Acta Palaeobot. 41(2): 355–364, 2001

Annual modern pollen deposition in the foothills of the Lagodekhi Reservation (Caucasus, East Georgia), related to vegetation and climate

ELISO KVAVADZE

L. Davitashvili Institute of Palaeobiology Georgian Academy of Sciences, 4 Potochnaya, 380008 Tbilisi, Georgia, e-mail: eliso@paleobi.acnet.ge

Received 10 October 2000; accepted for publication 20 September 2001

ABSTRACT. In the paper the results of pollen monitoring for 1996/1997 – 1998/1999 at two stations situated in the lowest part of the Lagodekhi Reservation foothills are presented. One is located in the flood plain forest with predominance of *Pterocarya pterocarpa*, and the other in the broad-leaved forest with predominance of *Carpinus caucasica*. It was found that *Fagus orientalis* and *Carpinus caucasica* have a maximum pollen deposition reaching in the average up to 117 206 grain/cm^2/year and 106 811 grain/cm^2/year, respectively. *Pterocarya pterocarpa* pollen deposition does not exceed 38 643 grain/cm^2/year. In general pollen deposition in every year was 2.5 time higher in the hornbeam forest than in the riparian forest. The aridization of climate have great influence on the pollen deposition in both hornbeam and riparian forests.

KEY WORDS: annual pollen deposition, pollen monitoring programme, *Pterocarya* forest, *Carpinus* forest, Lagodekhi, Caucasus

INTRODUCTION

The experimental investigation of modern pollen accumulated in special pollen traps is carried out for more objective interpretation of fossil pollen spectra. Similar works were first performed in Denmark (Tauber 1967), where pollen trapping took place not only on land but also in small lakes.

Somewhat later, experiments were performed in England (Peck 1973) and Sweden (Berglund 1973), Greenland (Fredskild 1973), Finland (Vuorela 1973, Hicks 1974). A number of long-term experiments to study pollen rainfall in mixed deciduous forests of South Jutland in Denmark are reported in the works by Andersen (1974, 1980).

In mountain regions pollen trapping first began in Switzerland, both in forest massifs and in open landscapes (Markgraf 1980).

Then the results of long-term pollen rainfall observations were compared and related to the climatic indices of the region under investigation, which makes it possible to reconstruct palaeoclimate according to palynological spectra (Spieksma et al. 1995, Hicks 1996, 1999). The above-mentioned studies also showed that the pollen productivity of plants is first of all affected by the temperature regime of the warm season (Hicks 1999).

In summer 1996 an international Working Group of the INQUA Holocene Studies Commission (coordinator – Sheila Hicks, University of Oulu, Finland) was launched for European Pollen Monitoring. The aim of the above mentioned programme was to create Pollen Monitoring stations in 15 countries of Europe, where the study of pollen rainfall was to be carried out according to the unified standard methods in established pollen traps of the same type.

