

# *Picea abies* (L.) H. Karst. – Spruce

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## PRESENT DISTRIBUTION IN THE WESTERN CARPATHIANS

*Picea abies* occupies the entire Polish part of the Western Carpathians, from their foothills to the sub-alpine zone (dwarf pine belt). The species forms its own associations or is a component of other ones, of a zonal type. Distribution of spruce is uneven and in the area of the Beskid Niski range it occurs only in minor amounts. In the past, this fact and the presence or absence of the mid-Carpathian disjunction in spruce distribution was a subject of a long-standing discussion (Środoń 1967, 1990a). According to Staszkiwicz (1993a), supporting the presence of disjunction, it provided an effective genetic barrier between spruces growing in the Eastern and Western Carpathians and producing cones with different morphological features. At present it is mainly assumed that the distribution of spruce in the Polish part of the Western Carpathians is continuous; however it occurs in smaller numbers in particular regions.

Spruces found at highest altitudes, still of a tree habit however, attain 1696 m a.s.l. (Radwańska-Paryska 1975). The upper montane belt, dominated by forests with *Picea abies*, covers the altitudes of 1250–1550 m a.s.l. in the Tatra Mountains and of 1150–1360 m a.s.l. In the highest parts of the Beskid Żywiecki range, whereas the Beskid Niski range, does not exceed 1000 m a.s.l. in height. The comparatively low altitude of this range may be considered to have affected the Holocene history of expansion of spruce in the Carpathians.

The montane stone pine-spruce forest, *Cembro-Piceetum* Myczkowski, Lesiński 1974, is a spruce association attaining the highest altitudes. It covers a small area of the Tatra Mountains and forms the upper forest limit at 1650 m a.s.l. However, there is no consensus on the basis of distinction of this syntaxon (Matuszkiewicz J.M. 2008). Areas of the upper montane belt with soils on crystalline bedrock are occupied by a poor subalpine spruce forest, *Plagiothecio-Piceetum* (Szafer et al. 1923) J. Mat. 1977, while those with calcareous soils support a spruce forest with a more diverse flora, *Polysticho-Piceetum* (Szafer et al. 1923) W. Mat. 1967.

Within the lower montane belt, spruce is a component of the fir-spruce forest, *Abieti-Piceetum* W. Mat. 1967, Carpathian mixed spruce-fir forest, *Galio-Piceetum* J. Mat. 1977, variable in particular parts of the Carpathians, and of the less common montane spruce forest on peat, *Bazzanio-Piceetum* Br.-Bl. et Siss. 1939, with abundant peat mosses (*Sphagnum* spp.). *Picea* is also a companion species in associations such as *Dentario glandulosae-Fagetum* Klika 1927 em. Mat. 1964 (lower montane belt) and oak-hornbeam forest, *Tilio-Carpinetum* Traczyk 1962 (submontane belt).

Within the Carpathians, the Beskid Śląski range provides conditions most advantageous for spruce, having the highest amounts of rainfall and snowfall as well as rocks, forming this range being subject to podzolisation (Sikorska 1997).

## ECOLOGY

Spruce displays exceptional polymorphism – numerous variants and forms are distinguished within the species. Its plasticity is expressed, i.e. in local varieties formed even under the same type of climate. *Picea* shows a broad range of occurrence and is highly capable of adapting to various ecological conditions. It grows well in a cool, relatively humid climate, however is also found in conditions of continental climate typified by snowfall intensive enough to serve as an abundant source of moisture throughout the entire growth period. Winter dormancy, that is its lack or insufficient length, limits the vitality of spruce and is important in this its development (Obmiński 1977).

*Picea abies*, regardless of its age, requires sufficient humidity of both air and soil. In areas with low amounts of rainfall in summer and a snow cover for only a short time in winter the species does not grow at all or is weak and vulnerable to the effects of various adverse factors. This fact, according to some authors, explains the continued presence of a spruceless zone in Poland as well as the lack of the taxon in comparatively arid areas.

Soil requirements of spruce are moderate, however, provided soil humidity is sufficiently high. The species grows on a very wide variety of soils, with a variable pH.

Under Polish climatic conditions spruce generally does not occur as a pioneer in forests (Obmiński 1977).

