THE HOLOCENE HISTORY OF DEVELOPMENT OF ZONAL FOREST COMMUNITIES IN THE WESTERN CARPATHIANS

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The history of particular Carpathian forest-forming trees may provide a basis for an attempt to determine the sequence of appearance of Holocene communities that were likely to initiate associations of the subalpine, upper montane and lower montane belt, and, to a certain extent, of the submontane belt also. Results of research on modern pollen and spore counts in montane areas (Obidowicz, Chapter: History of palynological studies..., this volume) seem to support such attempts at reconstructions. However, the presented estimations should be considered as preliminary and requiring further investigations, as the number of studies on the palynological record of the present-day Western Carpathian zonal associations is insufficient, with an exception only for the subalpine association of dwarf pine and the upper montane spruce forests of the Tatra Mountains and the Beskid Żywiecki range.

The following discussion covers the history of communities that gave origin to the dwarf pine association, *Pinetum mugo carpaticum*, the relict *Cembro-Piceetum* association, the Carpathian upper montane spruce forest, *Plagiothecio-Piceetum*, the upper montane calciferous spruce forest, *Polysticho-Piceetum*, and the lower montane *Dentario glandulosae-Fagetum* and *Abieti-Piceetum* associations. It should be expected that the spread of *Picea*, followed by migration of *Fagus* and afterwards *Abies*, may have resulted in the formation of other associations including these taxa and which now occupy present-day montane belts. However, the presented attempt to reconstruct the history of plant associations will be limited only to ones presently covering the largest areas in the Polish part of the Western Carpathians. In particular Carpathian regions, the material collected indicates also the development of riparian communities.

Reconstruction of the history of the foothill oak-lime-hornbeam communities seems to be far more difficult and only suggestions, based on interpretations of isopollen maps showing the history of *Carpinus* and *Tilia*, will be presented.

According to isopollen maps, in the Western Carpathians the beginning of the Holocene was marked by the dominance of forests including pine (Madeja et al., Chapter: *Pinus* subgen. *Pinus*, this volume). To a large extent, they were relicts from the close of the Pleistocene and expanded greatly in the first centuries of the Holocene. In the period of 9500–9000 BP, *Betula* sp. attained its maximum Holocene range of occurrence in the Western Carpathians; therefore it should be assumed that pine-birch forests were widespread as well. Peat bogs of the Orawa-Nowy Targ Basin were characterized by the initial deposition of *Pino-Betuleti* peats (Obidowicz 1990), later they formed under conditions of a swamp birch-pine forest association, *Vaccinio uliginosi-Betuletum pubescentis*. Between 5000 and 3500 BP the community became re-established in the Basin and the greatest abundance of birch populations was observed in this region of the Western Carpathians.

Following Szafer's opinion, it was assumed that the present-day vertical distribution of numerous Carpathian species reflects a record of their former history (Szafer 1966). Therefore, *Pinus mugo* may be considered the first taxon that formed its own belt in the highest parts of the Western Carpathians. As pollen grains of dwarf pine were not distinguished from pollen of common pine, conclusions on the occurrence and vertical extent of *Pinus mugo* were supported by its ecological requirements, which differ from those of *Pinus sylvestris*. Dwarf pine, as a pioneer species that invades consolidated screes, precipices and even rocky ridges (Piękoś-Mirkowa & Mirek 1996). Furthermore, it releases much less pollen, as confirmed by modern pollen spectra from patches of the dwarf pine belt. Therefore, the strong decrease in amounts of *Pinus* recorded in Tatra sections for 9500 BP seems likely to indicate that dwarf pine was the main pollen producer during this period (Obidowicz 1996).