Traps for the first stage of the programme

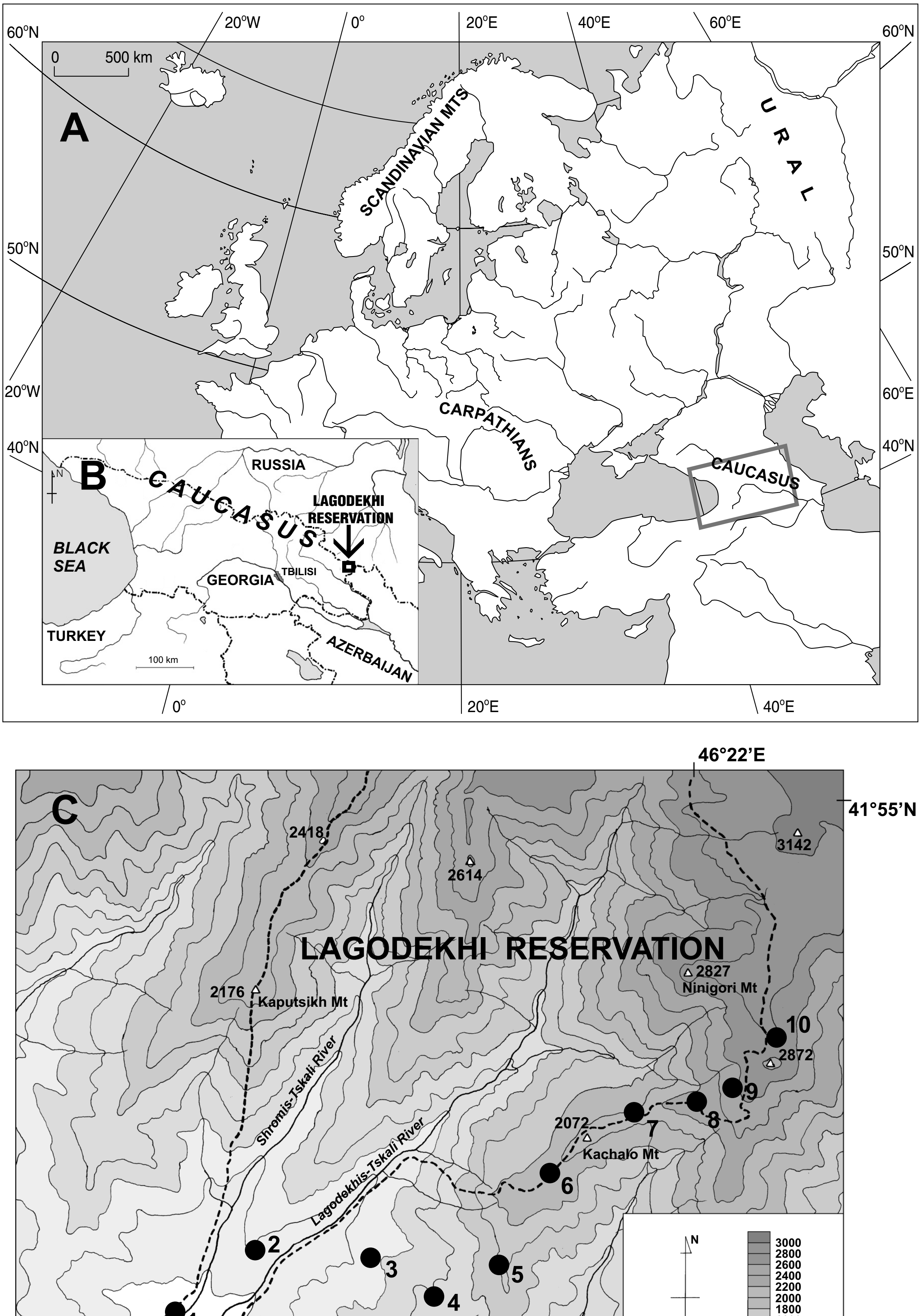

Fig. 1. **A** – map of Europe; **B** – map of Georgia with location of the Lagodekhi Reservation (in the square), **C** – map showing the position of the pollen monitoring site in the Lagodekhi Reservation

were established at the end of the flowering season (September-October) 1996. After that each addition of traps to the programme was to commence at the same time of the year (September-October) to ensure that the sampling period was always the same (Hicks et al. 1996). Besides the pollen percentage, particular attention was to be given to pollen deposition (grain/cm^2/year), since this index is a good indicator for distinguishing forested and unforested formations (Davis 1976, Davis et al. 1980).

In Georgia the studies within the framework of the Pollen Monitoring Programme began in September 1996 in mountain forests of the Lagodekhi Reservation (Fig. 1). Ten modified Tauber pollen traps were placed within the altitudinal range from 450 to 2 900 m a.s.l. Five traps were placed in the forest belts, two – on the tree limit and three traps – in the open landscapes with alpine and subalpine vegetation (Tab. 1). First results including the nature of the pollen accumulated for one calendar year (1996/1997) were published earlier (Kvavadze 1999). In the present publication the results of observations for three calendar years from 1996 to 1999 are given. Here the emphasis will be placed on recent pollen rainfall accumulated in the lowest belt of forest vegetation. Here two questions are of special interest: 1) the character of yearly variations in pollen deposition of such predominant broad-leaved species as *Pterocarya pterocarpa, Carpinus caucasica, Fagus orientalis, Tilia caucasica, Quercus iberica,* and *Acer velutinum*; 2) establishment of the dependence of variations in pollen deposition of the above-mentioned broad-leaved species on changes in climatic conditions.

GENERAL DESCRIPTION OF THE LAGODEKHI RESERVATION

The vegetation of the Lagodekhi Reservation is characterized by an unique floristic composition especially in the lower, piedmont belt. Here a marked increase in relict species and relatively young species with a narrow area should be mentioned (Dolukhanov 1989).

For the Lagodekhi Reservation forests and for the Caucasus, as a whole, the absence of monodominant forests is characteristic. Even *Fagus orientalis*, occupying 2/3 of the forest area of the Reservation, does not form pure stands (Lachashvili & Mamukelashvili 1986, Chikovani et al. 1990).

