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RECENT POLLEN SPECTRA OF THE MOUNTAIN FORESTS OF THE LAGODEKHI RESERVATION (EAST GEORGIA)

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ABSTRACT. Floristically, the region under investigation is unique. Numerous Tertiary relicts and endemics are concentrated here which are not only of Colchis, but also Talysh origin. Comparison of the pollen spectra with the vegetation composition on 20 test sites from different altitudinal zones, showed a number of important factors of subfossil spore-pollen spectra formation. Compared with the mountains of West Georgia the role of transported pollen here, from regions both near and far, is of much greater significance. The amount of pollen of *Fagus orientalis* is underestimated, while that of *Carpinus caucasica*, on the contrary, is overestimated. The roles of *Acer, Fraxinus, Hedera* and *Daphne* pollen shows up badly in the soil spectra.

KEY WORDS: East Georgia, broad-leaved forest, pollen transportation, pollen preservation

INTRODUCTION

The unique nature of Lagodekhi, and especially its vegetation, has attracted scientists attention since the last century. As in Colchis, a lot of Tertiary relicts and endemics of the Caucasus grow here. It is important, too, that, beside the Colchis elements, occurs in Lagodekhi vegetation of Talysh (Hyrcanian) origin (Dolukhanov 1942). Among the initiators and enthusiasts who organized the reserve there were L. F. Mlokosevich (1875, 1916), N. I. Kuznetsov (1911) and D. I. Sosnovski (1911). In 1912, due to their great efforts, the Russian Academy of Sciences and the Caucasian Department of the Geographical Society declared the gorge of the rivers Lagodekhiskhevi and Shromiskhevi as reservation. At the very beginning its area was no more than 3500 ha (Sokolov & Syrojechkovsky 1990). However, later on the reservation gradually expanded and at present it covers 17 818 ha. Over 2/3 of the territory is occupied by forest (12 146 ha).

The altitude ranges from 400 to 3500 m. Therefore, there exist several altitudinal zones. In each of them we took a few tens of samples for palynological analysis. For each sampling site a botanical description is given according to the Braun-Blanquet (1951) method.

The main purpose of our investigations was to seek answers to the following questions: does the composition of the pollen spectra correspond to that of the forest in each distinct altitudinal belt, what role in the spectra is played by transported pollen from neighbouring zones and what is the role of long-distance transport of pollen?

MATERIALS AND METHODS

The sampling of material was made during expeditions in June of 1989. Geobotanical descriptions of the vegetation were given for 20 test sites and at the same time soil samples were taken for spore-pollen analysis. At least 3 samples were taken from each site. Laboratory treatment of the soils was carried out in the Institute of Palaeobiology of the Georgian Academy of Sciences, first by the alkaline method and then by acetolysis. The pollen diagrams were obtained after computer processing, according to the program "Tilia" by Eric Grimm. Pollen and spore photography was carried out in the Palaeobotanical Department of the W. Szafer Institute of Botany, Polish Academy of Sciences.

PHYSICO-GEOGRAPHICAL CHARACTERISTICS

The reservation is situated in the far north-eastern part of Georgia (Fig. 1). The distance

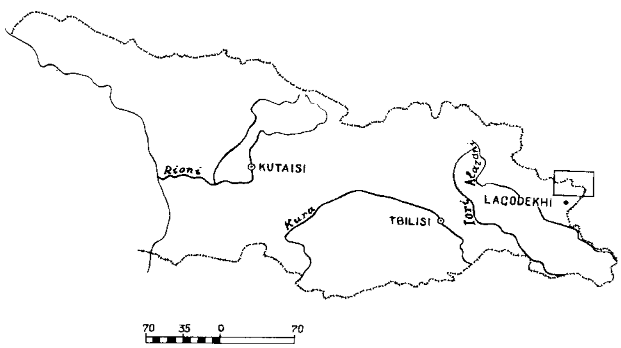


Fig. 1. Map of Georgia with location of the region under study

from Tbilisi to Lagodekhi is 162 km. The southern border of the reservation coincides with the lower tree line at an altitude of 450 m. The northern border runs along the Watershed Range of the Great Caucasus, i.e. it coincides with the state frontier with Daghestan. In the east it borders upon Azerbaijan along the river Matsimis-Tskali and in the west upon the Lagodekhi forest farm (Mamisashvili 1975).

The relief is characterized by deep dissection and steep slopes. All the main ridges descending meridionally southwards from the Watershed Range to the Alazani plain are the result of a fault. This site contains the narrowest southern slope of the Greater Caucasus, its width not exceeding 15 to 20 km (Maruashvili 1970). The main ridges are narrow, wooded and deprived of river terraces, a result of their geological structure. Rather soft mountain rocks dominate i.e. clayish shales and sandstones of the Jurassic. Erosion caused by rivers here has exposed Cretaceous deposits as well. The top part of the Watershed Range has a smoother relief.

The drainage system is well developed. The main rivers are the Shromis-Tskali, Ninos-Tskali and Lagodekhis-Tskali all flowing to the Alazani river basin.

The climate of the Lagodekhi Reservation changes with altitude. According to data from the meteorological station located at an altitude of 435 m in the town of Lagodekhi, the mean annual air temperature is 12.6° C. The January mean is 0.9° C while that in August is 24.1° C. The frost free period lasts for 239 days, from March 26th to November 21st. The growing season lasts for 209 days on average.

The mean annual rain fall does not exceed 993 mm with most occuring in the warm season. The average air humidity is 72% (Spravochnik po klimatu SSSR).

According to data from a second meteorological station located at an altitude of 1980 m, the mean annual temperature falls to 5.2° C. The temperature of the coldest month (February) is −4.2° C, while that of the warmest one (July) is 14.3° C. The growing season is reduced to 120 to 130 days. The annual rainfall rises to 1877 mm.

Because of the gradients existing here, at an altitude of 2600 to 3000 m the annual rainfall increases to 2000 to 2200 mm, i.e. it is almost twice as great as that in the lower and middle mountain zones. The mean annual temperature does not exceed 2° to 4° C. The growing season lasts only 2–3 months.

Because of the closed relief, the winds in the forest area are not strong. Usually only ten days a year are windy. Nevertheless in 1924, 1928 and 1957, hurricanes destroyed great parts of the forest. Not only beech and hornbeam woods, but oak forest was destroyed too (Lachashvili & Mamukelashvili 1986). In the upper parts of the mountains, west winds prevail. Along river gorges there are mountain-valley air currents.

Large differences of altitude, sharply dissected relief, variation in gradient and aspect of mountain slopes, deep gorges and rivers create very complicated physico-geographical conditions, in which the recent vegetation cover has arisen. 72% of the territory is occupied by forest at altitudes from 450 m to 2000–2300 m (Fig. 2). Above this height there are subalpine and alpine meadows. At an altitude of 3000 m a subnival zone begins with characteristically sparse vegetation.

As has been mentioned above, the Lagodekhi Reservation is remarkable for the diversity of its vegetation cover. Almost 2/3 of the plants which grow in Georgia can be found here (Mamisashvili 1975). The forests are mainly represented by broad-leaved species. There is no belt of coniferous forest consisting of fir-trees and spruce. One can only rarely come across pine (*Pinus hamata*).

Among broad-leaved plants, *Fagus* is dominant it covers 2/3 of the territory. Here it represents an interzonal element because it grows in all the belts from lowland forests and up to high-mountain ones. However, optimal conditions for beech forests exist only at altitudes from 800 to 1500 m (Dolukhanov 1941). Above and below these heights the conditions for beech growth gradually deteriorate and then

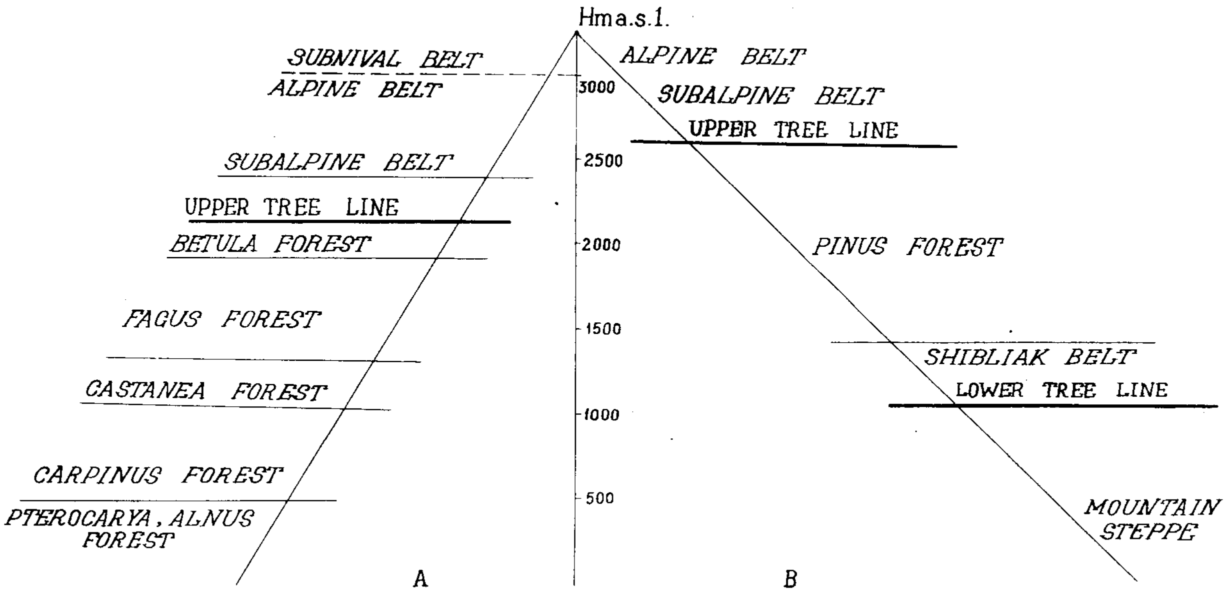


Fig. 2. The structure of the vertical vegetation belts of Lagodekhi (A) and Daghestan (B)

Fagus is only found as an admixture with other species.

The second dominant is *Carpinus caucasica*. In east Georgia pure hornbeam forest at altitudes from 500–800 m occurs only in the reserve. It is widespread on all aspects and slopes of the forest belt. This is a distinguishing feature of hornbeam forest compared with beech which prefers northern slopes. On the more sunlit southern slopes other species such as *Castanea, Quercus iberica* and *Carpinus orientalis* occur mixed with *Carpinus caucasica*. On the northern slopes *Carpinus caucasica* grows together with *Fagus, Ulmus foliacea* and *U. glabra*. In lowland areas, between gorges, pure hornbeam groves occur, in which, from time to time, *Juglans, Fraxinus* and several species of *Acer* (*A. velutinum, A. platanoides, A. campestre*) are admixed. Here it should be noted that maple woods in general, and woods consisting of *Acer velutinum* in particular, occupy the 3rd greatest area, after *Fagus* and *Carpinus caucasica* (Dolukhanov 1941). Among the forest component, the fourth and fifth subdominants are *Tilia caucasica* and *Ulmus elliptica*, respectively.

At the lowest levels scattered fragments of *Alnus* with an admixture of *Pterocarya* occur. They usually grow on alluvial terraces.

As one can see, the forest belt structure in Lagodekhi is almost identical to that in Colchis (Fig. 2). However, in Lagodekhi the coniferous forest belt is missing. The composition of growing to the north of the Watershed Range is quite different. This region of Daghestan is characterized by a less steep relief and in its mountain forests pine is the dominant (Shiffers 1953).

The type and diversity of soil in the Lagodekhi Reservation vary depending on aspect, character of the slopes and altitude above sea level. On northern slopes, there are lightly podsolic, deep and humic dark-brown soils. On southern slopes occur thin, dry soils. Above 1800 m dark-brown soils give way to subalpine and alpine ones (Mamisashvili 1975).

