a) and mollusc record (Ložek 2001, 2011). Putative relicts of the steppe flora during the coldest periods include *Agropyron pectinatum*, *Bassia prostrata* and *Taraxacum serotinum*, currently occurring rarely on eroded loess slopes with discontinuous vegetation cover in southern Moravia (alliance *Artemisio-Kochion prostratae*). However, it is possible that many, if not most, species of Czech dry steppes are Pleistocene relicts. With climatic amelioration in the early Holocene, the area of steppes was reduced due to the spread of forest, but human activity since the beginning of the Neolithic (ca 7500 cal. yr BP) reversed this trend: many lowland areas were deforested and steppe, as well as other types of grassland vegetation, spread again at the expense of forest. The key question is whether areas of steppe survived the period of a few centuries between the beginning of the presumably humid Atlantic period and the onset of Neolithic farming. Although spatial and taxonomic resolution of pollen data is not sufficient to answer this question, continuous persistence of steppe snails in the fossil record at some sites in northern Bohemia and southern Moravia, preservation of chernozem soils in the same areas and joint current occurrence of many plant species of

continental steppe (some of them with disjunct ranges) suggest continuous persistence of steppe vegetation in the forest-steppe areas throughout the Holocene not only on rock outcrops, but also on deeper soils (Sádlo et al. 2005, Ložek 2011). However, at most current sites dry grasslands developed in potential forest habitats after deforestation and under the impact of long-term grazing by livestock, and at more productive sites also mowing. After abandonment in recent decades, these secondary dry grasslands tend to decline due to expansion of tall grasses such as *Arrhenatherum elatius* and *Calamagrostis epigejos* (Fiala et al. 2011) and other herbs, shrubs and trees, although in many areas this process is being reversed by nature conservation management (Dostálek & Frantík 2008, Jongepierová 2008). On the other hand, dry grasslands of conservation importance can develop spontaneously on ex-arable land (Osbornová et al. 1990, Jírová et al. 2012) or in abandoned stone quarries (Novák & Konvička 2006) in dry and warm areas if remnants of dry grasslands in the neighbourhood serve as sources of seed.

Species composition and productivity of dry grasslands varies according to moisture availability, which depends on soil depth and precipitation. Dry grasslands on outcrops of various types of poorly weathered rocks are found mainly in northern and central Bohemia and southern Moravia (Fig. 20e). Most of these grasslands are dominated by the narrow-leaved tussocky grass *Festuca pallens*, which occurs both on siliceous rocks and limestone (alliance *Alyso-Festucion pallentis*). On the limestone outcrops in the Pavlovské Hills of southern Moravia, *Festuca pallens* is accompanied by sub-Mediterranean species such as *Fumana procumbens*, *Melica ciliata*, *Poa badensis* and *Teucrium montanum* (alliance *Bromo pannonici-Festucion pallentis*). *Festuca pallens* grasslands are confined to south-facing slopes, whereas north-facing slopes on limestone outcrops are covered by *Sesleria caerulea* grasslands (alliance *Diantho lumnitzeri-Seslerion*; Fig. 19g). *Sesleria caerulea* and some other species growing in the same grasslands (e.g. *Biscutella laevigata* and *Saxifraga paniculata*) are typical of the montane to subalpine belt of the limestone Alps and Carpathians. Their occurrence in the colline belt in northern and central Bohemia and southern Moravia is probably a relict of a broader distribution of these species at lower altitudes in the Pleistocene. However, at low altitudes these species are mixed with species of continental steppes and sub-Mediterranean rock-outcrop grasslands. Short-grass continental steppe (the ‘true steppe’ in Russian literature) occurs on both shallow (rendzina or ranker) or deep (chernozem) soils in the driest areas of northern and central Bohemia and southern Moravia. Dominant species include *Carex humilis*, *Festuca valesiaca*, *Stipa capillata*, *S. pennata*, *S. pulcherrima* and other feather grasses and at slightly more mesic sites also *Festuca rupicola* (alliance *Festucion valesiaca*; Kolbek 1975, 1978, Dúbravková et al. 2010; Figs 19f & 20f). More mesic soils on flat land or gentle slopes in the driest area in northern Bohemia and southern Moravia support patches of *Stipa tirsia* steppe. This species is the most moisture-demanding of the Czech feather grasses (Rychnovská & Úlehlová 1975). It may have dominated extensive areas on chernozem in the dry lowlands before these were converted to arable land. Nowadays only small fragmentary stands of *S. tirsia* steppe are preserved, although extensive stands still existed in the foothills of the Bílé Karpaty Mts in south-eastern Moravia in the first half of the 20th century (Sillinger 1929, Podpěra 1930). At some sites in southern Moravia, disturbed steppe on deep soil (e.g. on erosion-prone steep slopes, around rabbit colonies or on ex-arable land) harbours some competitively poor continental species, such as *Astragalus exscapus*, *Crambe tataria*, *Iris pumila* and *Taraxacum serotinum*. Short-grass steppes

have traditionally been used as pastures for livestock, typically for mixed herds of different kinds of animals grazing on common land. Semi-dry grasslands (Fig. 20g) are usually dominated by the broad-leaved rhizomatous grass *Brachypodium pinnatum*, but in some areas other species can also be important, e.g. *Bromus erectus*, *Koeleria pyramidata* (at higher altitudes), *Dorycnium pentaphyllum* agg. and *Inula ensifolia* (southern Moravia) and *Sesleria caerulea* (marlstone slopes in northern Bohemia). Based on their species composition, these grasslands are divided into suboceanic and continental types, corresponding respectively to the alliances *Bromion erecti* and *Cirsio-Brachypodium pinnati* (Illyés et al. 2007). In the Czech Republic, the former occurs mainly in the supracolline belt, i.e. areas with a wetter, more oceanic climate, whereas the latter is found in dry lowland and colline areas in the northern half of Bohemia and southern Moravia. *Cirsio-Brachypodium pinnati* grasslands correspond to tall-grass steppe or ‘meadow steppe’ of Russian literature. Semi-dry grasslands are characterized by a higher biomass production than other types of dry grasslands, therefore many of them used to be mown for hay once a year, usually late in summer (Jongepierová 2008), but some of them were also grazed by livestock. These grasslands are among the most species-rich vegetation types in the Czech Republic, both in terms of their regional species pool (Sádlo et al. 2007) and local species richness. In particular, the number of species of vascular plants in mown semi-dry grasslands in the Bílé Karpaty Mts in south-eastern Moravia is much higher than that in similar grasslands in adjacent areas and other vegetation types both in that area and beyond (Klimeš 1997, 2008). Typically these grasslands contain about 50 species of vascular plants per 1 m² and more than 100 species per 100 m² (Merunková et al. 2012). Observations of 13 and 44 vascular plant species per 0.004 and 0.25 m² (Klimeš et al. 2001) and of 105, 116 and 131 vascular plant species per 16, 25 and 49 m², respectively (Otýpková in Wilson et al. 2012), all from the Čertoryje National Nature Reserve in the south-western part of the Bílé Karpaty (Fig. 19h), have been reported as world records of local species richness per given areas (Wilson et al. 2012). This extraordinary species richness probably results from a combination of several factors conducive to high species richness: (i) no extreme values of climatic or soil factors, which is suitable for many species of the regional flora (Merunková et al. 2012); (ii) continuous existence of these grasslands for millenia (Hájková et al. 2011b), promoting species accumulation; (3) large areas of these meadows, which reduce the incidence of species extinction resulting from the island effects; (4) regular management with low fertilizer input and mowing, reducing the spread of strong competitors and preventing exclusion of competitively weaker species (Klimeš et al. 2000, Jongepierová 2008). Dry grasslands on acidic soils (alliance *Koelerio-Phleion phleoidis*) are poorer in species than semi-dry grasslands. They occur in dry and warm areas of the Bohemian Massif with poorly weathered rocks, especially in central Bohemia and south-western Moravia. Dominant species are mainly graminoids such as *Avenula pratensis*, *Carex humilis*, *Festuca ovina* and *F. rupicola* (Chytrý et al. 1997). The herbaceous vegetation of forest fringes is a specific type of dry grassland occurring in ecotonal habitats at the interface of forest and grassland. These communities are composed of both grassland species and species of forest herb layer, and dominated by broad-leaved dicots. Fringe vegetation dominated by *Dictamnus albus*, *Geranium sanguineum* or *Peucedanum cervaria* develops in dry and warm areas, often in an ecotone between dry grassland and thermophilous oak forest or xeric scrub (alliance *Geranion sanguinei*). In contrast, fringe vegetation with *Melampyrum nemorosum* or *Trifolium medium* develops in slightly cooler