One zonal association that survived until the beginning of the Holocene is *Cembro-Piceetum*, considered by Matuszkiewicz to be a specific form of the upper montane spruce forest found in the Tatra Mountains

(Matuszkiewicz W. 2008). However, the history of stone pine-larch communities, a relict of which the Tatra stone pine-spruce forest seems likely to be, provides a basis for recognizing this unit as a distinct syntaxon. This opinion is supported by Myczkowski and Bednarz, who stated that the *Cembro-Piceetum* stone pine forest and the upper montane spruce forests differ greatly in their shrub layer and the species composition of the ground layer (Myczkowski & Bednarz 1974).

However, it cannot be excluded that the composition of this forest changed during the Holocene. Most likely from the beginning of this period the community was marked by the presence of *Betula* and *Pinus mugo*, accompanied by a decline of *Larix*. Decrease in the proportion of the last-mentioned taxon is recorded for historical times (Myczkowski & Bednarz 1974). This causes problems in classification of this community or considering it as a geographical vicariant of the alpine *Larici-Pinetum cembrae* association, formed in the Late Glacial and gradually reducing its extent, being restricted by the expansion of spruce throughout the first thousand years of the Holocene. At the beginning of this period the decrease in area of stone pine-larch forests may also have been proceeding because of the rapid expansion of pine-birch forests.

After 9500 BP, tree stands of several Carpathian massifs (the Beskid Żywiecki, Beskid Makowski, and Beskid Wyspowy ranges) were characterized by a great increase in the frequency of *Picea*; however *Picea* did not become the dominant forest-forming tree in the area extending from the Beskid Śląski range to the Dunajec river valley before 7500 BP (Obidowicz et al., Chapter: *Picea abies*, this volume). There is no sufficient evidence to confirm that this period was already marked by the occurrence of spruce associations presently found in the upper montane belt. However, communities formed by spruce stands were undoubtedly a stage in the development of present-day associations. According to the available results, the presently recognized associations of the upper montane forest belt appeared 1500–2000 years later. Between 5500 and 4500 BP spruce forests and stands comprising this species covered the widest area in the Holocene history of this part of Polish Carpathians. Therefore, this could have been the time of formation of spruce associations, comparable with the present-day ones, on silicate and calcareous soils of the Tatra Mountains. This is supported particularly by the statistically significant similarity between a pollen spectrum from one Tatra profile from Zielony Staw Gąsienicowy (site no. 123) and modern pollen spectra from the interior of a spruce forest (Obidowicz 1996). Moreover, since ca 5000 BP, climate in the Carpathians was advantageous to the expansion of spruce, which became the main forest-forming tree over a large area of the mountains. Therefore, it may be assumed that upper montane spruce associations developed also in other ranges of the Western Carpathians.

At 8500 BP *Corylus* entered a period of rapid expansion, initiating the hazel phase. During this period, communities including hazel were dominant in various parts of the Western Carpathians and may even have formed their own zone locally in the Tatra Mountains. Possibly, hazel occurred abundantly in the developing riparian forests (see below) as well as forming its own associations, present-day equivalents of which are still unknown.

The hazel phase continued until ca 7000 BP, when the maximum distribution of *Fraxinus* was recorded as well. Therefore, a community conformable with the *Corylo-Fraxinetum* association, presently found in the northern part of the Iberian Peninsula (Mayer 1986), was likely to have been growing already in the Western Carpathians. That could be also the time of development of communities, which, after the arrival of *Carpinus betulus*, i.e. after 5500 BP, gave rise to the association of submontane ash forest, *Carici remotae-Fraxinetum*, presently occupying the submontane belt, particularly in valleys with fast-flowing streams and brooks (Matuszkiewicz J.M. 2008). This syntaxon initially inhabited the Orawa-Nowy Targ Basin and areas located more to the north-east, in the Dunajec river valley, and gradually expanded into the eastern part of the Carpathians.