RESULTS

SPORE-POLLEN SPECTRA OF LOWLAND FOREST

Geomorphologically, the right bank of the Shromis-Tskali river at altitudes between 500 and 520 m consists of a first and second fluvial terrace. Their surfaces are absolutely level and covered by lowland forest comprising various broad-leaved species (sites No. 5 and No. 6). The forest is old, but there are signs of regeneration. The trees are 25–30 m tall. On site No. 5 their trunks are up to 50 cm in diameter and on site No. 6 this increases to 100 cm (Tab. 1). There is also variation in the degree

Table 1. Description of the broad-leaved forests in the Łagodekhi Reservation

Number of site		3	4	5	6	7	8	9	10	11	12	16	19	20	21
Date		05.06. 1989	05.06. 1989	05.06. 1989	06.06. 1989	06.06. 1989	06.06. 1989	06.06. 1989	07.06. 1989	07.06. 1989	07.06. 1989	08.09. 1989	09.06. 1989	09.08. 1989	09.08. 1989
Altitude a. s. l. in m		690	720	520	500	510	520	600	950	1220	1400	2035	1720	1675	1650
Exposure		SE	SW	–	–	–	–	W	S	N	N	N	S	W	SE
Slope degree		15	30	–	–	–	–	5	30	45	45	60	45	20	15
Height of trees (maximum) in cm		30	30	25	30	30	25	20	25	35	30	30	35	30	25
Diameter of tree stem (maximum) in cm		120	100	50	100	120	120	30	80	100	80	100	150	90	80
Cover of tree layer %	(a)	80	90	80	90	90	90	90	80	90	80	80	80	90	90
Cover of shrub layer %	(b)	40	80	45	90	50	50	25	30	10	20	70	40	30	5
Cover of herb layer %	(c)	30	20	80	80	70	30	50	5	30	60	60	60	70	80
Trees:															
Fagus orientalis	(a)	4.4	5.5	4.4	3.3	1.1	–	+	3.3	3.3	2.2	5.5	2.2	3.3	3.3
	(b)	3.3	3.3	–	1.1	1.1	+	1.1	3.3	1.1	2.2	4.4	+	2.2	1.1
	(c)	1.1	1.1	–	+	+	–	+	1.1	–	1.1	–	+	–	–
Castanea sativa	(a)	1.1	2.2	–	–	–	–	–	–	–	–	–	–	–	–
	(b)	+	–	–	–	–	–	–	–	–	–	–	–	–	–
	(c)	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Carpinus caucasica	(a)	2.2	1.1	1.1	1.1	4.4	3.3	5.5	3.3	1.1	3.3	–	–	3.3	3.3
	(b)	+	–	–	+	2.2	1.1	1.1	+	–	–	–	–	+	+
	(c)	+	+	–	+	–	–	–	+	–	–	–	–	–	–
Fraxinus excelsior	(a)	2.2	1.1	3.3	3.3	1.1	3.3	+	–	–	–	–	–	–	–
	(b)	+	–	4.4	1.1	1.1	–	+	–	–	–	–	–	–	–
	(c)	+	–	–	–	2.2	2.2	–	–	–	–	–	–	–	–
Tilia caucasica	(a)	1.1	+	1.1	–	2.2	1.1	+	3.3	2.2	1.1	–	–	1.1	1.1
	(b)	+	–	–	–	+	+	+	–	–	–	–	–	1.1	–
	(c)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Quercus iberica	(a)	1.1	+	–	–	–	–	–	–	–	–	–	–	*1.1	2.2
**Q. macranthera*	(b)	+	–	–	–	–	–	–	–	–	–	–	–	+	–
	(c)	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Acer velutinum	(a)	4.4	–	2.2	–	1.1	1.1	+	–	–	–	–	–	–	–
	(b)	–	+	2.2	–	1.1	–	+	–	–	–	–	–	–	–
	(c)	–	–	–	–	–	–	+	+	1.1	–	–	–	–	–

Table 1. Continued

Number of site		3	4	5	6	7	8	9	10	11	12	16	19	20	21
A. campestre	(a)	1.1	–	1.1	.	.	1.1	–	–	–	–	–	–	–	–
	(b)	–	–	2.2	+	1.2	–	+	–	–	–	–	–	–	–
	(c)	–	–	–	+	+	1.1	+	–	–	–	–	–	–	–
A. pseudoplatanus	(a)	1.1	–	1.1	–	–	–	–	–	–	–	–	–	–	–
	(b)	–	–	3.3	–	–	–	–	–	–	–	–	–	–	–
	(c)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
A. trautvetteri	(a)	1.1	–	–	–	–	–	–	–	–	–	1.1	3.3	2.2	2.2
	(b)	–	–	–	–	–	–	–	–	–	–	–	1.1	–	–
	(c)	–	–	–	–	–	–	–	–	–	1.1	–	1.1	1.1	+
A. laetum	(a)	1.1	+	–	–	–	–	–	–	1.1	1.1	–	–	2.2	–
	(b)	1.1	+	–	+	+	–	+	–	–	+	–	+	+	–
	(c)	+	–	–	–	–	–	–	–	1.1	1.1	–	–	–	–
Pterocarya pterocarpa	(a)	–	–	+	3.3	–	–	–	–	–	–	–	–	–	–
	(b)	–	–	+	1.3	–	–	–	–	–	–	–	–	–	–
	(c)	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Alnus barbata	(a)	–	–	–	3.3	–	–	–	–	–	–	–	–	–	–
	(b)	–	–	–	+	–	–	–	–	–	–	–	–	–	–
	(c)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Juglans regia	(a)	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–
Corylus avellana	(a)	2.2	–	–	–	–	2.2	–	–	–	–	–	–	–	–
	(b)	3.3	1.1	+	1.1	1.1	+	–	–	–	–	–	–	–	–
	(c)	–	–	–	–	–	–	–	+	–	–	–	–	+	–
C. colurna	(a)	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1
Shrubs:															
Rubus caesius		2.2	–	–	1.1	–	–	–	–	–	–	–	–	–	–
R. idaeus		–	+	–	–	–	–	–	–	–	–	–	+	–	–
R. serpens		–	–	–	1.1	–	–	–	–	–	–	+	+	–	–
Rubus sp.		–	+	1.1	–	3.3	1.1	3.3	–	2.2	2.2	+	–	+	+
Ulmus elliptica		+	–	–	+	1.1	–	1.1	–	–	–	–	–	–	–
Hedera helix	(b)	–	+	+	3.3	1.1	1.1	2.2	+	–	–	–	–	–	–
	(c)	+	–	–	–	3.3	4.4	3.3	1.1	–	–	–	–	–	–
Sambucus nigra		–	–	–	–	–	–	–	–	–	+	+	–	–	–
Rhododendron flavum		–	1.1	–	–	–	–	–	–	–	–	–	–	–	–
Sorbus cancasigena		–	–	–	–	–	–	–	–	–	–	1.1	–	–	–

Table 1. Continued

Number of site	3	4	5	6	7	8	9	10	11	12	16	19	20	21
Herbs:														
Asperula odorata	1.1	–	4.4	2.2	1.1	3.3	1.1	+	+	3.3	1.1	3.3	3.3	3.3
A. tinctoria	–	–	–	–	–	–	–	–	–	–	–	–	1.1	+
Festuca sylvatica	2.2	2.2	+	–	–	–	1.1	+	–	–	–	3.3	1.1	+
Dryopteris filix-mas	+	+	+	+	1.1	1.1	+	+	3.3	1.1	3.3	3.3	3.3	3.3
D. spinulosa	–	–	–	–	–	–	–	–	–	–	+	+	–	–
Polygonatum multiflorum	+	–	–	–	–	–	–	–	–	–	+	–	–	–
P. verticillatum	–	–	–	–	–	–	–	–	+	–	+	–	+.3	–
Salvia glutinosa	+	–	–	–	–	–	–	–	–	–	–	+	–	–
Viola mirabilis	+	+	2.2	1.1	+	–	–	–	–	–	–	–	–	–
V. sylvestris	–	–	+	–	–	+	+	+	–	+	–	+	+	+
Euphorbia macrocarpa	+	–	1.1	+	–	+	–	–	+	–	+	1.1	1.1	1.1
Pteridium aquilinum	+.2	+	–	–	–	–	–	–	–	–	–	–	–	–
Circea lutetiana	+	+	–	–	+	–	–	–	–	–	–	–	–	–
Aristolochia cf. *iberica*	+	–	–	–	–	1.1	–	–	–	–	–	–	–	–
Geranium robertianum	–	–	+	1.1	–	+	–	–	–	–	–	1.1	1.1	1.1
Dentaria bulbifera	–	–	–	–	–	–	–	–	2.2	+	1.1	–	1.1	–
Moehringia trinervia	–	–	–	–	–	–	–	–	–	+	+	+	1.1	1.1
Polystichum braunii	–	–	–	+	+	+	+	–	+	+	–	–	–	–
Stellaria holostea	–	–	–	–	–	–	–	–	–	–	–	2.2	3.3	3.3
Poa nemoralis	–	–	+	+	–	1.1	–	–	–	–	–	–	1.1	+
Athyrium flix femina	–	–	–	+	+	–	–	–	–	–	–	–	+	+
Neottia nidus-avis	–	–	–	–	–	–	–	–	+	–	–	–	–	+
Astrantia maxima	–	–	–	–	–	–	–	–	–	–	–	–	+	+
Gentiana schistocalyx	–	–	–	–	–	–	–	–	–	–	1.1	–	1.1	–
Carex brizoides	–	+	+	–	–	–	–	–	–	–	–	–	–	–
C. sylvatica	–	–	+	+	1.1	1.1	2.2	–	–	–	–	+	–	–
Stachys sylvatica	–	+	1.1	+	–	+	–	–	–	+	–	–	+	+
Sanicula europaea	–	–	1.1	1.1	–	1.1	–	–	–	–	–	–	–	–

Table 1. Continued

Number of site	3	4	5	6	7	8	9	10	11	12	16	19	20	21
Primula macrocalyx	–	–	1.1	+	–	–	–	–	–	–	+	+	1.1	1.1
Commelina vulgaris	–	–	2.2	+	–	–	+	–	–	–	–	–	–	–
Galeopsis tetrachit	–	–	+	–	–	+	–	–	–	–	–	–	+	–
Geum urbanum	–	–	+	–	–	1.1	–	–	–	–	+	+	+	+
Phyllitis scolopendrium	–	–	–	1.1	–	–	+	–	–	+	–	–	–	–
Urtica dioica	–	–	–	+	–	–	–	–	–	+	–	–	+	–
Pachysandra macrophylla	–	–	–	+	4.4	3.3	–	–	–	–	–	–	–	–
Anthriscus nemorosa	–	–	–	–	–	+	–	–	–	–	–	+	–	+
Calamagrostis arundinacea	–	–	–	–	–	–	–	–	–	4.4	2.2	–	–	–
Impatiens noli-tangere	–	–	–	–	–	–	–	–	–	+	–	1.3	3.3	3.3
Sedum stoloniferum	–	–	–	–	–	–	–	–	–	–	+	–	+	+
Compositae (*Adenostyles*?)	–	–	–	–	–	–	–	–	–	–	1.1	+	1.1	+
Lapsana communis	–	–	–	–	–	–	–	–	–	–	+	+	–	+
Mycelis muralis	–	–	–	–	–	–	–	–	–	–	+	+	–	–
Veronica chamaedrys	–	–	–	–	–	–	–	–	–	–	–	+	–	+
Symphytum grandiflorum	–	–	–	–	–	–	–	–	–	–	–	+	–	+
Senecio sp.	–	–	–	–	–	–	–	–	–	–	+	+	–	–

Sporadic species: in site nr 3: *Lathyrus* sp. +, *Crataegus* sp. +, *Salix caprea* +, *Vicia cracca* +; 4: *Carex digitata* +, *Hypericum androsaemum* +; 5: *Ajuga reptans* +, *Alliaria officinalis* +, *Glechoma hederacea* +; 6: *Calystegia sylvatica* +, *Carex remota* +, *Dryopteris oreopteris* +, *Evonymus europaeus* +, *Festuca montana* +, *Sedum lenkorianicum* +; 7: *Pirus communis* +; *Chaerophyllum* sp. 2.2, *Smyrnium perfoliatum* 2.2; 9: *Lonicera* cf. *caucasica* +, *Platanthera bifolia* +; 10: *Cephalanthera* sp. +; 12: *Lathyrus* sp. +; 16: *Asplenium adiantum nigrum* +, *Athyrium alpestre* +, *Oxalis acetosella* +, *Rumex arifolius* +; 19: *Betula litwinowii* +, *Cardamine hirsuta* +, *Galeobdolon luteum* +, *Galium tauricum* +; 20: *Astrantia maxima* +, *Festuca montana* +, *Mespilus germanicus* +, *Senecio macrophyllus* +, *Solidago virga-aurea* +; 21: *Colchicum speciosum* 2.2, *Rumex tuberosus* +, *Scrophularia divaricata* +, *S. lateriflora* +, *Silene wallichiana* +, *Stellaria nemorum* +; 21: *Hesperis voronovii*+.