and wetter areas, typically at the transition between semi-dry grassland or mesic meadow and oak-hornbeam forest (alliance *Trifolion medii*).

Inland saline vegetation (Figs 19i & 20h) develops locally in dry lowlands of both areas of the forest-steppe biome. It used to be most diverse and rich in obligate halophytes in southern Moravia (Šmarda 1953, Vicherek 1962a, 1973), where solonchak (but not solonetz) soils developed in areas with salt-rich Miocene sediments, around mineral springs rich in calcium sulphate and on the shores of natural shallow saline lakes, which existed in the lowlands south-east of Brno but were drained in the first half of the 19th century. Most historical localities of saline vegetation have disappeared because of the lowering of ground-water table after draining and the regulation of rivers, or conversion to arable land or productive grassland (Grulich 1987). Some types of saline vegetation have disappeared entirely from the country, especially those occurring on soils with a very high salt concentration or in seasonally flooded habitats. In particular, species-poor vegetation with the succulent annual halophytes *Salicornia prostrata* and *Suaeda prostrata* (class *Thero-Salicornietea strictae*, alliance *Salicornion prostratae*) occurred at some sites in southern Moravia but has not been observed since the 1970s (Vicherek 1973, Grulich 1987). Also vegetation of annual halophytic grasses *Crypsis aculeata* and *C. schoenoides* (class *Crypsietea aculeatae*, alliance *Cypero-Spergularion salinae*), formerly recorded at several sites in southern Moravia (Vicherek 1973), has declined considerably. Last remnants of saline grasslands with *Carex distans*, *C. otrubae*, *C. secalina*, *Juncus gerardii*, *Lotus tenuis*, *Melilotus dentatus*, *Mentha pulegium*, *Plantago maritima*, *Puccinellia distans*, *Scorzonera parviflora*, *Spergularia media*, *Taraxacum bessarabicum*, *Trifolium fragiferum* and *Tripolium pannonicum* subsp. *pannonicum* (class *Festuco-Puccinellietea*, alliances *Puccinellion limosae* at drier sites and *Juncion gerardii* at wetter sites) occur at a few sites in southern Moravia, and impoverished stands that lack several specialized halophytes of continental distribution also occur in northern and central Bohemia (Toman 1988).

Ruderal and weed vegetation

The structure and species composition of the ruderal and weed vegetation in the Czech Republic mainly depends on the frequency and severity of disturbance. In frequently disturbed habitats in human settlements, along roads and on arable land, this vegetation is more open and composed mainly of annual plants. Where disturbance is less frequent or severe, ruderal vegetation becomes denser and biennial and perennial plants prevail.

In the pre-Neolithic landscape, ruderal vegetation was probably spatially restricted, confined to disturbed nutrient-rich sites such as sediment accumulations on floodplains, places where animals gathered and camps of Palaeolithic or Mesolithic hunter-gatherers. In the present landscape in the Czech Republic the native flora still makes up a considerable proportion of the vegetation in man-made habitats, accounting for about 35–40% of the regional species pool and about 40–70% of species in individual stands of annual vegetation, and about 60% of the regional species pool and about 55–80% of species in individual stands of perennial ruderal vegetation (Chytrý et al. 2005, Sádlo et al. 2007, Pyšek et al. 2012a). Human-mediated spread of alien species, initially mainly from southern Europe and the Middle East, started in the Neolithic. These pre-Modern Period invaders

(archaeophytes, defined as alien species that were introduced before 1500 AD; Pyšek et al. 2012b) are best represented in weed communities on arable land, where they represent on average about 35–55% of plant species at individual sites, and in annual ruderal vegetation, where their mean proportion is about 25–50%. However, in other types of ruderal vegetation they usually make up less than 35%. Aliens that arrived in the Modern Period, many of them from the Americas, eastern Asia and other continents (neophytes), make up 15–25% of the regional species pool of ruderal and weed vegetation. However, as most of them are rare, their percentage representation in individual vegetation stands is usually less than 10% of the total number of species (Chytrý et al. 2005, Sádlo et al. 2007, Simonová & Lososová 2008, Pyšek et al. 2012a).

Weed vegetation of arable land includes a high proportion of species from southern Europe and the Middle East, which were introduced into central Europe since approximately 7500 cal. yr BP, together with the Middle Eastern crops such as wheat, barley, pea, poppy and flax. Primitive agrotechniques used in the early Neolithic probably permitted many perennial species, mostly belonging to native flora, to occur as weeds on agricultural land, but with the improvements in ploughing technology from the late Neolithic onwards annual species became more prominent (Holzner & Immonen 1982, Kühn 1994). In the Middle Ages three-field crop rotation was used with spring cereal, winter cereal and fallow in the three sequential seasons. This system was gradually abandoned at the end of 18th century, when it was replaced by crop rotation with legumes (*Medicago sativa* and *Trifolium pratense*), cereals and root crops (namely potato and since the 19th century also beet). Maize planting was introduced in warm lowland areas in the 20th century. New agrotechniques needed for planting these new crops favoured new species of weeds. Neophytic weeds, mainly of American origin, spread especially in cultures of root crops and maize, while remaining less significant in cereal cultures; nevertheless, archaeophytic weeds have always been more important than neophytic weeds in all kinds of crops (Pyšek et al. 2005a, Lososová & Grulich 2009). In the 1950s small arable fields in former Czechoslovakia were merged into large fields managed by cooperative or state-owned farms, which introduced intensive agrotechniques relying on new crop cultivars, mineral fertilizers and pesticides. Improved techniques of seed separation led to a decline in species adapted to seeding with crop, e.g. *Agrostemma githago*, *Bromus secalinus*, *Bupleurum rotundifolium* and *Ranunculus arvensis* (Kornaš 1988). Local species richness of weed vegetation also decreased during the second half of the 20th century (Pyšek et al. 2005b) and its composition changed. Archaeophytes, especially rare ones, tended to decrease in abundance, while neophytes increased (Pyšek et al. 2005a, Lososová & Simonová 2008). In some weed species (e.g. *Amaranthus retroflexus*, *Chenopodium album* and *Echinochloa crus-galli*) herbicide-resistant populations evolved, which spread over large areas of arable land (Chodová et al. 2004). No-till farming with reduced soil disturbance, used on some farms since the 1990s, has led to the spread of perennial weeds, most notably *Artemisia vulgaris*, *Cirsium arvense* and *Elymus repens* (Mikulka & Kneifelová 2005). Generalist species adapted to modern agrotechniques are predominant in current weed vegetation, with *Chenopodium album* agg., *Cirsium arvense*, *Elymus repens*, *Fallopia convolvulus* and *Viola arvensis* being the most common (Lososová et al. 2008). Nowadays species-rich weed communities or those containing specialist weed species are found mainly at the field margins.