In the lowest piedmont part there are two pollen monitoring stations. One of them (trap No. 1) is located at an altitude of 450 m in the flood plain forest along the river Shromis-Tskali with predominance of *Pterocarya pterocarpa*. In the Caucasus this Tertiary relict, having a broken and narrow area, becomes rarer and rarer and needs protection. More detailed information on the spread of *Pterocarya* in the Caucasus both in time and space is given by Stuchlik and Kvavadze (1998).

The second station is situated in the broad-leaved forest with predominance of *Carpinus caucasica* (trap No. 2) at an altitude of 500 m. The detailed description (according to the method by Braun-Blanquet 1951) of flood plain and hornbeam forest vegetation is given

Table 1. Basic data of the location of each of the pollen sampling sites

Pollen trap	Location	Altitude (m a.s.l.)	Nature of surroundings	Coenosis dominant
1	41°51′15″N46°16′0.8″E	450	Closed	*Pterocarya, Carpinus, Fagus*
2	41°53′08″N46°17′10″E	500	Closed	*Carpinus, Tilia, Fagus*
3	41°53′10″N46°18′09″E	1000	Closed	*Fagus, Carpinus, Tilia*
4	41°53′30″N46°19′10″E	1250	Closed	*Fagus, Tilia, Carpinus*
5	41°53′11″N46°20′20″E	1500	Closed	*Fagus, Carpinus, Tilia*
6	41°55′10″N46°21′00″E	1800	Closed	*Fagus, Acer, Quercus macranthera*
7	41°57′30″N46°21′07″E	2000	Closed	*Acer, Sorbus, Fagus, Quercus*
8	41°57′07″N46°22′30″E	2250	Open	*Betula, Salix caprea, Sorbus*
9	41°55′08″N46°23′06″E	2500	Open	Poaceae, Cyperaceae
10	41°59′00″N46°23′15″E	2900	Open	Poaceae, Cyperaceae

in the earlier works (Kvavadze & Stuchlik 1996, Kvavadze 1999). Here we restrict ourselves to the description of local arboreal species growing directly near the pollen trap within the circle of 60 m in diameter. For better understanding of the presented material schematic maps of local arboreal vegetation on each sampling plot are prepared.

MATERIAL AND METHODS

A modified Tauber pollen trap for the region with high precipitation is a container of up to 5 litres and with a 5 cm diameter hole. The trap is sunk into the ground so that its top is at ground level. For better preservation of the trapped pollen the trap should contain a basic mixture of glycerin, formalin and thymol (Hicks et al. 1996, 1999). The pollen collected for the year together with rain water is settled in the laboratory conditions. After long-term settling of water the sediment is collected by centrifuging and the surface water was siphoned. If there are many mineral particles, they are separated from the pollen by centrifuging in cadmium liquid. The following treatment is performed according to the standard method (Hicks et al. 1996, 1999). To count the pollen deposition three *Lycopodium* tablets with batch No. 124961 were added (Stockmarr 1971, 1973). Two *Lycopodium* tablets were added only for the material from trap No. 2 for 1996/97. Spores of *Lycopodium* were added to the sediment after collecting pollen from the water by centrifuging and before the standard KOH and acetolize treatment was used. Generally the pollen sum was counted up to 500–700 specimens. Taxonomically pollen grains and spores were determined to the rank of species, genus or sometimes only to family rank. For determining the taxon names of pollen the "*Lexicon Botanicum*" by Makashvili (1961) has been used.

Around each pollen trap within a circle of 30–40 m diameter a schematic map of tree vegetation was made.

RESULTS AND DISCUSSION

Pollen monitoring station No. 1

As is seen from the schematic map (Fig. 2), 18 mature *Pterocarya pterocarpa* trees grow on this sampling plot. Here *Carpinus caucasica* (11 specimens) and *Fagus orientalis* (10 specimens) are met almost in equal amounts. *Acer velutinum* (3 specimens) is less important In the undergrowth there grow *Hedera helix, Corylus avellana, Euonymus europaeus, Rubus. Hedera* and *Rubus* are predominant. Directly near the pollen trap, at the distance of 4–5 m there grow *Pterocarya* and *Acer*. Even nearer *Euonymus* and *Rubus* bushes are found. Thus *Pterocarya* accounts for 43%, *Carpinus* – 26%, *Fagus* – 24% and *Acer* – only for 7% of the first tree layer (A). The shrub layer (B) is occupied by *Rubus caesius* and *Hedera helix*, and among herbs (C) layer *Asperula odorata, Viola mirabilis, Sanicula europaea* and *Phyllitis scolopendrium* prevail (the description of herbs was made in June).

