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A LATE GLACIAL-HOLOCENE HISTORY OF THE FORMATION OF VEGETATION BELTS IN THE TATRA MTS

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ABSTRACT. The present paper is a continuation of studies carried out by the author for many years in the Western Carpathians.

Investigations of modern pollen rain in particular vegetation belts have furnished the author with a basis for discussing the principles of the construction of pollen diagrams for the Carpathians. Studies of the history of the plant cover were conducted on seven profiles from the lakes Czarny Staw Gąsienicowy (1620 m a.s.l.), Zielony Staw Gąsienicowy (1671 m) and Kurtkowiec (1686 m); and the peat-bogs Żabie Oko (1390 m), Wyżnia Pańszczycka Młaka (1345 m), Siwe Sady (1545 m) and Molkówka (956 m).

The history presented here covers the last 13000 years. Steppe-tundra formation dominated the Tatra region in the Late Glacial. Some tree species like *Pinus sylvestris*, *P. cembra* and *Larix* sp., occurring there singly or in groups, moved deeper into the Tatra valleys in the warming phase of the Alleröd, establishing the timberline at an altitude of about 1200 m. In the stadial periods the timberline descended to the foot of the mountains or their forefield.

At the beginning of the Holocene the tree stands were dominated by *Pinus* and *Betula*, but *Picea* soon began to penetrate them. In the Boreal *Corylus* spread considerably, playing the role of a pioneer species. The non-forest associations of the subalpine and alpine belts were developing right to the end of the Boreal.
Carpinus, *Abies* and *Fagus*, among other trees, migrated there from their refugia in south-western Europe during the Atlantic. *Carpinus* entered into the composition of the submontane belt, whereas the remaining two genera invaded the valleys and slopes of the Tatras 5000 to 4500 years ago. The present system of vegetation belts had been formed by the end of the Subboreal. Changes taking place in the Subatlantic were chiefly of a quantitative nature. The oldest palynological traces of human activity occur in the Tatra forefield and date from 4100 BP. In the Tatras themselves such traces are more recent, dating from the Subatlantic. The significant impact of man upon the Tatra forests dates from the 16th century.

KEY WORDS: pollen analysis, Tatra Mts (Western Carpathians), vegetational history, Late-Glacial, Holocene

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INTRODUCTION

The Swedish botanist Wahlenberg (1814), when describing the Tatra Mts, was the first to pay attention to the zonal arrangement of the vegetation; earlier he had described plant belts in the Alps. In the Tatras he distinguished a belt of cultivated fields (equivalent to today's submontane-colline belt), a montane or beech belt (now the lower montane belt), a subalpine belt (present-day upper montane belt), a lower alpine belt (today's belt of dwarf mountain pine), an upper alpine belt (the present belt of alpine meadows) and an upper part of the alpine belt (now the belt of rocky peaks). Works published later, especially those by Kotula (1889–90) and Pawłowski (1956) gave the definitions of vegetation belts in the Tatras which are commonly accepted nowadays (Pawłowski 1972).

The possibility to reconstruct the history of the formation of these belts emerged much later, not before the turn of the century, when the method of pollen analysis was first put into practice. About 60 years have elapsed since the first palynological work carried out in the Tatras was published (Dyakowska 1932). In the meantime palynology has made considerable progress. Interdisciplinary studies have developed and made possible a more complete reconstruction of environmental changes which have occurred in the past. It is only now, however, that enough material has been collected to let us attempt the reconstruction of the course of changes which have taken place in the climate, soils and, above all, the plant cover of the Tatras over these last 13000 years.

HISTORY OF INVESTIGATIONS

The above-mentioned work by Dyakowska (1932), though carried out in the infancy of pollen analysis, when the list of determinable forms was very meagre, is valuable not only for historical reasons, but also for her perspicacity in assessing the role of particular trees and shrubs. She distinguished five phases of plant cover development in the Tatras: the pine, pine-hazel, spruce, beech-fir-spruce (or fir-spruce or fir) periods and a secondary pine period.

Koperowa's (1962) work on the Late Glacial and Holocene history of the vegetation of the Orawa-Nowy Targ Basin appeared thirty years later; additionally it dealt with a profile from the Molkówka peat-bog in the Tatras. The method of describing this profile measured up well to present-day standards and its perceptive interpretation meant that this and the remaining profiles published by Koperowa served as a basis for writing on the vegetational history of the Tatras and Carpathians for many years following (e.g. Fabijanowski 1962, Szafer 1966, Ralska-Jasiewiczowa 1972). Since the original palynological documentation had been preserved, it was possible to take a fresh look at Molkówka, using the POLPAL programme. This profile has been included in the present study as representative of the history of the forests in today's lower montane belt of the West Tatras.

In 1963 Krippel published the results of his study based on the Holocene profiles on the southern side of the Tatras. Unfortunately, he did not make full use of the possibilities which were already available to palynologists then.

Another profile come from a peat-bog called Wielka Pańszczycka Młaka (Obidowicz 1975). Its upper 5 meters, taken by means of a Russian sampler, illustrates local history, from the Atlantic onwards. Unfortunately, the lower portion, taken with a Hiller sampler, shows a high percentage of sporomorphs brought along from younger layers, which makes a precise interpretation of the beginnings of the Holocene difficult.

From among the profiles studied later, that located at Przedni Staw Lake in the Pięciu Stawów Polskich Valley (Krupiński 1984) is noteworthy; because of its particularly high regional pollen content it shows the necessity for critical treatment of the profiles of deposits accumulated in the wide open valleys of the subalpine zone.

Published accounts on further profiles provided a basis for new views on the course of fluctuations in the timberline (Obidowicz 1993, Libelt & Obidowicz 1994). An outline of the history of the plant cover in the sub-Tatra basins from the end of the Glacial onwards is also included (Jankovska 1991).

PRESENT-DAY ENVIRONMENT OF THE TATRAS

Geology and soils

The Tatras (Fig. 1) are the highest mountain group within the Carpathian range. Differences in the geological structure have created a variety of land forms making it possible to divide the Tatra massif into the High Tatras, West Tatras, Bielskie Tatras and Lower Tatras (Klimaszewski & Starkel 1972). The High Tatras are composed mainly of Carboniferous granite and the West Tatras of metamorphic rocks, gneiss and crystalline slates, also of Carboniferous age. The northern slopes of the West Tatras and the whole of the Bielskie and Lower Tatras are formed of sedimentary rocks of Mesozoic age, chiefly limestones, dolomites, sandstones and breccias. The Pleistocene glaciations left behind moraines and fluvio-glacial sediments.

The variability of the geological structure is responsible for great differentiation of soil cover in the Tatras. In the highest regions we encounter initial soils varying in skeleton thickness and in depth in the biological sense. They do not generally descend below 1250 m (Komornicki 1975). Cryogenic soils are also present in this zone above the timberline (Oleksynowa & Skiba 1977). In lower lying places different sorts of podzols and podzolic soils are dominant on a substratum of crystalline acid moraines, whereas initial, brown, and rendzinas with raw humus predominate on the calcareous substrata. In places rendzinas are accompanied by brown soils on limestone (Bednarek & Prusinkiewicz 1990). Hydrogenic soils have developed on diverse substrata as well.

Climate and plant cover

Today we are very well acquainted with the altitudinal differences in the elements of the Tatra natural environment. We have already

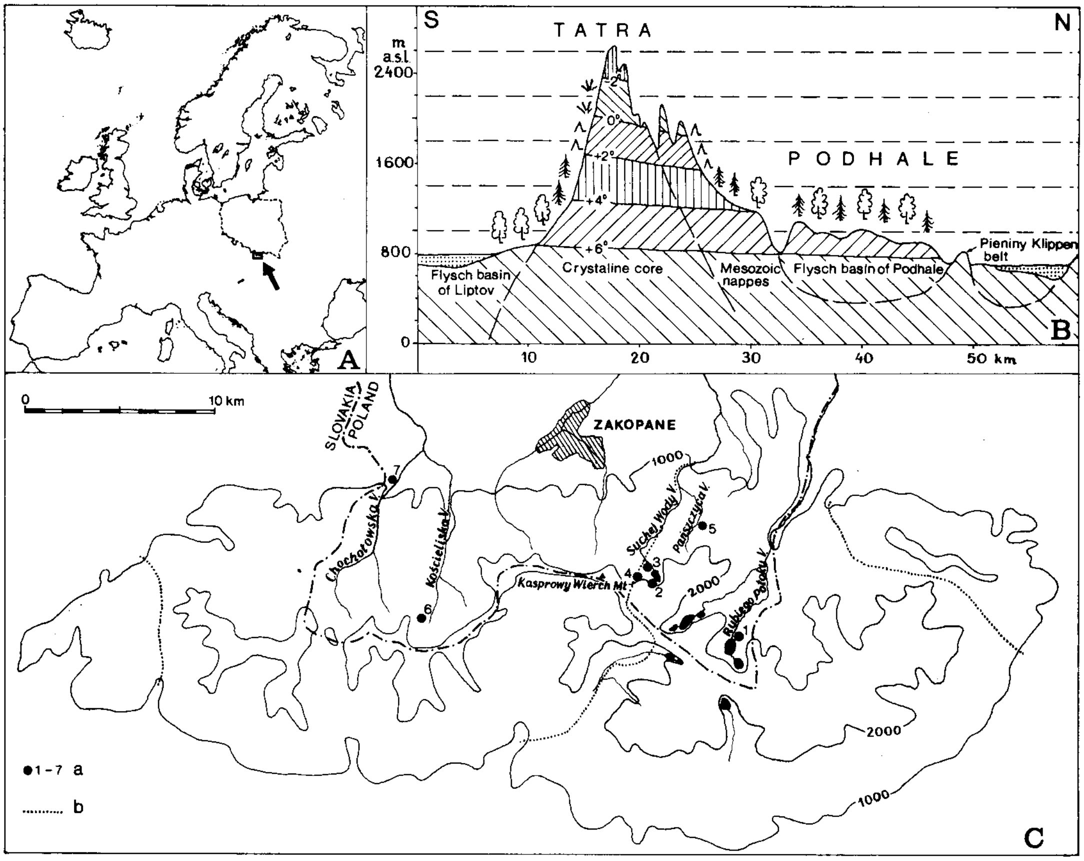

Fig. 1. A. Location of the Tatra Mountains on the map of Europe. B. Altitudinal belts of climate and vegetation in the Tatra Mountains (from Gerlach 1970). C. Geobotanical divisions of the Tatras. From left to right these are: the Siwy Wierch massif, the Western Tatras, the High Tatras, the Bielskie Tatras; a. distribution of examined sites: 1 – Żabie Oko, 2 – Czarny Staw Gąsienicowy, 3 – Kurtkowiec, 4 – Zielony Staw Gąsienicowy, 5 – Wyżnia Pańszczycka Młaka, 6 – Siwe Sady, 7 – Molkówka; b. boundaries between geobotanical subdistricts (after Mirek & Piękoś-Mirkowa 1992)

discovered the ranges of particular species, especially those of trees, shrubs and dwarf shrubs and we know which associations grow in the belts distinguished, which soils accompany them (Mirek & Piękoś-Mirkowa 1992, 1995) and how the climate changes (Hess 1965). Table 1 presents the most important items of this information.

Table 1. Natural vegetation and climatic belts in the Tatra Mts.

Altitude in m a.s.l.	Vegetation belts and important associations (after Mirek & Piękoś-Mirkowa 1992)	Climatic zones, mean annual t°, mean July t° annual rainfall, days with t°>5°C (after Hess 1965)
550–1200	lower montane belt: Abieti-Piceetum montanum, Galio-Piceetum carpaticum, Dentario glandulosae-Fagetum, Luzulo nemorosae-Fagetum	temperate cool 4°C 13°C 1400 mm 170
1200–1550	upper montane belt: Plagiothecio-Piceetum tatricum, Polysticho-Piceetum tatricum	cool 2°C 10.5°C 1600 mm 140
1550–1800	subalpine belt (=dwarf pine belt): Pinetum mughi carpaticum	very cool 0°C 8.2°C 1800 mm 100
1800–2250	alpine belt: Oreochloo distichae-Juncetum trifidi, Festuco versicoloris-Seslerietum tatrae	temperate cold -2°C 6°C 1750 mm 65 (at the lower zone boundary)
> 2250	subnival belt: Oreochloetum distichae subnivale	cold -4°C 4°C 1625 mm

POLLEN ANALYSIS IN THE MOUNTAINS

Our present-day knowledge of the size of the area from which sporomorphs in a palynological profile come (Heim 1970, Burga 1990) raises the question of what preconditions must be met for us to be able to interpret the profiles in such a relatively small group of mountains as the Tatras. For if at any spot of any vegetation belt we may expect to find sporomorphs windblown not only from the neighbouring zones but also from the forefield (Obidowicz 1993), the question arises as to whether there is a chance of a reliably reconstructing the history of the plant cover. In mountains such as the Tatras pollen analysis is stretched to its limit. If it is our aim to reconstruct the changes in the plant cover which led to the formation of the present-day vegetation belts, and to deduce the fluctuations in the timberline, we must first analyse the relationship between modern pollen rain and vegetation. We have to accumulate present-day palynological data in particular associations and vegetation belts, taking into consideration the diversity of the mountain relief. First of all it is vital to become familiar with the factors responsible for the transport of sporomorphs. Differences in the size of sporomorph production relative to altitude are of essential importance too (Lüdi 1937, Markgraf 1980). As far as the Tatras are concerned this last problem is noteworthy for the fact that in the course of the whole period of the Late Glacial-Holocene history included in this work, *Pinus sylvestris* and *P. mugo* may have been growing side by side in the West Carpathians. Morphologically the pollen of these species cannot be reliably distinguised. However, they do differ in their ecological requirements and also in the size of pollen production, which, in addition to identifiable macrofossils (cones, anatomical sections of needles), provide data enabling separate reconstructions of the histories of tree pine and dwarf mountain pain to be made. Nevertheless doubts still remain, for it is uncertain if the rate of pollen production of these species has been constant over the last 13000 years. Schneider (1984) even holds the opinion that today's pollen production of various trees cannot be applied to the past because of the impact exerted on it by climatic conditions.

Nearly fifty years ago observations were made in the lowlands on the part played by wind as a transporting agent of sporomorphs in forest, where this role is small, and in an open area, where it gains in significance (Bremówna & Sobolewska 1939). In mountains such as the Tatras, where forests, thickets of dwarf mountain pines and alpine meadows border one another, this becomes a key problem as far as the reconstruction of the history of vegetation belts is concerned. Experience acquired in investigations carried out in other mountains at various latitudes, can only be useful here to a limited degree on account of differences in the prevailing direction and force of the winds, air humidity and the extent of the massif. Thus the mean wind speed, which in the Caucasus Mts at 7–8 m/sec equals half the speed in the East Carpathians according to Kvavadze (1993), is responsible for a considerably smaller proportion of *Fagus* pollen in the surface spectra of the alpine and subnival belts of the Caucasus. In the Tatras the mean annual wind speed increases from about 2 m/sec at the foot of the mountains to more than 6 m/sec in the highest parts. The number of days with strong winds, that is at least 10 m/sec, essential for the transportation of sporomorphs, increases in the zone of the timberline so that at between 1400 and 1600 m a.s.l. it represents about a third of the year, while in the alpine belt it may even exceed 200 days (Hess 1965).

The pattern of sporomorph spread in the Tatras is complicated, as the directions of the winds are controlled by the relief forms; they blow along the valleys, basins, passes, etc. In the higher parts valley breezes blow towards the centre of the mountain mass during anticyclones in the warm season of the year (Hess 1965, Niedźwiedź 1984). Foehns too play an important role. Mountain chains extending transversely to the wind direction cause the upward movement of air masses and their undulation on the leeward side. The lowest portion of the air mass passing over the ridge rolls down the slope and deposits the sporomorphs carried by it immediately behind the ridge. These factors account for the particularly rich palynological material from long-distance transport which may occur in the alpine and subnival belts. If this phenomenon is accompanied by poor sporomorph production locally, then the AP/NAP ratio in the samples from these unwooded zones may closely approach that found for the belts of mountain forest.

Sporomorphs from particularly long distances, defined as long-distance transport proper (Bortenschlager 1970), sometimes even from 2000 km, have been recorded in the Tatras (Manecki et al. 1978). These are, however, incidental events and as such can enrich the spectra with "exotic" species but do not change the nature of the pollen zone.

The difficulties in interpretation we are faced with in the Tatras are well illustrated by the above-mentioned profile from Przedni Staw Lake in the Pięciu Stawów Polskich Valley at 1668 m, studied by Krupiński (1984). If, in its Holocene part, we analyse the course of single curves, the percentage values of maxima and the time of their occurrence, we notice a quite remarkable resemblance to the diagram for Puścizna Rękowiańska (Fig. 2) in Podhale (Obidowicz 1990). This is an example of the transfer of the Holocene pattern from the forefields of the mountains to the subalpine belt.

MATERIALS AND METHODS

Surface samples

Samples were collected along the transects marked out up the main valleys from the base to the ridge and also in all the important forest and thicket associations as well as meadow and grassland associations occupying fairly large areas. They consisted mainly of parts of cushions or carpets of mosses, more rarely the surface layer of raw humus. In the case of forest associations samples were gathered inside the stands, at their edges and in forest clearings. These last were designed to help interpret the samples from lake deposits which provide records of the periods when the water body was surrounded by forest. At least 500 pollen grains of trees and shrubs were counted in the spectra.

Lacustrine and peat-bog deposits

The study material come from the peat-bogs and lacustrine deposits listed below. The peat profiles were taken by a group of workers from the Department of Palaeobotany, W. Szafer Institute of Botany, Polish Academy of Sciences in Cracow, using a Russian sam-

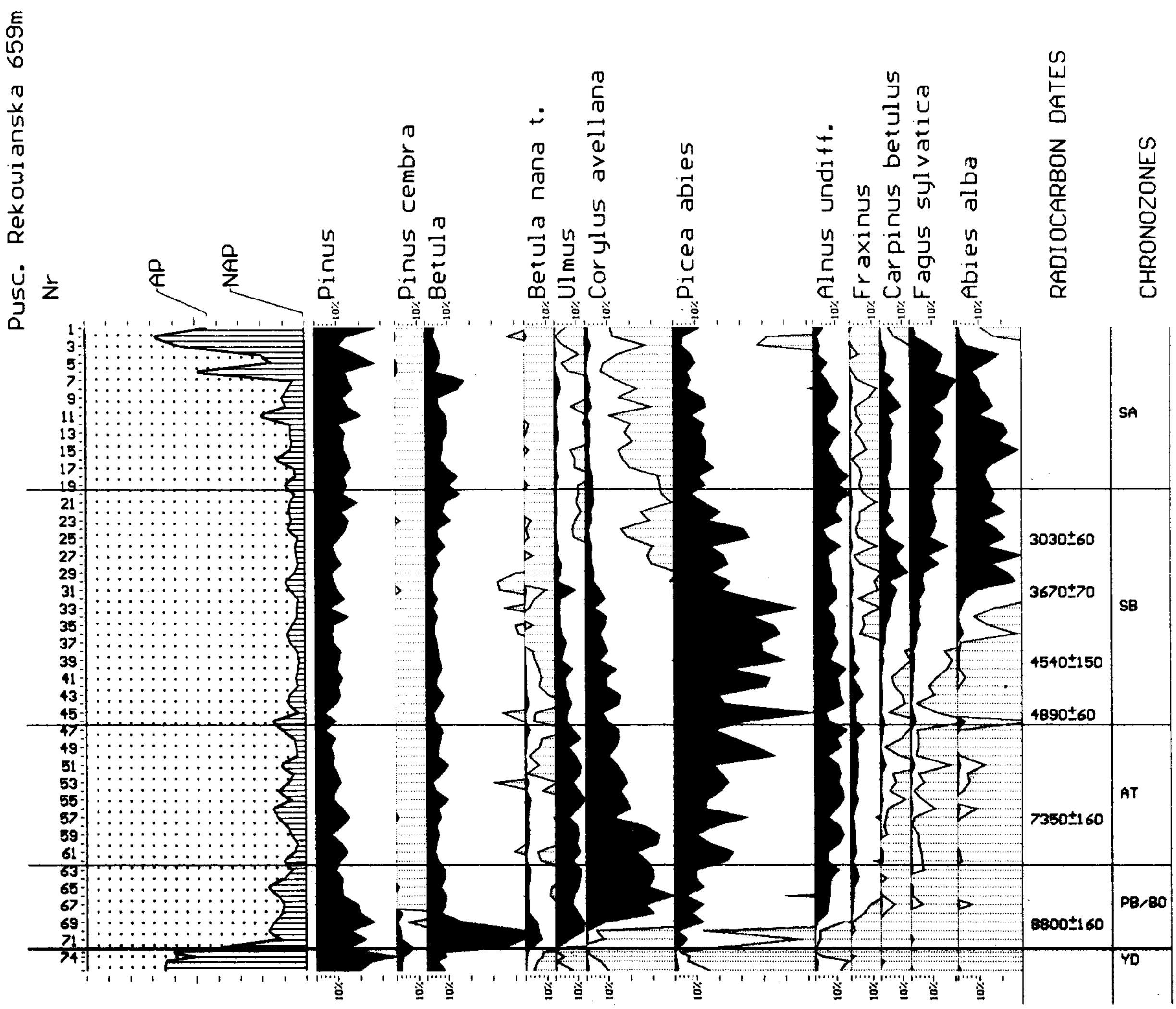

Fig. 2. Simplified percentage pollen diagram from the Puścizna Rękowiańska profile (Podhale), selected pollen taxa

pler with a chamber 80 or 100 mm in diameter. The profiles of lacustrine deposits were bored within a scheme of cooperation between the Department of Geomorphology, Institute of Geography, Polish Academy of Sciences in Cracow and Institute of Physical Geography of Uppsala University, Sweden, using a gravity corer (Baumgart-Kotarba & Kotarba 1993). Samples, 1 cm^3 in volume, were taken for palynological analysis at intervals of 2–10 cm. With *Lycopodium* tablets applied, up to at least 1000 pollen grains of trees and shrubs were counted in each spectrum. Diagrams were constructed on the principle presented on page 168.

In addition to pollen analysis the study of the peat deposits included also the determination of macrofossils: tissues, fruits, seeds, leaves and wood.

DESCRIPTION OF SITES

Żabie Oko

The site is a peat-bog situated in the Rybi Potok Valley, at an altitude of 1390 m, in the approaches to the moraines of Morskie Oko Lake. The plant cover was studied by Pawłowski, Sokołowski and Wallish (1927). They distinguished the following successional stages: Caricetum rostratae (phase with *Eriophorum angustifolium*), Caricetum fuscae or Hygronardetum (phase with *Eriophorum vaginatum*), dwarf pine association. They also described a patch, about 6 m^2 in area, with *Trichophorum alpinum*. The stratigraphy established in the profile bored in 1987 was: 0.00–0.35 m: moderately decomposed sphagnum peat (the most frequent species being *Sphagnum magellanicum*, *Drepanocladus exanulatus* and *Calliergon stramineum*); 0.35–0.50 m: poorly decomposed sphagnum peat (the most frequent species *Sphagnum magellanicum* and *Drepanocladus exanulatus*); 0.50–3.42 m: moderately decomposed moss peat (the most frequent species *Bryum pseudotriquetrum*, *Eurynchium pulchellum*, *Drepanocladus exanulatus*, *Phil-*

onotis fontana, *Ph. seriata*, *Schistidium apocarpum*, *Rhytidiadelphus squarrosus* and *Dicranum scoparium*) with thin interbeddings of fine-grained sand; 3.42–3.50 m: lamina of coarse-grained sand; 3.50–3.70 m: lightly striped grey clay; 3.70–3.80 m: coarse-grained grey sand; 3.80–3.94 m: fine-grained grey sand; 3.94–4.22 m: plant detritus; 4.22–4.50 m: grey clay; 4.50–4.66 m: ferruginous muds; 4.66–4.74 m: fine-grained sand; 4.74–4.81 m: ferruginous mud.

Wood determinations (Z. Tomczyńska, W. Szafer Institute of Botany): – 0.95–1.00 m: *Pinus cembra;* 1.35–1.40 m: *Pinus cembra*, *Pinus* sp.; 1.45–1.50 m: *Pinus sylvestris / mugo*; 2.45–2.50 m: *Pinus sylvestris / mugo*, *Picea* vel *Larix*, *Sorbus* sp.; 2.75–2.80 m: *Pinus cembra*, *Pinus* sp., *Picea* vel *Larix;* 3.05–3.10 m: *Pinus sylvestris / mugo*, *Picea abies*, *Picea* vel *Larix;* 3.40–3.45 m: *Pinus cembra*, *Pinus* sp., *Picea* vel *Larix*, *Salix* sp., *Sorbus* sp.; 3.45–3.50 m: *Picea abies*, *Picea* vel *Larix*.

Wyżnia Pańszczycka Młaka

A peat-bog, 0.9 ha in area, situated at an altitude of 1345 m in the Pańszczyca Valley, behind a lateral glacier moraine. Its present-day plant cover is composed of a mosaic of small stands, dominated by peat mosses: *Sphagnum papillosum*, *S. fallax*, *S. flexuosum*, *S. majus*, *S. magellanicum* and sporadically *S. compactum*. This mosaic is long established. Boreholes drilled at several points revealed different sequences of layers (Obidowicz 1975). The peat-bog arose as a result of the paludification of an open spruce forest and developed as a spring-water bog. A relatively short time ago parts of it entered the ombrotrophic phase. The stratigraphy of the palynologically analysed profile is: – 0.00–0.80 m: poorly decomposed sphagnum peat (mainly *Sphagnum magellanicum* and near the surface *S. compactum*); 0.80–1.00 m: poorly decomposed, extremely waterlogged cuspidatum peat (*Sphagnum cuspidatum* and *S. majus*); 1,00–2,00 m: poorly decomposed sphagnum-scheuchzeria peat (*Sphagnum cuspidatum*, *Scheuchzeria palustris* and *Carex limosa*); 2.00–3.60 m: moderately decomposed transition bog peat (*Sphagnum s. Subsecunda*, *S. palustre* and *Menyanthes trifoliata*); 3.60–3.75 m: strongly decomposed spruce peat.