Composition of Czech weed vegetation depends mainly on altitude (which summarizes the joint effects of lower temperature, higher precipitation and more acidic soils at higher altitudes), crop type (cereals vs. root crops) and time of year (Lososová et al. 2004). The percentage of annuals and aliens among weed species generally decreases with altitude. In early spring, when the cover of crops is still low, there are many small short-lived vernal annual weeds, such as *Arabidopsis thaliana*, *Erophila verna*, *Veronica hederifolia*, *V. sublobata*, *V. triloba* and *V. triphyllos*. As the crop cover increases and becomes denser, these short species disappear and the weed community then consists mainly of taller weeds that germinated in the previous autumn or early in spring (e.g. *Capsella bursa-pastoris*, *Caucalis platycarpus*, *Centaurea cyanus*, *Consolida regalis*, *Fallopia convolvulus* and *Sinapis arvensis*). These cool-season weeds make up a large proportion of the weeds in cereal fields. In contrast, hoeing or selective tillage in root crops provides space for late-germinating thermophilous weeds, such as *Chenopodium polyspermum*, *Echinochloa crus-galli*, *Mercurialis annua* and *Setaria pumila*. Populations of these weeds also develop in stubble fields after the cereal harvest (Lososová et al. 2006).

Classification of the weed vegetation in the Czech Republic reflects the variation in altitude, crop type and seasonal differences between spring and summer (Kropáč 2006, Lososová et al. 2006). All types of weed vegetation are assigned to the class *Stellarietea mediae*. The weed communities in cereal crops differ between warmer and drier lowland areas, where the soils are base-rich (alliance *Caucalidion*), and cooler and wetter mid-altitude areas, where the soils are usually acidic (alliance *Scleranthion annui*). Suboceanic weed communities in cereal fields on very poor sandy soils or wet podzols occurred rarely in the western part of Bohemia and their last locality is preserved in the Třeboňská Basin of southern Bohemia (alliance *Arnosseridion minimae*). Weed communities in root crops growing in warm, dry and base-rich habitats (alliance *Veronico-Euphorbion* on loamy or clayey soils and alliance *Spergulo arvensis-Erodion cicutariae* on sandy soils) also differ from those in cool, wet and base-poor habitats (alliance *Oxalidion fontanae*).

Ruderal vegetation is very variable depending on the frequency or intensity of disturbance, soil nutrients, soil moisture and climate. However, like in weed vegetation, the diversity of ruderal vegetation is also declining in terms of number of vegetation types, species richness and occurrence of archaeophytes (Pyšek et al. 2004). Most frequently disturbed sites with exposed bare soil are occupied by ruderal communities of annual species. These communities are dominated by either summer annuals of the genera *Atriplex*, *Chenopodium* or *Sisymbrium* (class *Stellarietea mediae*, alliance *Atriplicion*) or winter-annual grasses such as *Bromus sterilis*, *B. tectorum* or *Hordeum murinum* (class *Stellarietea mediae*, alliance *Sisymbriion officinalis*). Vegetation with low-growing archaeophytic annuals (e.g. *Anthemis cotula*, *Malva neglecta*, *M. pusilla*, *Mercurialis annua* and *Urtica urens*; class *Stellarietea mediae*, alliance *Sisymbriion officinalis*) occur especially at trampled sites in village yards and fowl runs, but has been declining due to village urbanization since the second half of the 20th century. Annual ruderal vegetation occurring on nutrient-poor sandy or gravelly soils is characterized by *Dysphania botrys*, *Plantago arenaria* and *Salsola kali* subsp. *rosacea* (class *Stellarietea mediae*, alliance *Salsolion ruthenicae*). On dry and nutrient-rich sandy or gravelly soils, both in ruderal (often trampled) habitats and on arable land, this vegetation is dominated by C₄ species such as *Cynodon dactylon*, *Digitaria sanguinalis*, *Eragrostis minor*, *Panicum capillare* and *Portulaca oleracea* (class *Stellarietea mediae*, alliance *Eragrostion cilianensi-*

minoris). Annual or short-lived species (e.g. *Lepidium ruderales*, *Matricaria discoidea*, *Poa annua* and *Polygonum arenastrum*) are also dominant in trampled habitats (class *Polygono arenastrum-Poëtea annuae*; Simonová 2008). At lower altitudes and drier sites, *Polygonum arenastrum* predominates and in places is accompanied by thermophilous species, such as *Eragrostis minor* or *Sclerochloa dura* (alliance *Coronopodo-Polygonion arenastrum*), while at high altitudes or wetter sites, more perennial species (e.g. *Lolium perenne*, *Plantago major* and *Trifolium repens*) and bryophytes occur in trampled habitats along with annual vascular plants.

