

Abies alba Mill. – Fir

ANDRZEJ OBIDOWICZ AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN THE WESTERN CARPATHIANS

Abies alba is a tree growing on mountains and uplands in Central and Southern Europe. In the Western Carpathians, communities including fir show regional variation. The tree is found in associations classified within two classes: *Quercus-Fagetum* and *Vaccinio-Piceetum* (Dzwonko 1986). Its best development is observed in acidophilous fir-spruce forests, *Abieti-Piceetum montanum* Szaf., Pawł. et Kulcz. 1923 em. J. Mat. 1978, occupying the poorest soils within the lower montane forest belt, and in the fertile Carpathian beech forest, *Dentario glandulosae-Fagetum* Klika 1927, em. Mat. 1964, at altitudes between 800 and 1200 m a.s.l. *Abies* also occurs in the fertile fir forest, *Galio rotundifolii-Abietetum* Wrab. 1959 (lower montane forest belt), montane acidophilous beech forest, *Luzulo nemorosae-Fagetum* (Du Rietz 1923) Markgr. 1932, em. Meusel 1937 (foothills and lower montane forest belt), and in the thermophilous limestone beech forest, *Carici albae-Fagetum* Panc.-Kotej. in W. Mat. 2001, particularly in its fir subassociation, *Carici albae-Fagetum abietetosum*.

Occasionally, fir grows in montane riparian alder forest – *Alnetum incanae* Lüdi 1921, and in oak-hornbeam forest – *Tilio-Carpinetum* Traczyk 1962 (submontane belt). According to Wojterski (1983), the species spreads readily and even colonises sites, where it has to compete with other established trees already well adapted to local conditions. In particular, a fir forms frequent stands in the Beskid Niski and the Beskid Sądecki ranges (Boratyński 1983). The highest locations where fir grows are in the Tatra Mountains at 1450 m a.s.l. (Komornicki 1974), and in the Beskid Żywiecki range at 1420 m a.s.l. (Borysiak & Stachnowicz 2004).

ECOLOGY

The ecological requirements of fir may be described as intermediate between those of beech and spruce (Jaworski & Zarzycki 1983). Optimum development of fir is limited by mean January temperature of -4.5°C and mean July temperature of 15°C . In all areas of high air humidity, fir shows good tolerance to very low temperatures. However,

it is sensitive to early and late mild frosts. Its northern range of occurrence corresponds to the annual isohyet of 600 mm, whereas in the Carpathians the annual rainfall of 700 or more millimeters provides optimum conditions. Periods of drought are likely to result in the death of trees (Jaworski & Zarzycki 1983).

Fir is a shade-tolerant species, inhabiting mainly fertile, deep and humid soils. The most abundant fir forests of the Beskid Sądecki range and the Tatra Mountains are found on brown soils. Poorer habitats where fir grows mostly possess sandy-loamy or strongly skeletal soils. In comparison with other coniferous trees, fir shows a visibly lower capacity as a pioneer species, as it avoids soils at an early stage of development.

In the Western Carpathians, natural plant rotation, including fir, is a frequent phenomenon. Examples of replacement of fir by beech, in the Babia Góra National Park (Beskid Żywiecki range), as well as of spruce by fir, are recorded. Transition from pine stands into fir ones and the expansion of *Abies alba* into larch and birch stands is also frequent (Jaworski & Zarzycki 1983).

The resistance of fir to tree-felling winds is of great importance for the protection of the surrounding tree stand, since the Carpathians are affected by frequent and very strong foehn winds (Komornicki 1974).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Within the Quaternary history of trees, the Mazovian interglacial was the time of dominance of *Abies alba* in Europe, to an extent never repeated in later periods (Środoń 1983). Fir still reached the coasts of the Baltic and North Seas in the Eemian interglacial. The present range of the species covers the central and southern part of the continent and is subdivided into smaller and larger islands, the locations of which are generally conformable with the distribution of mountain ranges and massifs. The western limit of fir occurrence covers the Black Forest range, the Vosges, the Swiss Jura Mountains, and the Alps, while the southern one – the Apennines, the Dinaric Alps and the mountains of the Balkan Peninsula.

As for the refugial areas of *Abies* during the last glaciation, there is general agreement that they were located in the mountains of the Apennine and Balkan Peninsulas. For other mountain massifs in Europe it has been difficult to confirm the presence of *Abies alba* during the last glaciation. This is particularly important when considering the Iberian Peninsula, where the tree is assumed to have been present (Lang 1994). However, according to Terhürne-Berson et al. (2004), fir refugial areas within that area were isolated and did not contribute greatly to the history of this species in Europe. Similarly, fir refugia in the central part of the Apennine Peninsula were also only of local importance.