Czarny Staw Gąsienicowy Lake

A lake situated at an altitude of 1620 m in the subalpine belt of the Gąsienicowa Valley. On the western, southern and eastern sides it is surrounded by rocky slopes, talus slopes and moraine ridges, above which the rocky slopes and faces of Mały Kościelec Mt., Wielki Kościelec Mt. and Żółta Turnia Mt. rise. It has an area of 17.9 ha, maximum depth of 51.0 m and possesses an outflow (Wit-Jóżwik 1974). The basin of Czarny Staw is the result of glacial overdeepening and is closed by a rocky bar transected by the Czarny Potok Stream flowing out of the lake and into the Sucha Woda Valley.

The deposit, 2.00 m thick, consists of brown-black gyttja, containing 10–30% of organic matter, with numerous mineral interbeddings. In the bottom section the organic matter content is very small (1–5%). The processes occurring on the slopes exerted an influence on the nature of the limnic sedimentation in the Late Glacial and throughout the Holocene (Baumgart-Kotarba & Kotarba 1993).

Zielony Staw Gąsienicowy Lake

A lake situated at an altitude of 1671 m in the subalpine belt in the Gąsienicowa Valley. It is 3.8 ha in area, and has a maximum depth of 15.1 m (Wit-Jóżwik 1974). On the southern side it is bounded by the rock walls of Żółta Turnia Mt., which are partly cut off from the lake basin by a moraine rampart. The basin of Zielony Staw is deep in the centre but a platform extending inwards from the shore creates a wide rim where the water is several meters shallower. Owing to this geomorphological situation only finest material reach the central part and there are no discontinuities in the deposits resulting from erosion (Baumgart-Kotarba et al. 1990, Baumgart-Kotarba & Kotarba 1993).

The lacustrine deposit is 2.35 m thick.

Kurtkowiec Lake

A lake situated at an altitude of 1686 m in the subalpine belt of the Gąsienicowa Valley. It is 1.53 ha in area and its maximum depth is 4.8 m (Wit-Jóżwik 1974).

The lacustrine deposit is 1.60 m thick.

Siwe Sady

This site is located at an altitude of 1545 m in the corrie of the Pyszniańska Valley in the upper part of the Kościeliska Valley. The profile, reaching 5.0 m in depth, is described in detail in a work by Libelt and Obidowicz (1994). Only a 0.7 m section of strongly compressed peat was analysed palynologically and divided as follows: 0.00–0.10 m: strongly decomposed sedge peat, 0.10–0.55 m: moderately decomposed moss peat, 0.55–0.70 m: strongly decomposed spruce peat.

Molkówka

A clearing extending from 945 to 990 m a.s.l. at the mouth of the Chochołowska Valley. The peat-bog occurring there was analysed palynologically by Dyakowska (1932) and next by Koperowa (1962). The latter paper contains a detailed description of the sediment, consisting of 5.0 m of peat and 0.35 m of underlying clay. The author's original documentation (110 samples) has been used for the purposes of the present publication and described by means of the POLPAL programme according to the rules adopted for the other profiles.

ANALYSIS OF SURFACE SAMPLES

Studies on the modern pollen rain have been carried out all over the world for many years, but the results, even if they come from mountains, cannot literally be transferred to any other mountain massif. It is, therefore, necessary to perform an analysis of modern pollen deposition in the Tatras in order to provide answers to several questions, namely, what do the pollen spectra of the most important plant associations characteristic of particular belts look like; is it possible to define the timberline using palynological methods; and how does the pattern of air currents in the sampling region influence the presence of regional sporomorphs.

The results of these studies have already been partly published (Obidowicz 1993, Libelt & Obidowicz 1994). The essential conclusions following from them will be discussed using the analysis of the transect Sucha Woda Valley – Hala Gąsienicowa – Sucha Stawiańska Valley – Kasprowy Wierch Mt. (Fig. 3) and the percentage data compiled in Table 2. In addition to the features which characterize particular vegetation belts, this table gives the proportion of cereal pollen, providing a measure of the extent of transportation of sporomorphs from the forefield of the mountains. The modern pollen rain analysis carried out by Stuchlik and Kvavadze (1995) gave similar results to those showed in Table 2.

The transect presented shows fairly clearly the relationship between modern pollen rain and present-day vegetation. The difference between the part of the transect in the mountain forest zone and its subalpine and alpine parts is very distinct. In the first part the proportion of tree and shrub pollen (AP) exceeds 70%. Even in a clearing or in open spruce forest (samples Nos 9 and 10) this proportion changes only slightly, being there complemented by pollen of *Alnus* and *Fagus*, no doubt blown from the nearby Olczyska Valley. On the other hand, the percentage of *Picea* pollen drops to about 40%, whereas in a close spruce stand it may sometimes reach 75% or more of the total (Tab. 2). Above the timberline the proportion of spruce pollen falls rapidly, accompanied by a rise in the total for herba-

Table 2. Pollen percentages for taxa characteristic of particular belts

Alpine belt	AP	37.1–72.8%
	NAP	**27.2–62.9%**
	Pinus	10.2–31.2%
	Picea	8.1–18.3%
	Abies	0.1–1.4%
	Fagus	1.0–3.3%
	Cereals	0.3–1.9%
Subalpine belt (=dwarf pine belt)	AP	46.6–79.3%
	NAP	**20.7–53.4%**
	Pinus	**23.2–48.8%**
	Picea	9.6–26.2%
	Abies	0.1–2.3%
	Fagus	0.6–3.9%
	Cereals	0.7–1.7%
Upper montane belt	**AP**	**71.9–91.5%**
	NAP	8.5–28.1%
	Pinus	3.9–20.3%
	Picea	**42.0–75.2%**
	Abies	0.2–2.1%
	Fagus	0.6–9.8%
	Cereals	0.2–1.0%
Lower montane belt	**AP**	**73.4–87.4%**
	NAP	12.6–26.6%
	Pinus	12.6–25.8%
	Picea	**14.7–40.5%**
	Abies	**0.8–3.7%**
	Fagus	**4.7–34.7%**
	Cereals	0.6–1.4%

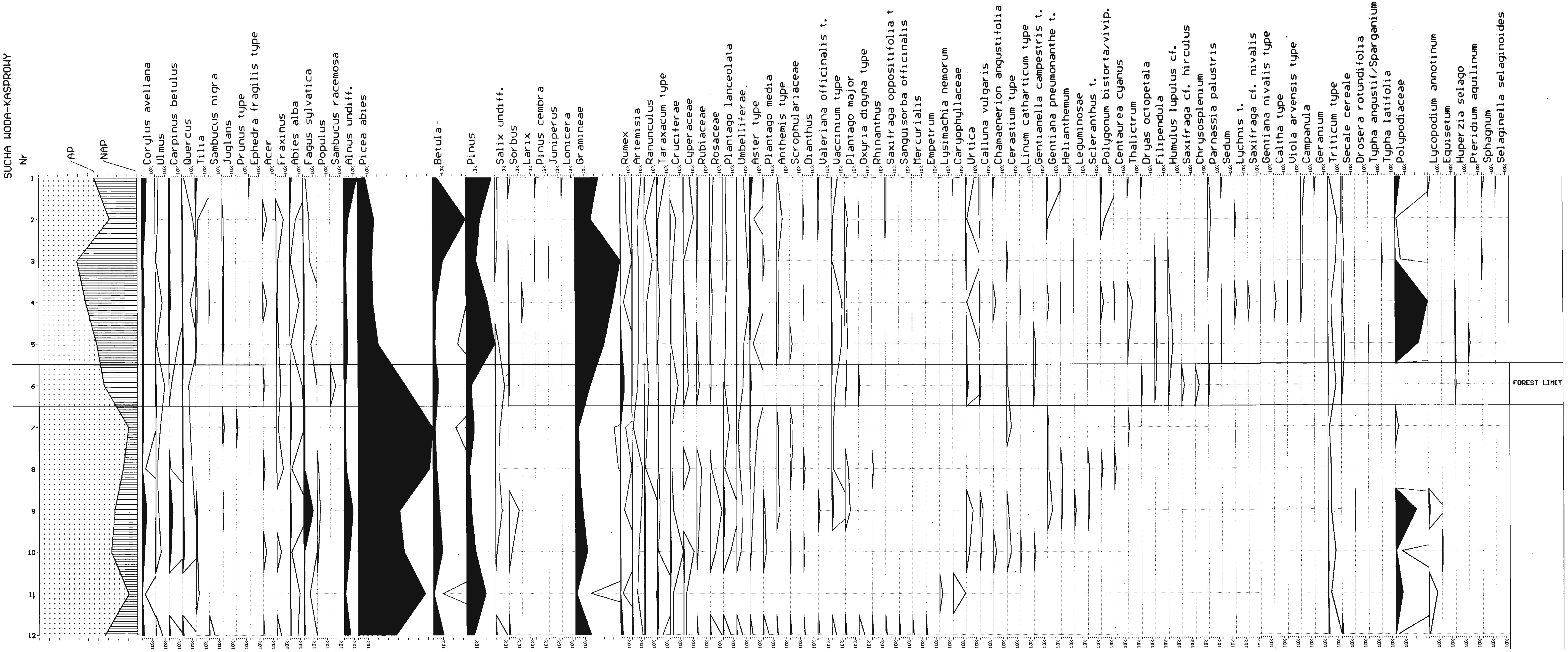

Fig. 3. Pollen diagram of surface samples taken from the longitudinal profile of Sucha Woda Valley – Kasprowy Mt

ceous plants (NAP), mainly because of Gramineae pollen.

The distinct increase in the proportion of *Rumex* in sample No 6 has been caused by a dense network of waymarked tracks and the proximity of the mountain shelter on Hala Gąsienicowa.

The boundary values of the proportions of individual components of contemporary spectra in neighbouring vegetation belts (Tab. 2) sometimes approach each other or even overlap. This creates a problem regarding the palynological definitions of these belts so that they can be related to pollen assemblage zones (PAZ).

The palynological determination of the timberline, which in the Tatras is the upper border of the spruce forest, is not possible on the basis of just one element of the spectrum, e.g. the AP/NAP ratio. The percentages of AP in the zone of the timberline exceeds 70%. A rise in this value increases the certainty that the sample has come from inside the forest. Above the timberline the AP values clearly dwindles, even falling below 40% in the alpine belt. Additionally, the list of herbaceous plants lengthens. And yet in this belt some spectra occur loaded with a considerable amount of regional pollen so that their AP values may also exceed 70%.

Another factor that should be taken into account is that the proportion of *Picea* should not fall below 50%. If, with the AP values exceeding 70%, the proportion of *Picea* lies between 40 and 50%, it is certain that the sample has come from a clearing in a spruce forest. Above the timberline the percentage value of *Picea* pollen in the spectra falls rapidly to little more than 10% and in some samples to below 10%.

In the subalpine (dwarf mountain pine) belt the proportion of *Pinus* pollen generally does not exceed 30% (Fig. 3). In the West Tatras, however, some spectra occur in which it even exceeds 50% (Libelt & Obidowicz 1994). This may be connected with the presence of *Pinus sylvestris* stands in this part of the Tatras. Sometimes the AP values in this belt falls below 50%, because even a dense scrub of dwarf mountain pine does not constitute such an effective umbrella against pollen rain as does a close spruce forest. Unfortunately, a comparison with the Alps is not always possible because of differences in the methods of counting the spectra. However, in the surface spectra of the subalpine belt in Karwendeltal (Kral 1988) the totals of both AP and *Pinus* pollen are much higher than in the Tatras.

The relatively good correlations between particular belts and their pollen spectra, as has been mentioned above, are somewhat distorted in the alpine belt (Fig. 3, samples 1–3). High values of *Betula* and *Alnus* pollen occur here; *Quercus*, *Tilia*, *Carpinus* and *Corylus* pollen grains are present as is some pollen of trees growing in the lower belts.

The transect under discussion occurs in a part of the Tatras where the typical mixed mountain forest belt with beech, fir-beech and fir-spruce forest is missing. The surface samples collected in these associations also show a high AP proportion, exceeding 85% of the total, the role of *Fagus* and *Abies* being considerably greater than in the remaining belts. In the Dentario glandulosae-Fagetum association beech forms more than 30% of the pollen spectra. The level of *Picea* in the spectra from mixed mountain forest is lower than that characteristic of spruce mountain forest (Tab. 2).

In spite of the fairly large number of surface samples analysed, the result patterns, especially those characterizing the timberline, are not conclusive and will need to be applied with caution.

Examination of the sample similarity matrix (see Walanus & Nalepka in print) for comparing the present-day and subfossil spectra makes it possible to identify the period of the Holocene when plant communities similar to or even identical with today's began to emerge (see page 201).

Attempts to compare the plant communities which appeared in the Holocene with present-day syntaxonomic units may be regarded as misguided. Criticisms have been expressed concerning this practice (Janssen 1970, Janssen & Birks 1994). If however, the forests of the Atlantic period dominated e.g, by *Alnus,* are to be compared with today's Alnetum incanae, this must be done on the basis of their lists of taxa being comparable, and also to a certain degree on the presence of similar proportion of pollen in the Atlantic pollen spectra and modern pollen rain in stands of Carpathian alder woods. Such an approach can be validated, in the case of some forest communities, by a comparative numerical analysis of the profiles and surface samples. The statement that, from a certain moment onwards, the Holocene thickets colonizing Carpathian valleys were of the Alnetum incanae type means that, at the very least those thickets may have given rise to the actual association Alnetum incanae.

CONSTRUCTION OF POLLEN DIAGRAMS

Taking into consideration the circumstances responsible for the possible distortion of the palynological profiles in the mountains by considerable amounts of regional pollen, we had to construct diagrams so that the regional influences could be eliminated or at least minimized. As a result of the first series of surface pollen spectra investigations (Obidowicz 1993) it seemed justified when constructing diagrams, to exclude from the total pollen sum (AP+NAP) not only cryptogam spores and grains of aquatic plants but also those which do not now grow above the submontane belt. The percentages of taxa of long-distance transport origin were calculated on the basis of the total sum (AP+NAP) + the pollen sum of the "regional" plants. The percentage calculations of taxa within the group of aquatic plants and cryptogam spores are based on the sporomorphs total (AP+NAP+aquatic+spores). All calculations were made using the POLPAL program (see Walanus & Nalepka 1996).

The group of plants treated as "regional" also includes taxa which do cross the boundary into the lower montane belt at particular places but whose range lies principally outside the mountains. And so pollen of *Quercus*, *Tilia*, *Carpinus*, *Corylus*, *Ulmus*, *Evonymus*, *Sambucus nigra*, *Hedera*, *Cornus sanguinea* and cereals were excluded from the total pollen sum. Some of these decisions call for more detailed justification.

Of the *Ulmus* species, *U. montana* does occur in the lower montane belt in the Tatras but, according to Pawłowski (1956), very rarely. It is connected with the association Phyllitido-Aceretum (Myczkowski & Lesiński 1974), although its stands have also been recorded from Alnetum incanae (Krzaklewski 1974). It is more frequent in the Bielskie Tatras (Radwańska-Paryska 1975). In Podhale, beginning from the phase with *Ulmus* (8800–8570 BP) through to the decline of the Atlantic period, *Ulmus campestris*, now common in the Carpathians, but may also have occurred in lower situations in various associations of broad-leaved forests growing there at that time (Obidowicz 1990). During this part of the Holocene the inclusion of *Ulmus* pollen grains in the pollen sum might distort the record of events in the Tatras themselves.

It is not easy to justify leaving *Corylus avellana* out of the pollen sum. Nowadays this shrub, according to Radwańska-Paryska (1995), is abundant in the Bielskie Tatras and in the Siwy Wierch range (in Slovakian territory), but apart from that it occurs rarely, mainly in Podhale. Myczkowski (1975) included it together with e.g. *Cornus sanguinea*, *Evonymus europaeus*, *E. verrucosus*, *Rhamnus frangula* and *Rh. cathartica* among the lowland species which avoid the Tatras. Neither have any of the shrubs mentioned above been included in the up-to-date list of important species growing in the Tatras (Mirek & Piękoś-Mirkowa 1995). The problem of *Corylus avellana* wil be discussed on pages 187–189.

In the opinion of early botanists, among them Kotula (Radwańska-Paryska 1975), *Fraxinus* must be ragarded as a tree wchich does not occur in the Tatras and all its sites in the Sub-Tatras are the result of planting. According to Myczkowski and Lesiński (1974), *Fraxinus* is scarce in the Tatras but may be found in the association Phyllitido-Aceretum. The practice of planting *Fraxinus* in quantity near houses in the Sub-Tatras, carried out from time immemorial, makes self-sowing possible in the lower montane belt. Radwańska-Paryska (1975) dispels these doubts. She claims that the ash is a tree "which certainly grew in abundance in the mixed mountain forest belt in old times but has been nearly utterly destroyed for its valuable wood". For this reason *Fraxinus* has been included in the total pollen sum.

Alnus is included too because of the essential role Alnetum incanae still plays in the Tatra valleys today. In the profile of the Kurtkowiec deposits it is, on average, twice as abundant as in other profiles from the Gąsienicowa Valley. A number of other features of the diagram from Kurtkowiec indicate a heavy presence of "regional" sporomorphs. In spite of this the pollen sum as a basis for calculations was not additionally corrected.

DESCRIPTION OF THE POLLEN ASSEMBLAGE ZONES (PAZ)

ZIELONY STAW GĄSIENICOWY
(Fig. 4)

ZS-1, *Pinus-Pinus cembra-Artemisia* PAZ (samples 43–47)

The AP values lie in the range 59.4–76.2% and *Pinus sylvestris/mugo* (max. 62.4%) is its main component; *Pinus cembra* reaches its maximum here (4.8%), while *Juniperus*, whose curve approaches 2%, is confined to this zone only. Single pollen grains of *Ephedra fragilis*-t., *E. distachya* and *Alnus viridis* are present.

For the NAP, the highest proportions are taken up by Gramineae (up to 12.5%), *Artemisia* (up to 5.6%), Chenopodiaceae (up to 3.2%) and Cyperaceae (up to 28.0%). *Taraxacum*-t., Rubiaceae, *Filipendula* and *Sedum* attain their highest frequencies in this zone.

Upper boundary: decrease in pollen of *Pinus sylvestris/mugo*, Gramineae, *Artemisia* and Chenopodiaceae, rise of *Betula* and the beginning of the ascending curve of *Picea*.

The ranges of the absolute concentrations of pollen, given to the nearest 100 grains/cm^3 for the AP and NAP are 31300–205100/cm^3 and 12400–140100/cm^3 respectively.

ZS-2, *Pinus-Betula* PAZ (samples 41–42)

The AP values exceed 80%; *Pinus sylvestris/mugo* is gradually reduced; *Betula* and *Betula nana*-t. (25.8 and 7.9%, respectively) have their maxima here; the *Pinus cembra* curve comes to an end, while the curves of *Picea* and *Ulmus* begin.

The zone has been dated ^{14}C at 10040±150 years BP (Ua-1446) (Jonasson 1991).

Upper boundary: decrease in *Betula* pollen, rise in Cyperaceae.

Pollen concentration: AP 268900–429400/cm^3, NAP 56300–61900/cm^3.

ZS-3, *Pinus*-Cyperaceae PAZ (samples 35–40)

The AP values fall drastically to a level of 52.0–61.5%, mainly because of a fall in *Pinus sylvestris/mugo* pollen; the proportions of *Betula* and *Betula nana*-t. are reduced to about a quarter of their values in the preceding zone. The ascending *Picea* curve exceeds 18% towards the end of the zone, whereas *Alnus* increases to more than 8% in sample No 37. Soon after the appearance of its continuous curve, *Corylus* reaches an absolute maximum (35.3%); the continuous curves of *Tilia*, *Quercus* and *Fraxinus* begin.

From among the NAP Cyperaceae reach their absolute maximum here; the continuous curve of Ericaceae begins.

A stoma of *Pinus* sp. occurs in sample No 39.

Upper boundary: increase in the AP values, fall in Cyperaceae.

Pollen concentration: AP 186300–460800/cm^3, NAP 149900–301600/cm^3.

ZS-4, *Pinus-Picea* PAZ (samples 26–34)

The AP values increase from 70.4% to 90.9%; *Pinus sylvestris/mugo* comes near to 40% in its final maximum; the steeply rising *Picea* curve exceeds 30% and the *Alnus* curve oscillates about its mean of 16%. *Corylus* remains at about 25%, whereas the maximum of *Ulmus* approaches 15%.

The NAP values fall rapidly, even below 10% as a result of a decrease in the proportion of Cyperaceae, which, however, are still dominant. *Typha latifolia* is present at the beginning of the zone.

The lowest part of the zone has been ^{14}C dated at 7000±380 years BP (Gd-4631) (Jonasson 1991).

Upper boundary: rise in *Picea*.

Pollen concentration: AP 121000–233300/cm^3, NAP 13800–81200/cm^3.

ZS-5, *Picea* PAZ (samples 13–25)

The percentages of AP lie between 81.7–95.4%. *Picea* with a maximum of 50.0% is the definite dominant. *Pinus* falls to about 20%, whereas the proportion of *Alnus* becomes stable at a level above 16%; the continuous curve of *Fagus* has its beginning halfway through the zone and so does the *Abies* curve although it is somewhat higher; the *Corylus* curve falls definitively. *Quercus* reaches its absolute maximum (6.2%) and the values of *Carpinus* pollen approach 7%.

A drop in the NAP below 10% is accounted for by a fall in Cyperaceae pollen, which is reduced to a proportion of merely 1–2%. The proportion of Filicales monoletae shows a large increase in this zone.

The lowest part of the zone has been dated at 4710±600 years BP (Gd-4629) and the middle part at 3730±350 years BP (Gd-4630) (Jonasson 1991).

Upper boundary: decrease in *Picea*, rise in *Abies*.

Pollen concentration: AP 74100–835200/cm^3; NAP 6400–45900/cm^3.

ZS-6, *Picea-Abies-Fagus* PAZ (samples 8–12)

The AP values remain within the limits 88.9–92.8%. The proportion of *Picea* falls rapidly but is still above 20%. Both *Abies* and *Fagus* approach 15%. *Carpinus* attains its highest values (about 10%) and the *Tilia* curve shows a discontinuity.

The boundary between zones ZS-6 and ZS-7 has been ^{14}C dated at 1760±180 years BP (Gd-4407) (Jonasson 1991).

Upper boundary: further fall in *Picea*.

Pollen concentration: AP 120600–397200/cm^3, NAP 9400–35600/cm^3.

ZS-7, *Pinus-Abies-Fagus* PAZ (samples 1–7)

The AP values fall to between 87.7–94.2%. The contribution of *Picea* pollen decreases to about a third of its highest percentages, whereas *Pinus* oscillates either side of 20%. In this zone *Abies* has its absolute maximum (25.3%) and the *Fagus* curve remains above 11%. *Alnus* still shows no essential change, while *Betula* increases slightly, approaching 10%.

The first pollen grain of *Triticum*-type appears in the top sample.

Pollen concentration: AP 109000–466500/cm^3, NAP 11800–33300/cm^3.

CZARNY STAW GĄSIENICOWY

(Fig. 5)

CzS-1, *Pinus*-Cyperaceae-*Betula nana* PAZ (samples 44–46)

The AP values fall rapidly from 82.1% in sample No 46 to somewhat above 50% in the succeding samples, mainly because of changes in the proportion of *Pinus sylvestris / mugo* pollen. The pollen values of *Betula nana*-t. approaches 7%.

With regard to the NAP, Cyperaceae reach their maximum, exceeding 35%; *Dryas octopetala*, *Helianthemum*, *Polygonum bistorta*-t., *Saxifraga oppositifolia*-t., etc. are present.

The zone has been ^{14}C dated at 12550±420 years BP (Gd-4540) (Baumgart-Kotarba & Kotarba 1993, 1994)

Upper boundary: rise in *Pinus sylvestris / mugo*, decrease in Cyperaceae.

Pollen concentration: AP 72700–126700/cm^3, NAP 14700–108600/cm^3.

CzS-2, *Pinus* PAZ (samples 41–43)

The AP curve rises above 80%, consisting mainly of *Pinus sylvestris / mugo* pollen whose maximum exceeds 70%. Initially *Betula* cf. *nana* still forms about 5%; later, however, its role shrinks considerably.

There are no significant changes in the taxonomic composition of the NAP; its total does not rise above 20%, whereas a quantitative drop, particularly drastic in the case of Cyperaceae, can be observed.

Upper boundary: decrease in *Pinus sylvestris / mugo*.

Pollen concentration: AP 97600–304300/cm^3, NAP 25500–47400/cm^3.

CzS-3, *Pinus-Pinus cembra-Artemisia* PAZ (samples 33–40)

The AP value averages somewhat above 70%, mainly due to the regress of *Pinus sylvestris / mugo*; maximum values are here attained by pollen of *Pinus cembra* (above 6%) and *Juniperus* (about 4%); *Salix* pollen forms 1%, *Betula nana*-t. more than 4%, while *Ephedra distachya*-t. is represented by a continuous curve and there are single pollen grains of *Ephedra fragilis*-t. and *Alnus viridis*.

Concerning the NAP, *Artemisia* shows a constant upward tendency and rises to above 12% at its maximum; Gramineae and Chenopodiaceae also have their highest values here, while *Dryas octopetala*, *Gypsophila muralis*, *Gentiana pneumonanthe*-t and *Sedum* are represented by single pollen grains.