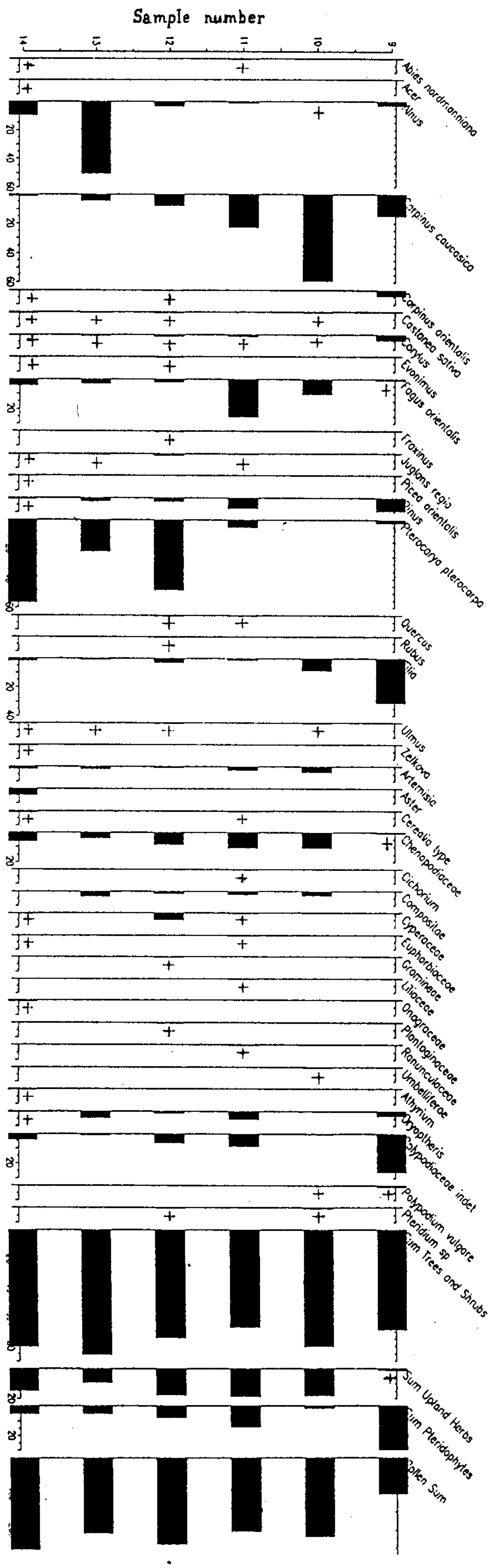


Fig. 3. Spore-pollen spectra of soil in lowland forest

of cover. On site No. 6 the cover of layers (a) and (b) is 90% and that of layer (c) 80%. In site No. 5 layer (a) covers 80% of the area and layer (b) only 45%. The cover of the third layer is 80%. Four components are dominants of the flood-plain forest: *Fagus, Pterocarya, Fraxinus* and *Alnus*. On site No. 5 considerable quantities of *Acer* occur in addition. However, the amount of *Pterocarya* is small. In addition to the elements of the first layer, the undershrubs include *Corylus, Hedera, Rubus, Evonymus* and *Ulmus* with *Fraxinus, Acer* and *Hedera* the most abundant. The herb cover is rather diversified, with large amounts of *Asperula odorata, Viola mirabilis, Commelina vulgaris, Sanicula europaea* etc. Ferns are represented by *Dryopteris filix-mas, D. spinulosa, Athyrium filix-femina* and *Polystichum braunii.*

Three samples from each site (Nos 9, 10, 11, 12, 13, 14) were taken for spore-pollen analysis which showed that the pollen content of the samples was small, markedly so in sample No. 9. Both pollen grains and spores were in a fair state preservation.

As a whole, the spectra are characterized by a predominance of AP pollen (up to 80%), which correponds to the current situation with a few exceptions. The prevalence of such genera as *Fraxinus* and *Acer* is not reflected in the spectra at all. Instead, in samples Nos 9, 10 and 11 (site No. 5), pollen of *Carpinus* and *Tilia* is dominant, although these species do not grow on the site, but in a neighbouring forest. The amount of *Fagus* pollen is also reduced (Fig. 3). The spectra of samples 12, 13 and 14 with a dominance *Pterocarya* and *Alnus*, appear to be better correlated with the current species distribution. It is significant that the pollen of these species reaches its maximun under their canopy. Sample 12 was taken under *Alnus* whose pollen percentage in the spectra reached 50.7%. Similarly, the pollen spectrum of sample 14 showed up to 56.2% of *Pterocarya*, because the sample was taken from directly under this tree.

The pollen of other AP genera, *Abies, Picea, Pinus, Juglans, Zelkova* and *Castanea* has been transported from long distances. All the shrubs are registered in the spectra, except *Hedera*.

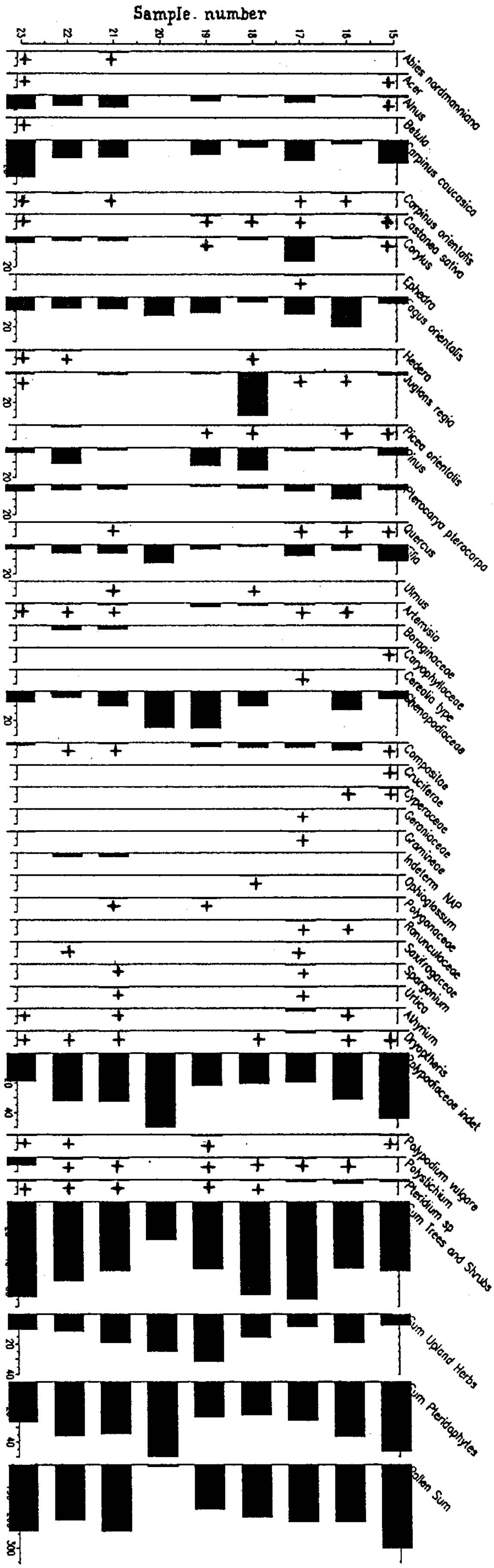


Fig. 4. Spore-pollen spectra of soil in hornbeam forest

Among NAP pollen in the spectra, ferns correlate well both qualitatively and quantitatively with their present day distribution. Only single spores of *Pteridium* and *Polypodium vulgare* were transported. The pollen of Chenopodiaceae was carried to the side in large amounts (up to 6–10.8%) and pollen of many other ruderal plants was also present. Cereal pollen occurs as single grains, transported by the wind from the south-eastern part of Eastern Georgia with various synanthropic elements. In Georgia cereal production is limited to this region.

SPORE-POLLEN SPECTRA OF HORNBEAM FOREST

Spectra of soil samples from hornbeam forest were taken from the river-terraces of the flood-plain of the Lagodekhis Khevi river. The altitude of the locality does not exceed 510–600 m where three sites (Nos 7, 8, 9) were studied. Hornbeam represented an independent formation on the 3rd fluvial terrace of the right bank of the Lagodekhis Khevi river (site No. 9). However, in other sites it grew as an admixture with many broad-leaved species: *Tilia, Fagus, Fraxinus, Acer velutinum* and *Juglans*. In site No. 7, which is also situated on the right bank, the trees were up to 30 m tall with a trunk diameter of 100–120 cm. In site No. 8 the trees were somewhat smaller, up to 25 m in height and diameter 80–90 cm. Site No. 9 was characterized by young forest. Until 1930, in the place where the hornbeam forest now grew, there stood a beech forest, completely destroyed by a hurricane. In 1989 the maximum height of the hornbeam trees did not exceed 20 m and their trunk diameter was 30 cm (Tab. 1). The degree of cover in area of layer (a) was 90% in all the three types of the forest. The cover in layer (b) was 25–50%, and that in (c) 50–70%.

From the hornbeam forest nine samples were taken and studied. As can be seen from the diagram (Fig. 4), the pollen spectra are of to the forest type. The role of fern spores increases their content may reach 50% (sample No. 20 from site No. 8). AP pollen makes up 46–65% of the total pollen content in which *Carpinus* pollen prevails. The second dominant here is *Fagus orientalis* and there is much pollen of *Tilia* and *Juglans*. The pollen of *Pinus* and *Alnus* (transported from long distances) is found in rather significant amounts while *Abies, Acer, Picea, Castanea, Quercus, Ulmus* and *Betula* are represented by single grains. *Betula*, however is not found at all in the spectra of the flood-plain forest of the Shromis-Tskali. Among shrubs one can always see pollen of *Corylus*, and *Carpinus orientalis* is also prominent in the spectra. Pollen grains of *Hedera* and *Ephedra* are found only in a few samples.

Among NAP species, as in the spectra from sites No. 5 and No. 6, transported pollen of Chenopodiaceae (12–25%) predominates, followed by Compositae. *Artemisia* pollen, transported by wind, is always found. Other NAP pollen can be observed in very small quantities among them cultivated Gramineae and ruderal plants (Fig. 4). The above account describes the general characteristics of the spectra. However, each site has its own specific peculiarities. For instance, in pure hornbeam forest the content of hornbeam pollen is not as high as that in the neighbouring site No. 5 (Fig. 1). This is probably because the hornbeam forest is rather young (not more than 60 years), while the forest in site No. 5 is much older.

SPORE-POLLEN SPECTRA OF THE SWEET CHESTNUT FOREST

Two sites were studied to the south-east of the Shromis-Tskali river gorge at altitudes of 690 and 720 m (sites Nos 3, 4), where *Castanea sativa* grew in admixture with *Fagus, Tilia, Carpinus* and *Fraxinus*. Here occured a small number of sweet chestnut trees. Among the AP *Fagus* is dominant (Tab. 1). The forest was located on a south facing slope with a 15° declivity. In site No. 3 the maximum height of the trees was 35 m with their diameter reaching 120 cm. However, in site No. 4 the forest was younger and the trees were not more than 30 m tall with diameters as small as 50 cm. The cover distribution for the 3rd site was layer (a) 80%, layer (b) 40% and layer (c) 30%. In the 4th site the cover was layer (a) 90%, layer (b) 80% and layer (c) 20%.

As has already been mentioned, *Fagus* dominated here in the past. Subdominants were *Castanea, Carpinus, Acer velutinum* and *Fraxinus* with *Quercus* and *Tilia* are also present. In addition to the elements of the first layer, the undergrowth includes *Corylus avellana, Rhododendron flavum, Rubus caesius, Hypericum androsaemum, Crataegus* and *Ulmus*. In the herb cover, *Festuca sylvatica* and *Asperula odorata* were predominant. Ferns were represented by *Dryopteris filix-mas* and *Pteridium aquilinum*.

