HISTORY OF PALYNOLOGICAL STUDIES IN THE POLISH PART OF THE WESTERN CARPATHIANS. REMARKS ON POLLEN ANALYSIS AT MONTANE SITES AND THE IMPORTANCE OF RESEARCH ON MODERN POLLEN RAIN

Andrzej Obidowicz

History of studies

It is not certain, when the earliest information on plants formerly occupying the Western Carpathians was recorded. In 1865, Morawski, describing the extraction of peat by the residents of the Orawa-Nowy Targ Basin, stated that "...occasionally a yew trunk is found" (Morawski 1865), while in 1922 Podkański wrote: "I myself heard stories about trunks of oaks, presently extinct, found in Ludźmierz" (Podkański 1922).

The beginning of palynological studies of the history of vegetation and changes in natural environment in the Western Carpathians dates back to the 1920s. This was the time when the novel method of pollen analysis was developed in palaeobotany and applied by Peterschilka (1927) and Dyakowska (1928) in the Orawa-Nowy Targ Basin and later by Trela (1929) in the Babia Góra Mountain (Beskid Żywiecki range) and Dyakowska (1932) in the Tatra Mountains. Profiles described by the authors are mostly of purely historical value; however, their numerous good interpretation ideas should be appreciated. If the original analysis data were still accessible and POLPAL could be used to plot diagrams for such profiles, then occasionally, as for the Litworowy Staw Lake (Dyakowska 1932, Obidowicz 1996), the trends in vegetational succession, as interpreted at that time, would show clear similarities to the ones observed in studies performed 50 or 60 years later.

In later years, when it became possible to identify also the pollen and spores of herbaceous plants, as well as those of trees and shrubs, the sites investigated made possible the determination of key stages in the development of postglacial vegetation (Koperowa 1962, 1970, Stuchlikowa & Stuchlik 1962, Pawlikowa 1965, Harmata 1969, 1995, Gil et al. 1974, Szczepanek 1987, 1989). The state of knowledge up to 1970 also provided the basis for a preliminary synthesis of the postglacial history of Polish Carpathian forests (Ralska-Jasiewiczowa 1972).

Studies of modern pollen rain were also undertaken, in an attempt to determine and present a set of palynological records that would accurately characterise the main plant communities related to particular altitudinal vegetation belts in the Western Carpathians (Libelt & Obidowicz 1994, Stuchlik & Kvavadze 1995, Obidowicz 1996).

The analysis of profiles, obtained from different altitudes a.s.l., and their interpretation, referring to studies on modern pollen rain, provided the basis for a reconstruction of the history of the formation of the altitudinal vegetation belts in the Tatra Mountains (Obidowicz 1996).

Taking into account the results of research carried out in various mountain ranges of the Western Carpathians and published within the recent years, the density of palynological profiles in this part of the Polish Carpathians is sufficient to present the Holocene history of vegetation using isopollen maps.

Pollen analysis at montane sites

There are several reasons why the application of pollen analysis to montane areas raises methodological problems. First of all, in the mountains there is the so-called "high mountain effect", which may have to be taken into account. Occasionally the pollen rain in high mountain areas is enriched by abundant pollen grains and spores that have a regional origin from plants growing beyond the mountains.

Secondly, vegetation, particularly of higher mountains, shows an altitudinal zonation, but when cores are collected within a given altitudinal belt, it must be expected that pollen and spores of species representing adjacent belts will also be present. This naturally causes problems when attempts are made to distinguish the boundaries of altitudinal belts, using palynology.

In order to minimize the effect of regional pollen on the shape of particular curves in pollen diagrams, Obidowicz (1996) counted spectra from Tatra profiles in a way that

excluded regional taxa from the total sum (AP+NAP). As a result, taxa forming present-day altitudinal vegetation belts were emphasized, with reference to their peaks, in defining the names of the pollen assemblage zones (PAZ) that could be distinguished.