Upper boundary: fall in Gramineae, *Artemisia* and Chenopodiaceae and further fall in *Pinus sylvestris / mugo*; rise in Cyperaceae.

Pollen concentration: AP 32700–277600/cm^3, NAP 11600–92900/cm^3.

Sample No 32 is palynologically void.

CzS-4, *Pinus*-Cyperaceae PAZ (samples 24–31)

Pinus sylvestris / mugo pollen falls to a mean value of about 35%, but it still dominates in the AP; *Betula* reaches a maximum of 19.1% in this zone and the *Betula nana*-t. again increases its values to attain 7.0% in a further maximum. The *Pinus cembra* curve comes to an end and *Larix* is represented by its last single pollen grains; the *Ulmus* curve begins and rapidly rises to nearly 8.0%; the beginning of the continuous curves of *Picea* and *Alnus* as well as *Quercus*, *Fraxinus* and *Tilia* occurs.

Cyperaceae, with a maximum of about 50%, definitively prevails in the NAP; the first pollen grain of *Hedera helix* occurs in the sample

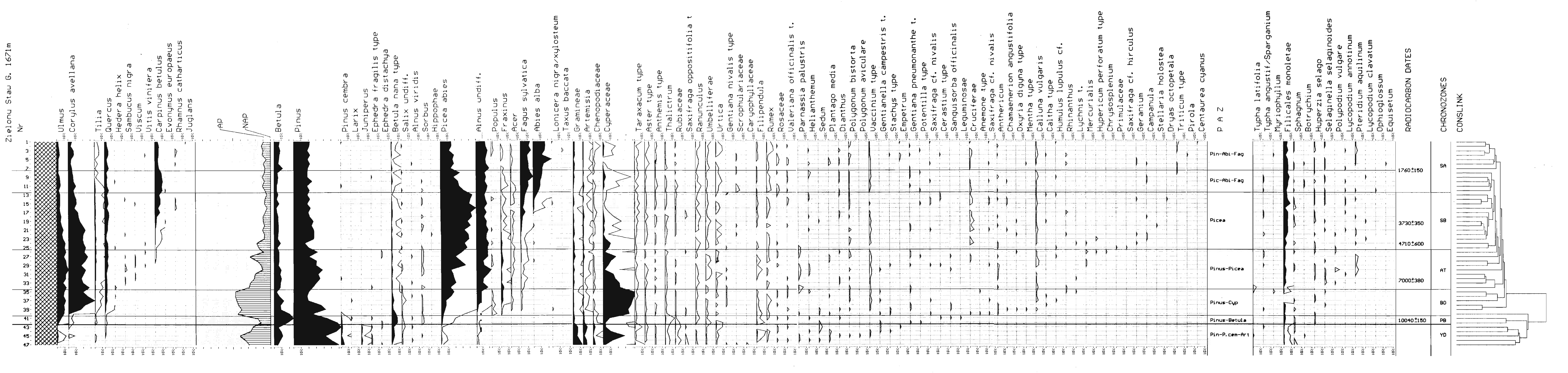

Fig. 4. Percentage pollen diagram from Zielony Staw Gąsienicowy

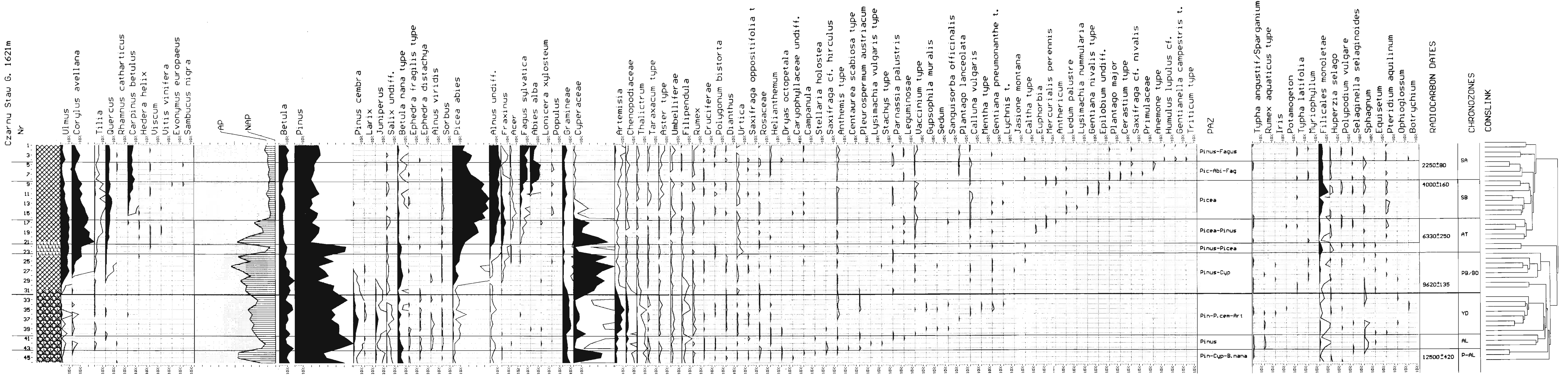

Fig. 5. Percentage pollen diagram from Czarny Staw Gąsienicowy

bordering the next zone; pollen of *Typha latifolia* and *Myriophyllum* appears.

The lowest part of the zone has been ^{14}C dated at 9620±135 years BP (Ua-1445) (Baumgart-Kotarba & Kotarba 1993).

Upper boundary: rise in *Pinus sylvestris/mugo* pollen, fall in Cyperaceae.

The zone is characterized by an exceedingly high pollen concentration: 104600–909600/cm^3 for the AP and 60700–675100/cm^3 for the NAP.

CzS-5, *Pinus-Picea* PAZ (samples 22–23)

Pinus sylvestris/mugo exceeds 60%, *Picea* 10% and *Betula nana*-t. 5% of the total. *Alnus*, *Fraxinus*, *Ulmus*, *Corylus*, *Quercus* and *Tilia* retain their levels from the preceding zone. A single pollen grain of *Ephedra distachya*-t. is present; *Viscum* appears.

As regards the NAP, Cyperaceae decreases to about 2% and Filicales monoletae have their first maximum here.

Upper boundary: fall in pollen values of *Pinus sylvestris/mugo* and *Betula nana*-t.; increase in *Picea*, *Alnus* and Cyperaceae.

Pollen concentration of the AP falls to about 50000/cm^3 and in the case of the NAP even more to about 7000/cm^3.

CzS-6, *Picea-Pinus* PAZ (samples 17–21)

The oscillating AP shows an upward tendency and reaches more than 80%. The proportion of *Picea* pollen rises rapidly, approaching 40%; *Pinus sylvestris/mugo* remains at about 30% and *Betula nana*-t. below 2%. *Alnus* increases gradually to above 11%, *Hedera helix* and *Viscum* occur in several horizons. The continuous *Fagus* curve begins in this zone.

The NAP total again shows a high proportion of Cyperaceae, which reaches 44.5% in its final maximum and then drifts downwards.

The lowest part of the zone has been ^{14}C dated at 6330±250 years BP (Gd-4628).

Upper boundary: further rise in *Picea* and marked fall in Cyperaceae.

Pollen concentration: AP 311100–661600/cm^3, NAP 55700–566100/cm^3.

CzS-7, *Picea* PAZ (samples 9–16)

The percentages of AP oscillate about a 90% mean. *Picea* is absolutely dominant with its values above 40% and a maximum of 48.9%. *Alnus* exceeds 15%, the continuous curves of *Abies* and *Carpinus* begin, while *Corylus* and *Ulmus* show a constant downward tendency.

A rise in the Ericaceae total (Ericaceae undiff., *Calluna*, *Ledum*) and a slight but perceptible increase in Gramineae take place in the NAP values. A 2.5–9.3% curve representing Filicales monoletae begins.

The final maximum in pollen values of *Picea* has been ^{14}C dated at 4000±160 years BP (Gd-4656) (Baumgart-Kotarba & Kotarba 1993).

Upper boundary: fall in *Picea*, rise in *Abies* and *Fagus*.

Pollen concentration: AP 244700–669100/cm^3, NAP 19100–41200/cm^3.

CzS-8, *Picea-Abies-Fagus* PAZ (samples 5–8)

Picea is retreating quickly but does not fall below 20% until the sample bordering the next zone. *Abies* and *Fagus* soon pass the 10% threshold, *Abies* reaching a maximum of 13%. The curve of *Alnus* undergoes no changes. At the start of the zone *Carpinus* exceeds 8%.

The continuous curve for *Plantago lanceolata* begins.

The top part of the zone has been ^{14}C dated at 2250±80 years BP (Gd-4928) (Baumgart-Kotarba & Kotarba 1993).

Upper boundary: decrease in *Abies*.

Pollen concentration: AP 444300–772000/cm^3, NAP 30900–75000/cm^3.

CzS-9, *Pinus-Fagus* PAZ (samples 1–4)

The AP total falls slightly below 90%. *Picea* and *Abies* distinctly lose significance; *Fagus* still averages above 10%, and *Pinus sylvestris/mugo* above 30%.

The first pollen grain of *Triticum*-t appears.

Pollen concentration: AP 328300–558400/cm^3, NAP 35700–60600/cm^3.

KURTKOWIEC
(Fig. 6)

Ku-1, *Pinus-Thalictrum* PAZ (samples 31–32)

The AP values somewhat exceed 70%, of which more than 20% falls to *Pinus sylvestris/mugo*; *Picea* is still below 15% but has an upward tendency. *Alnus* approaches 30%, *Betula* exceeds 15% and *Fagus* begins its continuous curve. *Ulmus* exceeds 14%, whereas *Corylus* reaches 44.6% in sample No 32, which is the highest proportion in all the Tatra Mts profiles.

As to the NAP, *Thalictrum* forms 2.5%.

Upper boundary: ascent of the curves of *Alnus* and *Picea*, fall in *Betula* and *Thalictrum* pollen values.

Pollen concentration: AP 7500–10800/cm^3, NAP 1500–2900/cm^3.

Ku-2, *Pinus-Picea* PAZ (samples 26–30)

The AP total reaches or even exceeds 80%. *Pinus sylvestris/mugo* approaches 30%, whereas *Picea*, showing a stable upward tendency, exceeds 20%; the *Betula* value drops below 10%, *Corylus* pollen decreases gradually but remains above 30%; *Ulmus* has its maximum here (15.6%); the *Alnus* pollen value averages about 30% and, at a maximum attains its peak for all the Tatra profiles (36.4%).

A single pollen grain of *Armeria* occurs in this zone.

Upper boundary: rise in the proportion of *Picea*.

Pollen concentration: AP 6100–14000/cm^3, NAP 1100–1900/cm^3.

Ku-3, *Picea* PAZ (samples 16–25)

The AP total gradually approaches 90%. *Picea* has its maximum values here, expressed by two peaks: 34.8% in sample No 23 and 35.4% in sample No 18 (converted to percentages of the total pollen sum AP+NAP after removing the *Alnus* value, these become 47.5% and 47.4%); *Corylus* decreases consistently from about 30% to below 10%; the continuous curve of *Carpinus* begins to ascend and in the uppermost sample attains a maximum (12.3%). The proportion of *Fagus* gradually increases and the *Abies* curve appears.

Single pollen grains of *Vitis* appear in several samples and a grain of *Juglans* occurs at the top of the zone.

Upper boundary: fall in *Picea* and an increase in the *Pinus sylvestris/mugo*, *Abies* and *Fagus* pollen values.

Pollen concentration: AP 8900–18400/cm^3, NAP 1100–2900/cm^3.

Ku-4, *Pinus-Abies-Fagus* PAZ (samples 9–15)

The proportion of *Picea* pollen falls to half of its value in the preceding zone, though the spruce stomata are still present. The mean *Pinus* pollen value rises again to above 30%; *Abies* soon exceeds 10% and attains 18.5% in a maximum. At the beginning of the zone *Fagus* reaches 18%, later it oscillates about a mean of 15%. *Betula* shows a distinct regression, its curve descending far below 10%.

In this zone the continuous curve of *Plantago lanceolata* has its beginning and Filicales monoletae their maximum.

Upper boundary: fall in *Pinus* pollen.

Pollen concentration: AP 10500–30800/cm^3, NAP (870) 1110–2700/cm^3.

Ku-5, *Abies-Fagus* PAZ (samples 1–8)

The AP total diminishes to its mean value of 80%. The *Pinus sylvestris/mugo* curve loses half of its previous value; *Abies* averages 14% and *Fagus* above 15%. In its course the *Alnus* curve has two maxima of about 25%.

The first pollen grain of *Triticum*-t. appears.

Pollen concentration: AP 9100–27600/cm^3, NAP 1700–2600/cm^3.

ŻABIE OKO

(Fig. 7)

ZO-1, *Pinus-P. cembra*-Cyperaceae PAZ (samples 44–49)

The NAP values oscillate about a mean of 35%, with two peaks: 43.9% and 47.1%. It consists chiefly of pollen of Gramineae, *Artemisia* and Cyperaceae which attain their greatest concentration here (above 110000/cm^3).

As regards the AP, *Pinus sylvestris/mugo* maintains about 45%, with a maximum of 54.5% and a rapidly increasing concentration; *Pinus cembra* exhibits two peaks: 10.7 and 11.0% and its greatest concentration (above 30000/cm^3). *Betula* has its maximum (11.9%) and *Betula nana*-t. averages 2.0% with a 3.7% maximum. *Juniperus* is represented by a continuous curve with a maximum of 1.0% and the *Larix* pollen value is below 1.0%.

Upper boundary: rise in the *Pinus sylvestris/mugo* curve, fall in *Pinus cembra* and Cyperaceae values.

Pollen concentration: AP (8500) 27800–215000/cm^3, NAP (4000) 9500–152800/cm^3.

ZO-2, *Pinus* PAZ (samples 41–43)

A rapid rise of the AP curve to above 80%, its principal component being pollen of *Pinus sylvestris/mugo* with a greatest value of 72.6% and its highest concentration (above 180000/cm^3).

The NAP, dominant in the previous zone, recedes and only *Artemisia* increases its proportion, approaching 8%.

Upper boundary: decrease in *Pinus sylvestris/mugo* pollen.

Pollen concentration: AP 128450–218900/cm^3, NAP 33300–53100/cm^3.

ZO-3, *Pinus-P. cembra-Artemisia* PAZ (samples 37–40)

The AP values fall rapidly to slightly over 50%. The proportion of *Pinus sylvestris/mugo* decreases, but with its pollen values of 40% to 50% it is still the main component of that total. The *Juniperus* curve comes to an end,

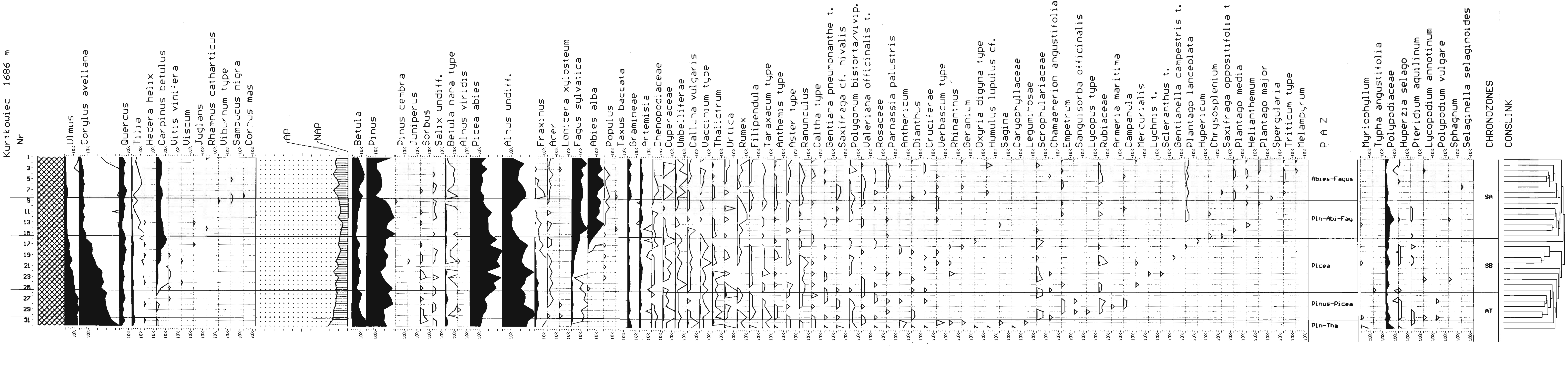

Fig. 6. Percentage pollen diagram from Kurtkowiec

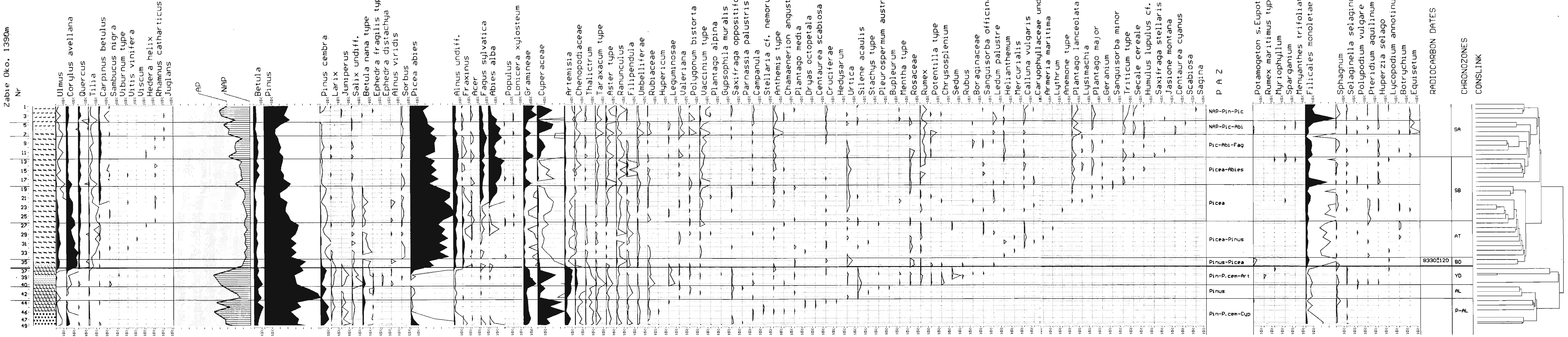

Fig. 7. Percentage pollen diagram from Žabie Oko

while *Salix* reaches 3.7% in its maximum and *Larix* 0.7%.

The NAP curve, approaching 50%, consists chiefly of *Artemisia* (on average 9%), Chenopodiaceae with a maximum of 3.7%, Gramineae and Cyperaceae; Rubiaceae has a continuous curve in this zone, pollen grains of *Sedum*, *Silene acaulis* and *Chrysosplenium* appear as well.

Upper boundary: rise in the AP values, drop in the curves of Gramineae, *Artemisia* and Chenopodiaceae.

Pollen concentration: AP 43100–129800/cm^3, NAP 27400–113100/cm^3.

ZO-4, *Pinus-Picea* PAZ (samples 35–36).

The AP values exceed 90%, of which *Pinus sylvestris / mugo* forms more than 50%. The *Picea* curve soon reaches 25%; the continuous curves of *Ulmus*, *Corylus*, *Quercus*, *Fraxinus* and *Alnus* appear, hazel pollen averaging 14%. Gramineae, *Artemisia*, Chenopodiaceae and Cyperaceae become insignificant. *Potamogeton* appears.

The zone has been ^{14}C dated at 8330±120 years BP (Gd-2799) (Baumgart-Kotarba & Kotarba 1994).

Upper boundary: rise in the *Picea* curve, fall of *Pinus sylvestris / mugo*.

Pollen concentration: AP 115100–121700/cm^3, NAP 11100–15200/cm^3.

ZO-5, *Picea-Pinus* PAZ (samples 27–34).

Picea pollen, averaging about 45%, has a maximum of 52.9%, its concentration (120000/cm^3) being three times as great as in the preceding zone. The *Corylus* pollen value decreases slightly but steadily; *Fraxinus* shows its highest values of the whole profile and has two maxima, each of 2.9%.

A single pollen grain of *Armeria maritima* was found.

Upper boundary: further rise in the *Picea* curve.

Pollen concentration: AP 70800–239800/cm^3, NAP (4200) 7500–18400/cm^3.

ZO-6, *Picea* PAZ (samples 19–26)

The proportion of *Picea* exceeds 50% and attains a maximum of 57.3%, with the pollen concentration exceeding 160000/cm^3.

The percentage values of *Pinus sylvestris / mugo* reduce gradually and the continuous curves of *Abies* and *Fagus* begin. The *Fraxinus* curve is discontinuous.

The proportion of *Corylus* decreases, while the continuous curve for *Carpinus* appears.

The continuous curve of *Plantago lanceolata* also bergins in this zone.

Upper boundary: fall in *Picea*, increase in *Abies*.

Pollen concentration: AP 138300–270200/cm^3, NAP 8000–15900/cm^3.

ZO-7, *Picea-Abies* PAZ (samples 13–18)

The pollen values of *Picea* drop to about 30%, the *Abies* curve rises steeply up to its maximum of 20.7%; there is a slight increase in the proportion of *Betula* expressed by two peaks (7.8 and 7.0%).

The NAP curve exceeds 10%, chiefly due to rises in the proportions of *Filipendula*, Ranunculaceae, Gramineae, *Rumex* and *Plantago lanceolata*; the first pollen grains of *Triticum*-t. and *Secale* appear.

Upper boundary: fall in *Abies*.

Pollen concentration: AP 51900–162100/cm^3, NAP 7900–37800/cm^3.

ZO-8, *Picea-Abies-Fagus* PAZ (samples 8–12)

Picea is still represented by proportions averaging about 30%; the ascending curve of *Fagus* reaches a maximum of 9.7%, while *Abies* decreases by several per cent in relation to the previous zone. *Alnus* has its maximum of 7.4% and *Carpinus* approaches 5%.

Upper boundary: the AP values drop to below 80%.

Pollen concentration: AP 65600–195700/cm^3, NAP 15100–48200/cm^3.

ZO-9, NAP-*Picea-Abies* PAZ (samples 5–7)

The course of the curves of *Abies* and *Fagus* shows a downward tendency; the mean proportion of *Picea* falls below 30%. The NAP increases rapidly to above 30%; apart from Gramineae and Cyperaceae the highest contributions to the total are made by *Artemisia*, *Taraxacum*-t., *Anthemis*-t., *Rumex* and *Plantago lanceolata*.

Upper boundary: rise of the curve of *Pinus sylvestris / mugo*.

Pollen concentration: AP 69900–92600/cm^3, NAP 31800–36400/cm^3.

ZO-10, NAP-*Pinus-Picea* PAZ (samples 1–4).

The proportion of *Pinus sylvestris / mugo* pollen is twice as high as in the previous zone, whereas the *Picea* curve is declining remains at or above below 20%. The *Abies* curve undergoes a sharp decline; *Ephedra fragilis*-t., present here in the late glacial, appears for the first time in the Holocene.

A further rise in the NAP brings it to a maximum above 40%. The proportion of *Triticum*-t. pollen approaches 1%. The curve of Filicales monoletae has its maximum here.

Pollen concentration: AP 78100–334700/cm^3, NAP 33900–103500/cm^3.

WYŻNIA PAŃSZCZYCKA MŁAKA
(Fig. 8)

WP-1, *Picea*-Gramineae PAZ (samples 37–38)

The AP values come close to 70%, its main constituent being *Picea* with a proportion of more than 40%; *Pinus sylvestris / mugo* somewhat exceeds 10%; the continuous curves of *Abies* and *Fagus* begin.

Corylus pollen grains exceed 20%.

As to the NAP pollen, Gramineae is clearly dominant, forming more than 20% of the total.

The zone has been ^{14}C dated at 4570±100 years BP (Gd-2323).

Upper boundary: increase in the NAP values, downward inclination of the Gramineae curve.

Pollen concentration: AP 60600–99400/cm^3, NAP 26300–57900/cm^3.

WP-2, *Picea* PAZ (samples 24–36)

The AP values exceed 80%; *Picea* is the absolute dominant with a mean proportion above 45%, rising to a maximum of 56.0%. The *Abies* curve rises steeply and, having reached its first maximum (11.6%), shows only a very slight further increase; *Fagus* behaves in a very similar way but always remains below 10%.

Ranunculus and *Taraxacum*-t. are the most abundant of the NAP taxa, whereas Gramineae pollen is reduced to half its value in the preceding zone.

The uppermost part of the zone has been dated at 3600±100 years BP (Gd-2324).

Upper boundary: decrease in *Picea*.

Pollen concentration: AP 19400–81300/cm^3, NAP 26300–57900/cm^3.

WP-3, *Picea-Abies* PAZ (samples 18–23).

The AP values exceed 90%. The spruce proportion decreases on average by roughly 12% and its curve proceeds erratically within the range 30–50%; *Abies* comes close to 20%. There is somewhat more *Fagus* pollen than in the preceding zone; the *Corylus* curve falls below 1%, while *Quercus* doubles its proportion.

As regards the NAP, only *Taraxacum*-t. maintains its level from the previous zone.

The middle part of the zone has been dated at 2570±100 years BP (GD-2320).

Upper boundary: successive fall in *Picea*, rise in the *Fagus* curve.

Pollen concentration: AP 13900–37000/cm^3, NAP 2500–10000/cm^3.

WP-4, *Picea-Abies-Fagus* PAZ (samples 9–17)

The AP values remain high at just below 90%. *Picea* averages above 35%, *Abies* has its highest proportions with a maximum of 24.2% and similarly the *Fagus* curve has its highest values in this zone, with a maximum of 20.1%. *Carpinus*, too, reaches its maximum of above 6%.

A number of the curves of the NAP species fall to insignificant values below 1%. The curve of Cyperaceae rises.

Upper boundary: decrease in the AP percentages, descent of the *Abies* and *Fagus* curves, rise in *Picea* values.