Under the canopies of the forests studied, seven soil samples were taken and analysed: samples 2 and 3 from site No. 3, and samples 4, 5, 6, 7 and 8 from site No.4. The pollen spectra are shown in Fig. 5. The content of AP and shrubs is high (up to 80%). There are far fewer spores of fern-like plants than in the hornbeam forest spectra. Here the percentage of pteridophytes is 3–13% on average to, while in the hornbeam formations 46–50% (Fig 4). In the AP group, pollen of *Fagus orientalis* predominates (14–45%) with the second subdominant *Castanea* (up to 30%). There is much *Carpinus* pollen (up to 27%) and *Tilia* is always present. Sample No. 8 taken directly from under a lime tree is distinguished by an abundance of its pollen with a content as high as 45%. The pollen of *Alnus, Pterocarya, Pinus* and *Quercus* is found in small amounts. There are very few pollen grains of *Fraxinus, Juglans, Ulmus* and *Picea* and among shrubs *Corylus* is dominant. *Hedera* occurs as single pollen grains. As one can see, the AP pollen spectra in general reflect the structure of the forest, but they do not show *Acer* pollen in them at all. In the NAP group the pollen of Chenopodiaceae predominates as in all the previous sites of lowland and hornbeam forest. The second subdominant is Compositae and there is little pollen of *Carex*, Gramineae, *Plantago*, Polygonaceae and Umbelliferae.

SPORE-POLLEN SPECTRA OF BEECH-HORNBEAM FOREST

On the left bank of the Lagodekhis-Tskali river along the so called Daghestan Path (the road leading to Daghestan), five sites of beech-hornbeam forest were studied (Nos 10, 11, 12, 20, 21) at altitudes from 950 m up to 1675 m. At lower levels (950 m) these forests grew only

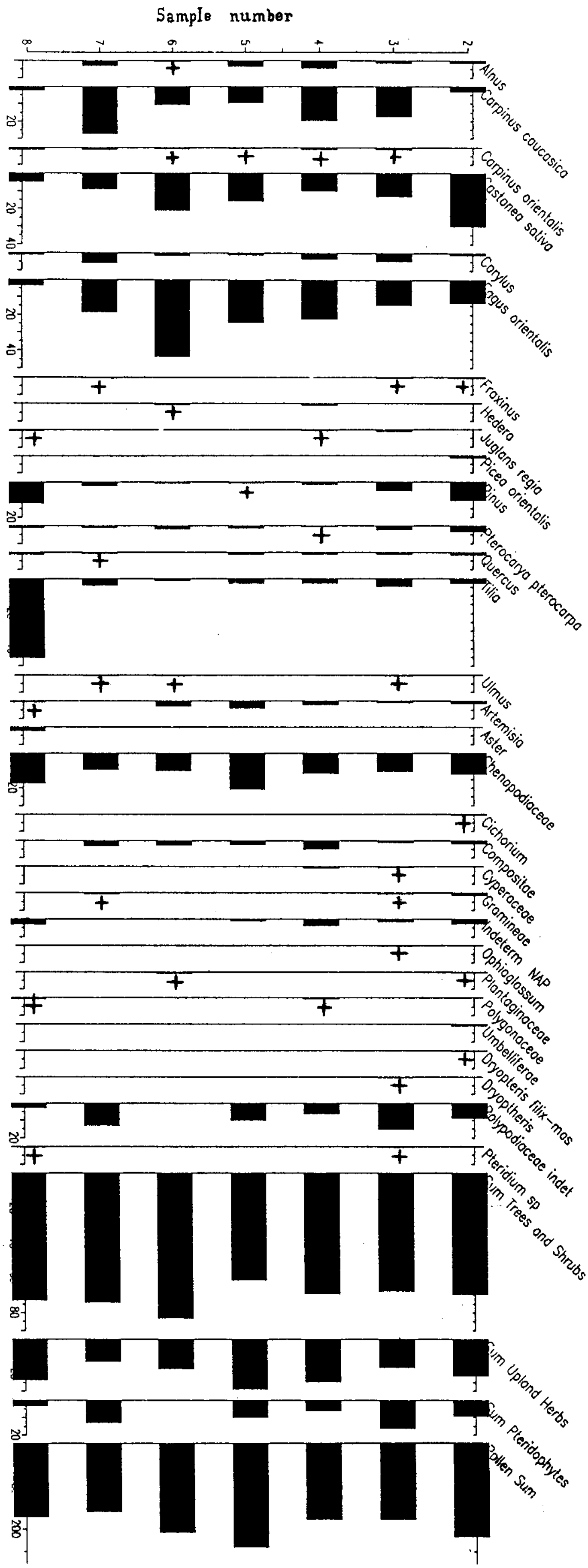


Fig. 5. Spore-pollen spectra of soil in sweet chestnut forest

in admixture with *Tilia*. Then, starting from 1250–1400 m, the role of *Tilia* was reduced and individuals of *Acer laetum* appeared. Still higher, at about 1650–1675 m. *A. letum* was accompanied by *A. troutvetteri*, *Quercus macranthera*, *Corylus colurna* (Tab. 1).

The first three sites were situated at altitudes from 950 to 1400 m. Site No. 10 was on a steep slope of southern aspect where the forest here was of uneven age. The height of the trees was about 25 m, and their trunk diameter up to 80 cm. The degrees of cover of layers (a), (b), and (c) were 80%, 30% and 5%, respectively. From this site, samples 24, 25 and 26 were taken for pollen analysis. Is spite of the fact that the three forest components contained similar numbers of individuals (Tab. 1), the pollen spectra show a dominance of *Fagus* (Fig. 6) with the amounts of *Tilia* and *Carpinus* equal. The AP group is characterized by large quantities of *Pterocarya pterocarpa* pollen (up to 12%) which has been carried here from below. This has evidently been caused by the southern aspect of the slope and its great steepness. Vertical slopes of the mountains serve as a screen where the pollen of many plants transported from lower belts is trapped. In addition to *Pterocarya*, the spectra contain *Alnus, Castanea, Juglans, Ulmus*. Some pollen has been carried from the higher mountain belts, for example, that of *Betula, Pinus*. As a result of transport from the west pollen of *Picea* and *Abies* occur, while pollen grains of *Ephedra, Artemisia*, Chenopodiaceae have been brought in from the steppes and forest-steppes of the lowland parts of East Georgia. There are also many spores of ferns (up to 45%).

At an altitude of 1230 m. on a still steeper slope with 45° declivity, site 11 was studied. However, here the slope faced north rather than south. The beech forest contained

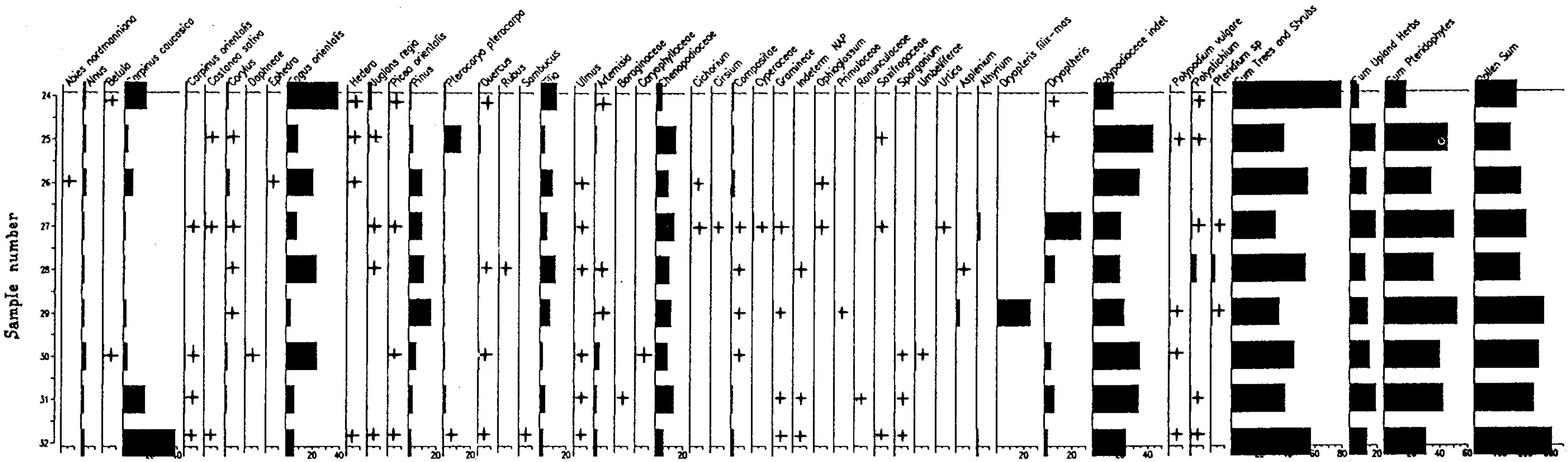


Fig. 6. Spore-pollen spectra of soil in beech-hornbeam forest

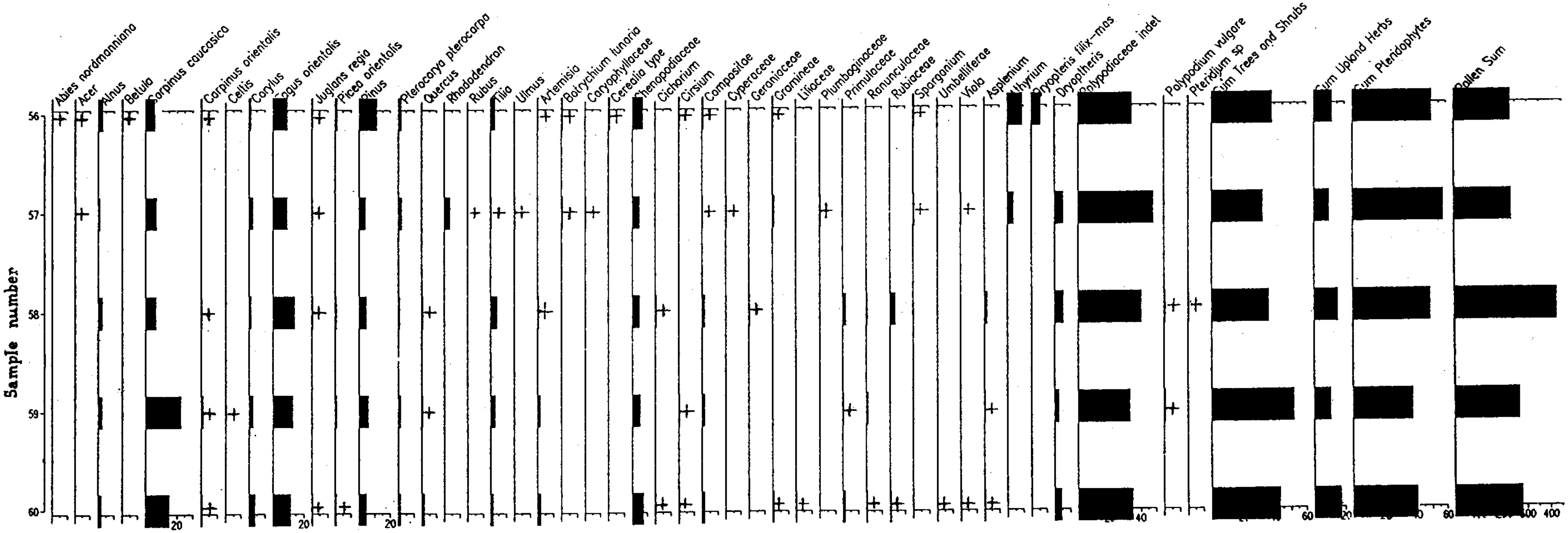


Fig. 6a. Spore-pollen spectra of soil in beech-hornbeam forest containing *Acer*

trees of different ages 30–35 m tall, with diameters reaching 100 cm. Layer (a) coverage was 90%, layer (b) 10% and that of layer (c) 30%.

The first dominant of the forest was *Fagus*, with *Tilia* second and *Carpinus* and *Acer laetum* subdominants. On site 11 soil samples 27, 28 and 29 were taken and analysed. As can be seen from the pollen diagram, local pollen is very well represented in the spectra. *Fagus* pollen prevails with *Tilia* as second dominant. Of the subdominants, only *Carpinus* is recorded. Apparently *Acer* pollen was not conserved in the soil samples. The other components of the spectrum, present a very interesting picture. Here there is very little pollen of plants growing in the lower belts, much less than in site 10. However, the amount of *Pinus* pollen increases sharply, mainly from trees in the pine forests on the northern slopes of the Greater Caucasus in Daghestan (Fig. 2).

Site 12 was situated on a steep slope facing west. This site was forest containing trees of all ages, of heights 20–30 m with trunk diameter 80 cm. Layer (a) had 80% cover layer (b) 20% and layer (c) 60%. The first and second dominants were *Carpinus* and *Fagus* respectively. The two subdominants, *Acer laetum* and *Tilia caucasica* were present in equal quantities (Tab. 1). On this site samples 30, 31 and 32 were taken.