In ruderal habitats with less frequent or weaker disturbance, biennial and perennial species are more common and eventually become dominant, although annual species are also well represented. On dry base-rich soils, e.g. on loess, limestone, and also on building rubble or in waste places, archaeophytes prevail, including *Artemisia absinthium*, *Carduus acanthoides*, *Marrubium peregrinum*, *Onopordum acanthium*, *Reseda lutea* and *R. luteola* (class *Artemisietea vulgaris*, alliance *Onopordion acanthii*). Currently this vegetation type is declining due to village urbanization. On dry and nutrient-poor anthropogenic substrates, often with a high content of gravel or dross, widespread biennial and perennial ruderal species are common, including *Artemisia vulgaris*, *Cirsium arvense*, *Daucus carota*, *Elytrigia repens*, *Melilotus albus*, *M. officinalis*, *Solidago canadensis*, *Tanacetum vulgare* and *Tussilago farfara* (class *Artemisietea vulgaris*, alliance *Daucocarotae-Melilotion*). On slopes with loamy soils subject to occasional landslides or solifluction, especially in dry and warm areas, semi-natural to ruderal herbaceous vegetation occurs that is dominated by species with extensive root or rhizome systems, e.g. *Bromus inermis*, *Convolvulus arvensis* and *Elytrigia repens* (class *Artemisietea vulgaris*, alliance *Convolvulo arvensis-Elytrigion repentis*). On mesic soils, infrequently disturbed ruderal vegetation is dominated by medium-tall to tall perennial dicots such as *Arctium lappa*, *A. tomentosum*, *Ballota nigra*, *Chenopodium bonus-henricus*, *Conium maculatum* or *Sambucus ebulus* (class *Artemisietea vulgaris*, alliance *Arction lappae*). In mesic to wet, infrequently disturbed habitats, large native umbellifers such as *Aegopodium podagraria*, *Anthriscus nitidus*, *A. sylvestris*, *Chaerophyllum aromaticum*, *C. aureum* and *C. bulbosum* dominate (class *Galio-Urticetea*, alliance *Aegopodion podagrariae*). Such habitats are frequently invaded by large perennial broad-leaved neophytes, including *Helianthus tuberosus*, *Heracleum mantegazzianum*, *Reynoutria ×bohemica*, *R. japonica*, *Solidago canadensis*, *S. gigantea* and *Symphyotrichum lanceolatum*. Similar habitats in the Jizerské Mts, Krkonoše and Orlické Mts locally support monodominant stands of the neophyte *Rumex alpinus* (class *Galio-Urticetea*, alliance *Rumicion alpini*).

In natural or semi-natural ecotonal or naturally disturbed habitats on nutrient-rich or wet soils, there is productive and dense vegetation dominated by dicot herbs, with a floristic composition similar to ruderal vegetation in man-made habitats. Along lowland and mid-altitudinal streams and channels, this vegetation is characterized by a frequent occurrence of *Epilobium hirsutum*, *Rubus caesius* and herbaceous lianas such as *Calystegia sepium*, *Cuscuta europaea*, *Echinocystis lobata*, *Fallopia dumetorum*, *Humulus lupulus* and *Silene baccifera* (class *Galio-Urticetea*, alliance *Senecionion fluviatilis*). The invasive alien *Impatiens glandulifera* is common in this vegetation. Herbaceous vegetation dominated by *Petasites hybridus* occurs along mountain streams; on some gravel accumulations in the Moravian-Silesian Beskids, this species is replaced by *P. kablikanus* (class *Galio-Urticetea*, alliance *Petasition hybridi*). Mesic, nutrient-rich

habitats at the edges of forest and in natural canopy openings (e.g. on screes, landslides and at windthrow sites) are dominated by tall dicot forbs such as *Aruncus dioicus*, *Eupatorium cannabinum*, *Impatiens noli-tangere*, *Lunaria rediviva*, *Parietaria officinalis*, *Stachys sylvatica* and *Urtica dioica* (class *Galio-Urticetea*, alliance *Impatienti noli-tangere-Stachyion sylvaticae*). In warmer regions, similar habitats are dominated by annual or short-lived species, e.g. *Alliaria petiolata*, *Anthriscus cerefolium*, *Chaerophyllum temulum*, *Chelidonium majus*, *Galium aparine* and *Torilis japonica* (class *Galio-Urticetea*, alliance *Geo urbani-Alliarion petiolatae*). In forest clearings, areas deforested by wildfires, insect outbreaks, wind storms or air pollution, in canopy gaps and forest fringes, soils are usually poor in bases but with temporarily increased availability of nitrogen. Herbaceous vegetation in such habitats usually contains a mixture of acidophilous and nitrophilous species, but also species of the former forest herb layer (class *Epilobietea angustifolii*, alliance *Fragarion vescae*). Dominant species include tall grasses (e.g. *Calamagrostis arundinacea*, *C. epigejos* and, in the mountains, *C. villosa*), tall dicot herbs (e.g. *Epilobium angustifolium* and *Senecio nemorensis* agg.), tall ferns (e.g. *Athyrium filix-femina* and *Pteridium aquilinum*) and dwarf to medium-tall shrubs (e.g. *Rubus idaeus* and *Vaccinium myrtillus*).

Current vegetation change

The above overview of vegetation types is largely based on data collected and concepts developed in the 20th century. However, during the last few decades the vegetation in the Czech Republic has been profoundly affected by socioeconomic, land-use and environmental changes. Sádlo & Pokorný (2003) suggest that the current changes occurring in the landscape and vegetation are of comparable magnitude to the major changes that occurred after the introduction of Neolithic agriculture and after the medieval colonization. The recent change is associated with a dramatic decline in small-scale disturbances caused by agricultural and forestry management, which used to occur in numerous rural subdivisions, mainly due to the activity of small land owners and village populations. Such landscape management, typical for the period between 1850 and 1950, changed dramatically after agricultural collectivization in the 1950s and the subsequent decline in the number of people involved in agriculture (currently less than 3% of Czech employees work in agriculture or forestry; Czech Statistical Office, <http://www.czso.cz/csu/2011edicniplan.nsf/publ/0001-11-2010>). Many areas of grassland that had formerly been mown or grazed were abandoned and former coppices and wooded pastures were converted to high forest or forestry plantations. Nowadays there is a much lower export of nutrients from grasslands and forests than a century ago. Nutrient accumulation in ecosystems is further enhanced by atmospheric nutrient deposition and widespread use of agricultural fertilizers. Exceedance of critical loads of nitrogen compounds in the Czech Republic, especially in the north-west, is among the highest in Europe (European Environment Agency 2007). As a result, open forests and oligotrophic grasslands typical of the first half of the 20th century, with light-demanding and stress-tolerant species, are developing towards species-poor vegetation types dominated by nutrient-demanding, highly competitive species (Bobbink et al. 1998, Verheyen et al. 2012). In addition to increasing the nitrogen content of soil, atmospheric deposition also results in soil acidification (Hédli et al. 2011). Current landscapes are char-

acterized by infrequent but strong disturbances of large spatial extent, which support fast-spreading ruderal (including alien) species, and extensive areas are left to spontaneous succession (Prach et al. 2001, Novák & Konvička 2006, Konvalinková & Prach 2010, Trnková et al. 2010). Abandoned arable land and grasslands continuously develop into shrubland and woodland (Kopecký & Vojta 2009, Jírová et al. 2012, Vojta & Drhovská 2012). Also the pattern of plant migrations has changed with increasing importance of long-distance dispersal, supported by international trade and extensive transport of various commodities. On average, four new alien plant species arrive in the Czech Republic every year (Pyšek et al. 2012b), mostly of American or Asian origin, and many of them invade natural vegetation outside man-made habitats (Chytrý et al. 2005, Pyšek et al. 2012a). Sádlo & Pokorný (2003) estimate that the greatest changes in Czech vegetation, marking the transition from the pre-1950 state to the current state, occurred in the 1970s–1980s, but a comprehensive quantitative analysis of these changes is missing. The effect of global warming on vegetation is currently much less pronounced than that of changes in land-use, however, its importance may increase in the future. Nature conservation is trying to halt or reverse these changes by applying management measures such as subsidized cutting and grazing, especially in protected areas, which include four National Parks, 25 Protected Landscape Areas and 2295 small-scale protected areas (National Nature Reserves, Nature Reserves, National Nature Monuments and Nature Monuments; <http://drusop.nature.cz/>, accessed on 8 June 2012). However, although some nature conservation measures have been successful, it may be very hard or impossible to halt some the current changes in the vegetation, especially in protected areas of small size.