According to possible migration pathways of *Abies alba* presented by Taberlet et al. (1998) and Linares (2011), fir arrived in the Carpathians primarily from the Balkan refugia, however, possibly, also from northern Italy. This statement is supported by genetic studies indicating that the Western Carpathians are an area of introgression and meeting of fir populations originating from those two centres (Konnert & Bergmann 1995). Recent studies rather point to the refugial areas of the Balkan Peninsula as the more important ones in the expansion of this species into the Western (=Northern) Carpathians (Liepelt et al. 2009). From results of genetic analysis of a montane fir population from southern Poland (Mejnartowicz 2004), it may be concluded that the tree entered the Polish part of the Carpathians from the south-west and south, i.e. from the Czech Republic and Slovakia.

Expansion of fir proceeded in montane areas and by the end of the Late Glacial (10 000 BP) it covered ca 10% of its present-day range (Lang 1994). It is difficult to determine the time in which *Abies* was undoubtedly present in the Western Carpathians on the basis of palynological studies alone. For a number of reasons Hicks (2006) suggests that absence of pollen grains in sediment may not indicate the absence of a particular taxon *in situ*, for example, if the climate was too arid or too cool and therefore made flowering impossible. However, it may be assumed that temperatures during the Atlantic period were already advantageous to *Abies*. Also the humidity of climate, at least locally, was already sufficient, which is indicated by the intensive development of ombrogenous peat bogs in the Orawa-Nowy Targ Basin (Obidowicz 1990). In the period of 8500–5800 cal. BP, in the northern Swiss Alps, located near the refugial areas of *Abies*, fir and European stone pine formed stands extending to the upper forest limit, while summers of that time were warm and long (Lotter et al. 2006). In the period of ca 6000 BP, fir forests were also found within the Bohemian Forest (Svobodová et al. 2002).

Therefore, climate does not appear to be the reason for such a late appearance of fir in the Western Carpathians.

HISTORY OF EXPANSION IN THE WESTERN CARPATHIANS
DURING THE HOLOCENE (Fig. 12)

10 000–9000 BP

At that time, *Abies* was still not found in the Western Carpathians. This observation is understandable, considering the distance of this part of the Carpathians from refugial areas, and the relatively low rate of expansion of fir, amounting to 40–300 m/year (Huntley & Birks 1983).

8500 BP

In the Orawa-Nowy Targ Basin and in the foreland of the Beskid Niski range, the first appearance of fir pollen grains is recorded. Their low amounts, resulting from long-distance transport, enable the identification of directions from which fir was likely to migrate, namely from the south-west and, presumably, also the south-east or the Eastern Carpathians.

8000–6000 BP

The number of sites with single *Abies* pollen grains increases. Their presence in several profiles from the Tatra Mountains, the Orawa-Nowy Targ Basin, and, for 6000 BP, also from the Beskid Niski range, probably indicates the migration of the tree from the west and south-east.

5500–5000 BP

The amount of *Abies* pollen grains increases in profiles from the Raba river valley and locally in the Beskid Niski range. Fir moves closer to the Polish part of Carpathians; however the question whether it already occurred in these mountains remains open. Its presence *in situ* is likely to be indicated by the beginning of a continuous curve for *Abies*, recorded for ca 5500 BP in the Lubogoszcz (site no. 275) and Pilsko (266) profiles. In the Bogdanówka-Beło profile (277), fir is also found at 5500 BP, however, its curve is still not continuous. It may be expected that a small population of fir migrated from the south-west and became a component of tree stands in the Beskid Wyspowy range. It is very likely that the species occurred in the Slovakian (southern) part of the Beskid Niski range (Regetovká, profile 61).

4500 BP

The western direction of expansion becomes evident. It may be assumed that small groups of fir were already found in the area extending from the Beskid Śląski range to the Dunajec river valley and indicated by the isopoll of 2%. Palynological profiles of this area are marked by the beginning of a continuous curve for *Abies*. In several profiles this curve begins even earlier, between 5000 and 4500 BP. At that time, fir already appears in the Tatra Mountains. Conditions particularly advantageous for its development were recorded locally, in the Beskid Makowski range. In the profile Bogdanówka-Beło (277), fir together with spruce, is one of the main components of forests.

To the east of the Dunajec river valley, fir is represented very poorly, and in the Jasło-Sanok Depression, part of the Beskid Niski range and further to the east it is not recorded at all.

4000 BP

Rapid expansion of *Abies* proceeded from the Upper Orava, through the Beskid Śląski, Beskid Mały, and Beskid Żywiecki ranges, higher parts of the Orawa-Nowy Targ Basin, and the Gorce Mountains, to reach the Dunajec river valley. Fir forests, or forests with an admixture of fir, are the dominant tree stands in the Beskid Makowski range and in a part of the Beskid Wyspowy range, where the proportion of *Abies* pollen attains at least 10%. The tree undoubtedly occurred in the Tatra Mountains, though still rather infrequently, at lower sites. This period may be considered to show the initial formation of the lower montane forest belt.

Numerous sites situated to the east of the Dunajec river valley bear a record of *Abies* as a continuous curve, therefore it was already found at these sites as well. It is probable, that at least to a part of this area the tree migrated from the southern part of the Western Carpathians. Even if we assume that two fir populations migrating from refugia in the Balkan Peninsula (one along the coast of the Adriatic Sea and second across the Eastern Carpathians) converged in the Polish part of the Western Carpathians, it did not happen before ca 4000 BP. Populations of *Abies alba* expanding from the two directions may have met even earlier, in the area of Slovakia.