Pollen concentration: AP 17500–105700/cm^3, NAP 2500–26000/cm^3.

WP-5, *Picea*-NAP PAZ (samples 1–8)

Picea displays similar values to those found in zone WP-2, attaining a maximum of 53.8%. The proportions of *Fagus* and *Abies* decrease distinctly and, in the final two samples, dramatically. The amount of *Pinus sylvestris / mugo* increases but remains small.

The NAP values rise rapidly reaching 33.5% in the uppermost sample; Gramineae pollen is the chief constituent with *Triticum*-t. represented by a continuous curve. *Secale* pollen appears and the proportions of *Rumex* and *Plantago lanceolata* increase; there is also more pollen of Ericaceae.

A further rise in the curve of Cyperaceae pollen occurs.

Pollen concentration: AP (2900) 7000–32800/cm^3, NAP (900) 1600–16400/cm^3; in samples 5–7 the concentration is the lowest in the whole profile.

SIWE SADY
(Fig. 9)

SS-1, *Pinus*-NAP PAZ (samples 16–19)

Among the AP pollen of *Pinus sylvestris / mugo* is absolutely dominant, reaching a maximum of 64.3%. *Betula* shows a maximum (15.3%) in sample 16, in which the *Ulmus* curve also reaches its highest point (13.2%).

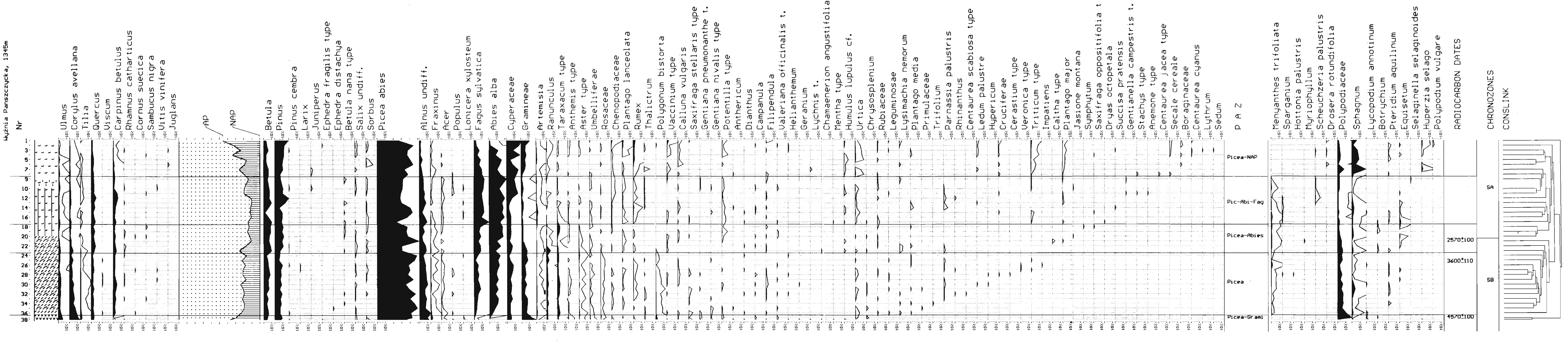

Fig. 8. Percentage pollen diagram from Wyżnia Pańszczycka Młaka

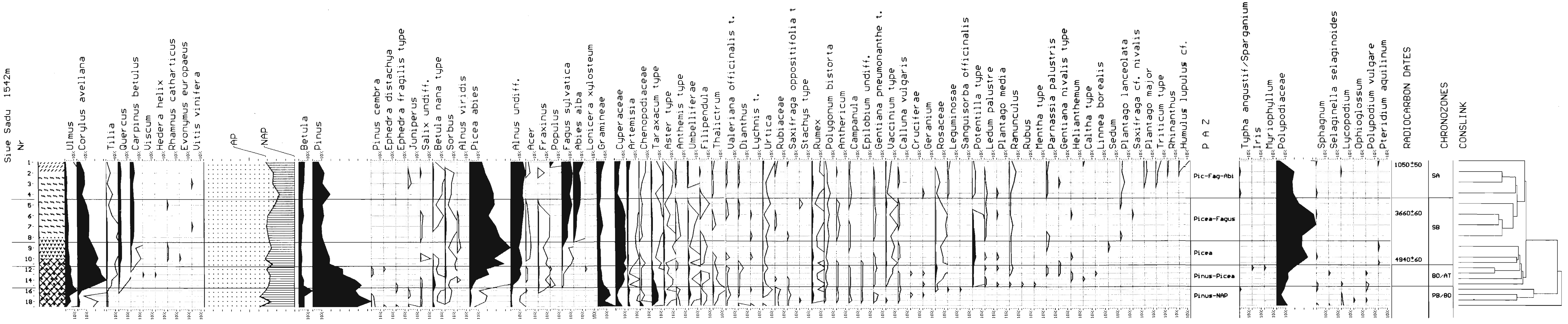

Fig. 9. Percentage pollen diagram from Siwe Sady

The NAP total averages 35% and its main constituents are: Gramineae with a maximum of 20.3%, *Taraxacum*-t. (max. 7.3%), *Aster*-t. (max. 2.8%), Umbelliferae (max. 3.1%) and in the lowest sample also Chenopodiaceae (4.1%).

Upper boundary: beginning of the rise of the *Picea* curve.

SS-2, *Pinus-Picea* PAZ (samples 12–15)

The AP values exceed 70%. *Pinus sylvestris/mugo* is continuously declining but it remains above 33%; the rapidly rising curve of *Picea* exceeds above 20%. In this zone *Sorbus* has its maximum (1.8%), *Betula* falls to one third of its highest values in the preceding zone, the continuous curves of *Fagus* and *Carpinus* begin and *Corylus* attains 32.4% as its maximum.

There occur single pollen grains of *Hedera helix*, *Viscum* and *Linnaea borealis*.

Within the NAP, Cyperaceae becomes dominant with Gramineae and *Taraxacum*-t. falling to half their previous values.

Upper boundary: fall in *Pinus sylvestris/mugo*, rise in *Picea*.

SS-3, *Picea* PAZ (samples 9–11)

The AP curve maintains its level above 70%, *Picea* being absolutely dominant, with a highest value of 46.2%. *Pinus* falls below 20%. *Corylus* continuously declines, ending at a level below 20%, while *Quercus* approaches 4%.

In the NAP values Cyperaceae and *Potentilla*-t. are particularly abundant. The percentage of Filicales monoletae more than doubles.

The lowest part of the zone has been ^{14}C dated at 4940±60 years BP (VRI-1.271) (Libelt & Obidowicz 1994).

Upper boundary: fall in *Picea* values, rise in *Fagus*.

SS-4, *Picea-Fagus* PAZ (samples 5–8)

The AP values average about 70%. The proportion of *Picea* pollen decreases but does not fall below 25%. The ascending *Fagus* curve attains 12.1% at its maximum; *Sorbus* has a second maximum (1.7%) and the continuous curve of *Abies* begins showing a distinct upward tendency.

Cyperaceae is dominant in the NAP values and the continuous curve of *Plantago lanceolata* begins. The proportion of Filicales monoletae attains a maximum.

The central part of the zone has been ^{14}C dated at 3660±60 years BP (VRI-1.270) (Libelt & Obidowicz 1994).

Upper boundary: beginning of a downward tendency in *Picea*, rises in *Abies* and *Pinus sylvestris/mugo* values.

SS-5, *Picea-Fagus-Abies* PAZ (samples 1–4).

The AP values decrease successively to 68.4% in the uppermost sample.

Despite its distinct decline *Picea* is still the main constituent of the spectra. The *Fagus* pollen value remains above 10%, with a maximum of 12.4%. In the uppermost sample *Abies* approaches 15% and *Populus* pollen forms 4.1%.

The NAP is dominated by Gramineae and Cyperaceae; the proportions of *Artemisia* and Umbelliferae are increasing, and the curves of *Triticum*-t. and *Plantago major* begin.

The uppermost part of the zone has been ^{14}C dated at 1050±50 years BP (VRI-1.269) (Libelt & Obidowicz 1994).

MOLKÓWKA
(Fig. 10)

Mo-1, *Pinus*-Cyperaceae-*Artemisia* PAZ (samples 96–110)

The AP values average about 85%. *Pinus* (*sylvestris/mugo* + *cembra)*, reaching its absolute maximum of 71.3%, is the main constituent of this total. *Salix* is represented by a continuous curve; *Hippophaë* and *Ephedra distachya* are present in several samples.

Cyperaceae, approaching 30% in a maximum, prevails in the NAP. Gramineae comes close to 10%. *Artemisia* with a maximum of 5.3% has its highest values of the whole profile. The presence of *Thalictrum* and Chenopodiaceae is illustrated by their curves; *Helianthemum* with a maximum of 1.1% occurs in consecutive samples.

Upper boundary: a considerable increase in the proportion of *Betula* and fall in the NAP percentage.

Mo-2, *Pinus-Betula* PAZ (samples 91–95)

The AP values exceed 85%. At its absolute maximum the *Pinus* curve reaches 83.4%. In the lowermost sample of this zone *Betula* attains its maximum of 42.0% to fall later below 10%. The beginning of the continuous *Alnus* curve occurs in the uppermost sample.

Regarding the NAP, only Gramineae retains its proportion from the previous zone, whereas the percentage values of Cyperaceae and *Artemisia* fall rapidly and the Chenopodiaceae curve displays a discontinuity.

Table 3. Correlation of the pollen assemblage zones distinguished in the Tatra profiles

^{14}C YEARS BP	CHRONOZONES	POLLEN ASSEMBLAGE ZONES						
		Czarny Staw	Zielony Staw	Kurtkowiec	Żabie Oko	Wyżyna Panszczycka	Molkówka	Siwe Sady
	SA	CzS-9 *Pinus-Fagus* CzS-8 *Picea-Abies-Fagus*	ZS-7 *Pinus-Abies-Fagus* ZS-6 *Picea-Abies-Fagus*	Ku-6 *Abies-Fagus* Ku-4 *Picea-Abies-Fagus*	ŻO-10 NAP-*Pinus-Picea* ŻO-9 NAP-*Picea-Abies* ŻO-8 *Picea-Abies-Fagus*	WP-5 *Picea*-NAP WP-4 *Picea-Abies-Fagus* WP-3	Mo-7 NAP-*Picea-Abies*	SS-5 *Picea-Fagus-Abies*
2500	**SB**	CzS-7 *Picea*	ZS-5 *Picea*	Ku-3 *Picea*	ŻO-7 *Picea-Abies* ŻO-6 *Picea*	*Picea-Abies* WP-2 *Picea* WP-1	Mo-6 *Picea-Abies* Mo-5	SS-4 *Picea-Fagus* SS-3 *Picea*
5000	**AT**	CzS-6 *Picea-Pinus* CzS-5 *Pinus-Picea*	ZS-4 *Pinus-Picea*	Ku-2 *Pinus-Picea* Ku-1 *Pinus-Thalictrum*	ŻO-5 *Picea-Pinus*	*Picea*-Gramineae	*Picea*	SS-2 *Pinus-Picea*
8000	**BO**	CzS-4 *Pinus*-Cyperaceae	ZS-3 *Pinus*-Cyperaceae		ŻO-4 *Pinus-Picea*		Mo-4 *Picea-Pinus*	SS-1 *Pinus*-NAP
9000	**PB**		ZS-2 *Pinus-Betula*				Mo-3 *Pinus-Picea* Mo-2 *Pinus-Betula*	
10000	**YD**	CzS-3 *Pinus-P. cembra-Artemisia*	ZS-1 *Pinus-P. cembra-Artemisia*		ŻO-3 *Pinus-P. cembra-Artemisia*		Mo-1 *Pinus*-Cyperaceae-*Artemisia*	
11000	**AL**	CzS-2 *Pinus*			ŻO-2 *Pinus*			
12000	**P-AL**	CzS-2 *Pinus*-Cyperaceae-*Betula nana*			ŻO-1 *Pinus-P. cembra*-Cyperaceae			

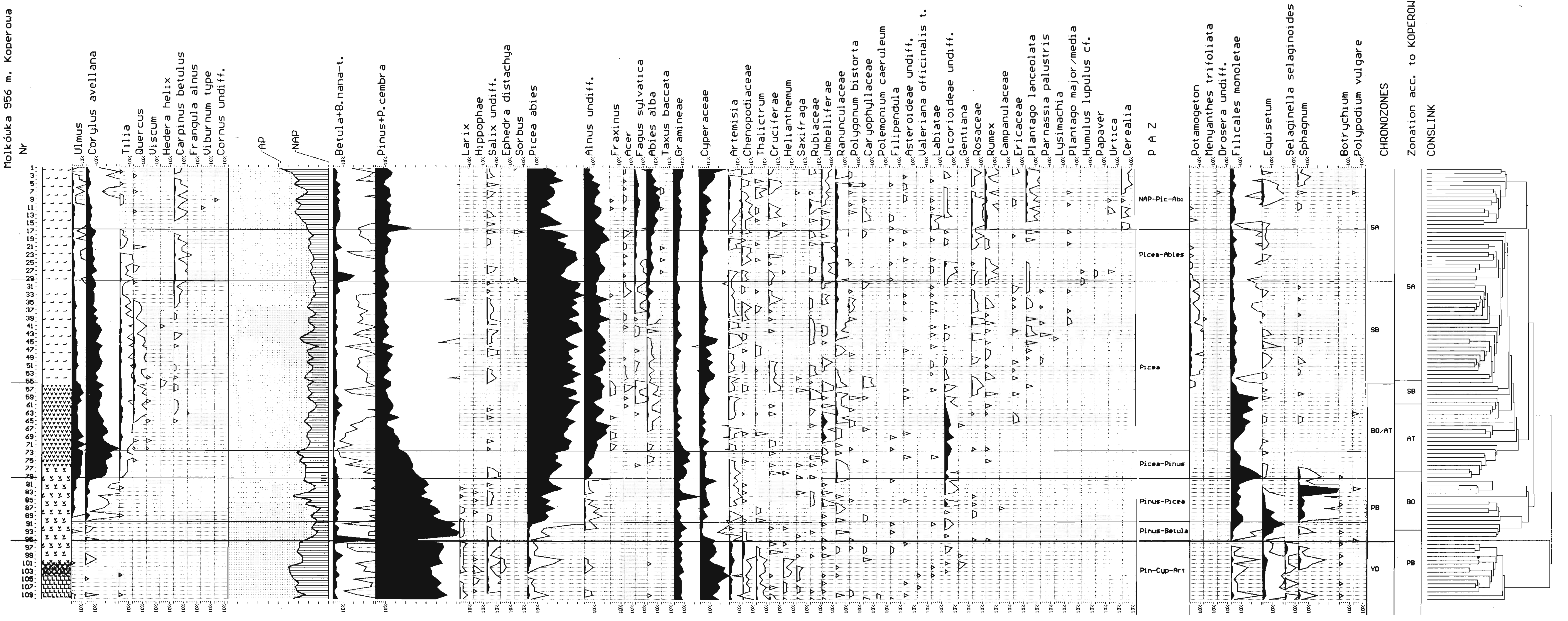

Fig. 10. Percentage pollen diagram from Molkówka (Koperowa 1962) recalculated and modified

Upper boundary: decrease in *Pinus*, increase in *Picea*.

Mo-3, *Pinus-Picea* PAZ (samples 80–90)

Pinus falls gradually but still remains above 50%. *Picea* rises sharply to 20% and at its maximum towards the end of the zone even exceeds 35%. The final appearances of *Larix* and *Hippophaë* and the beginning of the continuous curves of *Corylus* and *Ulmus* are seen.

The proportion of NAP varies within the range from 10% to more than 30%.

Upper boundary: fall in *Pinus*, rapid rise in *Alnus*.

Mo-4, *Picea-Pinus* PAZ (samples 73–79)

Pinus continues to decline but does not fall below 30%. *Picea* increases its proportion to over 30%. The rapidly increasing curve of *Corylus* exceeds 25%. *Ulmus* and *Alnus* are characterized by a distinct upward tendency and *Tilia* begins its continuous curve in this zone.

The final maximum of Gramineae (16.8%) and the highest values on the curve of Filicales monoletae are noted.

Upper boundary: a definite fall in *Pinus* pollen values and a regular and rapid increase of *Picea*.

Mo-5, *Picea* PAZ (samples 30–72)

The AP values maintain their level of about 80%; completely dominant is *Picea* with a maximum of 54.2%. *Alnus* shows a permanent upward tendency until it reaches 26.4%, after which it oscillates about a mean of 15%; *Fagus* is present sporadically, while *Abies*, although not numerous, is already represented by a continuous curve in this zone. After a maximum (14.2%) in the earlier part of the zone the proportion of *Ulmus* is reduced by half in sample No 40 and then, after a transitory rise, its curve gradually comes down to below 1%. The *Quercus* curve becomes discontinuous towards the top of the zone and *Carpinus* appears.

As regards the NAP, Gramineae falls to a third of its Mo-4 value. The proportion of Compositae increases rapidly and exceeds 10% in a maximum. The broken curve of Umbelliferae shows two peaks of 4.8% and 5.6% respectively. In the more recent part of the zone the curve of Filicales monoletae rises up to another maximum.

Upper boundary: decrease in *Picea*.

Mo-6, *Picea-Abies* PAZ (samples 17–29)

The proportion of *Picea* is somewhat smaller, although in sample No 24 it still exceeds 50%; *Abies* remains below 10%; *Betula*, after a second maximum at the beginning of the zone (21.3%) eventually falls to below 5%; the final maximum of *Alnus* occurs (26.0%).

The NAP values remain below 20% throughout the zone; the continuous curve of Umbelliferae attains its peak of 2.5%.

Upper boundary: dramatic decline in *Picea*, increase in *Abies* and the NAP total.

Mo-7, NAP-*Picea-Abies* PAZ (samples 1–16)

The AP values on the average fall below 65%. *Picea*, after an initial decrease in this zone, rises to a peak of 36.6%; *Abies* doubles its proportion and has a maximum of 14.1%. *Alnus* declines to just over 5%; *Tilia* has a discontinuous curve.

In the uppermost sample the NAP reaches 47.7%, made up chiefly of Gramineae and Cyperaceae pollen. The continuous curves of *Rumex* and *Plantago lanceolata*, the first pollen grains of cereals and the beginning of their discontinuous curve occur in this zone.

The correlation of particular pollen assemblage zones (PAZ) within chronozones after Mangerud et al. (1974) is shown in Table 3.

DISCUSSION

HISTORY OF CHANGES IN THE NATURAL ENVIRONMENT OF THE TATRAS FROM THE DECLINE OF THE PLEISTICENE ONWARDS

Pre-Alleröd (*Pinus*-Cyperaceae-*Betula nana* PAZ: CzS-1; *Pinus-P. cembra* – Cyperaceae PAZ: ZO-1)

In the profiles from Podhale and the Tatras published so far this zone is recorded from the bottoms of the Na Grelu peat-bog (Koperowa 1962) and the lacustrine sediment of Przedni Staw Lake (Krupiński 1984) in the form of an Oldest Dryas-Bölling-Older Dryas sequence. If the changes in the NAP values and the behaviour of the *Pinus sylvestris/mugo* curve are taken into account, the separation of the Older Dryas seems justified in both cases. The high total of herbaceous plant pollen in Przedni Staw chiefly consists of that of Gramineae, *Artemisia*, Chenopodiaceae, Caryophyllaceae and Rubiaceae, while at Na Grelu the components are Cyperaceae, Gramineae, Cruciferae and Caryophyllaceae. In both cases heliophytes, such as *Helianthemum* and Caryophyllaceae, are present. For the remaining Tatra profiles, extending to deposits from before the Alleröd Interstadial, we lack sufficient information to divide them up in greater detail (Obidowicz 1993).

The separation of the Older Dryas in profiles from the Alps has been creating problems long since ago. In Zoller and Kleiber's (1971) appraisal this part of the Late Glacial was poorly defined in the development of vegetation, at least in the colline and lower mountane belts, whereas it may have been apparent in places at higher altutudes, notably in the vicinity of local glaciers. Welten (1982) proposed a new stratigraphical division of the Late Glacial of the Alps, in which the Bölling and Alleröd Interstadials were not separated by the Older Dryas, since it did not distinguish itself clearly enough in the palynological profiles or the curves of palaeotemperature ($^{18}O/^{16}O$). Similar observations were made from both the Western and Eastern Alps (e.g. Wegmüller 1977, Schneider 1978, Kral 1979, Küttel 1982, Wahlmüller 1985, Oeggl 1988). Bortenschlager (1984) defined this phase as a period during which the pine-birch forest expansion slowed down. On the other hand, a climatic fluctuation dated to 12000–12300 BP was found in the forefield of the Alps (Lotter et al. 1992). This was markedly different from the North-European chronozone of the Older Dryas sensu Mangerud et al. (1974) wich fell in the period 11800–12000 BP.

In the palynological profiles from Żabie Oko and Czarny Staw a climatic deterioration preceding the Alleröd Interstadial is clearly visible. This is certainly due to the geographical position of the Carpathians within reach of the influence of a continental climate and chiefly that of the progressing thermal continentalization.

In the profile from Czarny Staw Gąsienicowy, the pre-Alleröd portion classified as CzS-1, *Pinus*-Cyperaceae-*Betula nana* PAZ, may correspond to the stadial cooling of the Older Dryas. It was a time of the development of communities of open, steppe-tundra areas, mainly with Cyperaceae, *Artemisia*, Chenopodiaceae, Gramineae and also *Thalictrum, Dryas octopetala*, *Helianthemum* and *Polygonum bistorta*.

The sample from the deepest level of the zone, distinguished by a particularly high proportion of *Pinus*, may represent the decline of the Bölling Interstadial. This supposition is supported by the radiocarbon date (12550±420 BP) obtained for the lowest part of the profile. In the remaining samples from the pre-Alleröd section the low AP total, slightly over 50%, indicates that pine, stone pine, birch or larch grew far below the Czarny Staw Gąsienicowy contour line, undoubtedly in small stands, at the foot of the Tatras. In 12000–13000 BP the Czarny Staw Gąsienicowy basin (1620 m) was already free from ice (Baumgart-Kotarba & Kotarba 1994). It seems therefore very probable that the timberline extended at an altitude of 700–800 m. The shrubs, *Betula nana* and *Juniperus* may have come relatively close to the Gąsienicowe Stawy Valley.

In the Rybi Potok Valley the pre-Alleröd is represented in the profile from Żabie Oko by pollen assemblage zone ZO-1, *Pinus-P. cembra*-Cyperaceae. Small groups of stone pine or stone pine, larch and pine may have been present close to this valley. Generally, however, trees would have been absent there, the vegetation resembling that found in the region of the Gąsienicowe Stawy Valley, with Gramineae, Cyperaceae, *Artemisia*, *Dryas octopetala*, various species of Compositae, *Thalictrum*, *Filipendula*, *Selaginella selaginoides* and *Helianthemum* present. Shrubs were represented by *Betula nana*, *Juniperus* and *Salix*.

The occurrence of pollen grains of *Picea*, *Corylus*, *Ulmus*, *Abies* and *Fagus* in the oldest samples of this zone, according to the present state of our knowledge of the Late Glacial in the Tatras, may be interpreted as the effect of the mechanical removal of trace amounts of material from the Holocene zones of the profile.

In attempts to determine the pre-Alleröd course of the timberline in the Tatras the profile from Żabie Oko, situated about 230 m below the Czarny Staw Gąsienicowy contour line provides local evidence. *Pinus cembra* seems to be a particularly useful species for this purpose. At present the largest group of stone pines on the northern side of the Tatras is situated on the slopes of Żabie, on the northern side of the Rybi Potok Valley. This species occurs in a zone between 1400 and 1659 m a.s.l. (Myczkowski & Bednarz 1974), forming a belt above the spruce mountain forest. Also the proportion of *Pinus cembra* pollen in the spectra of the pre-Alleröd part of the Żabie Oko profile is greater than that found in any other Tatra profile. This strongly suggests that the distribution of this tree in the Tatras, where it currently displays a preferance for the High Tatras, has changed little since the Late Glacial.

In those parts of the Alps with the most continental climate, *Pinus cembra* grew up to the altitude defined by the present day 7,5°C July isotherm (Landolt 1983). This corresponds to the highest current sites of stone pine in the Tatras, exceeding 2000 m a.s.l. However, in the Tatras, close stands of stone pine extend up to the 9.5°C July isotherm which corresponds with a mean annual temperature of 1°C; this isotherm runs through the middle of the mountain pine belt.

Küttel (1979) writes of pollen of regional origin in connection with those Alpine profile zones in which the proportion of *Pinus cembra* pollen does not exceed 10%. In the pre-Alleröd section of the Żabie Oko profile the proportion of stone pine exceeds this boundary value, but unfortunately this does not provide firm evidence of its former presence at the site. However, it may be supposed that if the climatic timberline ran at the foot of the Tatras at that time, the outposts of *Pinus cembra* reached about 150–200 m higher.

Alleröd (*Pinus*-PAZ: CzS-2, ZO-2)

In the Alleröd the plant cover of the West Carpathians was fairly uniform, with *Pinus sylvestris* playing the main role, supported by stone pine or stone pine-larch forest and locally high proportions of *Betula* or *Picea* (Koperowa 1970, Ralska-Jasiewiczowa 1972, Harmata 1987). Here and there an older birch phase can also be distinguished; it is characterized by larger proportions of plants which would have required higher temperatures than those of the younger pine phase (Harmata 1995). Such a division of the Alleröd, often encountered in the lowlands of Poland (Ralska-Jasiewiczowa 1991), has no parallel in the Tatras themselves. In the Alps, which show greater differentiation, notably on the southern side of the massif, the same species (*Betula*, *Pinus*, *P. cembra*, *Larix*), made up the tree stands (Kral 1979, Schneider & Tobolski 1985, Burga 1988).