*Picea* produces heavy pollen grains which sink to the ground relatively fast; therefore the horizontal range of their transport is limited (Bjune et al. 2009). Nevertheless, present-day pollen rain examined after episodes of stormy rainfall on the outskirts of the Western Carpathians, in Kraków and in its wide surroundings, shows high frequencies of spruce pollen, although large forests including this tree are not found in these areas (Szczepanek, unpubl.).

Values of 1% recorded in profiles for *Picea* already demonstrate the occurrence of single or small groups of trees, while amounts exceeding 2% already indicate adjacent large forest complexes (Latałowa & van der Knaap 2006 and references).

#### EXPANSION IN EUROPE DURING THE LATE GLACIAL

Carpathian refugia of *Picea abies* have been thoroughly discussed in literature (e.g. Środoń 1977, 1987, Lang 1994, Taberlet et al. 1998, Obidowicz et al. 2004a, Ravazzi et al. 2006). Presence of such refugia is confirmed by the record of macrofossil remains and the outline of pollen curves plotted for *Picea*, which, in most sections from the Polish part of the Western Carpathians, show a rapid increase already by the Preboreal period. Locations of spruce refugial areas in the western part of the Orawa-Nowy Targ Basin (Koperowa 1962) and in its southern surroundings, the Slovakian Upper Orava (Rybniček & Rybničková 2002), as well as in the Jasło-Sanok Depression, where Late Glacial macrofossil remains were observed (Harmata 1987), seem to be mostly justified. Another source of expansion of *Picea* in the Western Carpathians was the arc of the Eastern Carpathians (Lang 1994).

#### HISTORY OF EXPANSION IN THE WESTERN CARPATHIANS DURING THE HOLOCENE (Fig. 20)

##### 10 000 BP

The authors considered values exceeding 1% as indications of occurrence of spruce *in situ*, as, in most profiles, such amounts initiated a continuous curve for *Picea*. Consequently, two main centres from which the Polish Carpathians were colonised by the species are observed in the 10 000 BP map. One centre, the region between the Beskid Żywiecki range and the Orawa-Nowy Targ Basin, affected areas to the east, up to longitude ca 21°E, and was formed by populations of spruce likely to have locally survived the last glaciation.

The second centre, in the Bieszczady Mountains, influenced a smaller area to the east of longitude 22°E. The map includes also a region, extending from the Pogórze Ciężkowickie Foothills to the San river valley (between longitude 21° and 22°E), still not colonised by spruce.

However, due to the presence of *Picea* sp. macrofossil remains in profiles Tarnowiec (site no. 123) and Besko (232), it should be taken for granted that modest populations of this tree appeared locally in the Jasło-Sanok Depression.

##### 9500 BP

The distribution area of spruce forests and stands containing this species increases rapidly, particularly in the Beskid Żywiecki, Beskid Makowski and Beskid Wyspowy ranges. The eastern limit of occurrence of large complexes of spruce forests, with proportions of *Picea* pollen attaining at least 5%, overlaps the Dunajec river valley. The area devoid of spruce decreases noticeably; however the species is still infrequent in the zone between longitude 21° and 22°E.

##### 9000 BP

Highest values (20%) for *Picea* are recorded at sites in the Beskid Makowski, Beskid Mały, and Beskid Wyspowy ranges, part of the Beskid Żywiecki range and locally in the Tatra Mountains. In particular profiles the proportion of the species even exceeds 20%. The spruceless zone disappears. However, the taxon is still infrequent in the upper catchments of the Wisłoka and Wisłok rivers. This also applies to the profiles from the area between the Skawa and Raba rivers valleys, which were not used in this study, i.e. the Kotoń section (Margielewski et al. 2003) and Osieczkowa section (Margielewski 2006).

##### 8500–8000 BP

*Picea* becomes a more important component of West Carpathian forests and attains values exceeding 10% in most areas. The Beskid Makowski range, initially western and later its eastern part, becomes the most important centre of occurrence of this species. In the Tatra Mountains, spruce forests are found at altitudes exceeding 1390 m a.s.l. (Obidowicz 1996).

In part of the Beskid Niski range, amounts of spruce are still noticeably lower.