For the first sampling year 1996/97 the total pollen deposition in trap No. 1 reaches 240 745 grain/cm^2/year of which arboreal species amount to 155 840 grain/cm^2/year The first dominant among arboreal species is *Carpinus caucasica* (Fig. 3) whose pollen deposition reaches up to 33 714 grain/cm^2/year However, the pollen deposition predominant in *Pterocarya* coenosis, does not exceed 32 093 grain/cm^2/ year. Participation of *Fagus orientalis*, whose pollen deposition does not exceed 14 312 grain/cm^2/year, is also reduced. Acer amounts to 4 214 grain/ cm^2/year, *Rubus* – 2 809 grain/cm^2/year, *Hedera* – 2 809 grain/cm^2/year. The *Euonymus europaeus* pollen was not found in the sediment of trap 1 at all.

The second sampling year 1997/98 differed from the first one by an increase in warm season temperature, accompanied by nearly a twofold reduction in precipitation (the detailed data on the climate of Lagodekhi are given by Kvavadze and Stuchlik 1996). For this year the total amount of accumulated pollen was also twice as low and accounted for 145 792 grain/cm^2/year. The amount of arboreal pollen does not exceed 87 045 grain/cm^2/year. The pollen content of the arboreal group changed drastically. The *Pterocarya* pollen deposition (up to 38 643 grain/cm^2/year) is predominant; as is seen, its amount increased compared with the preceding year. However, the hornbeam pollen deposition reduced and accounted for 21 663 grain/cm^2/year. Even more dramatic changes took place in the beech pollen deposition up to 3 317 grain/cm^2/year. This index is nearly 5 times lower than that of 1996–97. The amount of *Acer* pollen reduced to 3 300 grain/cm^2/year. The *Hedera* and *Rubus* pollen deposition was more than three times less than that of the preceding year. However, in 1997–98 the *Euonymus* pollen was found in trap No. 1.

The third sampling year 1998/99 was characterized by normal, usual for this place climatic indices. The amount of arboreal pollen increased and was 99 852 grain/cm^2/year. Like

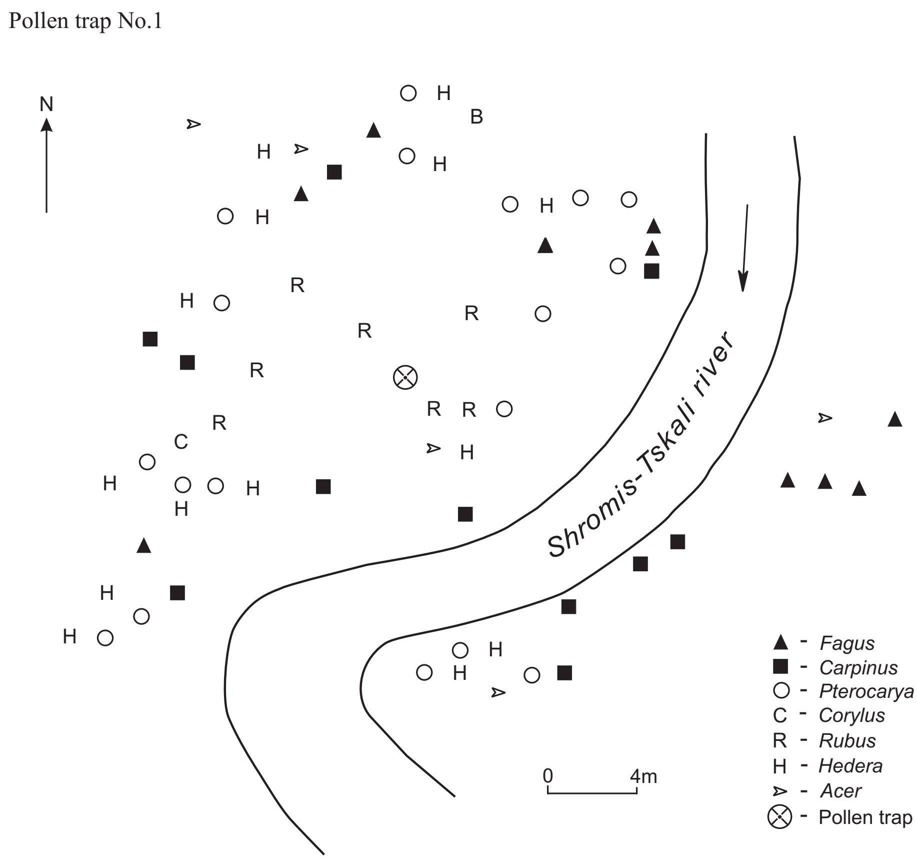

Fig. 2. Schematic map of vegetation (arboreal species and shrubs) around the trap No. 1

1996/97, *Carpinus caucasica* becomes the first dominant of the spectra (up to 27 846 grain/cm^2/year). The second place in predominance of pollen deposition is occupied by *Fagus orientalis* (up to 27 564 grain/cm^2/year), and the role of *Pterocarya* pollen places at the third place (up to 21 939 grain/cm^2/year). The *Acer* pollen deposition increased significantly (up to 7 313 grain/cm^2/year). However, in spite of the fact that the climatic conditions of the warm season became better, in the pollen rainfall collected for 1998/99 *Hedera*, *Rubus* and *Euonymus* pollen was not found at all.