The upper forest limit

The upper forest limit has in fact been defined in many ways and is occasionally assumed to be equivalent to the upper tree line. In the present study, the definition of the upper forest limit as being the boundary of dense tree stands is applied (Allaby 1996). If this boundary is natural, above its isohypse (i.e. contour height) dense stands pass into biogroups and eventually into single individuals, which, ca 100–300 m higher, form the tree limit. Nevertheless, the transition from dense stands into biogroups does not always indicate a climatic boundary, since shallow soil and presence of boulders is likely to produce a similar effect (Schuster 1979). However, in other cases, provided that the area does not display anthropogenic features, it should be considered a climatic boundary, as the dense forest extends to altitudes at which the mean daily temperature attains 10°C for at least three months. Such a property is observed for coniferous forests.

However, it is known that in the European mountains the upper forest limit may be formed by various different tree stands. In the Western Carpathians, these are mainly montane spruce forests, extending to ca 1550 m a.s.l., while in the Eastern Carpathians beech forests are found up to the altitude of ca 1300 m a.s.l. In the Alps the forest limit extends between 1650 and 2300 m a.s.l. In the humid and cool Northern Alps it is even located 400–600 m lower than in the more continental Central Alps, where it is formed by larch-stone pine forests. A different pattern is observed on the southern side of the Alps, where the limit is frequently shifted lower and overlaps the zone of beech forests. Mean January temperature of −4°C is then considered the limiting factor (Landolt 1983). In Germany and in the Polish Carpathians the upper limit of beech forests is associated with mean July temperature of 13°C (Dzwonko 1990).

The forest limit during the Late Glacial appears to be mostly physiological, related to the progressive processes of soil maturation (Welten 1982), while in the Holocene, until humans arrived, climate was the dominant factor.

For many decades palynologists have been concerned about the reasons for changes in the altitude of the forest limit during the Late Glacial-Holocene history of montane vegetation and, in particular, with trying to reconstruct these changes and their extent. Lang (1993, 1994), a researcher of great experience in applying pollen analysis to montane areas, is critical about the possibility of obtaining reliable information on the above-mentioned issues on the basis of pollen analysis alone. In his opinion, percentage diagrams plotted for montane areas need to be accompanied

by diagrams of absolute pollen frequency and analysis of macroscopic remains. Such a view stands to reason. Tinner et al. (1996), in their reconstructions of changes in the location of forest limits, analysed not only pollen and macroscopic remains but also the soil profiles, following the assumption that soil properties should be affected by changes at the forest-meadow boundary. Literature presenting research on oscillations of the forest limit, reconstructed on the basis of pollen analysis and examination of macroscopic remains, supported by the analysis of climatic change indicators, such as Cladocera and Chironomidae, is already impressive (Lang 2006, Lotter et al. 2006).

Palynological definition of the upper forest limit

The palynological estimation of the upper forest limit appears to be of exceptional importance. The ability to identify the upper forest limit for various periods in the geological past is crucial as it determines a number of climatic and habitat features, which are significant in the reconstruction of changes proceeding in the natural mountain environment.

Attempts have been made to form a palynological definition of the upper forest limit, deduced from studies of the modern pollen rain. Studies conducted in the Dachstein Massif by Kral revealed that the present-day vegetation and its palynological record are highly consistent (Kral 1971, 1973). The forest limit was indicated by the intersection of the curve plotted for the sum of pollen of climax trees (spruce + fir + beech + European stone pine + European larch) with the total curve for subalpine shrubs (dwarf pine + green alder).

In the Tatra Mountains, the boundary between the upper montane forest belt and the dwarf pine belt is recorded locally, as a change in the AP/NAP ratio, and generally, as a rapid decrease in the proportion of spruce, accompanied by an increase of *Pinus* (Obidowicz 1996). The definition of forest limit may not always be based only on the AP/NAP ratio. For example, in the Western Carpathians the belt of montane spruce forests, forming the upper forest limit, is adjacent to the belt of dwarf pine (*Pinus mugo*), pollen grains of which are included in the AP sum. Studies of the present-day pollen count in the Tatra Mountains, including over 80 surface samples, indicate that in the upper montane forest belt the AP sum attains 71.9–91.5%, with values for *Picea* amounting to 42.0–75.2%, while in the dwarf pine belt the AP amounts to 46.6–79.3%, with the *Picea* frequency of only 9.6–26.2%. Therefore, if the range of 71.9–79.3%, in which the AP values overlap, is excluded, it may be assumed that an AP sum exceeding 80% indicates a site located in the upper montane forest belt. The AP sum of 80% is also the limiting one for European stone pine stands, as suggested by surface studies performed in the European stone pine minizone of the Tatra Mountains (Obidowicz, unpubl.).