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Souhrn

Článek obsahuje první cizojazyčný souhrnný přehled o vegetaci České republiky. Popisuje základní abiotické faktory ovlivňující naši vegetaci, historii vegetace od poslední doby ledové, vymezuje čtyři biomy rozlišitelné na našem území (zonální biomy opadavého listnatého lesa a lesostepí a azonální biomy tajgy a tundry) a charakterizuje výškové vegetační stupně a krajiny s velkou diverzitou vegetačních typů (hluboká říční údolí Českého masivu, krasové oblasti, pískovcová skalní města, vulkanické kopce, horské ledovcové kary, nívy nížinných řek a oblasti s výskytem hadců). Jednotlivé vegetační typy jsou popsány podle fytoecologické klasifikace použité v monografii Vegetace České republiky s důrazem na jejich diverzitu, ekologii, historii a dynamiku. V závěru jsou shrnuty hlavní trendy současných změn vegetace.

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Appendix 1. – Important toponyms in the Czech Republic. Many Czech names of topographical features (e.g. mountain ranges, basins or lowlands) are derived from the names of settlements, rivers or regions, to which an adjective ending is added. For example, the name *Pavlovské vrchy*, literally meaning *Pavlov Hills*, is derived from the village name *Pavlov*. There are various English translations of such names; three basic options are used in the literature: *Pavlovské vrchy hills*, *Pavlovské Hills* and *Pavlov Hills*. The second option is preferred in this paper and alternative names are listed in this Appendix. For a few toponyms with well-established English equivalents, these equivalents are used here, but many Czech toponyms either do not have an English equivalent or the equivalent is rarely used and poorly known. In contrast, many Czech toponyms have German equivalents, which for most part are rarely used now, but were routinely used in older botanical literature. In this brief list, Czech names are followed by their English and German equivalents. The names used in this paper are in italics. Compare Fig. 1 for geographical locations.

Historical lands

Čechy – *Bohemia* – Böhmen
 Morava – *Moravia* – Mähren
 Slezsko – *Silesia* – Schlesien

Topographical features

Bílé Karpaty – White Carpathians – Weiße Karpaten
 Broumovsko – *Broumov region* – n/a
 České středohoří – n/a – Böhmisches Mittelgebirge
 Českokobudějovická pánev – *Českokobudějovická Basin*, České Budějovice Basin – Budweißer Becken
 Českomoravská vrchovina – *Bohemian-Moravian Highlands* – Böhmisches-Mährische Höhe
 Český kras – Český Karst, *Bohemian Karst* – Böhmischer Karst
 Český ráj – Bohemian Paradise – Böhmisches Paradies
 Český masiv – *Bohemian Massif* – Böhmisches Masse
 Chebská pánev – *Chebská Basin*, Cheb Basin – Egerer Becken
 Dokesko – *Doksy region* – n/a
 Doupovské hory – *Doupovské Mts*, Doupov Mts – Duppauer Gebirge
 Hradčanské stěny – *Hradčanské Cliffs*, Hradčany Cliffs – Kummergebirge
 Hrubý Jeseník – n/a – Altwatergebirge, Hohes Gesenke
 Jizerské hory – *Jizerské Mts*, Jizera Mts – Isergebirge
 Karpaty – *Carpathians* – Karpaten
 Kokořínsko – *Kokořín region* – Daubaer Schweiz
 Králický Sněžník – n/a – Glatzer Schneeberg
 Krkonoše – Giant Mountains – Riesengebirge
 Krušné hory – *Krušné Mts*, Ore Mts – Erzgebirge
 Křivoklátsko – *Křivoklát region* – n/a
 Labské pískovce – Elbe Sandstone Mts – Elbsandsteingebirge
 Moravskoslezské Beskydy – *Moravian-Silesian Beskids* – Mährisch-Schlesische Beskiden
 Moravský kras – Moravský Karst, *Moravian Karst* – Mährischer Karst
 Novohradské hory – *Novohradské Mts*, Nové Hrady Mts – Gratzener Bergland
 Orlické hory – *Orlické Mts*, Orlice Mts – Adlergebirge
 Ostravská pánev – *Ostravská Basin*, Ostrava Basin – Ostrauer Becken
 Pavlovské vrchy – *Pavlovské Hills*, Pavlov Hills – Pollauer Berge
 Slavkovský les – n/a – Kaiserwald
 Sudety – *Sudetes* – Sudeten
 Šumava – Bohemian Forest – Böhmerwald
 Třeboňská pánev – *Třeboňská Basin*, Třeboň Basin – Wittingauer Becken

Rivers

Czech names are used for all rivers throughout the text. Large rivers or those shared with other countries are internationally better known under their German names, which are usually used in English-language literature: Dyje – Thaya, Labe – Elbe, Morava – March, Odra – Oder, Ohře – Eger, Vltava – Moldau.

Appendix 2. – Phytosociological classification of Czech vegetation at the level of classes (in bold) and alliances according to that published in Volumes 1–3 of Vegetation of the Czech Republic (Chytrý 2007, 2009, 2011) and the manuscript of Volume 4 (forest and scrub vegetation). See Vegetation of the Czech Republic for information on associations.

Forests

LA. *Alnetea glutinosae* Br.-Bl. et Tüxen ex Westhoff et al. 1946 – Alder and willow carrs

LAA. *Alnion glutinosae* Malcuit 1929 – Alder carrs

LAB. *Salicion cinereae* Müller et Görs ex Passarge 1961 – Willow carrs

LB. *Carpino-Fagetea Jakucs 1967* – Mesic deciduous broad-leaved forests

LBA. *Alnion incanae* Pawłowski et al. 1928 – Ash-alder alluvial forests

LBB. *Carpinion betuli* Issler 1931 – Oak-hornbeam forests

LBC. *Fagion sylvaticae* Luquet 1926 – Eutrophic beech forests

LBD. *Sorbo torminalis-Fagion sylvaticae* Passarge et Hofmann 1968 – Calcicole beech forests

LBE. *Luzulo-Fagion sylvaticae* Lohmeyer et Tüxen in Tüxen 1954 – Acidophilous beech forests

LBF. *Tilio platyphylli-Acerion* Klika 1955 – Ravine forests

LC. *Quercetea pubescentis* Doing Kraft ex Scamoni et Passarge 1959 – Thermophilous oak forests

LCA. *Quercion pubescenti-petraeae* Br.-Bl. 1932 – Peri-alpide basiphilous thermophilous oak forests

LCB. *Aceri tatarici-Quercion* Zölyomi 1957 – Subcontinental forest-steppe oak forests

LCC. *Quercion petraeae* Issler 1931 – Acidophilous thermophilous oak forests

LD. *Quercetea robori-petraeae* Br.-Bl. et Tüxen ex Oberdorfer 1957 – Acidophilous oak forests