For the three years of the experiment the from longer distance transported pollen is also recorded in the pollen rainfall (Fig. 3). This is

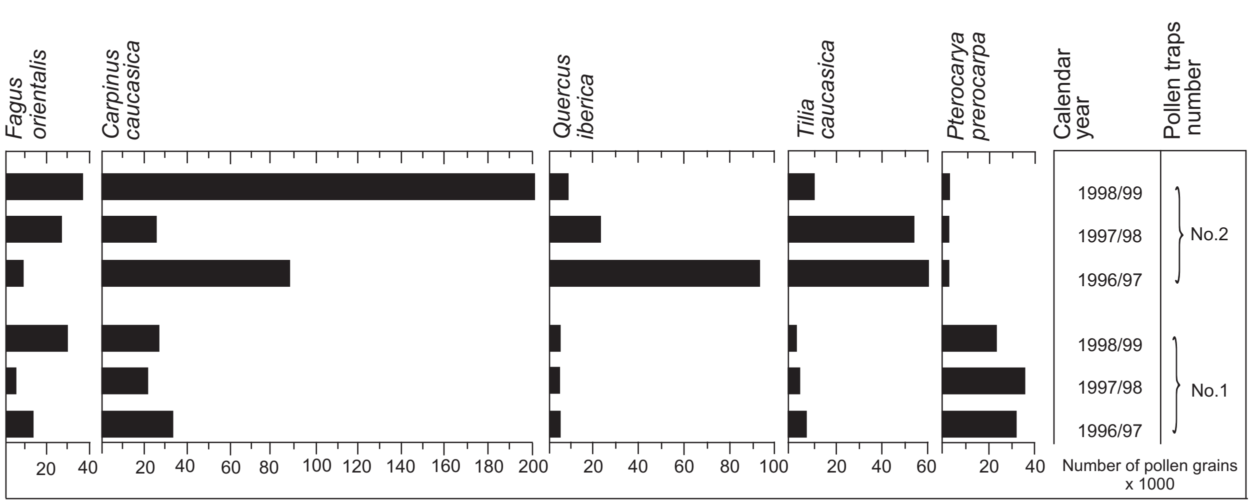

Fig. 3. Diagram showing the pollen deposition (in grain/cm^2/year) of dominant arboreal species in the pollen rain of traps No. 1 and No. 2 for three sampling years

essentially the pollen of plants growing in the neighbouring vegetation belts. In the transported pollen *Alnus barbata* growing a little higher along the river Shromis-Tskali is predominant. Significant quantities in the transported pollen occupy *Quercus iberica, Tilia caucasica* and *Corylus avellana*. *Carpinus caucasica, Juglans regia, Fraxinus excelsior* and *Ulmus elliptica* appear in less amounts. The components of high mountain forests 12–15 km away from the place of pollen sedimentation are found as single grains. This is *Betula litwinowii*.

Pollen monitoring station No. 2

On this sampling plot (altitude 500 m a.s.l.) 20 trees of *Carpinus caucasica*, 9 specimens of *Tilia caucasica*, 6 – *Fagus orientalis*, 3 – *Acer velutinum*, 2 – *Ulmus elliptica*, 2 – *Fraxinus excelsior*, 1 – *Quercus iberica* grow around the pollen trap situated on the slope of south-west exposition (Fig. 4). In the undergrowth *Rubus* sp. is predominant. Three *Cornus mas* bushes and one bush of *Corylus avellana* and *Carpinus orientalis* are recorded. Among herbs *Pachysandra macrophylla* (75%), *Asperula odorata* (15%), and *Carex sylvatica* (10%) are prevalent (the description of herbs was made in June).

As is seen, on the second sampling plot hornbeam accounts for 46.5% of the area, lime – 21%, beech – 14%, maple – 7%, elm and ash-tree – 4% each, and only 2% of the area is occupied by oak. In the immediate vicinity of the trap, 4 m to the north-east there grows hornbeam, and a little further, at the distance of 5 m a mature specimen of lime (Fig. 4).