Estimation of location of the upper forest limit according to the AP/NAP ratio has its followers (Treml et al. 2006). In the Tatra Mountains, the *Picea/Pinus* ratio is of great importance. Because of the variable floral composition and density of patches of dwarf pine, locally the forest limit is denoted by the presence of Poaceae, Ericaceae and Filicopsida (Filicales monoletae). In a series of surface samples collected from altitudinal vegetation belts of the Western Tatras (Libelt & Obidowicz 1994), the boundary between the upper montane forest belt and the dwarf pine belt is marked by a decrease in *Picea*, from 69.6 to 23.2%, and an increase in *Pinus*, from 8.5% to 13.7%, and eventually to 45.0%, as well as an increase in Poaceae from 5.8 to 43.3%, Ericaceae from 0.3 to 2.5%, and Filicales monoletae from 5.4 to 35.4%.

Changes in altitude of the upper forest limit in the postglacial period were presented graphically. In 1952, one attempt was made by Welten, who plotted an "altitudinal-temporal" diagram (Welten 1952). Using records from numerous pollen profiles obtained at various altitudes, he illustrated how the dominant tree stands shifted in the subsequent stages of the postglacial history of forests in the Simental Valley. The form of an altitudinal-temporal diagram was also used to present i.a. the history (Fig. 6) of tree stands and oscillation of the upper forest limit in the Central Alps (Burga 1988). The visible direct relationship between the oscillation of the snow limit and the altitude of the forest limit is likely to confirm the key importance of changes in the mean annual temperature in this matter.

However, Lang considered this type of diagram, used mainly by palynologists investigating the Alps, to be inconsistent with the present-day state of knowledge (Lang 1993, 1994). He suggested a different approach to graphic presentation of changes in the vertical pattern of the forest limit. In his method, the recognized altitude of the upper forest limit is deduced from pollen analysis alone or in combination with analysis of macroscopic plant remains. Reference is made to values from spectra of pollen and macroscopic remains of *Pinus cembra*, *Larix decidua*, *Picea abies*, and *Alnus viridis*.

In order to confront the issues discussed above, it is necessary to determine how various plant communities are recorded in pollen spectra. For this purpose, research on the modern pollen rain needs to be conducted in montane areas, including in particular altitudinal climatic-vegetation belts and various associations.

Modern pollen rain in the area of the Babia Góra Mountain (Beskid Żywiecki range)

Within studies of the postglacial history of vegetation in the Western Carpathians, the modern pollen rain was analyzed for particular altitudinal vegetation belts of the Babia Góra Mountain. The aim of this investigation was to identify the palynological record of specific zones and of the upper forest limit.