LDA. *Quercion roboris* Malcuit 1929 – Acidophilous oak forests

LE. *Erico-Pinetea Horvat 1959* – Basiphilous submontane pine forests

LEA. *Erico carnea-Pinion* Br.-Bl. in Br.-Bl. et al. 1939 – Basiphilous montane pine forests of central and south-eastern Europe

LF. *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 – Boreal coniferous forests

LFA. *Festuco-Pinion sylvestris* Passarge et Hofmann 1968 – Basiphilous continental pine forests

LFB. *Dicrano-Pinion sylvestris* (Libbert 1933) Matuszkiewicz 1962 – Acidophilous boreo-continental pine forests

LFC. *Piceion abietis* Pawłowski et al. 1928 – central European acidophilous spruce forests

LFD. *Vaccinio uliginosi-Pinion sylvestris* Passarge et Hofmann 1968 – Bog woodlands

Scrub

KA. *Salicetea purpureae* Moor 1958 – Riparian willow scrub and willow-poplar forests

KAA. *Salicion triandrae* Müller et Görs 1958 – Willow scrub of loamy and sandy river banks

KAB. *Salicion elaeagno-daphnoidis* (Moor 1958) Grass in Mucina et al. 1993 – Willow scrub on river gravel accumulations

KAC. *Salicion albae* de Soó 1951 – Willow poplar-forests of lowland rivers

KB. *Rhamno-Prunetea* Rivas Goday et Borja Carbonell ex Tüxen 1962 – Mesic and xeric scrub and *Robinia* groves

KBA. *Prunion fruticosae* Tüxen 1952 – Low xeric scrub

KBB. *Berberidion vulgaris* Br.-Bl. et Tüxen 1952 – Tall mesic and xeric scrub

KBC. *Sambuco-Salicion capreae* Tüxen et Neumann ex Oberdorfer 1957 – Mesic scrub in forest clearings, canopy openings and disturbed sites

KBD. *Aegopodio podagrariae-Sambucion nigrae* Chytrý ined. – Nitrophilous scrub in ruderal habitats

KBE. *Chelidonio majoris-Robinion pseudoacaciae* Hadač et Sofron ex Vítková ined. – Black locust groves with nitrophilous species

KBF. *Balloto nigrae-Robinion pseudoacaciae* Hadač et Sofron 1980 – Black locust groves on dry sandy soils

KBG. *Euphorbio cyparissiae-Robinion pseudoacaciae* Vítková in Kolbek et al. 2003 – Low black locust groves and scrub at dry and warm sites with shallow soil

KC. *Roso pendulinae-Pinetea mugo* Theurillat in Theurillat et al. 1995 – Subalpine krummholz vegetation

KCA. *Pinion mugo* Pawłowski et al. 1928 – Subalpine dwarf pine scrub

Alpine and subalpine vegetation

AA. *Loiseleurio-Vaccinieta* Eggler ex Schubert 1960 – Alpine heathlands

AAA. *Loiseleurio procumbentis-Vaccinion* Br.-Bl. in Br.-Bl. et Jenny 1926 – Arcto-alpine dwarf-shrub vegetation

AB. *Juncetea trifidi* Hadač in Klika et Hadač 1944 – Alpine grasslands on base-poor soil

ABA. *Juncion trifidi* Krajina 1933 – Wind-swept alpine grasslands on base-poor soil

ABB. *Nardo strictae-Caricion bigelowii* Nordhagen 1943 – Closed alpine grasslands on base-poor soil

AC. *Elyno-Seslerietea* Br.-Bl. 1948 – Alpine grasslands on base-rich soil

ACA. *Agrostion alpinae* Jeník et al. 1980 – Species-rich rock-outcrop grasslands in the Sudetes cirques

AD. *Mulgedio-Aconitetea* Hadač et Klika in Klika et Hadač 1944 – Subalpine tall-forb and deciduous-shrub vegetation

ADA. *Calamagrostion villosae* Pawłowski et al. 1928 – Subalpine tall grasslands

ADB. *Calamagrostion arundinaceae* (Luquet 1926) Jeník 1961 – Subalpine grasslands with *Calamagrostis arundinacea*

ADC. *Salicion silesiacae* Rejmánek et al. 1971 – Subalpine deciduous scrub and woodland

ADD. *Adenostylium alliariae* Br.-Bl. 1926 – Subalpine tall-forb vegetation

ADE. *Dryopterido filicis-maris-Athyrium distentifolii* (Holub ex Sýkora et Štursa 1973) Jeník et al. 1980 – Subalpine tall-fern vegetation

Rock and scree vegetation

SA. *Asplenietea trichomanis* (Br.-Bl. in Meier et Br.-Bl. 1934) Oberdorfer 1977 – Vegetation of rocks, walls and stable screes

SAA. *Cystopteridion* Richard 1972 – Vegetation of calcareous rock outcrops and walls

SAB. *Asplenion cuneifolii* Br.-Bl. ex Eggler 1955 – Vegetation of serpentine outcrops

SAC. *Asplenion septentrionalis* Gams ex Oberdorfer 1938 – Vegetation of siliceous rock outcrops and talus slopes

SAD. *Androsacion alpinae* Br.-Bl. in Br.-Bl. et Jenny 1926 – Vegetation of siliceous talus slopes in subalpine and alpine belts

SB. *Cymbalarium muralis-Parietarietea judaicae* Oberdorfer 1969 – Nitrophilous vegetation of walls

SBA. *Cymbalarium muralis-Asplenion* Segal 1969 – Wall vegetation with neophytes of Mediterranean origin

SC. *Thlaspietea rotundifolii* Br.-Bl. 1948 – Vegetation of mobile screes

SCA. *Stipion calamagrostis* Br.-Bl. et al. 1952 – Vegetation of calcareous screes

SCB. *Galeopsion* Oberdorfer 1957 – Vegetation of siliceous screes

Aquatic vegetation

VA. *Lemnetea* de Bolós et Masclans 1955 – Vegetation of free floating aquatic plants

VAA. *Lemnion minoris* de Bolós et Masclans 1955 – Vegetation of lemniids and free-floating aquatic ferns and liverworts

VAB. *Utricularion vulgaris* Passarge 1964 – Vegetation of bladderworts in mesotrophic to eutrophic water bodies

VAC. *Hydrocharition morsus-ranae* (Passarge 1964) Westhoff et den Held 1969 – Vegetation of large free-floating vascular plants

VB. *Potametea* Klika in Klika & Novák 1941 – Vegetation of aquatic plants rooted in the bottom

VBA. *Nymphaeion albae* Oberdorfer 1957 – Vegetation of aquatic plants rooted in the bottom and with leaves floating on the water surface

VBB. *Potamion* Miljan 1933 – Vegetation of aquatic plants rooted in the bottom

VBC. *Batrachion fluitantis* Neuhäusl 1959 – Vegetation of aquatic plants in streams

VBD. *Ranunculion aquatilis* Passarge 1964 – Vegetation of aquatic plants in shallow water bodies with fluctuating water table

VC. *Charetea* Fukarek ex Krausch 1964 – Vegetation of stoneworts

VCA. *Nitellion flexilis* Krause 1969 – Vegetation of stoneworts in calcium-poor water