For the first sampling year 1996/97 both the total pollen deposition and the arboreal pollen deposition in trap No. 2 reached very high values and amounted to 594 337 grain/cm^2/year and 527 226 grain/cm^2/year, respectively. These indices are significantly higher than the pollen deposition for 1996/97 in the flood plain forest (trap No. 1).

Among arboreal species *Quercus iberica* pollen is predominant (up to 98 656 grain/cm^2/year), in spite of the fact that here oak, as has been already mentioned, is represented by a single specimen. It should be mentioned that in the beech forest the first year is characterized by even higher values of the *Quercus hartwissiana* pollen deposition at an altitude of 1800 m

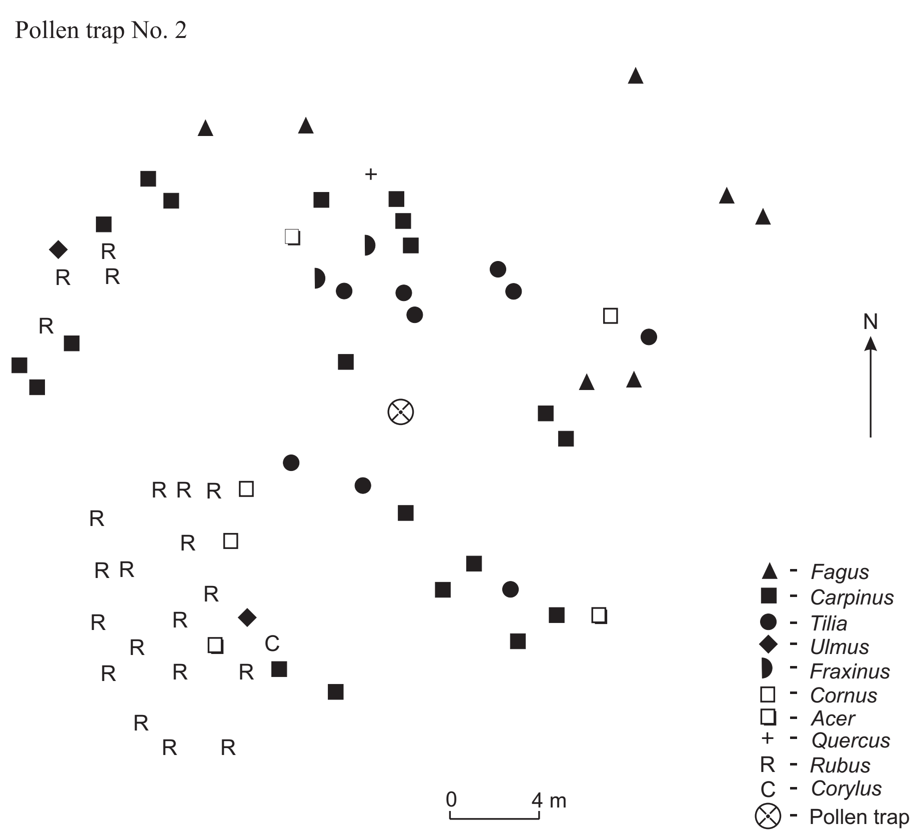

Fig. 4. Schematic map of vegetation (arboreal species and shrubs) around the trap No. 2

(up to 102 588 grain/cm^2/year), where only 2 specimens of oak are recorded. It seemed to be a year of optimum pollination for oak.

The second place is taken by the hornbeam pollen deposition (up to 79 363 grain/cm^2/year) and the third place – by lime (up to 68 453 grain/cm^2/year). The beech pollen deposition accounted for 67 111 grain/cm^2/year, maple – 3 355 grain/cm^2/year, elm – 2 944 grain/cm^2/year, and ash-tree – 2 725 grain/cm^2/year. Among bushes *Corylus*, growing here in a single specimen, has the highest pollen deposition values (up to 6 214 grain/cm^2/year). The *Cornus* pollen deposition is less important (up to 2 237 grain/cm^2/year) and the pollen of *Rubus*, growing on the west edge of the sampling plot, is not recorded in the trap sediments at all.

The second experimental year 1997/98 characterized by climate aridity, exhibits the following peculiarities of pollen rainfall. The total amount of pollen has decreased compared with 1996/97 and accounted for 205 540 grain/cm^2/year (against 594 337 grain/cm^2/year). The pollen deposition of arboreal species in trap No. 2 has decreased to 171 569 grain/cm^2/year (against 527 226 grain/cm^2/year) compared with the preceding year. In the group of arboreal species the highest pollen deposition value belongs to lime (up to 59 378 grain/cm^2/year. The second place is taken by hornbeam (up to 26 543 grain/ cm^2/year, the third – by beech (up to 25 692 grain/cm^2/year and the fourth – by oak (up to 21 695 grain/cm^2/year). Maple and ash-tree account for 2 115 grain/cm^2/year each, elm – 1 614 grain/cm^2/year, hazel – 6 848 grain/cm^2/year, *Cornus* – 570 grain/cm^2/year. As in the preceding year, accumulation of *Rubus* pollen in the pollen rainfall of trap No. 2 was not recorded.