Another association likely to be formed after 8500 BP was the riparian alder forest, *Alnetum incanae*, which developed in river valleys filled with fluvisols, and which is presently observed in the Carpathians, from the base of their foothills up to 900 m a.s.l. (Matuszkiewicz W. 2008). High pollen values of *Alnus*, recorded for the Atlantic period in several Tatra profiles, provide a basis for the assumption that this riparian forest, typical of montane regions, locally extended even to the lower montane belt.

After 8000 BP, *Tilia* and, in particular montane ranges, *Ulmus*, became frequent components of multispecies deciduous forests in the entire area of the Polish Carpathians. Only higher locations of the Tatra and Bieszczady Mountains were devoid of these taxa.

Small patches of elm-ash riparian forests, *Ficario-Ulmetum minoris*, at present not found in the Western Carpathians (Matuszkiewicz J.M. 2008), may have been formed locally.

Proportions of *Tilia* increased rapidly in the Jasło-Sanok Depression and the northern part of the Beskid Niski range, most likely occupied by stands, which included lime as a co-dominant species. The second centre of its occurrence was found in the Raba river valley. The outline of isopolls indicates an intensive expansion of lime across the entire study area within the Carpathians. Frequency of *Tilia* increased in the area of the Bieszczady Mountains, where the taxon inhabited lower submontane locations. This may have been the time of local development of montane and submontane slope forests included in the *Tilio platyphyllis-Acerion pseudoplatani* Klika 1955 alliance.

Such a conclusion is supported by the above mentioned presence of *Ulmus*, accompanied by *Acer* and *Fraxinus*, in the Western Carpathians. At present, such communities are infrequent in Poland, which lies at the limits of their range (Matuszkiewicz W. 2008).

Between 7000 and 5000 BP, climate remained warm and humid. Particular regions of the Western Carpathians were still dominated by hazel scrub or had stands in which *Corylus* was abundant. Locally, larger areas were covered by various types of mixed deciduous forests. Trees of the telocratic phase were only approaching the Polish Carpathians (*Abies*, *Carpinus*) or had already appeared locally, albeit in small populations (*Fagus*).

From ca 5000 BP, forests of the western part of the Western Carpathians may have already included hornbeam. The arrival of *Carpinus* was necessary for the development of the subcontinental oak-lime-hornbeam association, *Tilio-Carpinetum*. As the period of ca 4500–4000 BP was also marked by the expansion of *Abies* and *Fagus*, the formation of an association, presently described as the Malopolanian, which extends up to 600 m a.s.l. in the Western Carpathians (Dzwonko 1986), was probably already in existence at that time. This zonal community of the submontane belt covered its widest area at ca 3500 BP.

At ca 4500 BP, *Abies* undoubtedly occurred in the Beskid Makowski range and after 4000 BP continued its intensive expansion from the Upper Orava up to the Dunajec river valley. As the entire Western Carpathians were also already grown by larger assemblages of *Fagus*, this period may be considered the initial development of forest communities of the lower montane belt. The centre of formation of associations presently found in the belt may be assigned to the Beskid Makowski and, at least partly, the Beskid Wyspowy ranges.

Between 3500 and 2500 BP, beech-fir forests already inhabited large areas of the above mentioned mountain ranges and part of the Beskid Niski range. In the next centuries proportion of beech exceeded the frequency of fir in stands located to the east of the Wisłoka river valley. Dominance of *Fagus* was accompanied mainly by the displacement of spruce and shifted westwards in the Carpathians.

Numerous taxa, the history of which has been outlined in this study, such as *Pinus cembra*, *P. mugo*, *P. sylvestris*, *Larix* sp., *Betula* sp., and *Picea abies*, survived the last glaciation in the Western Carpathians or in their environs. Other taxa appeared in subsequent climatic phases. The formation of forest associations occurring as specific altitudinal vegetation belts in particular mountain ranges of the Western Carpathians is shown to be metachronous, and this has resulted from the sequence of immigration of taxa during the Holocene and from the direction of their migration.

The effect of human settlement on the history of the zonal forest communities considered here requires further investigations.