The pollen spectra are distinguished by a large *Carpinus* pollen content (up to 38.8%); followed by *Fagus* (up to 23%). There is a little *Tilia* pollen, but *Acer* does not feature in the spectrum at all, as was the case in other sites. The spectrum does not show such undershrub elements as *Rubus* which grows extensively in layer (b). However, there is pollen of forest species from neighbouring belts, namely *Castanea, Pterocarya, Juglans, Alnus, Corylus* and *Ulmus*. From belts further up, pollen of *Pinus, Betula, Abies* and *Daphne* has been transported while from the steppe regions of the east and south-east of Georgia, as is typical for other sites, pollen of *Artemisia* and Chenopodiaceae has been brought in. The spectra adequately register the local herbs and pterodophytes with the amounts of the latter fully matching the quantities in the present day communities.

As has been mentioned above, at the uppermost borders of the beech-hornbeam forest, appear such species as *Acer trautvetteri, Quercus macranthera* and *Corylus colurna*. Here sites 21 and 20 were located. The former was situated at an altitude of 1650 m on a slope with 15° declivity facing south-east. The trees were 25 m tall with trunks 80 cm in diameter. The layer (a), (b) and (c) covers were 90%, 5% and 80% respectively. The dominants were *Fagus* and *Carpinus*; the first subdominants were *Quercus, Acer,* and the second *Tilia* and *Corylus*. The undershrubs were poorly developed. In site 21 samples 58, 59 and 60 were taken with pollen spectra as shown in Fig. 6a. The pollen diagram shows the dominance of *Carpinus* and *Fagus* just as in the site at the time of study. Almost all the subdominants are represented as well. Single pollen grains of *Acer* are found only in sample No. 58 (0.24%). The slope aspect has limited the availability of pollen from the south of the region to that of *Artemisia,* Chenopodiaceae, *Juglans regia*, etc. Pteridophytes and other local herbaceous plants are adequately represented in the spectra.

Site No. 20 was situated at an altitude 1675 m in mixed forest. The north-west facing slope was not very steep (up to 20°). The height of the trees reached 30 m and their trunk diameter 90 cm. The cover of layers (a), (b) and (c) was 90%, 30% and 70% respectively. *Fagus* was the dominant, the first subdominants were *Carpinus caucasica, Acer trautvetteri* and *A. laetum* with the second subdominants *Tilia caucasica* and *Quercus*. In addition undershrub layer contained *Corylus colurna, Mespilus* and *Rubus* and the fern population was very large (Tab. 1). This site was represented by samples 56 and 57.

The spore-pollen spectra are characterized by a predominance of *Carpinus* and *Fagus* pollen. The third dominant is *Pinus*, since the slope is of north-western aspect, and here, as in site 11, the *Pinus* pollen has been transported from pine forests of Daghestan. From the higher belts there was pollen of *Rhododendron* and *Betula,* spores of *Botrychium lunaria*, and pollen of *Abies* and *Picea* has been transported from the north-west. The spectra also show elements from the lower belts including *Pterocarya, Juglans, Alnus* and *Ulmus*. However, elements of the steppe region are much more poorly represented than on the south facing slopes. Thus, there is no pollen of *Ephedra* and very little of *Artemisia*, cereals etc. There are many fern spores in the spectra.

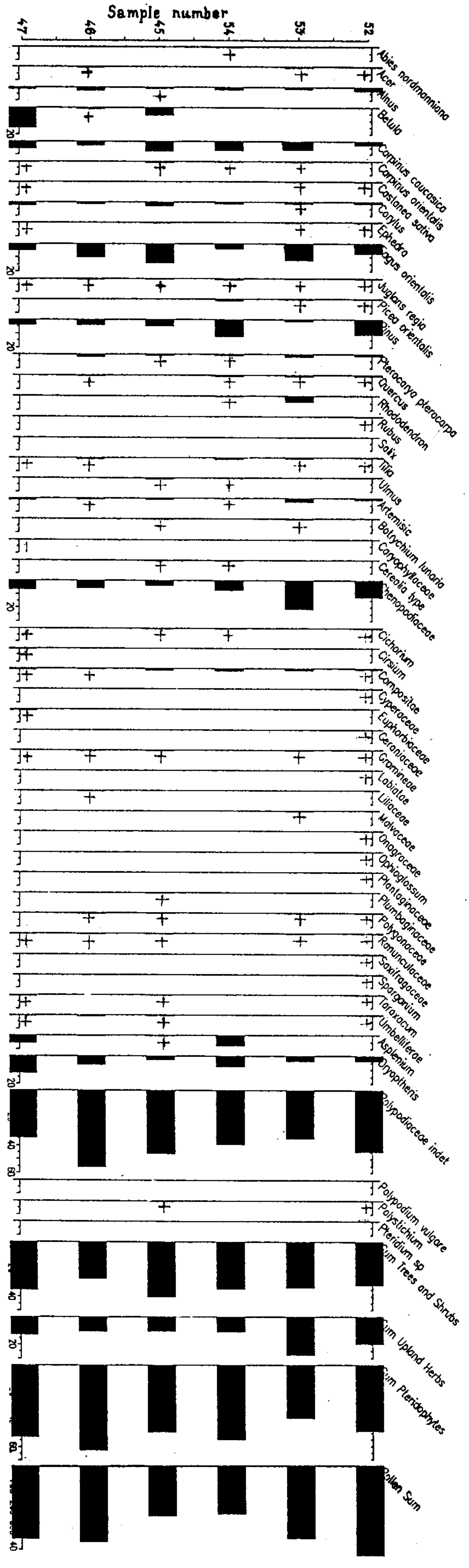


Fig. 7. Spore-pollen spectra of soil in beech forest

SPORE-POLLEN SPECTRA OF BEECH FOREST

At altitudes of 1720 and 2035 m, two sites of beech forest were studied, No. 19 (samples 52, 53, 54) and No. 16. The former was situated 3–3.5 km to the south of the meteorological station near the Daghestan Path. The forest with trees of all ages grew on a south facing slope with a 15° declivity. The trees reached 35 m in height, with a trunk diameter up to 150 cm (*Fagus*). The cover of layers (a), (b) and (c) was 80%, 40% and 60%, respectively. There were two dominants in the forest, *Fagus orientalis* and *Acer trautvetteri*. *Rubus* was the only additional undershrub. The herb layer was very rich (Tab. 1) with predominant *Asperula odorata* and *Stellaria holostea*. There were many ferns (*Dryopteris filix-mas*). The spore-pollen spectra (Fig. 7) are characterized by a dominance of sporiferous plants (Pteridophytes). A similar picture was obtained at the upper limit of the beech-hornbeam forest (Fig. 6a).

Among the AP group, the pollen of *Fagus*, *Pinus* and *Carpinus* predominates. The amount of *Acer* is reduced occuring in the spectra only in the form of single grains. There is also little pollen of *Rubus*.

Among the conifers, the pollen of *Picea* is always present, while that of *Abies* occurs only in one sample.

The elements of this lower belts are represented by fairly significant amounts of *Alnus barbata*, *Pterocarya pterocarpa*, *Juglans regia* and *Quercus iberica*. The pollen of *Tilia caucasica*, and *Carpinus orientalis* occurs in somewhat lesser quantities and there is little pollen of *Castanea sativa* and *Ulmus glabra*.

Among the shrubs the pollen of *Corylus* and *Ephedra* is ever present while to that of *Rhododendron* and *Rubus* is found in only a few samples.

Among the NAP group, Chenopodiaceae, *Artemisia* and Compositae predominate. It should be noted that here the Chenopodiaceae reaches high values (up to 21.2%), apparently as a result of the southern aspect. The same holds for *Artemisia* pollen (up to 2.6%).

Among sporiferous plants, apart from *Dryopteris*, there are spores of *Botrychium* and *Ophioglossum*. The former has most probably been carried in from the upper belts, while the latter has come in from below. The pollen of many NAP is found in small amounts. Included are elements of synanthropic vegetation.

Not far from the upper tree line at an altitude of 2035 m, the site of an old beech forest was studied, with grew on a steep (up to 35°) slope of northern aspect (site No. 16). Here the largest trees were 30 m tall with trunk diameters of 100 cm. The coverage of the layers (a), (b) and (c) was 80%, 70% and 60% respectively.

Obviously *Fagus* was a dominant in the forest. *Acer trautvetteri* and *Salix caprea* were found as single individuals. The undershrubs consisted of *Sorbus caucasigena, Betula litwinowii* and *Fagus orientalis*. The last predominated in this layer as well. Among the NAP group, there are many spores of *Dryopteris filix-mas* but pollen of *Senecio* and *Calamagrostis* is present only in small amounts.

On this test site, samples 45, 46, 47 were taken and analysed.

In the total spore-pollen diagram, the spores of Pteridophytes also prevail, reaching their maximum values (up to 62.4%).

Among the AP group the following taxa dominate: *Fagus* (up to 14.2%), *Carpinus* (up to 7.5%) and *Betula* (up to 14.9%). The large amount of the last indicates the proximity of the tree line. There is very little pollen of *Acer* and *Salix caprea*.

The spectra do not contain pollen of the conifers (*Abies* and *Picea*), most probably, because of the northern aspect. However, *Pinus* is always present with a pollen percentage of 37.5%. The quantities of *Alnus* and *Pterocarya* are fairly significant (up to 2.7% and 2.2% respectively). The percentages of some of the AP are somewhat smaller: *Tilia* (up to 0.8%), *Juglans* (to 0.9%), *Corylus* (to 0.8%), *Quercus* (to 0.5%), *Ulmus* (to 0.8%) and *Carpinus orientalis* (to 0.8%). *Castanea, Ephedera, Acer* and *Salix* are represented by single grains.

Among the NAP group, Chenopodiaceae and Polypodiaceae are dominants, while *Artemisia* (up to 1.1%) and other Compositae (up to 1.1%) can be considered as subdominants. The content of Euphorbiaceae and *Taraxacum* equals 0.9%, that of Gramineae and Umbelliferae 0.8%, and that of Ranunculaceae 0.5%.

There are many spores of *Dryopteris* and *Asplenium* (up to 12.4% and 5.5%, respectively).

The pollen of synanthropic vegetation occurs as single grains.

SPORE-POLLEN SPECTRA OF CROOK-STEM BIRCH FOREST

At the uppermost border of the forest at an altitude 2060 m, in an open crook-stem birch forest, site No. 13 was studied. It was situated on a very steep north facing slope (up to 60°). The trees were crooked with the tallest (*Betula litwinowii*) 10 m high with and a trunk diameter of up to 40 cm. *Betula* was predominant here. *Fagus orientalis, Sorbus caucasigena, Acer trautvetteri* and *Salix caprea* grew as isolated trees. *Daphne* occurred as an undershrub in addition to *Fagus* and *Betula*. The cover of layers (a), (b) and (c) was 50 %, 10% and 100%, respectively. In the herb layer *Senecio, Compositae* (*Adenosteles* ?) and *Calamagrostis* prevailed (Tab. 2). On this site samples 33, 34, 35 and 36 were taken. However, pollen and spores were found only in samples 34 and 36. Most probably, the steep gradient of the slope favoured the ablation of humus containing pollen.

The two spore-pollen spectra are characterized by a predominance of *Betula* pollen, (up to 18.6%) in sample No. 34, but as low as 2.6% in No. 36 (Fig. 8). It is very difficult to explain this fact. For *Fagus* the pollen content is almost the same in both samples (7.7% and 8.8%). Among forest forming species, *Acer* hardly registers (0.4%) while *Sorbus* and *Salix* are not found at all. Transported pollen of *Pinus* (up to 11%), *Alnus* (up to 4.8%), *Carpinus caucasica* (up to 3.5%) are subdominants

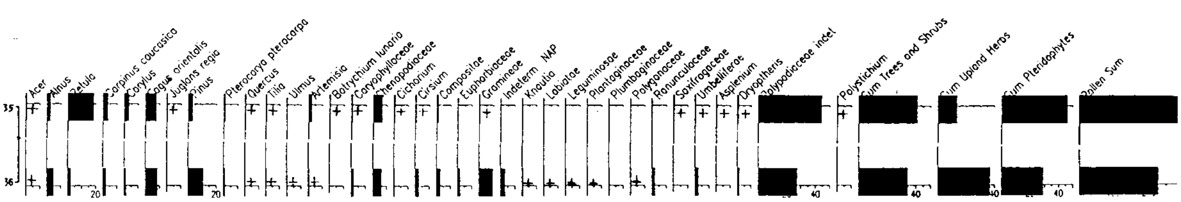


Fig. 8. Spore-pollen spectra of soil in open crook-stem birch forest

Table 2. Description of the open crook-stem birch forest on the timber-line, Lagodekhi Reservation, Daghestan Path, 2060 m a.s.l.