The Babia Góra Mountain is the only massif in the Western Carpathians, apart from the Tatra Mountains, with typically developed altitudinal climatic-vegetation belts, including a distinct alpine belt. The lower montane
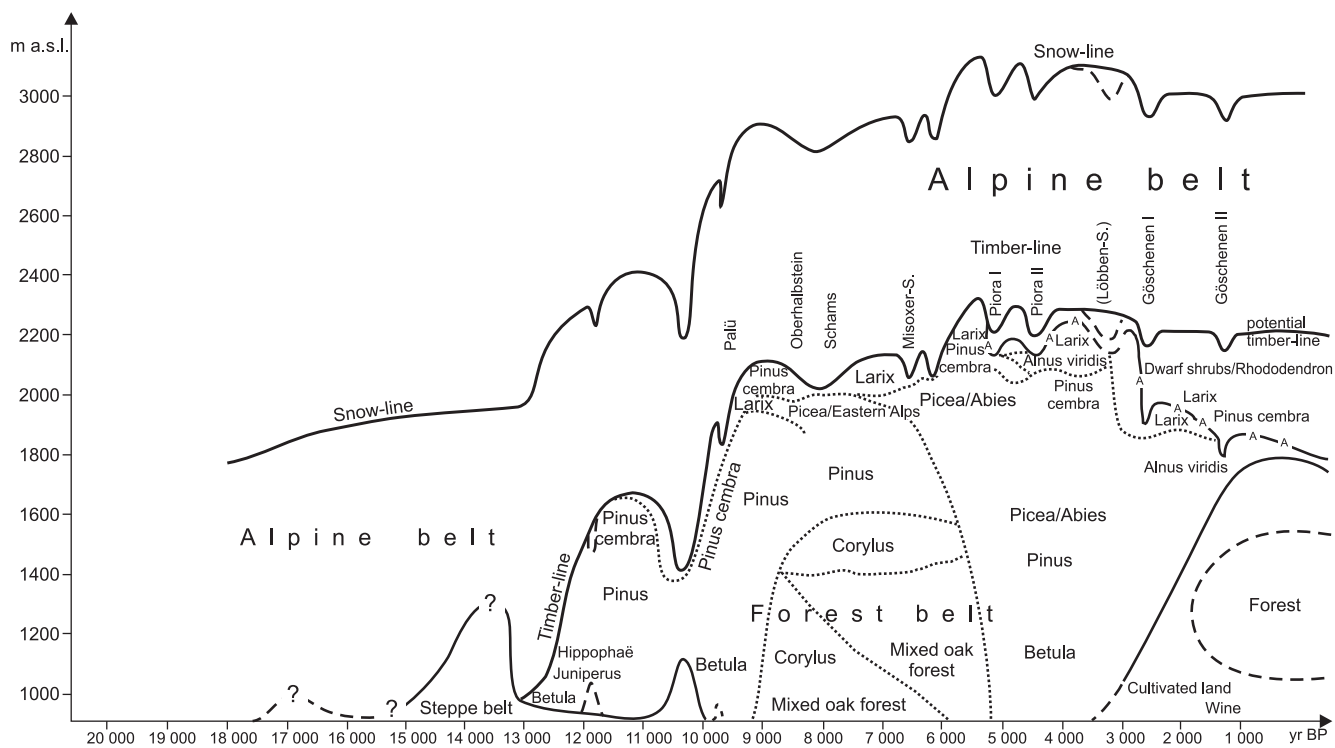

Fig. 6. Development of the Central Alpine forest belt of Switzerland since the Late-Würmian (after Burga 1988, slightly simplified)

forest belt includes the following associations (description of belts follows Parusel et al. 2004):

Abieti-Piceetum montanum Szaf., Pawł. et Kulcz. 1923 em. J. Mat. 1978, an association with a poor flora, dominated by *Picea abies* and with a constant proportion of *Abies alba* and *Fagus sylvatica*. The ground layer comprises the following constant and dominant species: *Dryopteris dilatata*, *Oxalis acetosella*, *Calamagrostis arundinacea*, *Luzula sylvatica*, *Athyrium filix-femina*, *Homogyne alpina*, and very numerous Bryophyta.

Dentario glandulosae-Fagetum W. Mat. 1964 ex Guzikowa et Kornaś 1969, an association of a medium floral abundance. The stand is dominated by beech and spruce, accompanied by commonly found fir and less frequent sycamore (*Acer pseudoplatanus*). In the ground layer, the highest constancy is recorded for: *Dentaria glandulosa*, *D. bulbifera*, *Polystichum aculeatum*, *Allium ursinum*, *Festuca altissima*, and *Symphytum tuberosum*. Species such as *Dryopteris filix-mas*, *Galeobdolon luteum*, *Dryopteris dilatata*, *Athyrium filix-femina*, *Oxalis acetosella*, *Rubus idaeus*, *R. hirtus*, *Senecio fuchsii*, and mosses like *Plagiothecium curvifolium* and *Polytrichum formosum*, are also present.

Alnetum incanae Lüdi 1921, an association having an abundant flora, with *Alnus incana* as a characteristic species. The ground layer is dominated by *Petasites kablikianus*, accompanied by taxa of a higher constancy such as *Stellaria nemorum*, *Petasites albus*, *Impatiens noli-tangere*, *Galeobdolon luteum*, and *Urtica dioica*.