##### 7500 BP

Spruce forests become the dominant component of vegetation in the area of the Beskid Śląski, Beskid Żywiecki, Beskid Mały and Beskid Makowski ranges, the Gorce Mountains and the western part of the Orawa-Nowy Targ Basin. In the Tatra Mountains, and more to the east, spruce forests are less frequent and are replaced by other forest communities.

The lowest proportions of *Picea* are still recorded in part of the Beskid Niski range.

##### 7000–6000 BP

The boundary of the area dominated by spruce forests (50%) gets closer to the Dunajec river valley and crosses the river. More to the east, in the Beskid Sądecki range and

part of the Pogórze Ciężkowickie and Dynowskie Foot-hills, amounts of *Picea* exceed 10% and area enclosed by this isopoll systematically increases.

Throughout the entire millennium, in the Jasło-Sanok Depression and the Beskid Niski range spruce seems to be present only as a minor component in forests dominated by other tree species or to occupy only particular habitats.

#### 5500–4500 BP

Spruce forests and stands including *Picea* cover the largest area within the part of Polish Carpathians under investigation in their Holocene history. This was the time when a montane spruce forest, comparable with the present-day association, was formed in the Tatra Mountains (Obidowicz 1996) and, most likely, also in other ranges of the Western Carpathians. In all mountain ranges (from the Beskid Śląski to the Beskid Sądecki range) spruce forests formed the upper forest limit which attained its highest Holocene altitudes. Examination of wood of *Picea* found in Siwe Sady profile (site no. 268) indicates that the limit extended to at least 1542 m a.s.l. in the Tatra Mountains.

In areas of the Beskid Niski range, represented by sites Regetovká (61) and Jasiel (125), occurrence of spruce is noticeable; however other tree communities are dominant.

At 4500 BP, spruce stands became nearly the only forest communities of the eastern part of the Beskid Makowski range and of part of the Beskid Wyspowy range.

#### 4000–3500 BP

*Picea* shows the first symptoms of a decrease in its relative abundance in West Carpathian forests, however its distribution is still not affected by significant changes. Withdrawal of spruce is recorded mostly in the eastern part of the Beskid Niski range, where the species was not found at all at the beginning of the Holocene and later occurred only in minor amounts, as a component in stands with other dominants. Nevertheless, slightly more to the west, at site Szymbark (126), *Picea* attains its maximum values in Holocene spectra, confirmed by the presence of macrofossil remains.

#### 3000–1500 BP

In the first instance, a noticeable decrease in the frequency of *Picea* is observed in forests at lower locations in the Western Carpathians. In the area of the Beskid Makowski and Beskid Wyspowy ranges and at least in part of the Beskid Niski range this process is strongly associated with the expansion of fir. Large complexes of spruce forests are still found in the Tatra Mountains, part of the Orawa-Nowy Targ Basin and in the Beskid Żywiecki range.

In the Beskid Niski range, the mid-Carpathian zone of limited occurrence of spruce begins to develop and rapidly increases its area.

#### 1000–0 BP

The proportion of *Picea* proceeds to decrease in Carpathian forests, particularly at lower altitudes, which is mostly visible in the area to the east of longitude 21°E. Larger populations are still found in the western part, up to the Dunajec river valley, and to the south of it, in the Beskid Sądecki range.

#### CONCLUSIONS

The south-western region of the Western Carpathians provided conditions in which *Picea* could locally survive until the end of the Late Glacial. It may be assumed that here were the main population centres from which much of the study area was subsequently colonized. From 10 000 BP onwards spruce was spreading to the east and crossed the 21°E line of longitude already by 9500 BP. Simultaneously, the Western Carpathians were colonized by spruce from the Eastern Carpathians, though to a limited extent. Up to ca 9000 BP a spruceless zone separated the two ranges of occurrence.

Spruce forests and stands containing *Picea* covered their greatest area between 5500 and 3500 BP. At ca 3000 BP, a zone of limited occurrence of spruce appeared and proceeded to gradually extend and cover large parts of the Beskid Niski range. Since ca 1000 BP, a noticeable division of the Western Carpathians has developed, into an eastern part, with sites showing a decreasing proportion of spruce, and a western part, with relatively numerous populations of the species.