Number of site	13
Date	08.06.1989.
Exposure	N
Slope degree	60
Height of trees (maximum) in m	10
Diameter of trees stem (maximum) in cm	50
Cover of tree layer	50%
Cover of shrub layer	10%
Cover of herb layer	100%
(a) Trees:	
Betula litwinowii	4.4
Fagus orientalis	1.1
Acer trautvetteri	+
Salix caprea	+
Sorbus caucasigena	+
(b) Shrubs:	
Fagus orientalis	1.1
Betula litwinowii	+
Daphne mesereum	+
(c) Herbs:	
Calamagrostis anundinacea	3.3
Acer trautvetteri	2.2
Compositae (Adenostyles ?)	2.2
Senecio	2.2
Myosotis sylvatica	1.1
Ranunculus ?	1.1
Veratrum lobellianum	1.1
Veronica gentianoides	1.1
Alchemilla	+
Alectorolophus	+
Astrantia maxima	+
Athyrium alpeste	+
Betula litwinowii	+
Cerastium alpinum	+
Cirsium	+
Dryopteris filix-mas	+
Dryopteris spinulosa	+
Euphorbia	+
Galium sylvaticum ?	1.1
Gentiana schistocalyx	+
Polygonatum verticillatum	+
Rumex	+
Serophulania divaricata	+
Sedum stoloniferum	+
Silene	+
Vaccinum myrtillus	+
Valeriana alliariaefolia	+

of the spectra. There is also pollen of *Pterocarya* (up to 1.3%) and *Quercus, Juglans, Tilia* and *Ulmus* (up to 0.4% in each case). As on the northern slopes of the previous site No. 16, *Abies* and *Picea* pollen is absent. Among shrubs, the spectra register only *Corylus* pollen (up to 2.8%) with no *Daphne* pollen at all.

In the NAP group, the picture is somewhat different. Gramineae (up to 10%) are dominants instead of Chenopodiaceae (up to 6.1%) with Compositae as subdominants. Umbelliferae pollen is present in fairly significant amounts (up to 2.6%) and the pteridophytes spore content amounts to 46%.

SPORE-POLLEN SPECTRA OF THE SUBALPINE AND LOWER ALPINE BELTS

In the subalpine belt at the limit of the forest that is delimited by *Rhododendron flavum*, we studied sites No. 17 and 18. The altitude of the locality was 1880 m and it was situated to the south of the meteorological station near the Daghestan Path. During our in situ investigations (June 8, 1989), *Rhododendron* was in full bloom and was most impressive. The locality was relatively level, and surrounded by forest containing *Acer trautvetteri, Fagus orientalis, Sorbus caucasigena.* Among shrubs, in addition to *Rhododendron flavum* which was obviously dominant occured *Rubus* and *Acer.* In the dense herb layer, Ranunculaceae (especially *Ranunculus*), *Calamagrostis arundinacea, Doronicum* and *Circaea alpina* were dominant (Tab. 3).

The spore-pollen spectra (Fig. 9) are characterized by a significant reduction in the role of the AP and shrub groups (down to 31.6–21.1%). In the NAP group, the pteridophytes and *Botrychium* contents are rather high, 53% and 12.3%, respectively. In some spectra of the AP group, *Alnus* and *Fagus* predominate, up to 8.5% and 6.5%, respectively. There is a noticeable amount of *Pinus pollen* (up to 3.9%), *Carpinus caucasica* (up to 2.9%), *Pterocarya* (up to 2.2%). The pollen of *Juglans* (up to 0.6%), *Betula* (up to 0.4%), *Picea* (0.8%), *Quercus* (up to 0.8%), *Tilia* (0.6%), *Ulmus* (0.4%) and *Corylus* (0.9%) are consistently present. *Abies, Ephedra, Rubus* and *Carpinus orientalis* pollen are found as single grains. It should be emphasized that although *Rhododendron flavum* was in flower, its pollen content on the test sites did not exceed 8.1%. Among the NAP group, Chenopodiaceae (up to 15.4%), Gramineae (up to 3.7%), Ranunculaceae (up to 2.2%) and Umbelliferae (1.9%) dominate. Many elements of

Table 3. Description of the *Rhododendron flavum* thicket in the Lagodekhi Reservation, Daghestan Path 2–3 km south of the Meteorogical Station 1880 m a.s.l.

Number of site	17	18
Date	08.06.1984.	08.06.1989.
Exposure	NW	–
Slope degree	30	–
Cover of the shrub layer %	100	100
Cover of the herb layer %	10	25
(b) Shrubs:		
Rhododendron flavum	5.5	5.5
Rubus idaeus	2.2	1.1
Acer trautwetteri	+	1.1
Daphne glomerata	1.1	–
D. mesereum	–	+
(c) Herbs:		
Ranunculus	+	2.2
Rumex cf. *arifolius*	–	2.2
Calamagrostis arundinacea	+	1.1
Circea alpina	–	1.1
Doronicum austriacum	+	1.1
Myosotis alpestris	+	1.1
Alchemilla	+	+
Anthriscus sylvaticus	+	–
Dryopteris filix-mas	+	+
Galium vernum	–	–
Gentiana schistocalyx	+	–
Geranium sylvaticum	–	+
Polygonatum verticillatum	+	+
Pyrethrum roseum	–	+
Senecio	+	+
Urtica dioica	+	–
Viola	–	+

subalpine and alpine formations register in small amounts.

Among the sporiferous plants of this site, *Lycopodium selago* spores are found for the first time.

It is interesting to record that in *Rhododendron* thichets the pollen concentration was very high, and microfossil preservation is good that almost all fern spores had retained their perisporium (Plate 1). This phenomenon is extremely rare in soils. However, dense *Rhododendron* thickets contribute to an accumulation of humus with an acidic reaction.

At a distance of about 2 km from the meteorological station, up the Daghestan Path at an altitude 2100 m, site No. 14 was studied. Here were lower alpine meadows, but situated on the faced south rather steep slopes of the ridges (30°–60°). Herbs here were represented by Gramineae with an abundance of *Festuca ovina* and *F. varia*. There was also much *Anthoxantum odoratum, Galium verum* and *Veronica gentianoides*.

Description of the vegetation cover 14: *Festuca ovina* 4.4; *Anthoxantum odoratum* 3.3; cf. *Galium verum* 3.3; *Pyrethrum roseum* 3.3; *Anemone fasciculata* 2.2; *Betonica grandiflora* 2.2; *Myosotis alpestris* 2.2; *Nardus stricta* 2.2; *Veronica gentianoides* 2.2; *Daphne glomerata* 1.1; *Festuca varia* 1.1; *Luzula spadicea* 1.1; *Psephellus* ? 1.1; *Thymus alpinus* 1.1; *Ajuga orientalis* +; *Alchemilla caucasica* +; *Campanula glomerata* +; *C. tridentata* +; *Centaurea cheiranthifolia* +; *Gentiana schistocalyx* +; *Linum alpinum* +; *Orchis* +; *Polygala alpicola* +; *Rumex arifolius* +; *Trifolium caucasicum* +; *Tripleurospermum caucasicum* +; *Viola*+; soil samples 37 and 38.

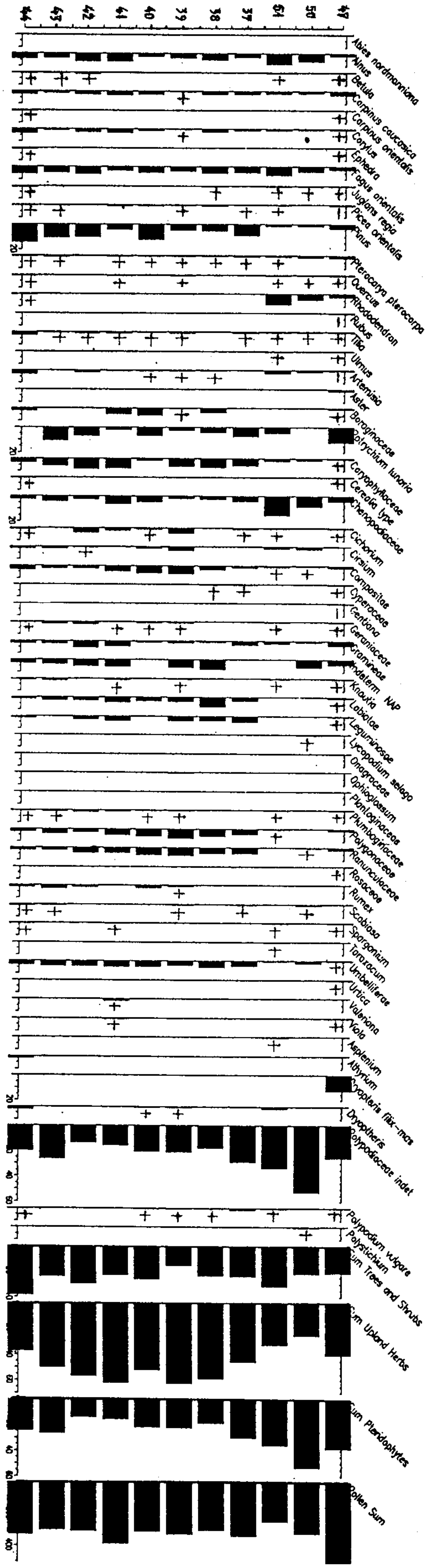


Fig. 9. Spore-pollen spectra of soil of subalpine and lower alpine regions

Somewhat higher, above the timber line at an altitude 2260 m we studied two ather sites No. 15 and No. 15a.

Description of the site 15; local erosion cander west facing slope 15°, 2260 m a.s.l. date 08.06.1989. The species *Rumex alpinus* 5.5 and *Doronicum austriacum* 3.3 were widespread. Other taxa: Gramineae 4.4; *Veronica gentianoides* 1.1; Labiatae 3.3; *Alchemilla* cf. *caucasica* 1.1; *Chaerophyllum sibiricum* +; *Cirsium* +; *Myosotis alpestris* +; soil samples 39 and 40.

Description of the site 15a: dense clumps of *Daphne glomerata* on a very steep (60°) north facing slope, 2200 m a.b.s.l. date 08.06.1989. Vegetation cover: *Anemone fasciculata* 3.3; *Calamagrostis arundinacea* 3.3; *Daphne glomerata* 2.2; *Vaccinium myrtillus* 2.2; *Astrantia maxima* 1.1; *Cirsium* 1.1; *Gentiana schistocalyx* 1.1; *Myosotis alpestris* 1.1; *Ranunculus alpestris* 1.1; *Alchemilla caucasica* +; *Daphne mesereum* +; *Galium verum*+; *Pedicularis caucasica*+; *Poa pratensis*; soil samples 43 and 44.

From similar alpine vegetation at an altitude 2400 m a.s.l. soil samples 41 and 42 were taken.

We shall not discuss the individual spectra for each sample, but only characterize them in general, because all of them were taken from the same belt. The spore-pollen spectra are distinguished by the small amount of AP group pollen (not more than 30% on average). Here the dominants are *Pinus* (up to 14.4%) and *Alnus* (up to 6.2%). *Fagus* (up to 5.8%) and *Carpinus* (up to 3,1%) can be considered subdominants. The pollen of *Abies* and *Picea* is found in large amounts in the samples taken on the western slopes (for example, samples Nos 39, 40, 41). Among the elements of the upper tree line, only *Betula* registers in the spectra. *Salix, Sorbus, Acer* and *Rhododendron flavum* which form great thickets, are not found at all. Under the bushes of *Rhododendron caucasica* its pollen is found only as single grains and in the *Daphne* thickets *Daphne* pollen was not found at all. In so far as appear in other trees and shrubs are concerned almost all elements of the lower belts appear in the spectra. Included are *Juglans, Pterocarya, Ulmus, Tilia, Corylus, Quercus, Ephedra* and *Carpinus orientalis*.

In the NAP group it is almost impossible to distinguish any dominants. There are very small differences among such elements as Caryophyllaceae (5–8%), Polygonaceae (4–7%), Umbelliferae (3.6–5%), Gramineae (3–5%), Compositae (4–6%), Chenopodiaceae (4–6%) and Boraginaceae (4–5.5%). The first dominant among sporiferois plants are the pteridophytes (up to 24%), and the second *Botrychium* (up to 10.5%). The pollen of synanthropic vegetation has also been carried to the alpine belt (Fig. 9).