VCB. *Charion globularis* Krausch 1964 – Vegetation of stoneworts in calcium-rich or brackish water

- VD. *Littorelletea uniflorae* Br.-Bl. et Tüxen ex Westhoff et al. 1946** – Vegetation of oligotrophic water bodies
 VDA. *Littorellion uniflorae* Koch ex Tüxen 1937 – Submerged vegetation of oligotrophic water bodies
 VDB. *Eleocharition acicularis* Pietsch ex Dierßen 1975 – Vegetation of amphibious plants in shallow, oligotrophic to mesotrophic water bodies
 VDC. *Sphagno-Utricularion* Müller et Görs 1960 – Vegetation of oligotrophic pools with bladderworts

Wetland vegetation

- MA. *Isoëto-Nano-Juncetea* Br.-Bl. et Tüxen ex Br.-Bl. et al. 1952** – Vegetation of annual wetland herbs
 MAA. *Eleocharition ovatae* Philippi 1968 – Vegetation of short-growing annual herbs on exposed bottoms of fisponds
 MAB. *Radiolion linoidis* Pietsch 1973 – Vegetation of short-growing annual herbs on wet sand
 MAC. *Verbenion supinae* Slavnić 1951 – Vegetation of annual herbs on base-rich exposed bottoms in warm areas
MB. *Bidentetea tripartitae* Tüxen et al. ex von Rochow 1951 – Vegetation of annual nitrophilous wetland herbs
 MBA. *Bidentition tripartitae* Nordhagen ex Klika et Hadač 1944 – Nitrophilous vegetation of exposed bottoms and wet ruderal habitats
 MBB. *Chenopodium rubri* (Tüxen 1960) Hilbig et Jage 1972 – Nitrophilous vegetation with *Chenopodium* and *Atriplex* in wet habitats
MC. *Phragmito-Magno-Caricetea* Klika in Klika et Novák 1941 – Marsh vegetation
 MCA. *Phragmition australis* Koch 1926 – Fresh-water reed vegetation
 MCB. *Meliloto dentati-Bolboschoenion maritimi* Hroudová et al. 2009 – Continental brackish marsh vegetation
 MCC. *Eleocharito palustris-Sagittarion sagittifoliae* Passarge 1964 – Vegetation of large wetland herbs in habitats with periodical changes of water level
 MCD. *Phalaridion arundinaceae* Kopecký 1961 – Reed and tall-sedge vegetation on river banks
 MCE. *Glycerio-Sparganion* Br.-Bl. et Sissingh in Boer 1942 – Medium-tall reed stands along brooks and on floating islands
 MCF. *Carici-Rumicion hydrolopathi* Passarge 1964 – Vegetation of wetland herbs on organic muddy sediments
 MCG. *Magno-Caricion elatae* Koch 1926 – Tall-sedge vegetation in littoral zones of oligotrophic and mesotrophic water bodies
 MCH. *Magno-Caricion gracilis* Géhu 1961 – Tall-sedge vegetation in littoral zones of eutrophic water bodies

Spring and mire vegetation

- RA. *Montio-Cardaminetea* Br.-Bl. et Tüxen ex Klika et Hadač 1944** – Vegetation of springs
 RAA. *Caricion remotae* Kästner 1941 – Vegetation of non-calcareous forest springs
 RAB. *Lycopodo europaei-Cratoneurion commutati* Hadač 1983 – Vegetation of calcareous forest springs with tufa formation
 RAC. *Epilobio nutantis-Montion fontanae* Zechmeister in Zechmeister et Mucina 1994 – Vegetation of subatlantic, submontane springs in open habitats
 RAD. *Swertio perennis-Dichodontion palustris* Hadač 1983 – Vegetation of non-calcareous alpine and subalpine springs
RB. *Scheuchzerio palustris-Caricetea nigrae* Tüxen 1937 – Vegetation of fens, transitional mires and bog hollows
 RBA. *Caricion davallianae* Klika 1934 – Calcareous fens
 RBB. *Sphagno warnstorffii-Tomentypnion nitentis* Dahl 1956 – Fens with calcicolous species and calcitolerant peat mosses
 RBC. *Caricion canescenti-nigrae* Nordhagen 1937 – Slightly acidic fens
 RBD. *Sphagno-Caricion canescentis* Passarge (1964) 1978 – Acidic fens (transitional mires)
 RBE. *Sphagnion cuspidati* Krajina 1933 – Vegetation of bog hollows
RC. *Oxycocco-Sphagnetes* Br.-Bl. et Tüxen ex Westhoff et al. 1946 – Bog vegetation
 RCA. *Sphagnion magellanici* Kästner et Flössner 1933 – Continental and subcontinental bogs
 RCB. *Oxycocco palustris-Ericion tetralicis* Nordhagen ex Tüxen 1937 – Oceanic and suboceanic bogs
 RCC. *Oxycocco microcarpi-Empetrium hermaphroditii* Nordhagen ex Du Rietz 1954 – Boreal bogs