The interstadial warming in the Alleröd is revealed in the profile of Czarny Staw Gąsienicowy as a time of expansion of pine and pine-birch forest. Since it is impossible to distinguish the pollen of *Pinus sylvestris* and *P. mugo*, it is difficult to estimate the role them played by dwarf pine, especially as its macrofossils are not known in the West Carpathians from before the Younger Dryas (Koperowa 1962). Our present-day knowledge of the ecology of *Pinus sylvestris*, including the fact that it produces far more pollen than does dwarf pine (Markgraf 1980, Kvavadze et al. 1992), suggests that the Tatra forests of the Alleröd were for the most part pine forests. Pine macrofossils occurred in several Vistulian West Carpathian floras (Środoń 1968, Mamakowa et al. 1975).

The picture of the Alleröd recorded in the profile from Żabie Oko resembles that of Czarny Staw Gąsienicowy only in that the pollen values of *Pinus sylvestris/mugo* in the spectra are particularly high. It may be claimed that if Scots pine has ever had an optimum in the Tatras, then it was in the Alleröd. It may well be that the present stands of the relict association Vario-Pinetum are remnants of the extensive pine forests of that interstadial. Stone pine and stone pine-larch forests played a minor role, at least on the northern side. On the southern side of the Tatras *Pinus sylvestris*, *P. cembra* and *Larix* were present in the forests in different proportions, the occurrence of stone pine being confirmed also by macrofossils (Jankovska 1984, 1988, 1991).

In today's montane belt of the continental Alps, dominated by pine forest, the climate is characterized by low rainfall, big differences in temperature and high insolation (Landolt 1983). Studies on the ecology of the Tatra pine show that the thermal conditions of the growing season are important to the development of its shoots, needles and production of biomass (Łysek 1974). The continental climate of the Alleröd was therefore characterized by relatively warm summer months.

It is difficult to determine the altitude at which the upper boundary of the pine forest extended in the Alleröd Interstadial. According to Koperowa (1962), it lay about 1050 m a.s.l. and in Krupiński's opinion (1984), even at 1100 m. Now single pines grow in the Tatras up to about 1500 m, whereas groups of trees do not as a rule range beyond 1200 m (Łysek op.cit.). It seems impossible that in the Holocene, when pine began to give way to the more competitive dwarf pine and spruce it managed to expand upward. And so in the Alleröd the timberline, formed by pine forests, probably ran at about 1200 m. The climatic timberline certainly extended somewhat higher, as is suggested by the presence of *Pleurospermum austriacum* in the Żabie Oko region. A narrow zone of dwarf pine may already have developed above the pine forest. This happened in the Gąsienicowe Stawy Valley as is confirmed by the discovery of stomata and funnel vessels of *Pinus* in the Alleröd segment of the Czarny Staw Gąsienicowy profile. In the Rybi Potok Valley stone pine persisted close to the upper boundary of the pine forest.

Younger Dryas (*Pinus-P. cembra-Artemisia* PAZ: CzS-3, ZO-3, ZS-1; *Pinus* – Cyperaceae-*Artemisia* PAZ: Mo-1)

There are several accounts of the stadial oscillation of the Younger Dryas in the West Carpathians (Koperowa 1958, 1962, 1970, Pawlikowa 1965, Gerlach et al. 1972, Krupiński 1984, Harmata 1987, Szczepanek 1987 & Obidowicz 1990). In Podhale and in the Tatras the deterioration of the climate brought about a very distinct decrease in the forested areas, well reflected by a remarkable rise in the NAP total. The regression of forest communities affected mainly pine forest, while the stone pine and stone pine-larch forests retained their Alleröd presence, which, allowing for the decline of the Scots pine, is revealed by an unchanged (Żabie Oko) or higher (Czarny Staw Gąsienicowy) proportion of *Pinus cembra* pollen. To be sure, *Larix* is still represented by, at most, a small number of pollen grains, but in sufficient quantity to confirm its presence as a constituent of the on site vegetation (see Kral 1983). Its macrofossils have also been found (Koperowa 1962). From among shrubs which survived mainly macrofosils of *Juniperus*, *Salix*, *Betula nana*, and also dwarf mountain pine have been found.

In many respects the Younger Dryas in the Tatras is a recurrence of the situation from before the Alleröd Interstadial. There are, however, some perceptible local differences. It was not until the later period that the Czarny Staw Gąsienicowy profile contained fairly large amounts of pollen of *Pinus cembra* and *Juniperus* and at Żabie Oko also that of *Ephedra distachya*, *Sorbus* and *Alnus viridis*. However, the distinctive characteristics of the Younger Dryas are, above all, higher proportions of Gramineae, *Artemisia* and Chenopodiaceae; in this connection the treeless formation of that time is often termed steppe-tundra. The expansion of *Artemisia* in the Younger Dryas distinguishes this stadial in many regions of the northern hemisphere (Wright 1989). Recorded in numerous profiles also from the Alps, it was an element that exerted pressure on the then existing communities, encroaching upon the areas abandoned by the receding forest. The role of *Artemisia* was, however, sometimes incomparably smaller there than was the case before the Alleröd, especially in the pioneer communities of the Oldest Dryas (Zoller & Kleiber 1971, Küttel 1979, Seiwald 1980, Welten 1982, Bortenschlager 1984, Wahlmüller 1985, Schneider & Tobolski 1985, Wegmüller & Lotter 1990).

The above-mentioned features of the Younger Dryas are also recorded in the lowest segment, distinguished as *Pinus*-Cyperaceae-*Artemisia* PAZ, in the Molkówka profile. Koperowa (1962) recognized this section as Preboreal, placing its boundary higher by two samples and explaining that "in the composition of its spectra it resembles the period of the Younger Dryas...". In addition to the herbs known from the remaining profiles, and dominant at that time, namely Gramineae, Cyperaceae, *Artemisia*, Chenopodiaceae, *Thalictrum*, *Helianthemum* and the trees, *Pinus sylvestris*/*mugo* and *P. cembra*, sea-buckthorn (*Hippophaë rhamnoides*) was present as well. The similarity matrix for the samples from Molkówka and Zielony Staw Gąsienicowy justifies the decision to separate the Younger Dryas in the profile from Molkówka (Fig. 11).

The date and lithology of deposits from the Late Glacial section of the Żabie Oko profile, in which sample No 43 is estimated to have originated in 9780±350 (Gd-4172), from the basis for regarding this period as marking the beginning of the Holocene (Baumgart-Kotarba & Kotarba 1994). The similarity matrix for the samples from the Czarny Staw Gąsienicowy and Żabie Oko profiles, however, shows a very strong correlation with the Late Glacial segments (Fig. 12). Assuming the accuracy of palynological criteria, one should regard sample No 43 from Żabie Oko as having been postdated by the radiocarbon method. It comes from the period of the radiocarbon plateau (see about the item Goslar et al. 1995) and has

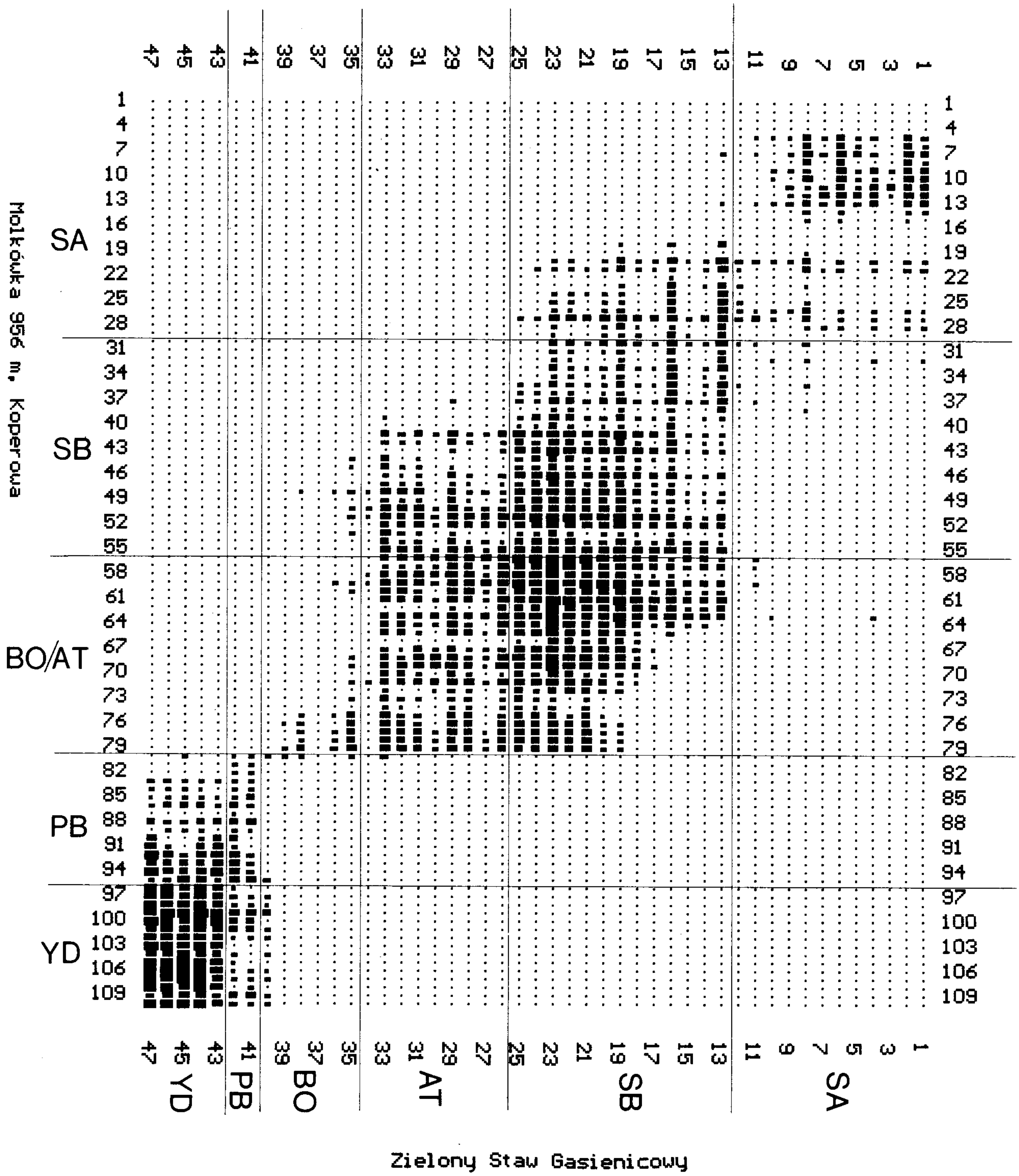

Fig. 11. Similarity matrix for the samples from Molkówka and Zielony Staw Gąsienicowy

been omitted from the various versions of the diagram presented here.

The literature on the decline of the Pleistocene provides information about this type of difficulty. Burga's opinion, based on observations made in the Alps (Burga 1988), is significant: "Radiocarbon dates are often problematic, and moreover there are sometimes hiatuses which make it difficult to interpret both the palaeovegetational and palaeoclimatological significance of the transition from the Late Würmian to the Holocene". These problems are encountered in the profile from Żabie Oko.

The Pleistocene/Holocene boundary

The onset of the Holocene brought a noticeable warming. Based on numerous palaeotem-

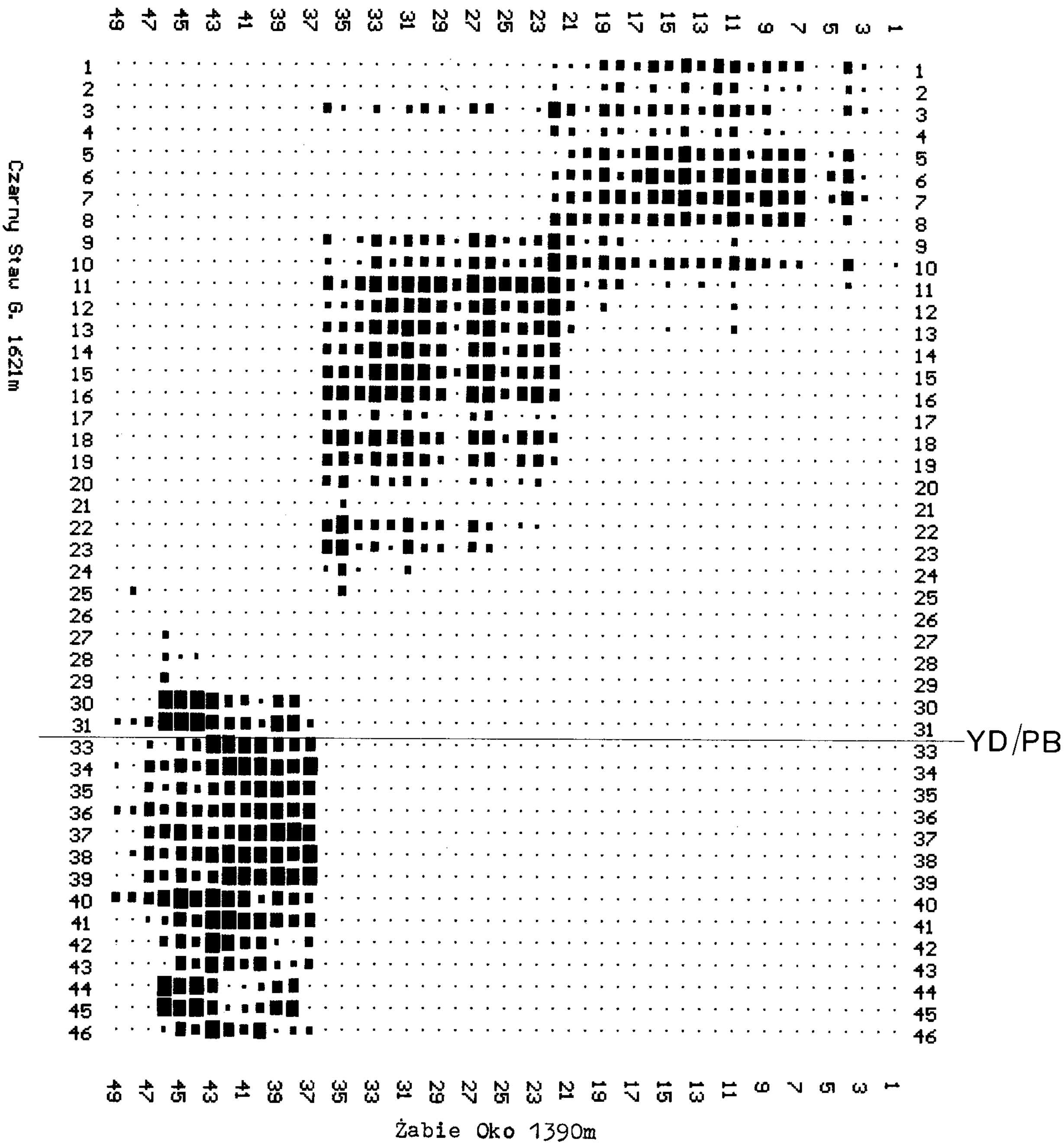

Fig. 12. Similarity matrix for the samples from Czarny Staw Gąsienicowy and Żabie Oko

perature curves for different regions of the Atlantic Ocean, it has been estimated that the rise in temperature averaged 5°C. At latitudes between 40° and 50° N increases in excess of 7°C occurred (Barash 1988). In the Alps the temperature during the growing season rose by 2–4°C (Bortenschlager 1991). Koperowa (1962), basing her opinion on the index values of *Betula*, *Pinus* and *Typha latifolia*, estimated that the mean July temperature rose to at least 14°C in the forefield of the Tatras. Nevertheless, it is not clear to what altitude this July mean isotherm extended.

The basic changes in climate that occurred at the Pleistocene/Holocene boundary are recorded in the profiles from Czarny Staw Gąsienicowy, Zielony Staw Gąsienicowy, Żabie Oko and Molkówka. Because of differences in altitude between locations, this boundary varies somewhat among the profiles. In order to bring out the most important changes (Figs 13–15), separate cumulative diagrams were

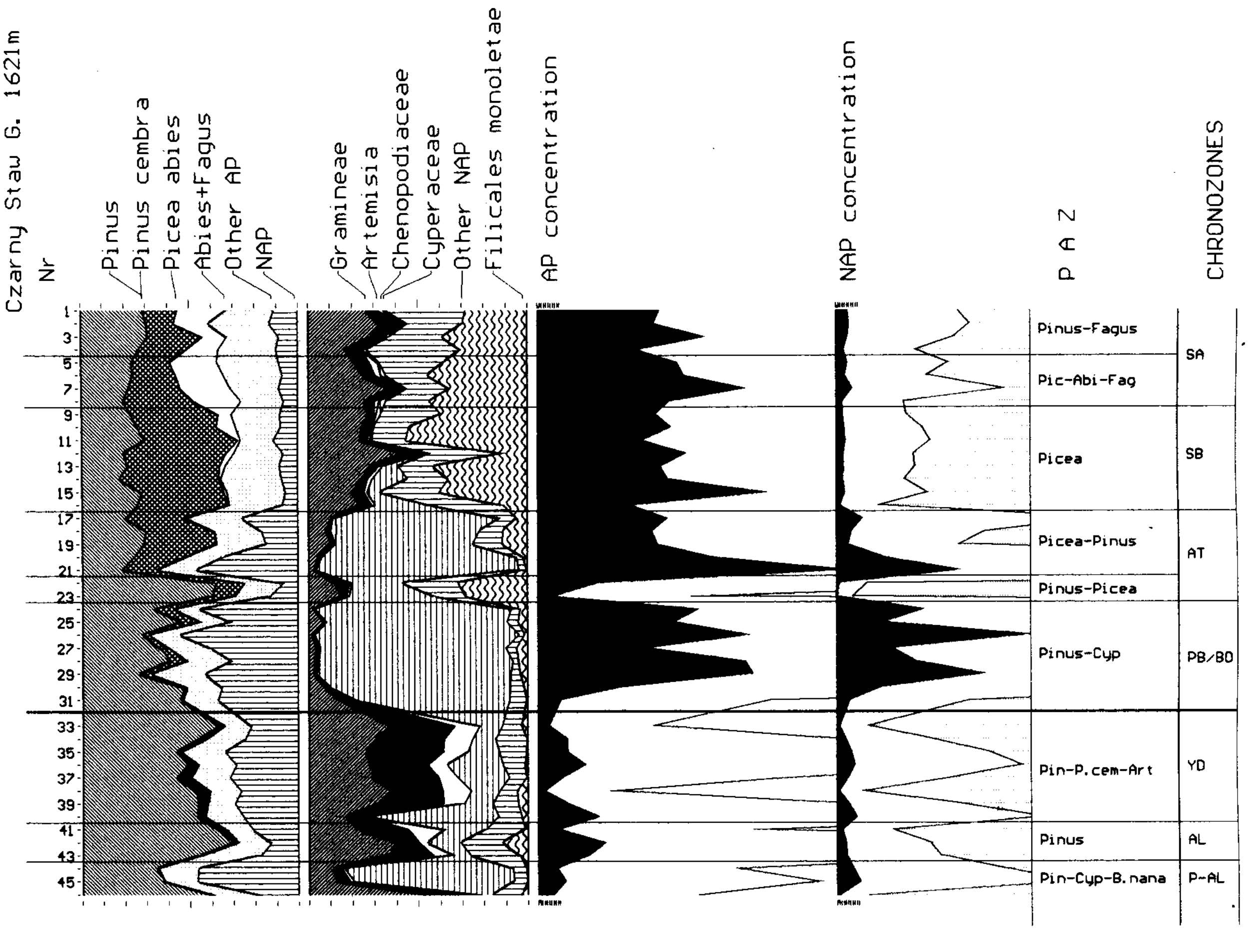

Fig. 13. Pleistocene/Holocene boundary recorded in the profile from Czarny Staw Gąsienicowy

used for the AP and NAP in which the taxa whose proportions in the plant cover had changed dramatically were specified. The curves of pollen concentrations of the AP and NAP were also used; with no essential changes in the types of deposit, they may point to variation in the size of sporomorph production and consequently a change in temperature during the growing season.

In the Tatras the Late Glacial was a period of steppe-tundra-type communities, though it was not entirely treeless, and in the Alleröd Interstadial forest expansion even took place. *Pinus sylvestris* and *P. cembra* were the main trees of the Late Glacial in the Tatras; at different times they occurred in various ratios, occupying areas varying in size. Their presence in the West Carpathians in the Late Pleistocene has been corroborated by several macrofossil finds. The Pleistocene/Holocene boundary ended this arrangement. Both species were rather soon relegated to marginal habitats by the expanding spruce. The composition of herbaceous communities too was changing rapidly and radically with the increasingly humid climate eliminating steppe elements from them. The steppe-tundra type formation, abounding in *Artemisia* and Chenopodiaceae, disappeared almost instantly.

The rapid rise in the mean annual temperature and the warmer, extended growing season caused a considerable increase in pollen production, expressed in the profile from Czarny Staw Gąsienicowy by a very great and sudden increase in the concentration of sporomorphs per cubic unit of deposit. In the profile from Zielony Staw Gąsienicowy an immediate rise in concentration is visible in the AP curve, whereas the NAP curve's response is slightly delayed. In the Żabie Oko profile the lack of a Preboreal segment and the change of deposit from inorganic to peaty has meant that the concentration of sporomorphs does not show such differences.

The similarity matrix for the samples from particular profiles (Figs 11–12 and 16–17) exhibits a marked correlation of the Late Glacial segments, whereas the events recorded in the

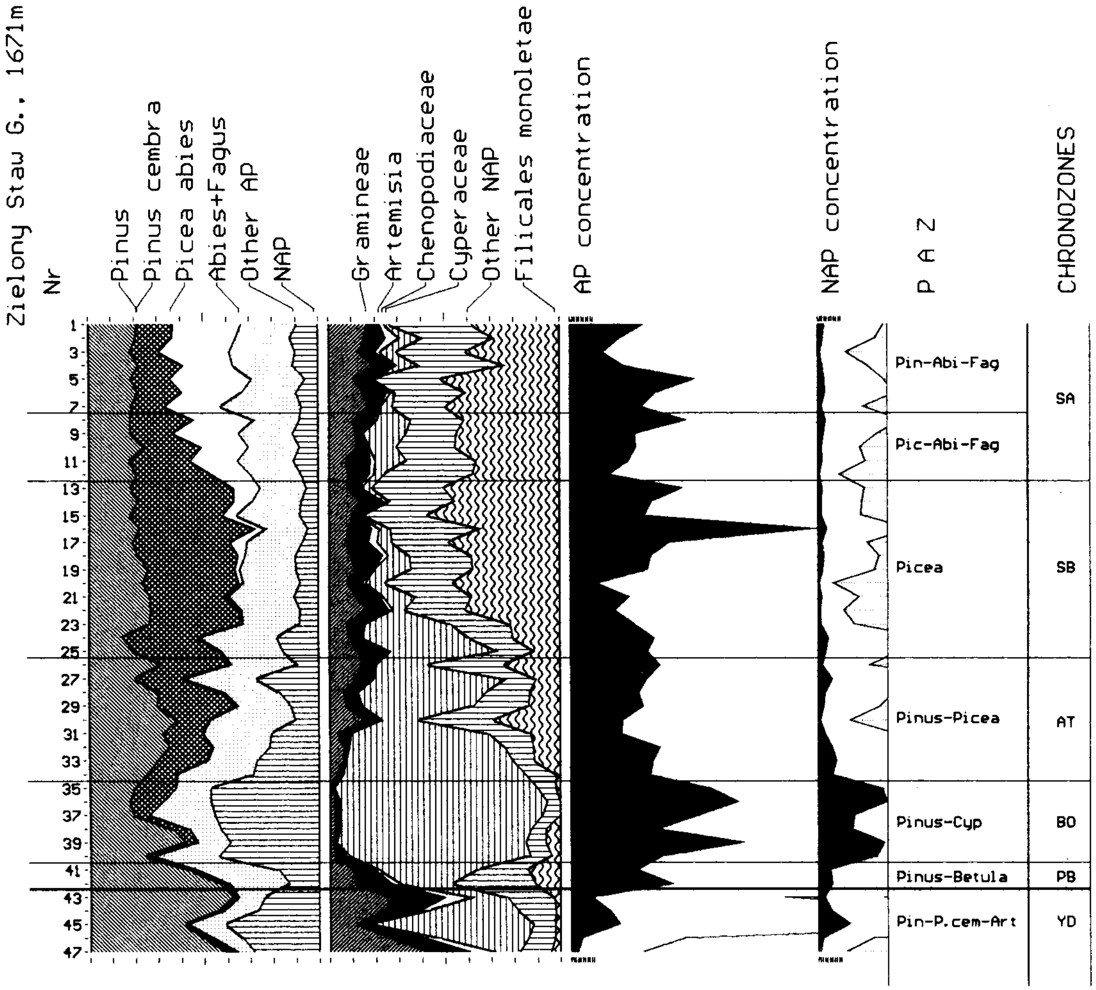

Fig. 14. Pleistocene/Holocene boundary recorded in the profile from Zielony Staw Gąsienicowy

Holocene segments are not so strongly correlated. The differences in altitude among particular localities under comparision, exceeding 700 m in the extreme case (Molkówka – Zielony Staw Gąsienicowy), are of decisive significance here. Therefore, we may assert that the Late Glacial vegetation of the Tatras and Podhale was relatively homogeneous. On the other hand, the different climatic and vegetational belts in the Holocene are revealed in different ways in the profiles from different altitudes, due to the vertical displacement of particular communities.