Caltho-Alnetum (Zarz. 1963) Stuchlik 1968, this represents associations of the most abundant floras in the area of the Babia Góra Mountain. The tree layer is formed mainly by *Alnus incana*. Many patches are dominated by *Alnus glutinosa*; occasionally *Fraxinus excelsior* is the prevailing species. The ground layer is most frequently characterized by *Crepis paludosa*, *Caltha laeta*, *C. palustris*, *Chaerophyllum hirsutum*, *Poa remota*, *Carex remota*, *Ranunculus repens*, *Myosotis palustris*, *Cardamine pratensis*, and *C. amara.*

The upper montane forest belt and the area of the upper forest limit include the following associations (following Parusel et al. 2004):

Plagiothecio-Piceetum (*tatricum*) Szaf., Pawł. et Kulcz. 1923, an association with a poor flora. The stands are formed almost exclusively of spruce. Fir and *Sorbus aucuparia* are found only occasionally. The luxuriant ground layer is dominated by *Athyrium distentifolium*, *Calamagrostis villosa*, and *Plagiothecium undulatum*, accompanied by *Vaccinium myrtillus*, *Luzula sylvatica*, *Dryopteris dilatata*, *Homogyne alpina*, *Deschampsia flexuosa*, *Oxalis acetosella*, and mosses such as *Plagiothecium curvifolium*, *Polytrichum formosum*, and *Dicranum scoparium.* Altitudinally, the association extends between 1150 and 1390 m a.s.l.

Athyrio-Sorbetum (Wojt. 1956; Cel. et Wojt. 1960, 1961 n.n.) Borysiak (1978) 1986, an association with a restricted flora.

A layer of low-growing trees is formed by rowan, in poorer patches accompanied by spruce. The ground layer, with *Athyrium distentifolium* as the prevailing species, is very luxuriant. *Doronicum austriacum*, *Adenostyles alliariae*, *Rumex arifolius*, *Stellaria nemorum*, *Oxalis acetosella*, *Vaccinium myrtillus*, *Homogyne alpina*, *Dryopteris dilatata*, and *Calamagrostis villosa* show high constancy. These scrub patches occur within the upper forest limit and montane spruce forests. Altitudinally, the association extends in a belt located from 1160–1415 m a.s.l.

The zone of dwarf pine (subalpine belt) is occupied by the *Pinetum mugo carpaticum* Pawł. 1927 association, dominated by *Pinus mugo*, constantly accompanied by spruce. The characteristic species are represented by *Ribes petraeum* var. *carpaticum*, *Sorbus aucuparia* var. *glabrata*, *Rosa pendulina*, *Salix silesiaca*, *Athyrium distentifolium*, *Leucanthemum waldsteinii*, *Veratrum lobelianum*, and *Geranium sylvaticum*. Altitudinally, the association extends between 1200 and nearly 1700 m a.s.l. The dwarf pine scrub includes patches characterized by the dominance of dwarf juniper (*Juniperus communis* ssp. *alpina*). Dwarf juniper may form its own stands as well (Parusel et al. 2004). Another natural community of the subalpine belt is *Empetro-Vaccinietum* Br. Bl. 1926, comprising *Empetrum hermaphroditum*, *Polytrichum strictum*, and *Sphagnum capillifolium* (Balcerkiewicz & Pawlak 2004).

Windthrow hollows and steep slopes within the upper montane forest belt and dwarf pine belt are inhabited by tall fern communities composed mainly of *Athyrium distentifolium* (Balcerkiewicz & Pawlak 2004).

The alpine belt is dominated by alpine grasslands with highland rush (*Juncus trifidus*) and tufted fescue (*Festuca airoides*), forming the *Junco trifidi-Festucetum airoides* Wal. 1933 association. It comprises also i.a. *Hieracium alpinum*, *Pulsatilla alba*, and *Agrostis rupestris* and develops on the highest parts of the massif at altitudes which exceed 1600 m a.s.l. (Balcerkiewicz & Pawlak 2004). Ridges of the Babia Góra Mountain are covered with patches of crowberry-bilberry heaths, *Empetro-Vaccinietum*, with tufts of Bryophyta like *Polytrichum strictum* and *Sphagnum capillifolium.*