Grasslands and heathlands below the timberline

- TA. *Crypsietea aculeatae* Vicherek 1973** – Vegetation of annual graminoids in saline habitats
TAA. *Cypero-Spergularion salinae* Slavnič 1948 – Inland salt marshes with annual halophilous grasses
- TB. *Thero-Salicornietea strictae* Tüxen in Tüxen et Oberdorfer 1958** – Vegetation of annual succulent halophytes
TBA. *Salicornion prostratae* Géhu 1992 – Inland salt marshes with annual succulent halophytes (now extinct)
- TC. *Festuco-Puccinellietea* Soó ex Vicherek 1973** – Saline grasslands
TCA. *Puccinellion limosae* Soó 1933 – Intermittently dry saline grasslands
TCB. *Juncion gerardii* Wendelberger 1943 – Mesic and wet saline grasslands
- TD. *Molinio-Arrhenatheretea* Tüxen 1937** – Meadows and mesic pastures
TDA. *Arrhenatherion elatioris* Luquet 1926 – Lowland to submontane mesic meadows
TDB. *Polygono bistortae-Trisetion flavescens* Br.-Bl. et Tüxen ex Marschall 1947 – Montane mesic meadows
TDC. *Cynosurion cristati* Tüxen 1947 – Mesic pastures and perennial grasslands of trampled habitats
TDD. *Molinion caeruleae* Koch 1926 – Intermittently wet, nutrient-poor meadows
TDE. *Deschampsion cespitosae* Horvatič 1930 – Lowland floodplain meadows
TDF. *Calthion palustris* Tüxen 1937 – Wet tall-herb meadows
- TE. *Calluno-Ulicetea* Br.-Bl. et Tüxen ex Klika et Hadač 1944** – *Nardus* grasslands and heathlands
TEA. *Nardion strictae* Br.-Bl. 1926 – Subalpine *Nardus* grasslands
TEB. *Nardo strictae-Agrostion tenuis* Sillinger 1933 – Montane *Nardus* grasslands with alpine species
TEC. *Violion caninae* Schwickerath 1944 – Submontane and montane *Nardus* grasslands
TED. *Nardo strictae-Juncion squarrosi* (Oberdorfer 1957) Passarge 1964 – Wet *Nardus* grasslands
TEE. *Euphorbio cyparissiae-Callunion vulgaris* Schubert ex Passarge in Scamoni 1963 – Dry lowland and colline heathlands
TEF. *Genisto pilosae-Vaccinion* Br.-Bl. 1926 – Submontane to subalpine *Vaccinium* heathlands
- TF. *Koelerio-Corynephoretea* Klika in Klika et Novák 1941** – Pioneer vegetation of sandy and shallow soils
TFA. *Corynephorion canescens* Klika 1931 – Open sand grasslands
TFB. *Thero-Airion* Tüxen ex Oberdorfer 1957 – Vegetation of annual grasses on sandy soils
TFC. *Armerion elongatae* Passarge 1964 – Closed sand grasslands
TFD. *Hyperico perforati-Scleranthion perennis* Moravec 1967 – Submontane acidophilous vegetation of shallow soils
TFE. *Arabidopsion thalianae* Passarge 1964 – Acidophilous vegetation of vernal therophytes and succulents
TFF. *Alyssio alyssoidis-Sedion* Oberdorfer et Müller in Müller 1961 – Basiphilous vegetation of vernal therophytes and succulents
- TG. *Festucetea vaginatae* Soó ex Vicherek 1972** – Sand steppes
TGA. *Festucion vaginatae* de Soó 1929 – Pannonian sand steppe grasslands
- TH. *Festuco-Brometea* Br.-Bl. et Tüxen ex Soó 1947** – Dry grasslands
THA. *Alyssio-Festucion pallentis* Moravec in Holub et al. 1967 – Hercynian rock-outcrop vegetation with *Festuca pallens*
THB. *Bromo pannonici-Festucion pallentis* Zólyomi 1966 – Pannonian vegetation of limestone outcrops
THC. *Diantho lumnitzeri-Seslerion* (Soó 1971) Chytrý et Mucina in Mucina et al. 1993 – *Sesleria caerulea* grasslands
THD. *Festucion valesiaca* Klika 1931 – Narrow-leaved dry grasslands and short-grass steppes
THE. *Cirsio-Brachypodion pinnati* Hadač et Klika ex Klika 1951 – Subcontinental broad-leaved semi-dry grasslands and tall-grass steppes
THF. *Bromion erecti* Koch 1926 – Suboceanic broad-leaved semi-dry grasslands
THG. *Koelerio-Phleion phleoidis* Korneck 1974 – Acidophilous dry grasslands
THH. *Geranion sanguinei* Tüxen in Müller 1962 – Dry herbaceous fringe vegetation
THI. *Trifolion medii* Müller 1962 – Mesic herbaceous fringe vegetation

Ruderal and weed vegetation

XA. *Polygono arenastri-Poëtea annuae* Rivas-Martínez 1975 corr. Rivas-Martínez et al. 1991 – Vegetation of trampled habitats

XAA. *Coronopodo-Polygonion arenastri* Sissingh 1969 – Annual vegetation of dry trampled habitats

XAB. *Saginion procumbentis* Tüxen et Ohba in Géhu et al. 1972 – Annual vegetation of mesic trampled habitats

XB. *Stellarietea mediae* Tüxen et al. ex von Rochow 1951 – Annual vegetation of arable land and ruderal habitats

XBA. *Caucalidion* von Rochow 1951 – Thermophilous weed vegetation of cereal fields on base-rich soils

XBB. *Veronico-Euphorbion* Sissingh ex Passarge 1964 – Basiphilous weed vegetation in root-crop fields

XBC. *Scleranthion annui* (Kruseman et Vlieger 1939) Sissingh in Westhoff et al. 1946 – Weed vegetation of cereal fields on acidic soils

XBD. *Arnoseridion minimae* Malato-Beliz et al. 1960 – Weed vegetation of cereal fields on nutrient-poor acidic soils

XBE. *Oxalidion fontanae* Passarge 1978 – Weed vegetation of cereal and root-crop fields in cool areas

XBF. *Spergulo arvensis-Erodion cicutariae* J. Tüxen in Passarge 1964 – Weed vegetation of dry sandy soils

XBG. *Atriplicion* Passarge 1978 – Ruderal vegetation of tall annual herbs

XBH. *Sisymbrium officinalis* Tüxen et al. ex von Rochow 1951 – Ruderal vegetation of winter-annual grasses

XBI. *Malvion neglectae* (Gutte 1972) Hejný 1978 – Ruderal vegetation of prostrate annual herbs on nutrient-rich soils

XBJ. *Salsolion ruthenicae* Philippi 1971 – Annual ruderal vegetation of disturbed gravelly and sandy soils

XBK. *Eragrostion cilianensi-minoris* Tüxen ex Oberdorfer 1954 – Late-summer thermophilous ruderal and weed vegetation of sandy soils

XC. *Artemisietea vulgaris* Lohmeyer et al. ex von Rochow 1951 – Xerophilous ruderal vegetation with biennial and perennial species

XCA. *Onopordion acanthii* Br.-Bl. et al. 1936 – Thermophilous archaeophyte-rich ruderal vegetation with biennial and perennial herbs

XCB. *Dauco carotae-Melilotion* Görs ex Rostański et Gutte 1971 – Ruderal vegetation with biennial and perennial herbs on stony and gravelly soils

XCC. *Convolvulo arvensis-Elytrigion repentis* Görs 1966 – Ruderal vegetation with perennial herbs on dry or intermittently dry soils

XCD. *Artemisio-Kochion prostratae* Soó 1964 – Relict vegetation of the Pleistocene loess steppes

XCE. *Arction lappae* Tüxen 1937 – Nitrophilous ruderal vegetation with biennial and perennial species in man-made habitats

XD. *Galio-Urticetea* Passarge ex Kopecký 1969 – Nitrophilous perennial vegetation of wet to mesic habitats

XDA. *Senecionion fluviatilis* Tüxen ex Moor 1958 – Nitrophilous herbaceous fringes of floodplain forests

XDB. *Petasition hybridi* Sillinger 1933 – Vegetation of montane and submontane floodplains with *Petasites*

XDC. *Impatienti noli-tangere-Stachyion sylvaticae* Görs ex Mucina in Mucina et al. 1993 – Nitrophilous vegetation of forest fringes, canopy openings and clearings with perennial herbs

XDD. *Geo urbani-Alliarion petiolatae* Lohmeyer et Oberdorfer in Görs et Müller 1969 – Nitrophilous vegetation of disturbed forest fringes with annual and biennial herbs

XDE. *Aegopodion podagrariae* Tüxen 1967 – Nitrophilous ruderal vegetation with broad-leaved perennial herbs

XDF. *Rumicion alpini* Scharfetter 1938 – Montane nitrophilous vegetation of broad-leaved herbs

XE. *Epilobietea angustifolii* Tüxen et Preising ex von Rochow 1951 – Herbaceous vegetation of forest clearings and disturbed habitats in forest environments

XEA. *Fragarion vescae* Tüxen ex von Rochow 1951 – Herbaceous vegetation at sites of disturbed forest