Preboreal (*Pinus*-Cyperaceae PAZ p.p.: CzS-4; *Pinus*-NAP PAZ p.p.: SS-1 p.p.; *Pinus-Betula* PAZ: ZS-2, Mo-2; *Picea-Pinus* PAZ: Mo-3)

It is not clear to what altitude the slope covers formed in the Carpathians during the Vistulian (Kowalkowaki 1988) possessed soil properties by the beginning of the Holocene. In the Tatras this may have been determined by the altitudine distribution of the steppe-tundra formation dominant in the Late Glacial. The presence of relict Pleistocene soils found by Jahn (Oleksynowa & Skiba 1977) above the present-day timberline allows us to suppose that the relatively fast expansion of forests, observable in the Tatras, was possible due to the soil cover inherited from the Pleistocene.

The communities which had persisted during the cooling of the Younger Dryas began to colonize the Tatras at the beginning of the Holocene. These were pine-birch forests, and a short-lived episode associated with their expansion is revealed in the profiles from Molkówka, Zielony Staw Gąsienicowy and, less strongly, from Siwe Sady. Such beginnings of the Holocene succession are fairly commonly seen both in the Carpathians and the Alps (Ralska-Jasiewiczowa 1972, Szczepanek 1989,

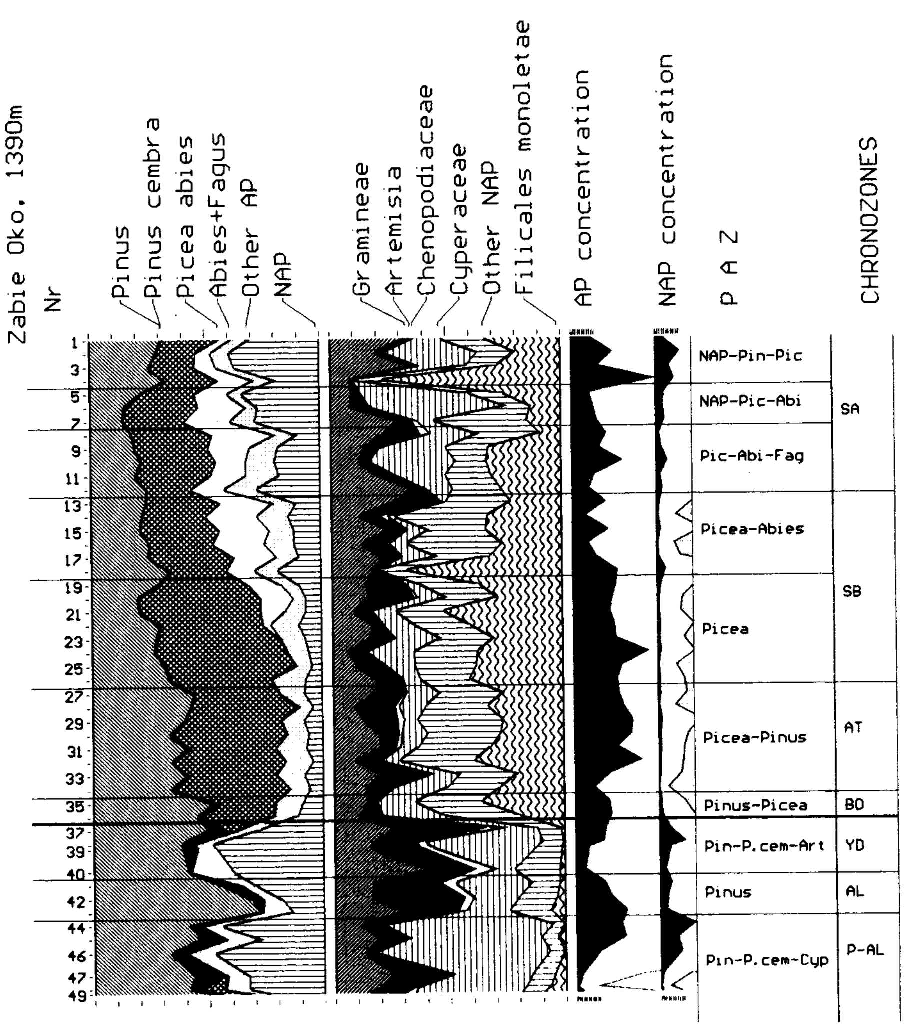

Fig. 15. Pleistocene/Holocene boundary recorded in the profile from Żabie Oko

Wegmüller 1977, Wahlmüller 1985, Burga 1988). There are, however, some regions in the Alps where the beginning of the Holocene caused these forests to disappear (Bortenschlager 1984). Their composition was similar over a large area of Central and Western Europe. Swamp forests were common in the forefield of the Tatras at that time and they survived until the Boreal leaving behind traces in the form of peat layers abounding in remains of *Betula* and *Pinus* (Obidowicz 1990). In the Preboreal the expansion in the Tatras of forests of pine and birch on mineral soils ended owing to the early spread of spruce. This is particularly well seen in the profile from Molkówka at the foot of the Tatras. The survival of stands of sea-buckthorn at this altitude supports Reynaud's (1976) suggestion concerning the adaptability of this species to both a cold, dry climate and a cool humid one.

In the region of the Gąsienicowe Stawy Valley the *Pinus-Betula* PAZ recorded in the profile at Zielony Staw reflects events which took place several hundred metres lower. In general, this profile contains far more sporomorphs transported from lower lying habitats than that from Czarny Staw, which may account for the lack of an analogous PAZ in the latter. It is possible that in the profile from Czarny Staw the pine-birch episode corresponds with the palynologically void sample No 32. In this profile the beginning of the Holocene marks the start of the large-scale development of the communities found in today's alpine belt, in which sedges were dominant even then (pages 194–196).

In the Preboreal, the pine-birch and pine forest invaded the wooded valleys of the West Tatras and formed the timberline adjacent to the developing dwarf pine belt. Communities

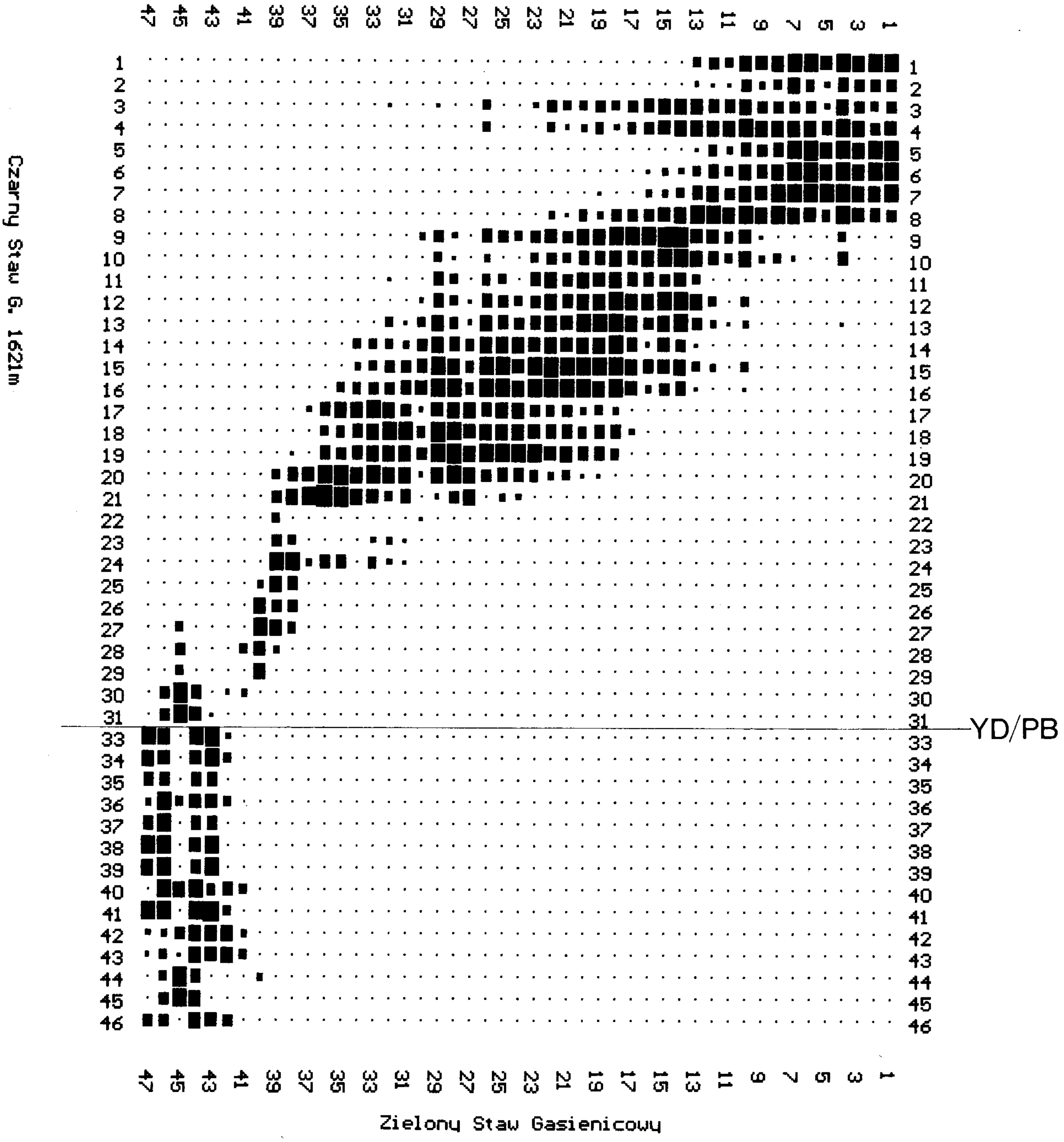

Fig. 16. Similarity matrix for the samples from Czarny Staw Gąsienicowy and Zielony Staw Gąsienicowy

of alpine grassland, occupied the higher positions. These differed from those of the High Tatras possessing greater proportions of Gramineae, *Taraxacum*-t., *Aster*-t. and Umbelliferae and having fewer Cyperaceae.

Spruce was spreading in the lower parts of the Tatras during the Preboreal. Its expansion ousted *Pinus sylvestris* from its hitherto optimal habitats and displaced *Pinus cembra* and *Pinus mugo* upwards. Spruce therefore succeeded, at least locally, in separating *Pinus sylvestris* forest from the developing dwarf pine belt.

Boreal (*Pinus*-Cyperaceae PAZ: CzS-4 p.p., ZS-3; *Picea-Pinus* PAZ: Mo-4; *Pinus* – NAP PAZ p.p.: SS-1 p.p.; *Pinus-Picea* PAZ: ZO-4, SS-2 p.p.)

This period is distinguished by a series of significant changes in the natural environment of the West Carpathians. About 8300 BP

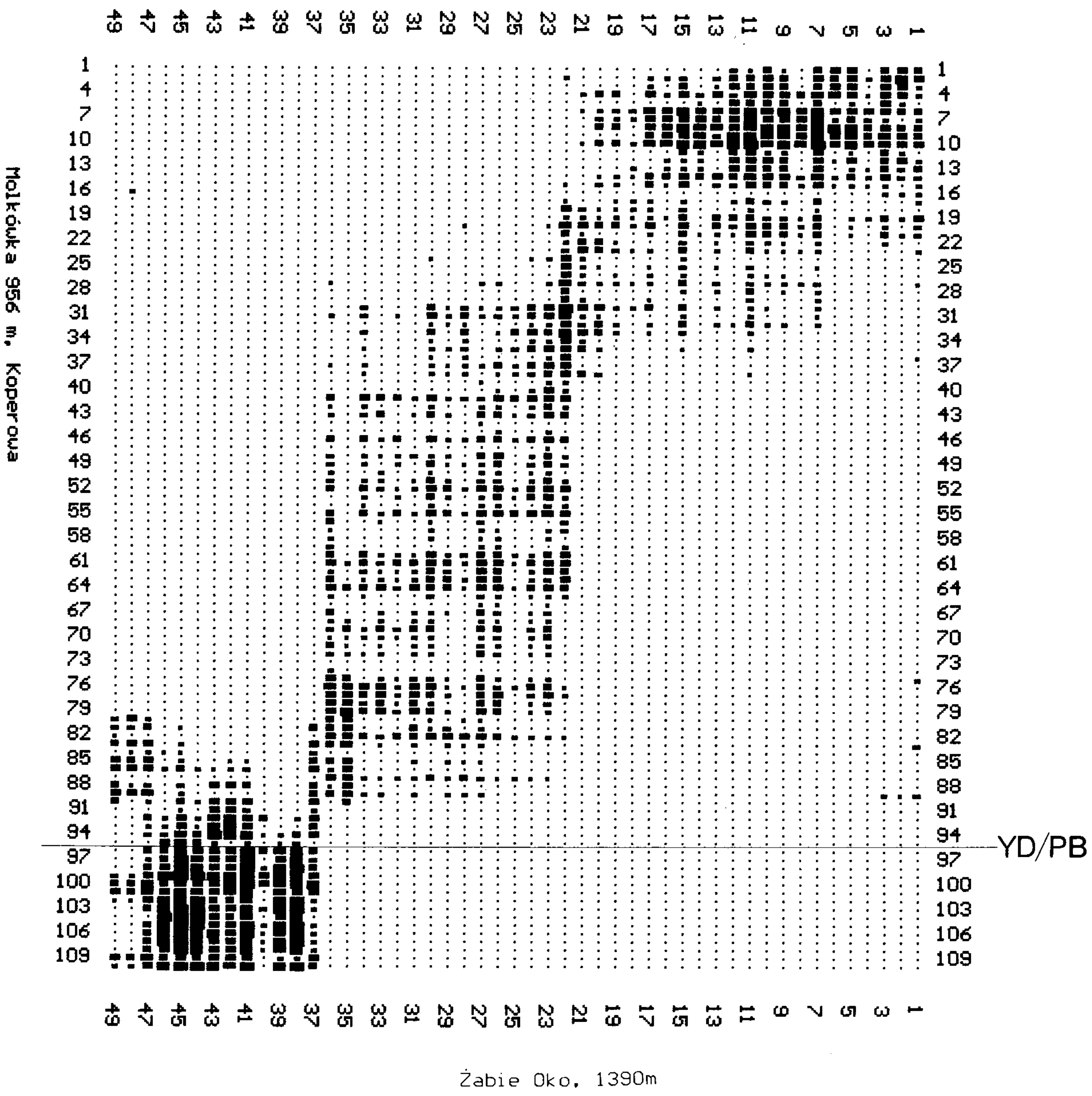

Fig. 17. Similarity matrix for the samples from Molkówka and Żabie Oko

the earliest peat-bogs of Podhale reached the ombrotrophic phase, so the rainfall in the growing season exceeded the rate of evaporation. The high pollen concentration in the profiles from Gąsienicowe Stawy confirms the existence of favourable thermal air currents in the summer months. From the Boreal of the High Tatras we have macrofossil material of *Pinus cembra*, *P. sylvestris/mugo*, *Picea abies*, *Picea* vel *Larix*, *Salix* sp. and *Sorbus* sp. (identified by Z. Tomczyńska) from an altitude of about 1400 m (Żabie Oko).

The progressive warming and increasing humidity of the climate brought a rapid expansion of species with higher thermal requirements. At that time in Podhale the formation of riverine woods comparable to today's woods of the Alnetum incanae or Fraxino-Ulmetum type was in progress (Obidowicz 1990). In these woods *Corylus avellana* may have been present; it also formed its own communities, mainly on south-facing slopes. The hazel phase began in Podhale about 8500 BP and lasted till about 7300 BP. In the Boreal portion of this phase the proportion of hazel pollen in the spectra exceeds 35%.

The problem of the role played by hazel in the Tatras in the Older Holocene cropped up in

Dyakowska's (1932) work. One of the profiles she analysed comprised lacustrine sediments from Litworowy Staw (1618 m) in the Gąsienicowe Stawy Valley. Because of the preserved original documentation it has been possible to work out this profile using the POLPAL programme (Fig. 18); Dyakowska limited her counting to several taxa of the AP in accordance with the state of knowledge at that time, omitting herbaceous plants entirely, while the total number of pollen grains counted did not generally exceed 200. This notwithstanding, the basic tendencies in the courses of particular curves are consistent with the profiles from other lakes of the Gąsienicowe Stawy analysed by me 60 years later. The proposed division into chronozones for the Litworowy Staw profile shows that it covers the whole of the Holocene. In this and other profiles studied by Dyakowska *Corylus* is represented by high proportions of pollen, a fact that led her to state that hazel had occurred then "in the whole Tatra region and much higher than it does now at that" and "we have to assume that then hazel spread about 500–600 m above its present range". As the highest site of this shrub known in the Tatras during her time occurred at an altitude of 1060 m (Kotula 1889–1890), in its optimal period hazel was supposed to have extended above the present timberline.

The new Tatra profiles presented here show that the Boreal was actually a time of spread for *Corylus*. The highest point on its curve for the Zielony Staw profile bears an interpolated date of about 8500 BP. In general, in the Tatras and Podhale, the highest values of the *Corylus* curves are therefore the determinant of the Boreal. The proportion of hazel pollen in the lowest sample from Kurtkowiec, approaching 45%, presents a problem of interpretation. The lack of radiocarbon datings could invalidate the statement that the lowest part of the profile extended into the Boreal. The similarity matrix for the samples from Kurtkowiec and Zielony Staw leaves no room for doubt that the correlation of these profiles began in the Atlantic (Fig. 19). As has already been mentioned, because of its open location in the Gąsienicowe Stawy Valley, Kurtkowiec is particularly contaminated with pollen of regional origin. At the same time it is to be expected that in the Boreal the range of *Corylus* persisted locally in the Tatras at least until the be-

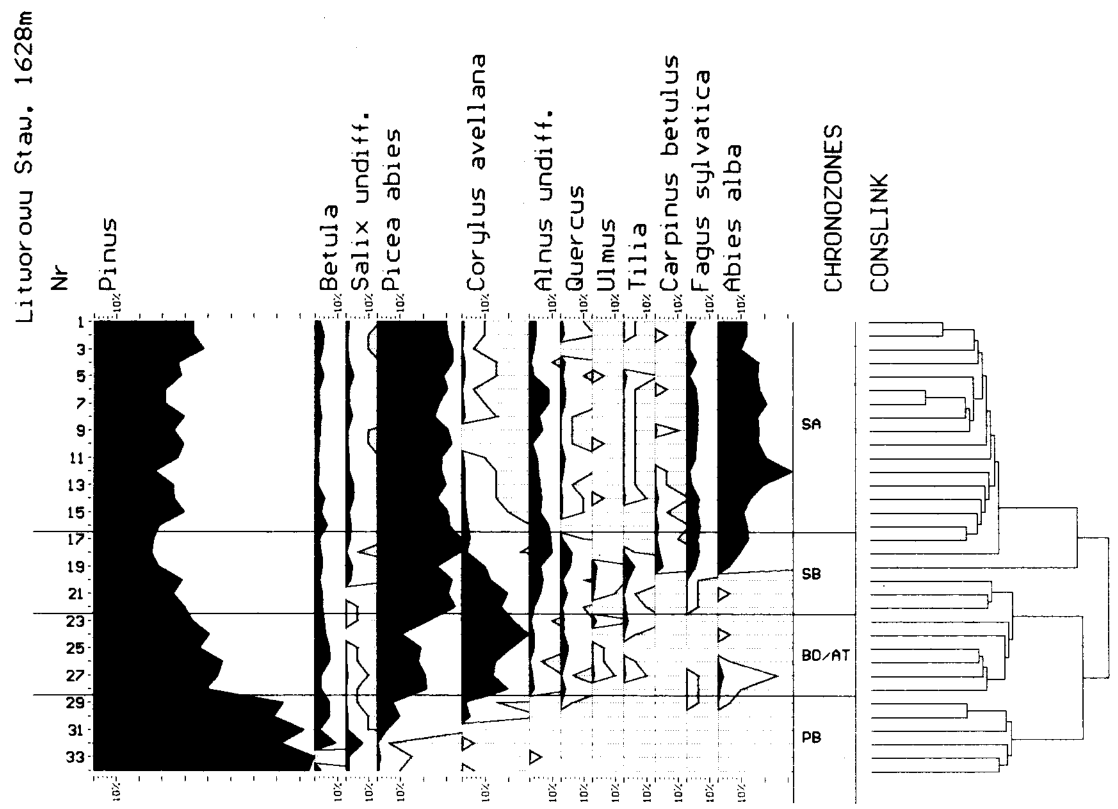

Fig. 18. Pollen diagram from Litworowy Staw (Dyakowska 1932), modified. The proposed chronostratigraphic division takes into consideration radiocarbon dated events in other pollen profiles from the Gąsienicowa Valley

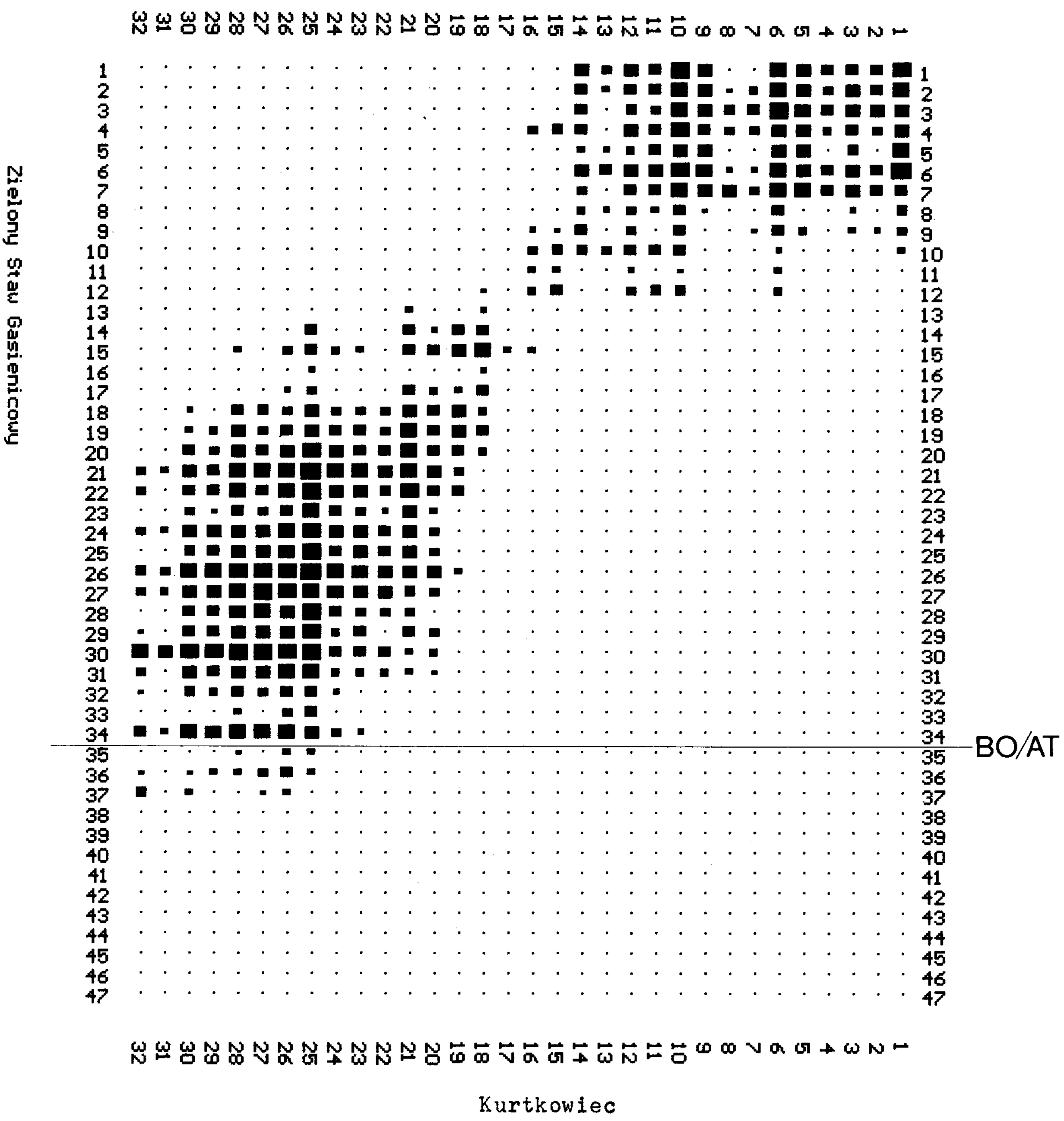

Fig. 19. Similarity matrix for the samples from Zielony Staw Gąsienicowy and Kurtkowiec

ginning of the Atlantic. Records of the phase of fast expansion of hazel in the profile from Czarny Staw have been eroded by mineral material inwash into the lake basin. This event (see page 190) was caused by high-energy geomorphic processes on the slopes surrounding the lake (Baumgart-Kotarba & Kotarba 1993). In the profile from Siwe Sady the highest point of the hazel curve occurs in the strongly compressed segment jointly comprising the Boreal and Atlantic periods.

The particularly high proportions in the spectra seem to indicate that hazel could even have penetrated deep into some of the forested valleys, notably in the West Tatras, so it could have occurred in the Starorobociańska Valley, where this shrub certainly formed large colonies (Obidowicz 1995). Unfortunately, this fact has not been confirmed as yet by any finds of hazel macrofossils.

In the Tatras the Boreal was above all a period of the progressive expansion of *Picea* and decrease in the area of *Pinus sylvestris*. Migrating rapidly up the northern slopes of the High Tatras, spruce surpassed the Żabie Oko contour line (see page 197). This was responsible for the masking of events from the forefields of the mountains in the profile from

Żabie Oko and, in consequence, the species which were expanding in lower lying places (*Ulmus*, *Corylus*, *Alnus*) are represented by low values.

The pine forests, ousted initially by spruce from low lying habitats (Molkówka), persisted longer in the West Tatras. Above the valley floors, at about 1200–1300 m, the pine forests were still merging into the belt of dwarf mountain pines throughout the Boreal, a fact indirectly confirmed by the present-day distribution of *Pinus sylvestris*, which is more abundant in the West Tatras, where it forms fairly large colonies (Łysek 1974). Scree vegetation, grassland, herbaceous and other treeless communities developed in the higher parts; nowadays they grow above the timberline. *Alnus incana* began to invade the lower valleys.