METHODOLOGY OF POLLEN RAIN INVESTIGATIONS

The above-mentioned altitudinal vegetation belts were subjected to surface sampling of fragments of tufts or carpets formed by mosses. The samples were distributed in a row marked out along the main ridge of the massif and passing through all the altitudinal belts (Fig. 7). Samples 1–3 were collected from the upper montane forest belt and the area of the upper forest limit, samples 4–5 (the dwarf pine belt), samples 6–9 (the alpine belt), samples 10–11 (the dwarf pine belt), samples 12–14
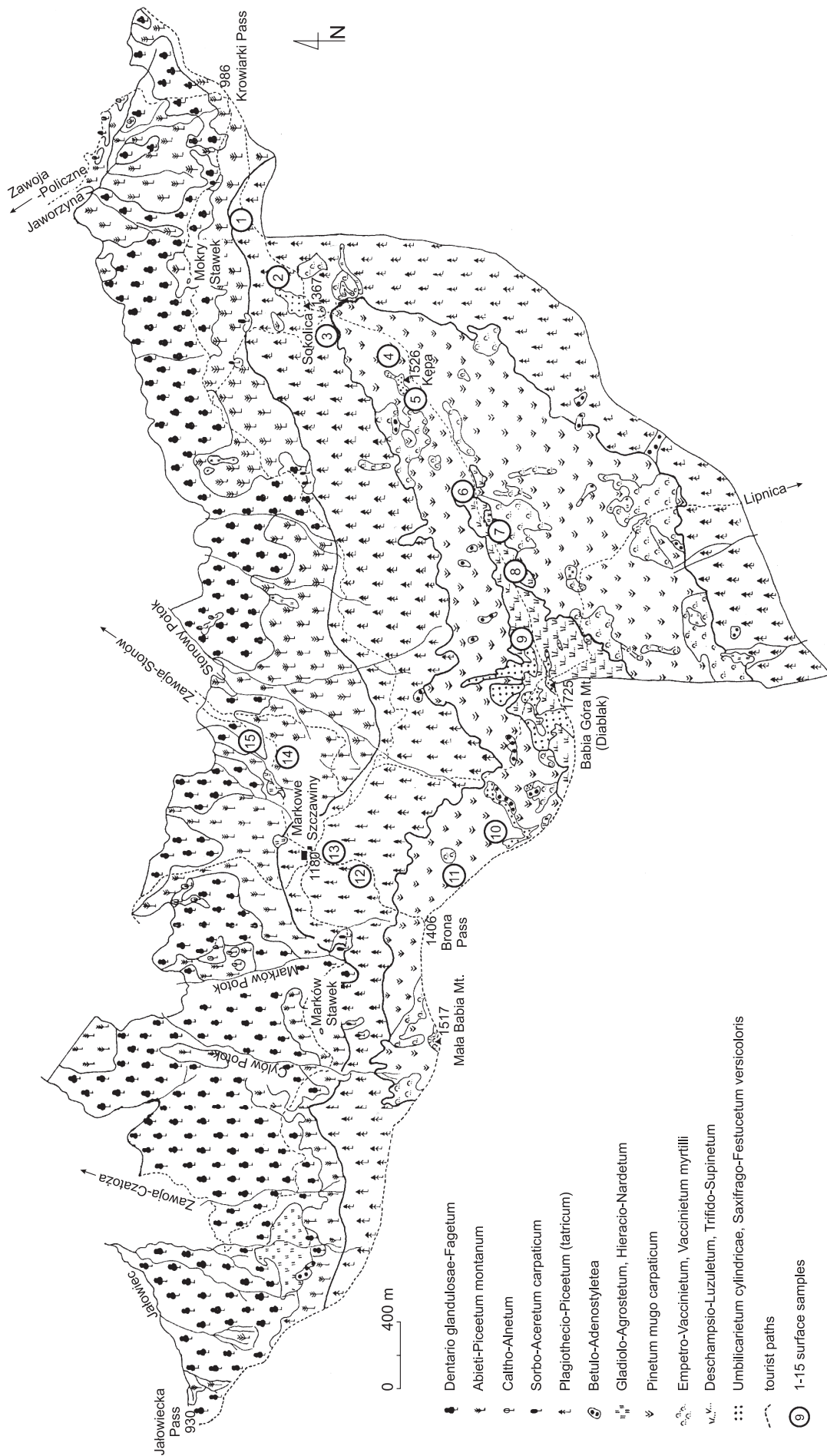