DISCUSSION

The thorough analysis of the pollen spectra of each individual vegetation belt has shown that, in general, the pollen and spore compositions of the spectra are consistent with the present-day vegetation of the belt. However there are some exceptions which we must discuss.

In lowland forest the amounts of *Pterocarya* and *Alnus* in the spectra reach their expected values whereas that of *Fagus* is significantly reduced. There are almost no pollen grains of *Acer, Fraxinus* and *Hedera*, even where these components were dominants in the community.

Though the *Carpinus* content is dominant in pure hornbeam forest, it is represented better quantitatively in neighbouring sites where it is mixed with other broad-leaved species. This fact cannot yet be explained. Perhaps chemical or physical properties of the soil may be exerting an influence on the preservation of hornbeam pollen grains.

In the spectra from the canopy of forest containing *Castanea* the pollen of *Rhododendron flavum* is not found at all, although it is a significant member of the undershrub layer there. However, its pollen content does reach higher values in spectra obtained from samples within *R. flavun* thickets in the subalpine belt (Fig. 9). A similar phenomenon was observed by us for the Colchis spectra as well (Stuchlik & Kvavadze 1987).

It is interesting to note that the *Fagus* pollen content reaches its maximum, not in pure beech forest at lower levels, but in an admixture with *Castanea* (Fig. 5) and *Carpinus* (Fig. 6, 6a). In association with *Castanea* its percentage is up to 43%, with *Carpinus* up to 38%, while in the spectra from beech forest its pollen value does not exceed 14% (Fig. 7). This fact can be explained as follows. Pure beech forest is situated in high-mountain areas, where increased wind velocity and duration, bring more pollen from both the lower and upper belts. For example, from above comes pollen of *Betula* and from below that of *Carpinus, Alnus, Pterocarya, Tilia*, etc. Here too the quantity of pollen of Chenopodiaceae and *Artemisia* transported from the adjacent lowland steppes reaches its maximum, up to 21% and 3% repectively.

At the upper limit of the forest vegetation, the role of *Betula litwinowii* is also reduced (Fig. 8), although it can still be the spectrum dominant (up to 18%). This reduction seems to be caused by an increase of both AP and NAP transported pollen content as well.

Most probably, the under-representation of subalpine vegetation pollen from *Rhododendron* thickets in the high-mountain region cannot be explained by an increase in transported pollen alone. Other factors contribute as well, in particular, poor preservation of *Rhododendron* pollen in soils of the type found there, and probably, low pollen productivity. A similar explanation accounts for the absence of the Caucasian species of *Daphne, Rubus, Salix, Sorbus, Acer* and *Fraxinus*. A similar phenomenon has been observed in other regions of the Caucasus (Kvavadze 1993).

As is clear, in spite of all the factors hindering the formation of pollen spectra in the forest, subalpine and lower-alpine belt soils, the spectrum of each vegetation formation has its own clear-cut peculiarities by which it can be identified fairly precisely. It should also be noted that in the Lagodekhi Reservation unlike many other regions in West Georgia, pollen transported from both short and long distances is of considerable significance (Plates 2, 3). One reason for this is the dry climate in which pollen and spores are more easily spread by air, than, for instance, in the extremely humid maritime climate of Colchis (Kvavadze 1990). It is also significant that the mountain slopes here are very steep, they rise above the Alazani valley like a wall. As a result, all the vegetation belts are compressed to lie within a band 20–25 km wide (the distance from the foot of the mountains up their summits). The consequent transportation of pollen and spores to the summits and ridges of the Lagodekhi peaks means, that the spectra are broadened and register vegetation spread across (Fig. 10). As can be seen from the ac-

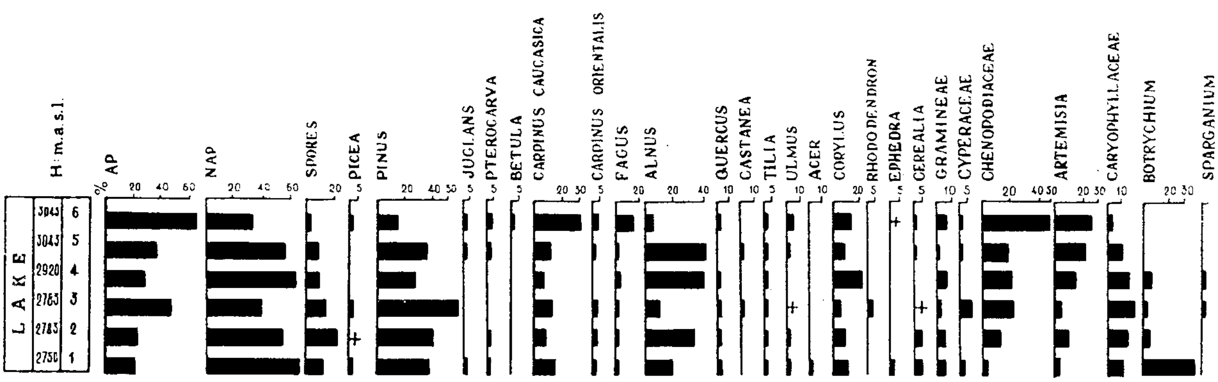


Fig. 10. Spore-pollen spectra of soil of lake sediments in Lagodekhi

companying diagram, the spectra have a fairly extensive area registered not just the forest vegetation belts, but the adjacent steppes as well. Here the source of a large amount of *Artemisia* pollen is the semi-deserts of Azerbaijan and its border territories, whose pollen spectra have been studied by us previously (Kvavadze & Stuchlik 1993).

Thus, the spectra have registered the vegetation structure not only of the Caucasian mountains of the Lagodekhi Reservation and Daghestan, but also that of the whole of eastern Transcaucasia. Hence, the abundance of transported pollen in this case plays a positive role. However, the interpretation of fossil mountain spore-pollen spectra should take into account the ecological requirenments of individual elements in the community and place them in corresponding vertical vegetation belts.

CONCLUSION

Comparison of the spore-pollen spectra of the Lagodekhi Reservation forest with the vegetation actually growing there shows that the spectra give an inadequate representation of *Fagus orientalis* which is the first dominant there and occupies 2/3 of the territory. Meanhwile, the role of pollen of *Carpinus caucasica* (the second dominant of the forest) is somewhat overestimated. The same holds true for *Tilia caucasia*. However, the values for *Acer, Fraxinus, Salix, Rubus, Sorbus, Hedera, Rhododendron* and *Daphne* show that these genera are rather under represented in the pollen spectra.

In the region under study pollen spread by air over both short and long distances plays a much greater role, than in West Georgia. In addition to the direction and strength of the wind, which reachae its maximum in summer, the dry air is a very important factor. Pollen and spores are spread much more easily here than in the saturated damp masses of Colchis.

The floristic composition and quantity of transported elements in the spore-pollen spectrum in the mountains of the Lagodekhi Reservation are strongly influenced not just by the altitude, but also by the aspect of slopes. For example, on the north slopes facing the highest part of the Watershed Range, transport from higher, more cold-loving vegetation increases. On the whole, in the transported pollen of the southern slopes, there are more elements from lower (heat-loving) vegetation belts. This peculiarity of the spectrum, as well as all the others, should be taken into account when interpreting Holocene spore-pollen spectra.

REFERENCES

BRAUN-BLANQUET J. 1951. Pflanzensoziologie. Grundzüge der Vegetationskunde. Springer Verl. WIEN

DOLUKHANOV A. G. 1941. Kratkii ocherk rastitel'nosti Lagodekhskogo zapovednika (A brief description of the Lagodekhi Reservation). In: "Lagodekhskii zapovednik" ("The Lagodekhi Reservation") Issue 1, Izdatel'stvo ANGSSR, Institute of Zoology.

DOLUKHANOV A. G. 1942. Rastitel'nost Lagodekhskogo zapovednika (Vegetation of the Lagodekhi Reservation). Trudy Tbil. Botan. Inst. 8, Tbilisi.

KUZNETSOV N. N. 1911. Lagodekhskoe ushchel'ye v Kakhetii na Kavkaze kak pamiatnik prirody podlezhaschii okhraneniyu. (The Lagodekhi gorge in Kakheti, the Caucasus, as a nature sanctuary to be protected). Izd. Akad. Nauk, St. Petersburg.

KVAVADZE E. V. 1990. Aktuopalinologicheskie aspekty biostratygrafii i paleogeografia golotsena gornykh regionov Zakavkazia (Actuopalynological aspects of biostratygraphy and paleogeography of the Holocene of the Transcaucasian mountain region). Avtoreferat doktorskoy dissertatsii (Thesis of Doctor degree). Tbilisi (in Russian).

KVAVADZE E. V. 1993. On the interpretation of subfossil spore-pollen spectra in the mountains. Acta Palaeobot., 33(1), 347–360.

KVAVADZE E. V. & RUKHADZE L. P. 1989. Rastitel'nost i klimat Golotsena Abkhazii. (Vegetation and climate of the Holocene in Abkhazia). Metsniereba, Tbilisi (in Russian).

KVAVADZE E. V. & STUCHLIK L. 1993. Subfossil polen spectra of the steppe regions of East Georgia. Acta Palaeobot., 33(2): 365–376.

LASCHASHVILI I. YA. & MAMUKELASHVILI V. G. 1986. Flory Lagodekhskogo gosudarstvennogo zapovednika. (Floras of the Lagodekhi State Reservation. Metsniereba, Tbilisi (in Georgian).

MAMISASHVILI K. D. 1975. Zapovedniki Gruzii. (Reservations of Georgia). Department of Reservations and Hunting under the Council of Ministers of the GSSR, Tbilisi.

MARUASHVILI L. I. 1970. Fizicheskaya geografiya Gruzii (Physical Geography of Georgia). Izdat. Tbil. Gosud. Universit. part II (in Georgian).

MLOKOSEVICH L. F. 1878. Zametki o periodicheskikh yavleniyakh prirody v okrestnostiakh urochishcha Lagodekhi Signakhskogo uyezda Tiflisskoi gubernii. (Notes on periodical natural phenomena in the vicinity of the Lagodekhi reservation of the Signakhi District, Tiflis Province). Izv. Kavk. Obshch. Lubit. Yest. i Al'p.Kluba, No.1, Tiflis.

MLOKOSEVICH L. F. 1916. Les Lagodekhskogo ushcheliya. (The forest of the Lagodekhi gorge). Izv. Kavk. Otd. Russk. Geogg. Obshch., 24(2), Tiflis.

SOKOLOV S. Ja. & SYROJECHKOVSKY (eds.) 1990. Zapovedniki SSSR. (Reservations of the USSR. Reservations of the Caucasus) Mysl', Moskva, (in Russian).

SOSNOVSKII D. I. 1911–1912. Lagodekhskoe ushchelie kak predmet okhrany. (The Lagodekhi gorge as an object to be protected). Izv. Kavk. Otd. Russk. Goegr. Obshch., 21(2), Tiflis.

SHIFFERS E. V. 1953. Rastitel'nost' Severnogo Kavkaza i yego prirodnyjekormovyje ugodiya. (Vegetation of the North Caucasus and its natural grasslands). Academic Press, Moscow-Leningrad.

SPRAVOCHNIK PO KLIMATU SSSR. (Reference book for the climate of the USSR), vol. 14. Georgian SSR, part 1, 1971, part 2, 1973, Gidrometeodizdat, Leningrad.

STUCHLIK L. & KVAVADZE E. V. 1987. Subrecent spore-pollen spectra and their relation to recent forest vegetation of Colchis (West Georgia, USSR), Palaeontographica Abt. B, 207, Ltg., (1–6): 133–151.