Basing their views on sedimentological criteria, Baumgart-Kotarba & Kotarba (1993, 1994) detected a cold climatic oscillation in the profiles from Czarny Staw Gąsienicowy and Żabie Oko and referred it to the Alpine Venediger oscillation. In the profile at Żabie Oko it is, in their opinion, represented by a 20-cm-thick insertion of coarse and medium sands below the level dated at 8330±120 BP (samples 38–40, Fig. 7). The palynological criteria demand that we should ascribe this segment univocally to the Younger Dryas. On the other hand, in Czarny Staw, a 5–10 cm thick layer of coarse sand (samples 22–23, Fig. 5), occurring at the beginning of the Atlantic in the palynological profile, would be a vestige of the Venediger climatic recession. In addition to the abnormally low pollen concentration, signalling the rapid nature of the sedimentation process, the part of the profile under discussion differs very distinctly, not only from the samples of the Boreal section, but also from the Atlantic spectra, in the proportions of *Pinus* and Cyperaceae pollen present. However, the presence of *Viscum*, which in the Tatras has not been noted from layers preceding the Atlantic phase of the Holocene, is decisive for including the profile in the Atlantic. The stratigraphic placing of the critical segment has been confirmed by numerical methods (Fig. 20). And so in my opinion the previously mentioned spontaneous inwash of minerogenic sediment into the basin of Czarny Staw, causing the erosion of part of the Boreal segment, took place at the beginning of the Atlantic.

There are, however, some findings which

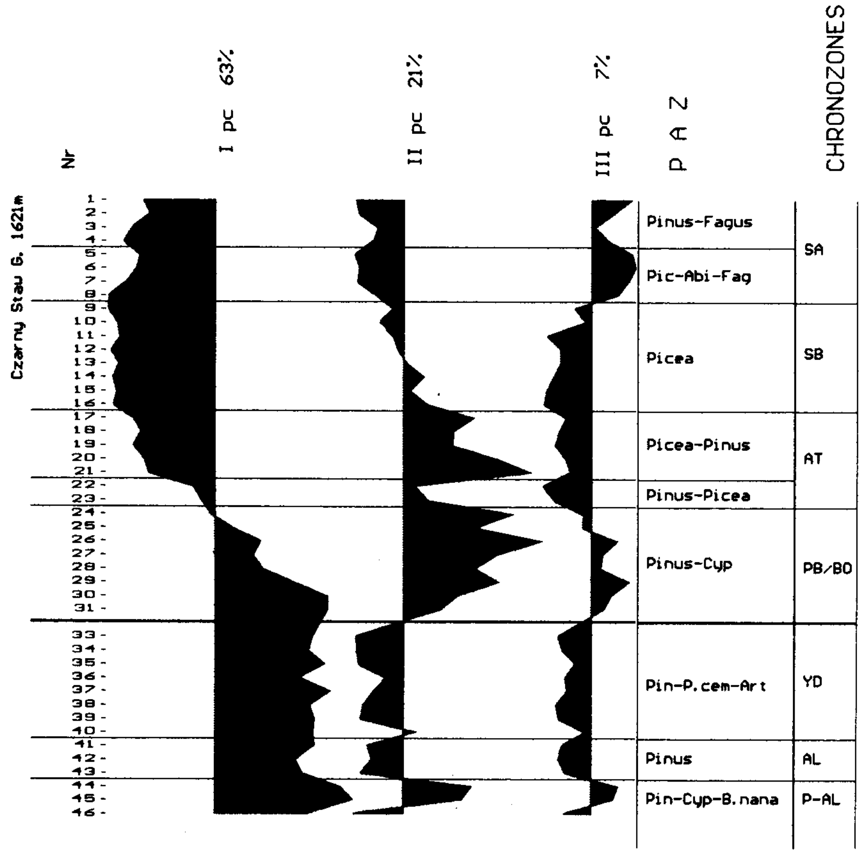

Fig. 20. Graph of principal component analysis performed on the major pollen taxa from Czarny Staw Gąsienicowy

can be interpreted as evidence of a cool oscillation coincident with the Venediger oscillation of the Alpine glaciers. In the course of the curves of pollen concentration for the profiles from both Czarny Staw and Zielony Staw Gąsienicowy, the phase of rapid rise at the beginning of the Holocene is followed by a considerable temporary fall (Figs 11 and 12). It may reflect cooler conditions in the growing season. Since it occurred during the period of rapid expansion of hazel in lower lying places, it could not have been very profound and has been recorded only in the region of Stawy Gąsienicowe.

Atlantic (*Pinus-Picea-Thalictrum* PAZ: Ku-1; *Pinus-Picea* PAZ: CzS-5, ZS-4, Ku-2, SS-2 p.p.; *Picea-Pinus* PAZ: CzS-6, ZO-5; *Picea* PAZ: Mo-5)

The Holocene thermal maximum occurred during the Atlantic, the mean annual temperature in Europe being 1–3°C higher than it is nowadays. Hess (1968) calculated that, for southern Poland, this difference was 1.8°C. The estimates of temperatures in the Atlantic may differ fairly significantly, depending on the criteria applied. Hantley and Prentice pointed out (Magny 1993) that the mean July temperature in the area of the high mountains of Central Europe was up to 5°C higher about 6000 years ago than it is at present.

Various authors place this maximum between 7000 and 6000 BP (Barash 1988) or between 6000 and 5000 BP (Budyko 1984). At about 6000 BP the glaciated area on the earth shrank to a minimum (Webb III 1985). At that time the rate of increase of peaty deposits in Podhale dropped to half the value found for the time interval 8570±90 – 7350±160 BP (Obidowicz 1990). In a number of profiles in the West Carpathians the organic parts representing the Atlantic (Besko – Koperowa 1970, Tarnawa – Harmata 1987) are extremely short, a fact which may be interpreted as the result of the compression of strongly decomposed peat.

In the Tatra profiles from the highest situations the Atlantic period begins with a remarkable increase in the AP values. This is connected with a further upward movement of forest in which the proportion of spruce rose, and the area occupied by dwarf mountain pine increased. At the lower lying sites (Molkówka, Żabie Oko) the percentage of spruce pollen in the spectra indicates the occurrence of dense forest. The distribution of Carpathian alder woods with added *Fraxinus* became stable at that time. The common presence of ash pollen in the profiles may also be due to the approach of riverine woods, growing in the area of forefields already in the Boreal (Obidowicz 1990). In the region of Gąsienicowe Stawy it was the time of development of herbs, with abundant *Thalictrum* (Kurtkowiec) and locally large proportions of *Filipendula* and Umbelliferae (Zielony Staw). At present *Thalictrum* absent from this part of the Tatras (Mirek oral comm.).

In the Siwe Sady region the occurrence of *Linnaea borealis* at that time is well documented. This species, characteristic of spruce forest in the subalpine belt of the Alps (Ellenberg 1978), is scarce in the Tatras now.

The history of the following Tatra peat-bogs has its origin in the Atlantic: Toporowy Staw Wyżni (1135 m), Wielka Pańszczycka Młaka (1265 m) and Kotlinowy Staw (1280 m). On the Slovakian side, among other sites, the bottom of Trojrohe pleso (1650 m) in the subalpine belt is also of Atlantic origin (Hüttemann & Bortenschlager 1987).

Out of the group of classical indices of the thermal optimum, *Hedera* appeared as early as the decline of the Boreal (Czarny Staw, Zielony Staw) and from the Atlantic onwards *Viscum* was also present. Both these genera persisted in the region of the Gąsienicowe Stawy Valley up to the beginning of the Subboreal and in profiles from lower lying sites up to the SB/SA turn.

The presence of *Typha latifolia* pollen in the Atlantic parts of the profiles from Gąsienicowe Stawy, if not of long-distance transport origin, suggests that the July isotherms of 10.5°C, marking the position of the climatic timberline, neared an altitude of 2000 m then. For orographic reasons, however, forest never extended so high in this part of the Tatras. On the Slovakian side the dense spruce forest ascended to 1900–2000 m at that time (Rybničkova & Rybniček 1993).

Since none of the profiles examined comes directly from an area of present-day *Pinus cembra* forest we lack confirmation of the considerable upward migration of stone pine woods, which now reach 1659m in the Valley of Rybi Potok (Myczkowski & Bednarz 1974).

Nevertheless, it seems possible that they went up to at least 1800 m a.s.l. Stone pine, which cannot compete with spruce in conditions of exceedingly high summer rainfall (Hofmann 1970), was restricted to small enclaves in the High Tatras. Only in the Atlantic segment of the Żabie Oko profile, located in the floor of the Rybi Potok Valley, does the curve of *Pinus cembra* come close to or exceed 1%. In the remaining profiles its pollen is either missing or sporadic. The distribution of spruce forest on the northern side of the Tatras did not attain its maximum altitude until the succeeding period.

The upward movement of the vegetation belts fundamentally affected the geomorphic processes on the Tatra slopes. The Atlantic is generally characterized by a decrease in their dynamics (Libelt 1990, Baumgart-Kotarba & Kotarba 1993).

Subboreal (*Picea*-Gramineae PAZ: WP-1; *Picea* PAZ: CzS-7, ZS-5, Ku-3, ZO-6, WP-2, Mo-5, SS-3; *Picea-Abies* PAZ: ZO-7, WP-3 p.p., Mo-6; *Picea-Fagus* PAZ: SS-4)

The Subboreal period was characterized by renewed intensification of the dynamics of the Tatra environment. The lacustrine deposits reflect the phases of mineral deposition and erosion, providing evidence of the great energy involved slope processes (Baumgart-Kotarba & Kotarba 1993). An increase in the activity of these processes can also be found at many sites in the West Tatras (Libelt 1990, Libelt & Obidowicz 1994).

The decline of the Atlantic and the beginning of the Subboreal (Starkel 1995) saw a phase of increased flooding in the Vistula Valley. The rate of peat accumulation rose exceptionally in the peat-bogs of Podhale at the beginning of the Subboreal, even though the composition of the peat forming communities remained unchanged. In the interval between 5000 and 4500 BP the rate went up to 171 mm/100 yrs. A fresh phase of peat formation began in Podhale, which saw the formation of new peat-bogs (Przymiarki), or the expansion of existing ones (Puścizna Rękowiańska, Bór na Czerwonem). These changes were obviously connected with the increased humidity of the climate. Since spruce was dominant then in tree stands it may be assumed that the greater humidity resulted from a decrease in the mean summer temperature and a consequent fall in the evaporation rate (Obidowicz 1990). The presence of *Hippophaë rhamnoides*, noted at the beginning of the Subboreal in the Valley of Gąsienicowe Stawy (Zielony Staw), was recorded for the final time from the Holocene of the Tatras. It indicates that at about 1600 m the mean July temperature was not lower than 11°C (Paus 1989). If the *Typha latifolia* pollen found here (Zielony Staw) was of local origin, July may have been warmer still.

In Southern Poland the mean annual temperature fell by 0.5°C in comparison with that in the Atlantic (Hess 1968), causing the climatic timberline to descend by about 100 m. However, it still ran high enough not to influence the potential course of the upper boundary of the spruce forest (see pages 198–199). It is not clear, however, how the stone pine woods responded.

The dominance of spruce, and certainly the formation of its major associations, are generally characteristic of the Subboreal in the West Tatras. This process shows local metachronicity and differs in duration in various parts of the West Tatras. In Podhale the spruce phase (*Picea* PAZ) is associated with the period between 5000 and 3670±70 BP (Obidowicz 1990).

The *Picea* PAZ covers the whole of the Subboreal (Czarny Staw, Zielony Staw, Kurtkowiec) or its older part (Żabie Oko, Wyżnia Pańszczycka Młaka, Molkówka, Siwe Sady). This means that spruce forest or forest with a spruce componend occupied the largest area in the Tatras in the first millenium of that period. The expansion of spruce forest was accompanied by an increase in the proportion of Ericaceae (*Vaccinium*-t., *Calluna*, *Ledum*). About 4500 years ago *Abies* and *Fagus* entered the zone of today's mountain forests. Beech appeared first, but the more invasive fir fairly quickly occupied a considerably larger area on the northern slopes. *Fagus* prevailed only locally in the West Tatras (Siwe Sady). At the same time *Carpinus* arrived in the lower lying regions and, together with the *Tilia*, *Acer*, *Fraxinus* and *Quercus* already present there, started to form a community of the Tilio-Carpinetum type, currently growing in the submontane (collin) belt.

A change occurred in the climate of Podhale between about 3600 and 3000 BP which in the peat-bog deposits of that region is recorded by layers of peat from hollows in reised bog dominated by *Sphagnum majus*. This may indicate that a remarkable amount of rainfall was transferred to the growing season (Obidowicz 1990). This change occurred simultaneously with the Löbben oscillation of glaciers in the Eastern Alps (Patzelt & Bortenschlager 1973). The beginning of this phase in Podhale was also accompanied by an intense expansion of *Abies*.

In the profile from Wyżnia Pańszczycka Młaka the date 3600±110 BP is somewhat in advance of the *Picea* PAZ/*Picea-Abies* PAZ boundary, but in the High Tatras an intensive spread of fir had already survived since about 4570±100 BP (see page 199).

In the Siwe Sady profile the date 3660±60 BP marks the beginning of the accumulation of peat from hallow in reised bog with *Drepanocladus fluitans*. The peat-bog was therefore permanently inundated and constituted a forest clearing, which in the diagram is expressed by a fall in the *Picea* curve and a rise in the proportion of Filicales monoletae. Spruce, however, persisted in the West Tatras at a greater altitude than it does today, as is clear from spruce cones found in the upper part of the Starorobociańska Valley, at an altitude of 1422 m, in the layer dated at 3590±80 BP (Libelt 1990). A pollen analysis carried out for this sample (Obidowicz unpubl.) points to a progressive thinning of these forests. Pollen analyses (Obidowicz unpubl.) made for the profile of deposits arising from the flow of rock debris filling Dudowe Stawki (1690 m), which are thought to be of Subboreal age (Libelt 1990), have shown that the timberline must have run considerably lower.

The area occupied by *Abies* and *Fagus* increased slightly in this part of the Tatras.

Subatlantic (*Picea-Abies-Fagus* PAZ: CzS-8, ZS-6, Ku-4, ZO-8, WP-4; *Pinus-Abies-Fagus* PAZ: ZS-7; *Pinus-Fagus* PAZ: CzS-9; *Abies-Fagus* PAZ: Ku-5; NAP-*Picea-Abies* PAZ: ZO-9, Mo-7; NAP-*Pinus-Picea* PAZ: ZO-10; *Picea*-NAP: WP-5; *Picea-Fagus-Abies* PAZ: SS-5; *Picea-Abies* PAZ: WP-3 p.p.)

The remarkable similarity of surface samples from particular belts to the Subatlantic segments of profiles located in corresponding belts, confirms that today's associations existed as early as the Subatlantic and that the changes which were taking place were merely quantitative in nature. They affected the sizes of the regions occupied by the main species of trees and shrubs defining particular belts.

The profiles from Gąsienicowe Stawy show a general tendency for the spruce forest area to diminish with a simultaneous expansion of fir and beech. This tendency, although not so distinct, can also be seen in the profiles from the mountain forest belts. It is generally accompanied by a thinning of the forest, indicated by an increase in the proportion of Filicales monoletae.

Taxus baccata appeared in the Subatlantic. It belongs to the set of trees like beech, fir and hornbeam, which became relatively late constituents of forest in the West Carpathians. The same situation occurred in the lowland of this part of Europe. The fossil remains of this species found so far are for the most part of Subatlantic age (Środoń 1975). To be sure, the first sign of the presence of yew in Podhale comes from as early as the Atlantic (Obidowicz 1990), but in attempting to penetrate the Tatras it faced competition with spruce and, later, with trees which formed the mixed mountain forest belt.

Now yew is threatened with utter extinction. Of the several tens of extant specimens of *Taxus* nearly all occur on the south-eastern and southern slopes, up to 1250–1300 m (Zembrzuski 1975).

In the younger part of the Subatlantic the boundaries of the altitudinal ranges of particular trees were descending. This process was, however, slow and *Abies*, for example, was still growing in the Siwe Sady region in 1050±50 BP (macrofossils), that is about 300 m above its present gregarious distribution range.

By interpolation the age of the first palynological data from Podhale containing information about changes produced by man can be calculated as 4100 BP. The first appearance of cereal pollen (*Trirticum*-t.) is dated at 3030±60 BP (Obidowicz 1990). The signs of man's economic activities are less distinct in the Tatra diagrams than in those from Podhale and, as a rule, reflect events occurring in the forefields of the Tatras. In the profile from Wyżnia Pańszczycka Młaka *Triticum*-t. pollen appears in sample No 27 bearing the date 3600±110 BP, making this occurrence of cereal pollen grains the earliest recorded in the West Carpathians. In the other profiles cereal pollen occurs in the mid-Subatlantic, therefore, they are generelly much later than those found in Podhale.

Of the profiles under discussion only three comprise a record of Holocene events which have continued until the present time. Of these Molkówka has no radiocarbon datings, but, in the profiles from Żabie Oko and Wyżnia Pańszczycka Młaka, the beginning of a steep fall in the AP values and a rise in the curve of cereals to 1% or higher is dated by interpolation at about 500 BP. From that time onwards some events in the natural environment of the Tatras can be associated with the presence of man, although the contemporary spectra, notably those from the belts above the timberline, call for much caution in their interpretation.

Our reluctance to recognise possible traces of man's economic activity in the Tatra forests is also due to the likelihood of their having been superimposed by changes in the mountain environment caused by the Little Ice Age which occurred in the Tatras between 1400 and 1857 A. D. (Kotarba 1995).

HISTORY OF THE FORMATION OF THE VEGETATION BELTS

As the profiles under analysis have come from various altitudes, it has been possible to attempt a reconstruction of the history of the vegetation belts. Cumulative diagrams (Fig. 21), listing the most important taxa defining individual belts, are helpful, in illustrating this problem. The profile from Puścizna Rękowiańska (Figs 2 and 21) represents Podhale and allows an appraisal to be made of the differences existing between the Tatras and their forefield in relation to the time of arrival and spread of important trees and shrubs.

Subalpine, alpine and subnival belts

The times of formation of plant communities characteristic of particular belts seem to be closely related to the altitudinal differences in the present-day plant cover of the Tatras. The higher vegetation belt the sooner started forming its floristic composition in the Holocene or already in the Late Glacial.

In his extremely interesting discussion on the problem of the steppe and tundra vegetation of the glacial periods, Frenzel (1987) enquired to what extent today's alpine vegetation is related to the stadial vegetation of the glacial periods. In order to establish the genealogy of the present-day communities of the alpine and subnival belts, and the open communities of the subalpine belt, we must go back to the Denekamp Interstadial of the last glaciation in the West Carpathians. The flora from Dobra, dated at 32550±450 BP (Środoń 1968) and that from Sowliny, bearing the date 29650±650 BP (Środoń 1987), come from that interstadial. Many species now extending into the alpine belt or having their main ranges there, and which also grow in the subnival belt, were present in those floras. These are species of scree communities and communities of hollows with late snow lie, like *Arabis alpina*, *Cerastium lapponicum*, *Doronicum stiriacum*, *Ranunculus montanus*, *Salix herbacea*, *Saxifraga oppositifolia*, *Silene cucubalus*, species of alpine grasslands, like *Callianthemum coriandrifolium*, *Dianthus speciosus*, *Dryas octopetala*, *Helianthemum alpestre*, *Leontodon pseudotaraxaci*, *Linum extraaxillare*, *Minuartia sedoides*, *M. verna*, *Polygonum viviparum*, *Potentilla aurea*, *Selaginella selaginoides*, *Silene acaulis*, *Soldanella carpatica* and many others. Their composition, complemented by the results of pollen analyses, serve as a basis for inferences about the similarity to alpine meadows occurring close to the timberline in the Tatras (Dobra) or the mountain tundra (Sowliny). One's attention is drawn to the presence of such genera and species in these floras which make up or are in genetic relationship with the continental steppe species of Asia *(Alyssum*, *Artemisia*, *Aster alpinus*, Chenopodiaceae, *Festuca*, *Filipendula*, *Helianthemum* and *Potentilla heptaphylla*). Discussions on the nature of the Late-Glacial floras in Central Europe (Walter & Breckle 1984, Frenzel 1987, Lang 1994) support the proposed classification of the formation then prevailing as steppe-tundra.

In the composition of their NAP values the Late-Glacial parts of the profiles, especially the Younger Dryas from Czarny Staw Gąsienicowy, Zielony Staw Gąsienicowy, Żabie Oko and Molkówka, show the dominance of *Artemisia*, and to varying degrees, Caryophyllaceae, Chenopodiaceae, Compositae *(Taraxacum*-t., *Aster*-t., *Anthemis*-t.), Cyperaceae, *Filipendula*, Gramineae, Rubiaceae and *Thalictrum*. Of the shrubs, *Betula nana*, *Ephedra*,

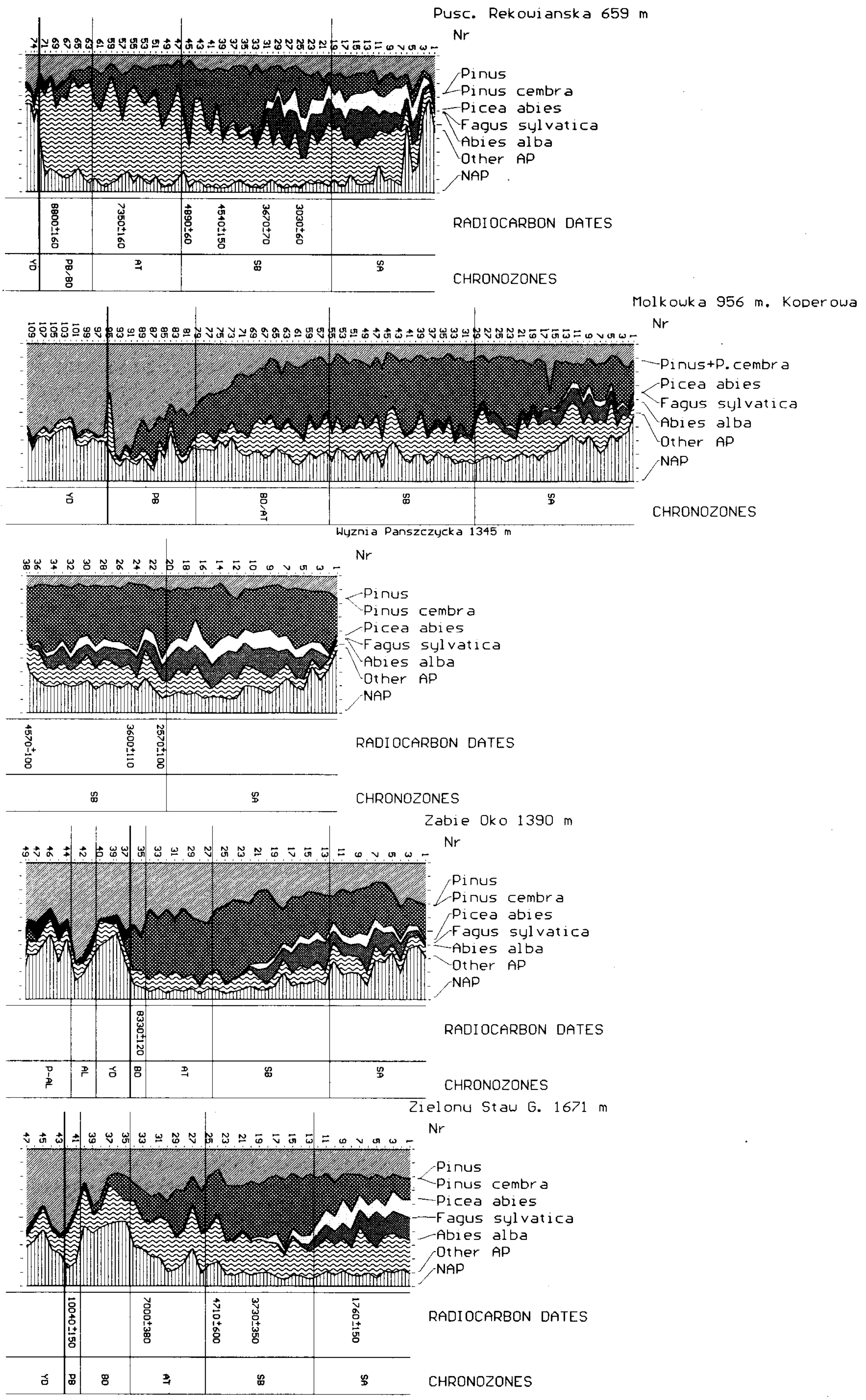

Fig. 21. Cumulative diagrams showing the Late Glacial-Holocene history of the formation of vegetation belts in the Tatra Mts

Hippophaë, *Juniperus* and *Salix* are present but Ericaceae are poorly represented. The periglacial vegetation of the Vistulian, and that from the decline of the Pleistocene, have, therefore, many features in common, lending weight to the view that the steppe-tundra formation persisted all through the Pleistocene and gave rise to the communities now growing above the timberline in the West Carpathians. The present-day associations of the highest belts are, however, different in their composition and relative abundance of species. They lack a series of taxa reported from the abovementioned fossil floras or the Late-Glacial segments of palynological profiles. Therefore, in today's flora of the Tatras *Alyssum montanum*, *Betula nana*, *Ephedra (fragilis*-t. and *strobilacea*-t.), *Hippophaë*, and *Thalictrum alpinum* are absent. Frenzel's (1987) opinion that the natural alpine vegetation of today is a Holocene formation is thus confirmed.