The third experimental year 1998/99 with normal climatic conditions was characterized by the following features of the pollen spectrum. The total pollen deposition was 333 424 grain/cm^2/year of which the arboreal species accounted for 296 205 grain/cm^2/year. These indices, though somewhat lower than those of the first year, are still much higher than the pollen deposition for the second arid year.

In the group of arboreal species the hornbeam pollen deposition has the highest values (up to 214 528 grain/cm^2/year, the second dominant is the beech pollen (up to 34 634 grain/cm^2/year) and the third – the lime pollen (up to 10 855 grain/cm^2/year). As we see, the role of lime is reduced nearly 6 times compared to the preceding year and nearly 7 times compared to the first year. The oak pollen deposition got also reduced drastically (to 7 754 grain/cm^2/year against 21 685 grain/cm^2/year for the second year and 98 656 grain/cm^2/year – for the first year). Thus, in the first case the pollen deposition decreased nearly 7 times, while in the second case – nearly 14 times. The maple pollen accounted only for 978 grain/cm^2/year. In 1998/99 the ash-tree and elm pollen was not recorded in the pollen rainfall of trap No. 2 at all. Among bushes the hazel is predominant, whose pollen deposition accounted for 5 168 grain/cm^2/year. The *Rubus* pollen appeared (up to 1 242 grain/cm^2/year).

For all these years in trap No. 2 like in trap No. 1 the transported pollen is recorded, where the pollen of plants from the neighbouring belts is predominant. From distant places (from highland forests) pollen of pine and birch was transported. The transportation of pollen of *Cedrus deodara* growing in the introduction (as an ornamental plant in gardens and parks of Lagodekhi at least 3–3.5 km away from pollen monitoring station No. 2) is observed.

Thus, the analysis of the character of the pollen accumulated in piedmont broad-leaved forests indicates that the pollen deposition of all arboreal species and bushes is not constant and varies from year to year. *Quercus iberica* and *Tilia caucasica* exhibit most significant changes in the pollen deposition – from 7 000 to 98 000 grain/ cm^2/year and from 10 000 to 68 000 grain/cm^2/year, respectively. *Pterocarya pterocarpa* is characterized by lower fluctuations in this index (from 21 000 to 38 000 grain/cm^2/year).

Among all arboreal species growing on the two sampling plots *Carpinus caucasica* shows maximum pollen values. Its averaged index for the three years in the pollen rainfall of trap No. 2 is 106 811 grain/cm^2/year. Such high values of hornbeam pollen deposition are not reached at other altitudes (Fig. 5), since exactly in the piedmont belt up to 500–600 m hornbeam has most favourable growing conditions and here this plant is a predominant species of coenosis. Similarly, the maximum pollen deposition of *Fagus orientalis* is recorded at an altitude of 1500 m, where there are more favourable ecological conditions for it (Dolukhanov 1989). It should also be mentioned, that