3500 BP

Fir stands, or forests with a high proportion of this species, spread to the east and crossed the Dunajec river valley. They also expanded into the Orawa-Nowy Targ Basin, not, however, over its entire area, since vast tracts of peat bog occur at the bottom of basin. At numerous localities where cores were taken from these peat deposits, occurrence of *Abies* was not observed (Obidowicz 1990). In this area, fir may have inhabited altitudes above 800 m a.s.l.

In the area of the Beskid Makowski and the Beskid Wyspowy ranges, forests including fir rapidly replaced the declining spruce forests (Obidowicz et al., *Picea abies*, this volume). In profiles Pcim-Sucha (265) and Lubogoszcz (275), the proportion of *Abies* even exceeds 40% of the total sum. This process, continued for only 200–300 years, and appears to have two causes. To a rather minor extent, it may result from a phase of increased humidity recorded for this period and responsible for the activation of slope processes (Margielewski 2006), likely to cause local damage within areas occupied by spruce forests. However, the activity of groups of shepherds, burning down the Carpathian forest for farming purposes, seems to be a more likely reason. It is supported by the presence of a charcoal layers in profile

Lubogoszcz (275), in a pollen zone dated to approximately 3900 BP (interpolated date, Margielewski 2006).

The frequency of fir in forests of the Gorce Mountains, the Beskid Sądecki range, and, locally, also the Beskid Niski range is clearly higher than 500 years earlier. At that time, the tree was found, more or less commonly, across the entire Western Carpathians.

3000–2500 BP

Tree stands abundant in *Abies* clearly extended their range towards the east of the Polish part of the Western Carpathians. Apart from the Beskid Makowski and the Beskid Wyspowy ranges, with fir as the dominant tree in their forests since at least 4000 BP, a large population of this species have developed in the area between the Beskid Niski range and the Pogórze Ciężkowickie Foothills. For both these areas, high values of fir pollen are indicated by the 50% isopoll. Profile from the Beskid Makowski range (Szymbark, 126) records an event relating to a period 600–800 years ago and almost certainly having anthropogenic causes. In that area a rapid replacement of spruce stands by forests dominated, by fir and beech took place. High amounts of *Abies* in pollen spectra are also observed in the borderland between the Beskid Żywiecki range and Beskid Śląski range, reflecting the influence of fir stands of the Upper Orava (Zlatnická Dolina, 286).

The proportion of *Abies* in the forests also increased in the Jasło-Sanok Depression and in the San river valley.

2000 BP

The boundary of the area being covered, at least locally, by dense fir stands, is seen to retreat to the Wisłoka river valley. Nevertheless, frequency of *Abies* still attains at least 20%. A relative regression of the species is recorded exclusively in the Tatra Mountains.

1500–1000 BP

The limit of the area abundant in forests with a high proportion of *Abies* again shifts towards the east, moving closer to the Wisłoka river valley. The Beskid Żywiecki, Beskid Śląski and, presumably, also the Beskid Mały ranges became dominated by fir stands. Higher parts of the Orawa-Nowy Targ Basin or, more likely, the Gorce Mountains are marked by a temporary increase in the amount of fir.

500 BP

Two areas, i.e. the adjacent Beskid Śląski and Beskid Żywiecki ranges as well as the Pogórze Ciężkowickie Foothills, are still characterized by a significant proportion of fir, exceeding 20%. It is particularly worthy of note is that the Tatra Mountains, for the first time in their Holocene history, were covered by the 20% isopoll. However, from this time onward we have to be aware of the effects of deforestation, the felling of trees both with the spread of human settlement and with the establishment of foundries, requiring quantities of wood for smelting.

0 BP

The growth of human settlement in the Western Carpathians, particularly intensive since the 14th century (Przyboś 1995), undoubtedly contributed to the restriction of forested areas, as well as of the reduction of *Abies*, cut down for economic purposes. Relatively large areas of forests comprising of fir were still retained in the Beskid Żywiecki range.

CONCLUSIONS

Abies alba migrated to the Polish part of the Western Carpathians from its refugial areas in the Balkan Peninsula between 5500 and 5000 years ago. Its initial immigration,

from the south-west, through the Beskid Śląski range, resulted in the formation of the first centre of its occurrence in the Beskid Makowski range. Several hundred years later, fir migrated also from Slovakia, through the Beskid Niski range. At about 4000 BP, the eastern margins of the Western Carpathians were probably also colonized by fir that had migrated across the Eastern Carpathians. At about 3900 BP, fir forests began to replace spruce stands. This process proceeded in particular mountain ranges over a period of 600–800 years, largely as a result of human economic activity. Within the last 500–600 years, the intensive development of human settlement in the Carpathians has strongly restricted the area covered by fir.