The beginning of the Holocene brought a vigorous development of grassland associations with sedges dominant in the Tatras. This can be seen clearly in the Preboreal-Boreal segments of the profiles from Czarny Staw Gąsienicowy and Zielony Staw Gąsienicowy. At the same time the role of some genera and families which constitute the characteristic features of the non-forest associations of the Younger Dryas, namely *Artemisia*, Chenopodiaceae, *Filipendula*, Gramineae and *Thalictrum*, is markedly restricted. The continued presence of considerable quantities of *Betula nana* pollen, and also the essentially unchanged proportions of the pollen of Caryophyllaceae, Compositae, Cruciferae, *Ranunculus* and Umbelliferae, mean that the elements of dwarf shrub tundra were mingling with the communities which would dominate the alpine belt during the Holocene. On the other hand, the scree associations may have persisted unchanged retaining a composition similar to that reconstructed on the basis of the Pleistocene floras.

The main non-forest communities, now growing from the subalpine belt to the subnival, had been formed by the end of the Boreal, as is indicated by the lack of significant differences in the lists of identified forms of NAP, from the Atlantic onwards. Changes occurring in the later phases of the Holocene may have consisted in the dying out of single species. For example the *Armeria* sp. which grew in the region of Gąsienicowe Stawy (Kurtkowiec) during the Atlantic, is now known only from sites on the southern side of the Tatras.

On the assumption that in today's altitudinal arrangement of species some traces of past history are preserved (Szafer 1966), we may deduce that dwarf mountain pine in association with birch, was among the first trees and shrubs to enter the Tatras at the beginning of the Holocene. The difference in the size of pollen production now found between the pine stands and the belt of mountain pine suggest that the fall in the *Pinus* curves at the beginning of the Holocene is accounted for by the replacement of *Pinus sylvestris* by *Pinus mugo*. The rainfall total, increasing with altitude, contributed to the altitudinal division of the area occupied by these two species. In its present dense stands in the Tatras, *Pinus sylvestris*, as a rule, does not go beyond the zones in which the annual rainfall is about 400 mm lower than in the subalpine belt of dwarf pine (Atlas TPN 1985). The problem of the time of formation of the association Pinetum mughi carpaticum remains open, although the existence of its primary framework was evident as early as the decline of the Boreal.

The remarkable spread of *Corylus* in the Boreal, discussed in pages 187–189, was an important factor in the colonization of the Tatras by trees, which, in the later periods of the Holocene, formed mountain forest belts. One may justifiably conclude that hazel, which is able to occupy terrain with shallow, stony soils, acted as a pioneering species in the Tatras by preparing the habitats for the expansion of trees into the present-day belt of mountain forests.

Upper montane belt (*Picea abies*)

The presence of spruce in the West Carpathians is proved by pollen grains and macrofossils found in the Vistulian floras varying in age (Środoń 1968, Mamakowa et al, 1975).

Its occurrence in the vicinity of the Tatras in the Late Glacial, according to some authors, at least from the Alleröd, is undeniable (Koperowa 1962, Środoń 1967, Ralska-Jasiewiczowa 1982). Środoń (1967), however, when discussing the presence of *Picea* in the relevant segment of the profile from the "Na Grelu" peat-bog (Koperowa 1962), writes that rather large amounts of pollen of a series of thermophilous trees, "no doubt redeposited", were found in this sediment. He also recalls Szafer's (1935) earlier opinion that centres of spruce expansion existed in the Tatra region in the post-glacial period. Środoń's (1990) statement that there are no grounds on which to deny the possible existence of spruce refuges in the West Carpathians may be regarded as valid, because in some sites it is represented by macrofossils, even continuously, in the Late-Glacial segments.

Doubts accompanying the analysis of these last 13000 years of spruce history mainly concern the Tatras themselves, for there the vestigial quantities of *Picea* pollen in the Alleröd portions of the profiles from Żabie Oko and Czarny Staw are undoubtedly of regional origin. Consequently Krupiński's (1984) opinion that spruce was growing in situ in the Tatras, even before the Alleröd, seems questionable, even though its comparatively distinct presence in the pre-Alleröd part of the Żabie Oko profile seems to support his view.

The spruce forest communities in the West Carpathians underwent a marked reduction in the Younger Dryas because of an essential change in the climate. Nonetheless, spruce persisted there untill the Holocene, as is clear from the presence of macrofossils from as early as the beginning of the Preboreal (Koperowa 1962, Pawlikowa 1965), and a simultaneous, relatively steep rise in the *Picea* curve in the profiles from Podhale (Koperowa 1962, Obidowicz 1990).

While not denying the existence of Late-Glacial refuges of *Picea abies* in the West Carpathians, one should not overestimate their role in the later history of the spread of this species, for it is probable that this tree arrived in the West Carpathians from its refuges in the South Carpathians, covering that distance at a speed of 230–250 m/year (Lang 1994). It had been spreading in Podhale since the beginnings of the Holocene, where, as has been mentioned above, it had survived the Late Glacial. In the Tatras its expansion was somewhat delayed (Fig. 21) and began in the course of the Preboreal, as recorded in the profile from Molkówka (956 m). In the remaining profiles the rate of ascent of the curves seems to depend on the altitude of the site. In the Boreal, spruce crossed the 1390 m contour line in the High Tatras so the site at Żabie Oko found itself in the middle of a spruce forest. This can be inferred, not only from the behaviour of the *Picea* curve and the accumulation of its macrofossils, but also from the fact that after the date 8330±120 BP the concentration of pollen of herbaceous plants fell to its lowest values in the whole profile, accompanied by their low proportion in the percentage diagrams.

In the Atlantic, some 8000 to 5000 years ago, the area occupied by spruce was still increasing, a fact reflected in all the profiles comprising this phase of the Holocene.

In the West Tatras the upper boundary of spruce forest had already been formed, in contiguity with the dwarf pine belt, by the end of the Atlantic. It reached the altitude of Siwe Sady, i.e. above 1500 m, as is indicated by the presence of *Picea* wood at the bottom of the Subboreal chronozone of this profile.

The phase of maximum spread of this tree in the Tatras occurred in the older part of the Subboreal (5000–4000 BP), virtually in agreement with Środoń's (1967) view. At that time a distinct correlation appears between the spectra of the pollen zones and the modern pollen rain spectra of the present-day upper montane belt (Fig. 22). It may therefore be inferred that the associations resembling today's spruce stands in the coniferous mountain forest belt developed at the beginning of the Subboreal. Wyżnia Pańszczycka Młaka, where deposits began to accumulate in 4570±100 BP., originated as a forest bog surrounded by spruce woodland.

At the beginning of the Subboreal, spruce forests made their appearance in the Gąsienicowa Valley. Both the AP/NAP ratio and the proportions in the spectra show that spruce was present in the neighbourhood of Gąsienicowe Stawy. The arrival of the timberline in this region is confirmed in the profile from Zielony Staw Gąsienicowy by the presence of *Picea* needles, dating from the decline of the Atlantic.

In the younger part of the Subboreal the area occupied by spruce began to contract in favour of *Fagus* and *Abies*, but its upper border still persisted high up.

The problem of the fluctuation of this boundary in the Holocene has long been discussed. In our present discussion we are concerned with the answers to two questions:

- when did this boundary have its maximum altitudinal range ?
- how high did it run at this time ?

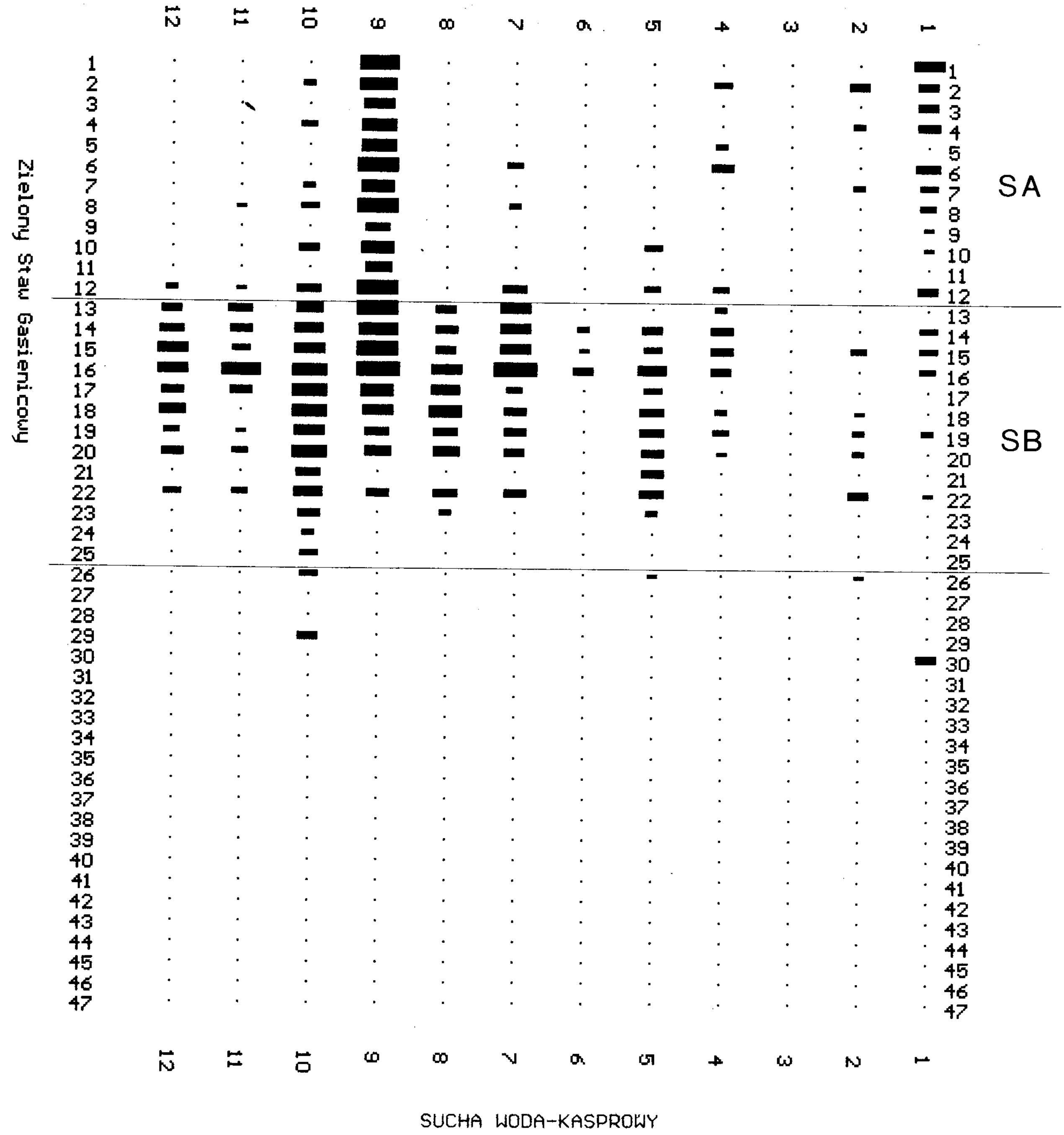

Fig. 22. Similarity matrix for Zielony Staw Gąsienicowy and surface samples from the longitudinal profile of Sucha Woda Valley – Kasprowy Mt showing the possible correlation since the Subboreal

Generally authors are rather agreed that the timberline extended highest in the Atlantic (Fabijanowski 1962, Ralska-Jasiewiczowa & Starkel 1975, Krupiński 1984). Opinions differ, hovewer, as to its highest position, with altitudes of 1900 m being given by Fabijanowski (op.cit.) and even 1950 m by Krupiński (op.cit.). The profiles presented in this work enable us to discuss these opinions critically.

The time at which the highest range of spruce forest occurred must have coincided with the above-mentioned maximum spread of *Picea* in the Tatras in the older part of the Subboreal (5000–4000 BP). We see therefore a distinct delay of that phenomenon in comparison with the period of the thermal optimum. This was also observed, at least locally, in the Alps (Kral 1979). The profiles presented provide confirmation of the fact that *Picea* migrated above the Kurtkowiec contour line (1686 m), the highest examined of the lakes of Gąsienicowe Stawy. As further evidence we may also cite the highest present-day situation of the spruce association stands described by

Myczkowski (1964) from about 1700 m in the dwarf pine belt. It seems fairly certain that the upper boundary of spruce forest during its highest range in the Gąsienicowe Stawy region ran at an altitude of 1700–1750 m, that is 150–200 m higher than it does now. On the other hand, at that time in the West Tatras, at least in the Siwe Sady region, it did not extend above 1550 m (Libelt & Obidowicz 1994), chiefly because of orographical conditions.

Lower montane belt
(*Abies alba*, *Fagus sylvatica*)

In order to reconstruct the history of the formation of the mixed mountain forest belt it is necessary to investigate the history of the two species which define this belt, namely *Abies alba* and *Fagus sylvatica*.

Fir did not occur in the floras of the younger interstadials of the last glaciation, described from several sites in the Carpathians and their forefield (Środoń 1983). Its presence in Podhale in the Alleröd (Koperowa 1962) is called into question, as redeposition cannot be ruled out (Ralska-Jasiewiczowa 1983).

An isopollen map for *Abies* of the area south of the West Carpathians shows that the main direction of migrations 5000 years ago was from the south-west (Rybničkova & Rybniček 1988). A similar direction of migration is shown by the isopollen map of the Sudetes and West Carpathians for the same period (Ralska-Jasiewiczowa 1983). Basing his opinion on more recent profiles, Lang (1994) pointed out that *Abies* arrived in the Carpathians from its refugia in the Balkan Peninsula. It appeared in the northern forefield of the Tatras (Podhale) about 5000 years ago and its intense expansion, visible in the profile from Puścizna Rękowiańska, started 3600 years ago (Obidowicz 1990).

Earlier, as much as 4500 years ago, fir began to spread in the Tatras themselves, ousting spruce from the lower lying places or forming stands in company with it. Some suggestions concerning the causes of such a considerable delay in the expansion of *Abies* in Podhale in relation to the Tatras themselves can be found in the rich palynological literature relating to the Alps. The reasons given for the delay in the expansion of fir observed in various parts of the Alpine chain include different distances from its refugia, climatic differences (mainly in humidity), and also competition from the tree stands already present (Müller 1972, Wegmüller 1977, Schneider 1978). At the time of the arrival of fir at the foot of the Tatras, about 5000 BP, their northern forefield was to a large extent covered by peat-bogs, for the most part already ombrogenic (Obidowicz 1990). The river valleys were occupied by riverine woods of the Alnetum incanae type and others which can be compared with the present-day Fraxino-Ulmetum or Carici remotae-Fraxinetum associations. Mixed forests with *Tilia cordata*, *T. platyphyllos*, *Acer* sp., *Fraxinus excelsior*, *Ulmus* sp. and, in places, *Quercus* sp. grew on the south-facing slopes. These habitats were inaccessible or, under the climatic conditions of that time, difficult for fir to access.

Nowadays a very dynamic intrusion of firs into the pine stands is observed in the Carpathians. This process is probably caused by the presence of dispersed light rich in the blue part of the spectrum, humus of the moder type and a favourable set of soil fungi (Jaworski & Zarzycki 1983). Similar conditions cause the replacement of spruce by fir in mixed stands and, therefore, such conditions may have existed about 4500 BP in the zone of today's lower montane belt, dominated by spruce woodlands at that time. The humidification of the climate at the beginning of the Subboreal favoured the expansion of *Picea*, but *Abies*, resembling spruce in its moisture requirements (Jaworski & Zarzycki 1983), as a shade tolerant species could compete with it effectively. Fir began entering the Tatra forest communities first in the lower parts of the Sucha Woda Valley and the Pańszczyca Valley (Wyżnia Pańszczycka Młaka); somewhat later, but still before the mid-Subboreal, it appeared in the Rybi Potok Valley (Żabie Oko) and in the West Tatras (Siwe Sady). In Podhale suitable conditions for its appearance existed from 3670±70 to 3030±60 BP, when the rainy spells shifted to the growing season (Obidowicz 1990). This was also when fir covered the largest area in the West Carpathians throughout its Holocene history.

The glacial refugia of *Fagus sylvatica*, very much like those of fir, were situated in the mountains of the Apennine and Balkan Peninsulas (Lang 1994 and literature quoted there). The route of its migration from there to the West Carpathians resembled that of *Abies*.

The speed of spread for both species was similar, with a maximum of 300 m/year (Lang 1994). Their time of arrival in the West Carpathians, however, varied somewhat. While it is indisputable that *Abies* arrived about 5000 years ago, the beginning of the continuous curve of *Fagus* occurred earlier.

The first isopollen of beech to the south of this part of the Carpathians, in the territory of the former Czechoslovakia, can be reconstructed for the time around 7000 BP, the Hungarian Lowland being one of the routes of migration suggested (Rybniček & Rybniček 1988). The approaching of *Fagus* to the West Carpathians is indicated in the highest situated Tatra profiles, starting from the Boreal. In Podhale the continuous curve of beech emerges in the Atlantic and attains nearly 3% (Puścizna Rękowiańska). Consequently we can say that this tree arrived in the West Carpathians more than 5000 years ago. The picture of the process of its further penetration is equivocal. There is a widely accepted opinion that beech expansion was associated with neolithic colonization, as a result of the concurrence of the development of this settlement and the rapid rise in the proportion of beech pollen in the diagrams at the transition of the Atlantic into the Subboreal (Środoń 1990).

Two profiles representing Western Podhale (Grel – Koperowa 1962 & Puścizna Rękowiańska – Obidowicz 1990) point to its presence as early as the Atlantic. In other sites in the forefield of the Tatras (Zubrzyca Górna – Stuchlikowa & Stuchlik 1962, Palenica – Harmata 1969, Bór na Czerwonem – Obidowicz 1990) beech was already established in the Subboreal, and locally (Przymiarki – Obidowicz 1990) attains higher values than fir in the spectra. In the Bryjarka profile (Pawlikowa 1965), from eastern Podhale, beech pollen did not appear before the younger part of the Subatlantic and even then in vestigial quantities.

Both these species may have contributed to the formation of the Tilio-Carpinetum-type forest, which had been developing there since the mid-Subboreal. Today these subcontinental lime-hornbeam-oak woods are preserved in the submontane belt of various parts of the Carpathians (Matuszkiewicz 1981, Dzwonko 1986).

In nearly all profiles from sites in the present lower and upper montane belts, comprising sufficiently long sequences of deposits, the continuous curve of beech precedes the beginning of the continuous curve of fir, indicating the order in which these trees entered the Tatras. Only in the profile from Molkówka is the situation reversed. Differences between the times of arrival of *Fagus* and *Abies* in the valleys and on the northern slopes did not prevent the more expansive fir from achieving a distinct dominance which it maintained during the Subboreal.

The upward progression of these two trees from the altitude of the Gąsienicowe Stawy Valley was not apparent before the beginning of the Subatlantic, when the area occupied by spruce forests was shrinking noticeably.

Our present knowledge of beech ecology seems adequate for explaining its relatively slow colonization of new terrain in comparision with fir when both species had arrived almost simultaneously. We need not invoke man's interference, although in the case of the Tatras and Podhale this would be justified well enough. The significant factor impeding the expansion of beech was rodents feeding on its seeds. Even under favourable environmental conditions and with good beechmast crops, they may have prevented beech from regenerating successfully and in the struggle for new areas it would often have been defeated by fir, whose seeds were to a considerably smaller degree threatened by rodents (Dzwonko 1990).

The account of the differentiation of the lower montane belt can be supplemented with the history of *Fraxinus excelsior* and *Acer pseudoplatanus*.

Both these species and also *Ulmus scabra*, behave like beech with respect to their altitudinal distribution. This has been confirmed in the Alps (Landolt 1983) and supposedly a similar situation prevails in the Tatras (Mirek & Piękoś-Mirkowa 1992, Myczkowski & Lesiński 1974).

It is not quite clear where the refugia of *Fraxinus* were situated. Perhaps they were the same regions in north-western Greece in which beech and fir survived (Willis 1992). Mayer (1984) localized them in southern and south-western Europe. Ash may have persisted in the Iberian Peninsula, in the Alps and in Bulgaria (Lang 1994). A continuous curve of this tree appears in diagrams from the south of the Czech Republic at the PB/BO boundary and during the Boreal it began to spread, contributing to the formation of the riverine woods of that time (Jankovska 1980).

Fraxinus appeared in the West Carpathians before *Abies* and *Fagus*, which was possible because it migrated at almost twice the speed of fir and beech. In the profiles from Podhale its continuous curves appear at the outset of the Boreal (Puścizna Rękowiańska), but it is sometimes represented only in vestigial form (Grel, Bryjarka). At the same time it turned up also at the base of the High Tatras (Żabie Oko).

The optimal development of the Fraxino-Ulmetum- or Carici remotae-Fraxinetum-type forest of that time occurred in the Atlantic (Obidowicz 1990). Temperature inversion and the formation of cold air pockets on the northern side of the Tatras favoured the movement of forest containing *Fraxinus* and *Ulmus* to the higher regions of Podhale. Ash also entered the Tatras then, as part of the developing Alnetum incanae, no doubt in rather high places at that, as it is noted from the Atlantic segments of the profiles from Gąsienicowe Stawy. The process still continued during the Subboreal which, in some regions of Podhale (Palenica) turned out particularly favourable for forests containing ash. The arrival of *Abies* and *Fagus* deprived *Fraxinus* of most of its stands, pushing it down to lower lying areas, although a small slight number of specimens managed to remain in the Alnetum incanae and beech-fir forests. This was possible because of temperature changes in the climate at about 5000 BP. It is known that the occurrence of ash depends on the length of the frost free period (Hulden 1941). At present, in the lower montane belt, this averages 135 days (Hess 1965) and this fact, as well as human activities in historical times, adequately account for the sporadic presence of *Fraxinus* in the Tatra forests. However, it is unnecessary to question whether or not this tree is an indigenous species in the Tatras.

Lang (1994) mentions eight possible refugia for the genus *Acer*, chiefly in western and south-western Europe but also in the Alps and Carpathians as well as the east of Europe. The first pollen grains from this genus appeared in the forefield of the Tatras in the Boreal (Grel, Puścizna Rękowiańska), while in the diagrams from the younger Atlantic parts of the profiles from Podhale and the Tatras *Acer* forms continuous curves. It is impossible to decide which species it was, but in the then developing associations comparable to today's Carici remotae-Fraxinetum or Phyllitido-Aceretum it could have been *Acer campestre*, *A. platanoides* or *A. pseudoplatanus*.

As a result of the cooling and humidification of the climate, which started about 5000 BP, forests with *Acer campestre* and *A. platanoides* dropped to below 700–800 m where they joined the forest communities of the Tilio-Carpinetum type, developing at that time. On the other hand, sycamore (*A. pseudoplatanus*), more frost resistant than beech or yew (Bednarz & Krzaklewski 1975), infiltrated the developing beech-fir woods of the lower montane belt and the Carpathian sycamore wood (Sorbo-Aceretum carpaticum), of the upper montane belt.

Dense populations of sycamore are not found above 1350 m in the Tatras today, but single specimens occur even in the region of the timberline (Bednarz & Krzaklewski op.cit.).

The framework of the associations of the present-day lower montane belt was therefore formed during the Subboreal. A critical stage in this process was the separation of the areas dominated by beech-fir forest from the belt of spruce forest. However, the moment when these associations became identical with today's, indicated by analyses of the matrices of similarity between surface samples from the transects in the lower montane belt and the samples from various profiles, dates, at the earliest, from the beginning of the Subatlantic (Obidowicz unpubl.). This was when the process of differentiation of the Tatra vegetation belts, controlled mainly by climatic zonation and ecological processes ended.

CONCLUSIONS

1. There is a relationship between the zonal arrangement and the period in which the plant communities contributing to the formation of particular belts arose. The associations of today's alpine and subnival belts had developed first, by the end of the Boreal. The association of dwarf pine in the subalpine belt is undoubtedly of similar age. The differentiation of the mountain forest belts, i.e. the separation of spruce forest from the forest with beech and fir took place during the Subboreal. A compari-

son of the subfossil spectra with modern ones shows that the clear-cut boundary of correlations never falls below the AT/SB chronozone boundary. The associations of the upper montane belt, as defined today, came into existence in the first millenium of the Subboreal, whereas those of the lower montane belt arose at the beginning of the Subatlantic. The movements of their boundaries, stimulated by changes in the climate and by competition, were still going on in the Subatlantic.

2. In various parts of the Tatras, and in various phases of the Late Glacial-Holocene history of their plant cover the timberline was formed by pine, stone pine, stone pine-larch, stone pine-spruce and spruce forests. In view of the lack of ^{14}C datings for subfossil pieces of wood from the Atlantic and Subboreal, the highest position of the timberline has been estimated on the basis of the presence of other macrofossils (seeds, needles, periderm), palynological findings and also on the contemporary gregarious range of dense tree populations and the range of their single specimens. Spruce forest reached a maximum altitude of 1700–1750 m in the Subboreal. The stone pine (stone pine-spruce) forest may even have excended above 1800 m, perhaps as early as the Atlantic.

3. By comparision with the short-lived climatic oscillations described from the Holocene of the Alps, the pollen profiles presented here suggest that corresponding oscillations in the Tatras occurred in the time ranges from approximately 8500–8000, 5000–4500 and 3600–3000 BP. The records are not uniform, but depend on the situation of the given profile. This means that the changes attributed to these oscillations can be inferred from the course of particular curves, the type of deposit or pollen concentration and, more rarely, from all these elements simultaneously. In this connection, the actual basisfor these changes calls for confirmation by other methods.

4. Knowledge of the history of the main trees which make up the Tatra forests can be put to good account in renovating these forests, for it seems sensible not to reintroduce those species which disappeared from the stands in particular valleys for climatic reasons or through competition. This applies especially in the neighbourhood of the timberline.

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