PLATES

Plate 1

Spores of ferns found in *Rhododendron* tickets of the subalpine belt (slide 49)
Figs 1,2 × 750
Figs 3–9 × 1000

1. *Dryopteris* sp.
2. *Asplenium* sp.
3. a, b – *Athyrium alpestre*
4. a, b – *Athyrium* sp.
5. *Dryopteris spinulosa*
6. *Polystichum braunii*
7. a, b – *Asplenium* sp.
8. a, b – *Asplenium ruta-muraria*
9. a, b – *Cystopteris regia*

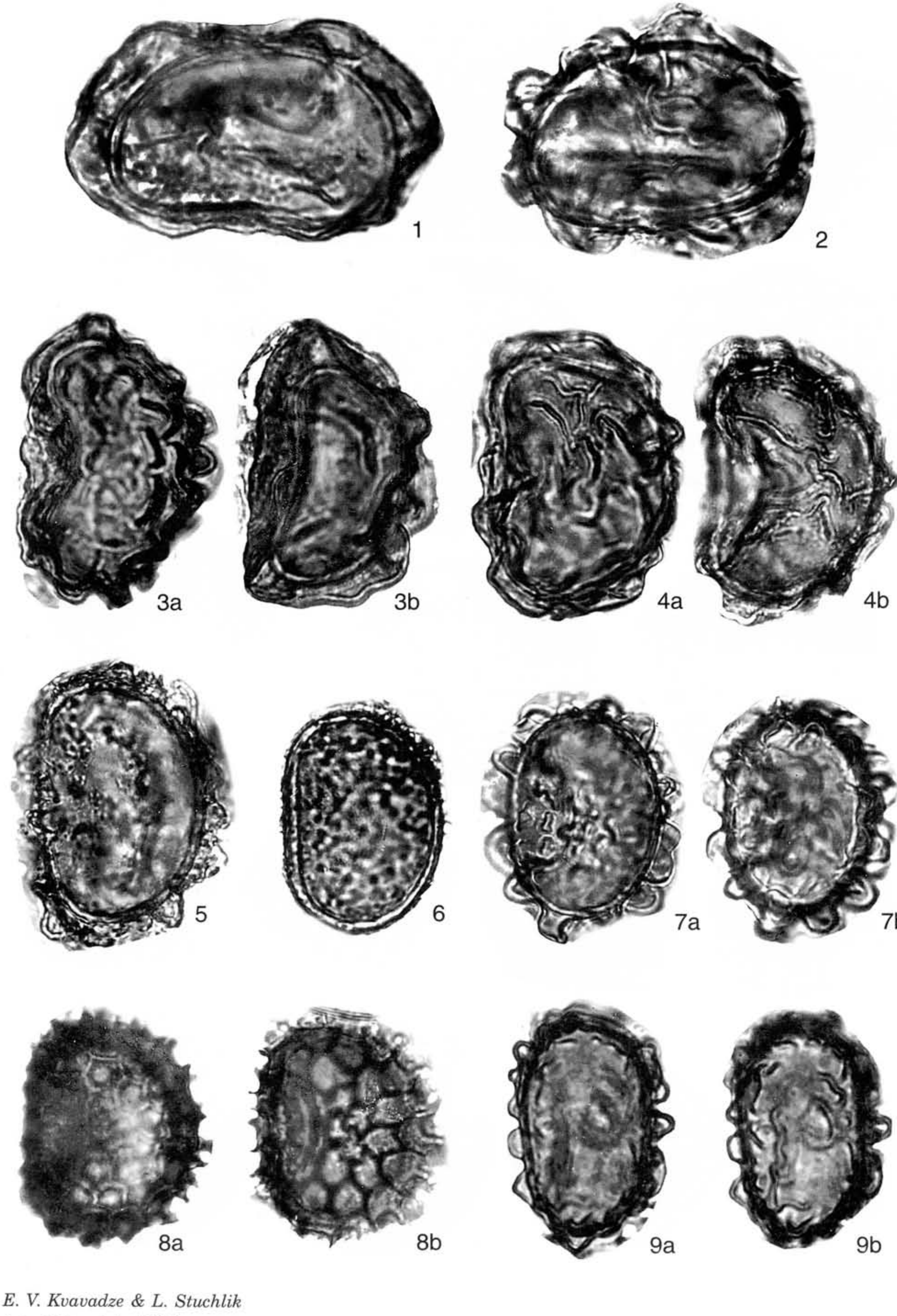

1
2
3a
3b
4a
4b
5
6
7a
7b
8a
8b
9a
9b

Plate 2

Pollen transported to the subalpine belt from neighbouring belts (slide No. 49)
× 1000

1. a, b, c – *Fagus orientalis*
2. a, b – *Tilia caucasica*
3. a, b – *Tilia caucasica*
4. a, b, c – *Carpinus caucasica*
5. *Corylus colurna*
6. a, b – *Ulmus glabra*
7. a, b – *Acer* sp.
8. a, b – *Alnus incana*

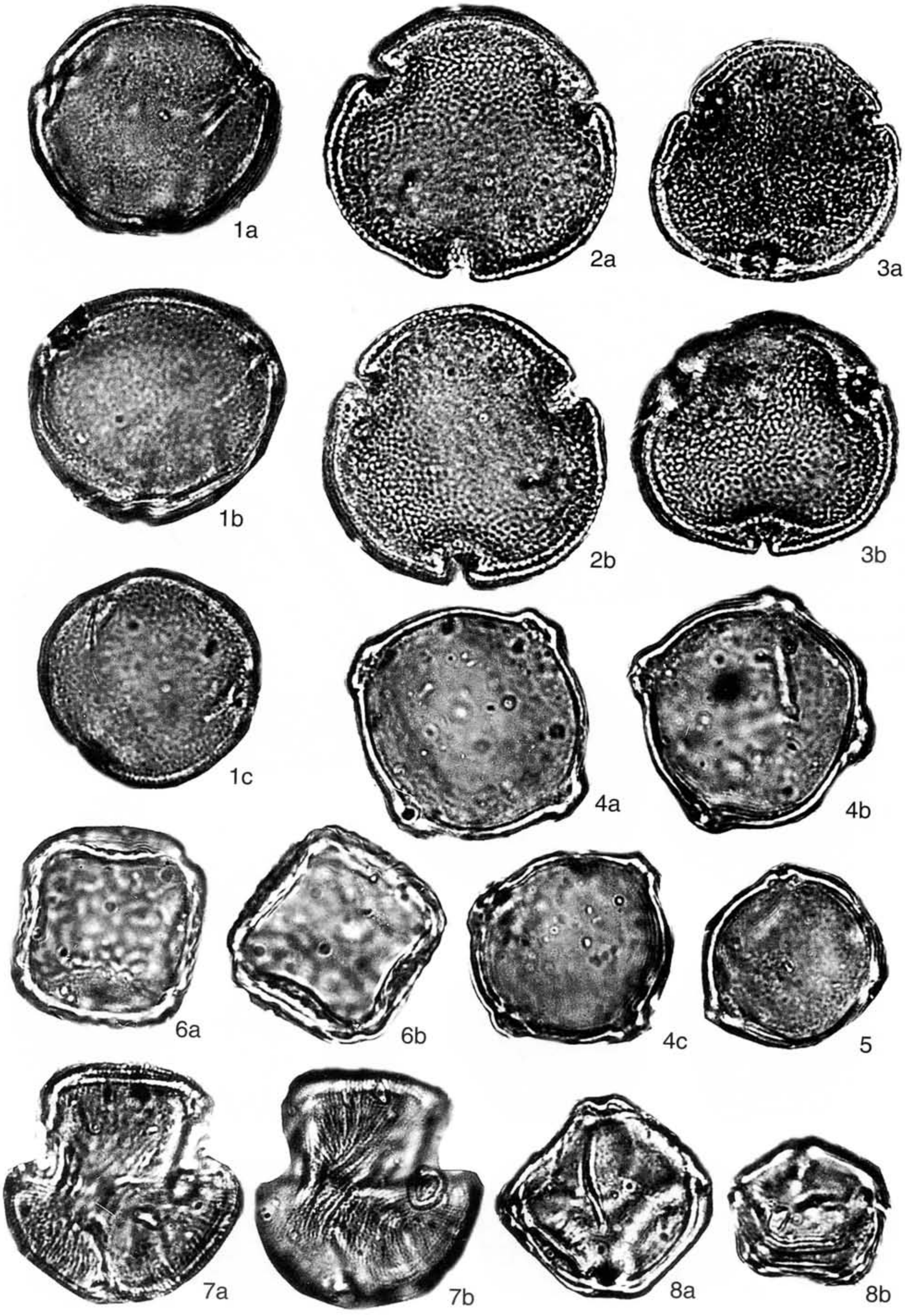
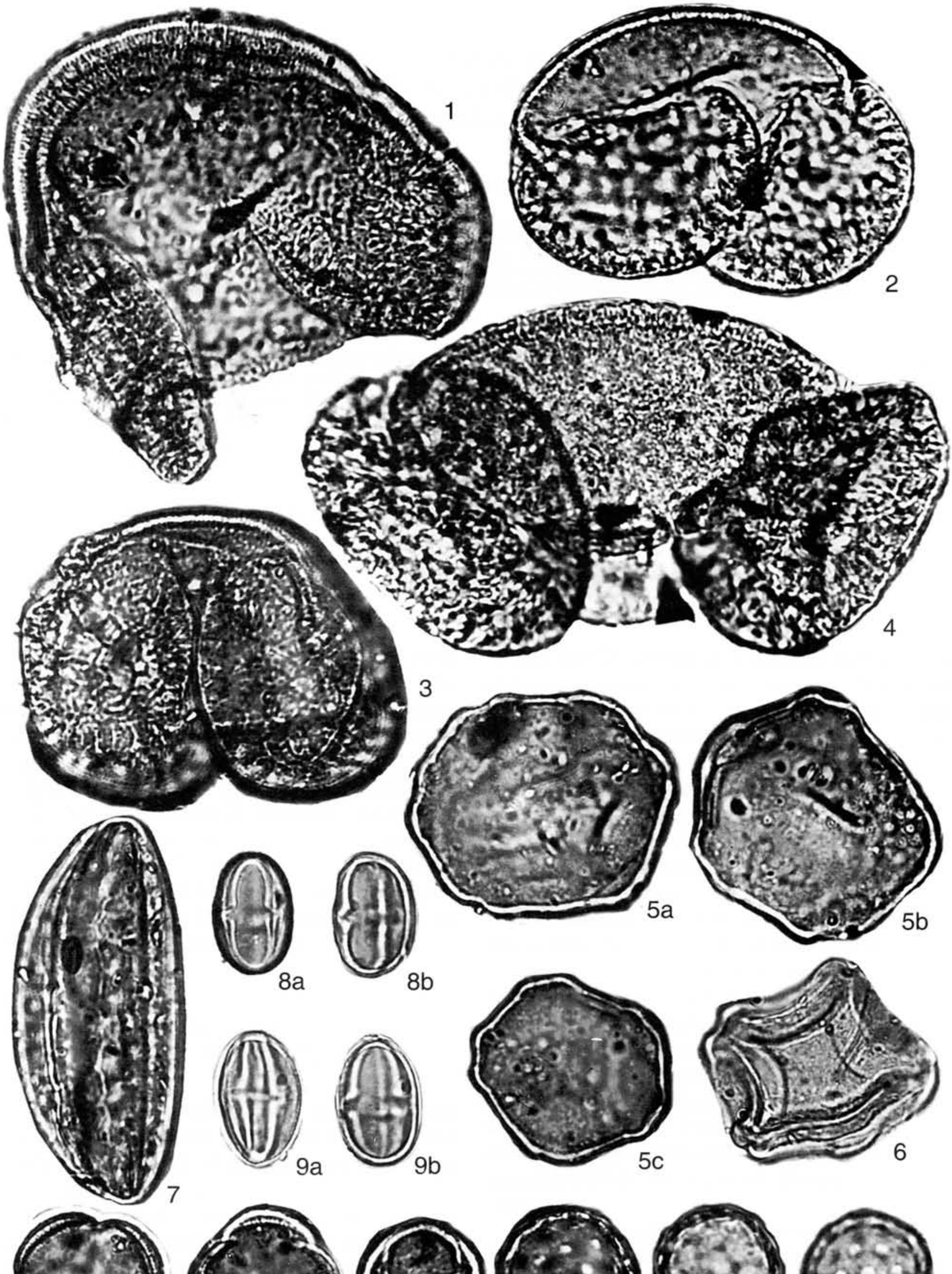

1a
2a
3a
1b
2b
3b
1c
4a
4b
6a
6b
4c
5
7a
7b
8a
8b

Plate 3

Pollen transported to the subalpine belts from distant regions (slide 49)
Figs 1–4 × 750
Figs 5–11 × 1000

1. *Cedrus libani*
2. *Pinus hamata*
3. *Pinus* sp.
4. *Abies nordmanniana*
5. a, b, c – *Pterocarya pterocarpa*
6. *Alnus barbata*
7. *Ephedra procera*
8. a, b – *Castanea sativa*
9. a, b – *Castanea sativa*
10. a, b, c – *Artemisia* sp.
11. a, b, c – Chenopodiaceae


1
2
4
3
5a
5b
7
8a
8b
9a
9b
5c
6
10a
10b
10c
11a
11b
11c