Fig. 7. The distribution of the main plant communities of the Babia Góra Mt. (after Celiński & Wojterski 1983, slightly simplified) and distribution of surface samples
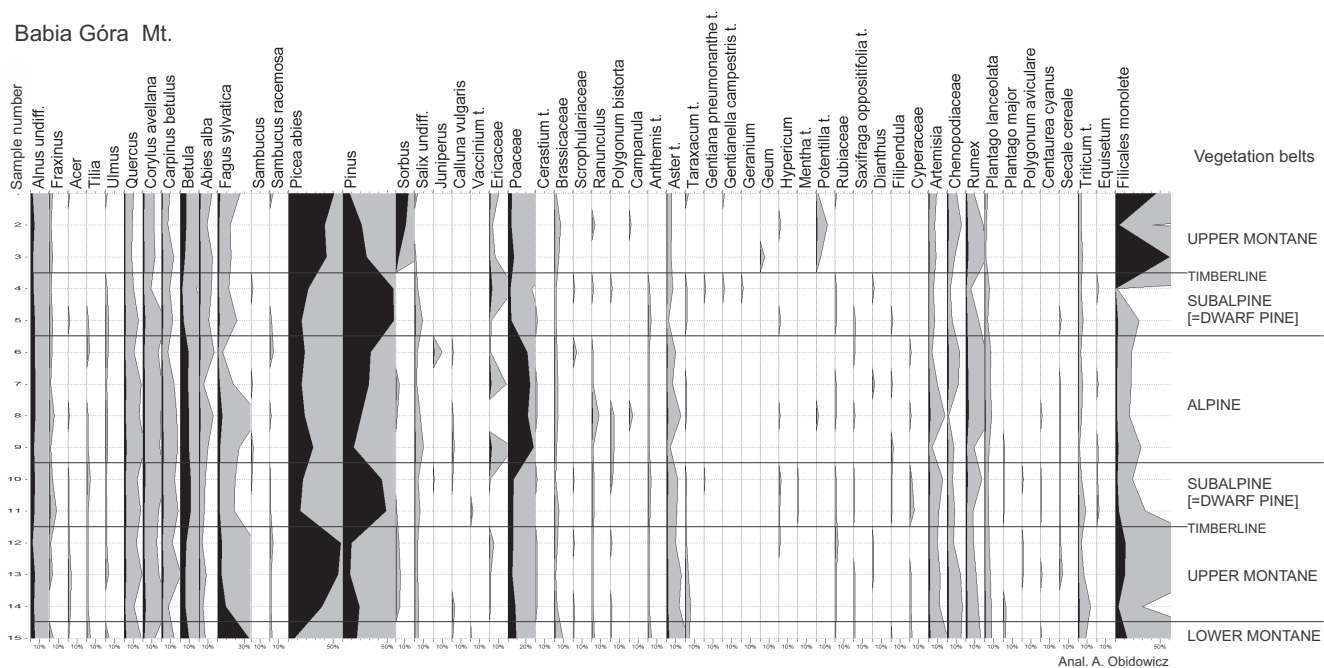
Dentario glandulosae-Fagetum
Abieti-Piceetum montanum
Caltho-Alnetum
Sorbo-Aceretum carpaticum
Plagiothecio-Piceetum (tatricum)
Betulo-Adenostyletea
Gladiolo-Agrostetum, Hieracio-Nardetum
Pinetum mugo carpaticum
Empetro-Vaccinietum, Vaccinietum myrtilli
Deschampsio-Luzuletum, Trifido-Supinetum
Umbilicarietum cylindricae, Saxifrago-Festucetum versicoloris
tourist paths
1-15 surface samples

Fig. 8. Pollen diagram of surface samples taken from the transect running across the vegetation belts of the Babia Góra Mt. (selected pollen taxa)

(the upper montane forest belt), and sample 15 (the lower montane forest belt). Samples intended for pollen analysis were prepared following the method of Faegri and Iversen (1989). Spectra were counted to the AP sum of at least 500 grains, however mainly to ca 1000 sporomorph grains. The results are presented graphically in Figure 8, while the percentage values for the most important taxa, characteristic for particular altitudinal belts in Table 2.

Discussion

The results of pollen analysis show that the floral composition of particular altitudinal vegetation belts is generally conformable with their palynological record. Within the lower montane forest belt, a sample taken from the patch of *Fagetum carpaticum* is dominated by *Fagus* pollen (34.2%), while a sample from the *Abieti-Piceetum montanum* patch is marked by a frequency of *Fagus* amounting to 9.0%, of *Abies* to 0.5%, with the highest values being attained by *Picea* (37.2%). In the upper montane forest belt with patches of *Plagiothecio-Piceetum*, *Picea* pollen occurs most frequently (max. 57.4%), while *Sorbus* is occasionally co-dominant (max. 13.2%). In the dwarf pine belt, it is *Pinus* that displays the highest value in the spectra (56.6%), whereas in the alpine belt it is Poaceae (max. 28.4%). Among taxa

characteristic for associations of this belt, *Juniperus* attains its maximum value of 1.0%, Ericaceae its maximum of 2.9%, *Empetrum* a value of 0.3%, *Campanula* 0.4%, and *Ranunculus*-type 0.8%.

In all altitudinal vegetation belts, spectra include regional sporomorphs. Although the identified taxa show low percentage frequency or are recorded only as single pollen grains, their list is long and comprises i.a. *Carpinus*, *Corylus*, *Quercus*, *Tilia*, *Secale*, *Triticum*-type, and *Typha latifolia*. This demonstrates transport from distances even exceeding 10 km. When considering quantity, it is in the alpine zone that the highest percentages of regional sporomorphs and of sporomorphs originating from adjacent vegetation zones are recorded.

Spruce, forming dense tree stands ca 400 m from the site of collection of the samples within the alpine belt, is found in its spectra in a maximum value of 27.3%. *Pinus*, most likely, exclusively *P. mugo*, which forms a scrub directly, bordering on the alpine belt, attains a proportion of 30.6% in this zone.

Spectra from sites situated below the forest limit are clearly different from ones obtained from areas above. However, it is locally observed in the Tatra Mountains that the difference is not in the AP/NAP ratio. On the Babia Góra Mountain, the NAP sum remains within the

Table 2. Highest pollen percentages for taxa characteristic of particular belts

	Pinus	*Picea*	*Fagus*	*Sorbus*	Poaceae	Ericaceae	*Juniperus*
Lower montane belt	18.3%	**37.2%**	**34.2%**	0.5%	8.7%	0.5%	0.0%
Upper montane belt	27.8%	**57.4%**	4.2%	**13.2%**	5.9%	1.0%	0.0%
Subalpine	**56.6%**	22.0%	2.1%	0.1%	5.9%	2.8%	0.1%
Alpine	30.6%	27.3%	4.6%	0.4%	**28.4%**	**2.9%**	**1.0%**

range of 10.2–23.3% in forest belts and in the dwarf pine belt and increases to 29.9–36.2% only in the alpine belt. The forest limit, encountered twice in the row of surface samples (samples 3/4 and 11/12), shows a slightly different record. The key indicator of this limit is the rapid increase in pollen values for *Pinus*, accompanied by a similarly rapid decrease in the frequency of *Picea*. However, locally (3/4) a visible decrease is also noticed for *Sorbus* and Filicales monoletae (Fig. 8), which results from the variability of patches of montane spruce forests forming the limit. On the Babia Góra Mountain, unlike the Tatra Mountains, the dominance of fern spores is here encountered in spectra obtained for spruce forests, growing close to the forest limit. This matter requires further investigation.

Therefore, while analyzing a montane section obtained for an altitude, which was found below the forest limit in a given period of the Holocene, we may determine the time of this event. However, in order to specify how high the limit extended it is necessary to examine profiles from sufficiently high locations as well as findings of macroscopic remains of wood.

The results of studies presented here support the view that pollen spectra may provide a basis for assuming whether the sites they represent are situated above or below dense spruce stands. However, in order to interpret the historical shifts in the upper forest limit properly, it is necessary to investigate present-day sporomorph counts on particular mountain massifs. That is because there are numerous reports which have shown that mountains in Europe, depending on the size of different massifs, their aspect of exposure and the directions of dominant winds, may differ significantly in their present-day sporomorph counts. This diversification may be exemplified in the shape of the total AP and NAP curves, which, when plotted for the Babia Góra Mountain, not enable an unequivocal determination of the upper forest limit.