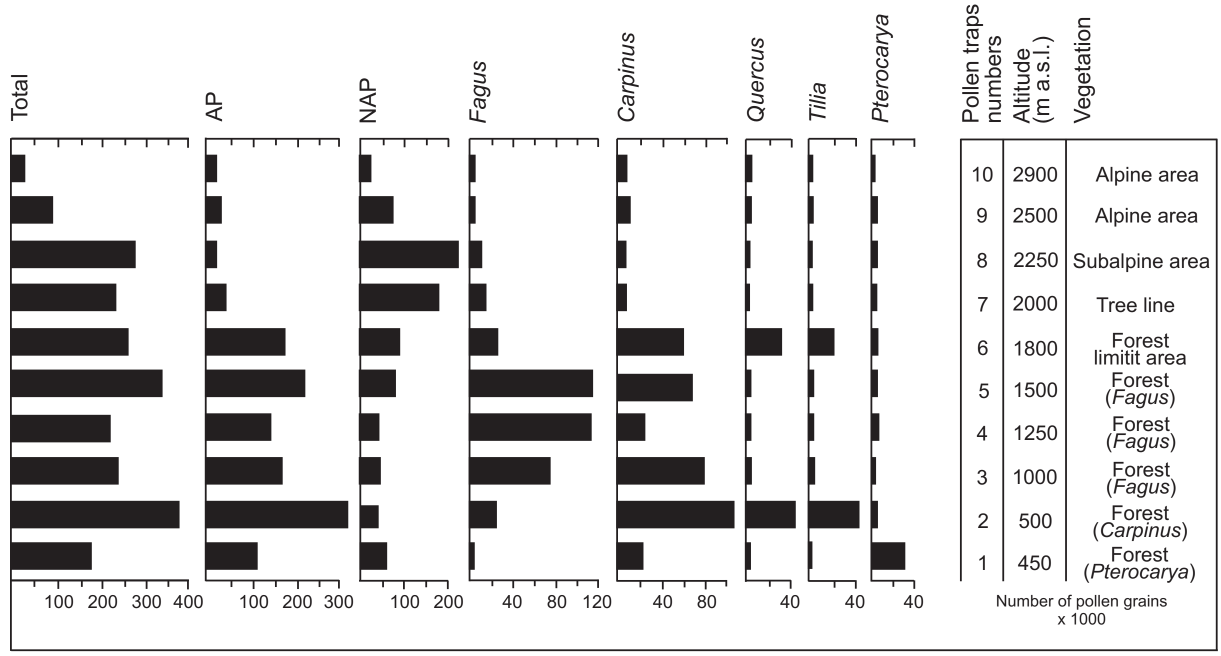

Fig. 5. Diagram showing the averaged (over a period of three years) pollen deposition (in grain/cm^2/year) of dominant arboreal species in the pollen rainfall of ten pollen traps located at different altitudinal levels of mountain ridges

the averaged index of beech pollen deposition is somewhat higher than that of hornbeam and accounts for 117 206 grain/cm^2/year. The third place in pollen deposition abundance is occupied by *Tilia caucasica* (up to 46 228 grain/cm^2/year) and the fourth place – by *Quercus iberica* (up to 42 701 grain/cm^2/year). Maple participation in the coenosis in trap Nos 1 and 2 was adequately reflected in the pollen spectra. This is also true for *Ulmus* and *Fraxinus* whose pollen amount in the spectrum corresponds to their role in vegetation. However, *Rubus* and *Euonymus* are characterized by a very low pollen deposition for the years under consideration. A little reduced, especially in the arid year, is the amount of *Hedera* pollen in trap No. 1.

As for the pollen productivity response of the arboreal species under consideration to climate drying and warming, it should be noted that beech appeared to be most sensitive, its pollen deposition reduced nearly seven times (trap No. 1). The hornbeam and oak pollen deposition reduced nearly three times (trap No. 2). Rather peculiar was the pollen productivity response of *Tilia caucasica*. A sharp decrease in the pollen deposition took place in a year, when the pollen deposition reduced nearly six times, while exactly in the arid year a decrease in the pollen deposition of lime was rather insignificant (Fig. 3).

Climate drying and warming exerted positive influence only on the pollen quantity of *Pterocarya pterocarpa*, whose pollen deposition in the arid year increased and appeared to be maximum (up to 38 643 grain/cm^2/year). This phenomenon can also be explained by ecological requirements of *Pterocarya*. Of all Tertiary elements it is the most heat-loving plant. It never grows in mountains higher than 500 m (Gulisashvili 1964). During the drought *Pterocarya* compensates the lack of moisture from always moist flood plain soil.

From the comparison of the average pollen deposition indices for the three sampling years (Fig. 5) we see that the local vegetation of the both sampling plots and its character are adequately reflected in the pollen rain. On the first plot, where *Pterocarya* prevails, it is most important in the pollen spectrum. On the second sampling plot the coenosis dominant – hornbeam is characterized by maximum and predominant participation in the spectrum of the pollen accumulated for the three years.

CONCLUSION

In spite of quite a short time of observations, carried out within the pollen monitoring programme, some rather interesting regularities of modern pollen spectrum formation in the piedmont belt of broad-leaved forests of the Lagodekhi Reservation have been revealed.

1. The pollen deposition of all considered arboreal species and shrubs is not a constant value and varies significantly from year to year. In every year it was 2.5 time higher in the hornbeam forest (*Carpinus caucasica, Quercus iberica, Tilia caucasica*) than in the riparian forests (*Pterocarya pterocarpa*).

2. Among all arboreal species growing on the two sampling plots *Carpinus caucasica* shows the highest pollen deposition. *Tilia caucasica* takes the second place in this index, while the third place is occupied by *Quercus iberica*. However, at other altitudinal levels, where, for example, there are optimal ecological conditions for beech forests, beech reaches maximum pollen deposition values. It should also be mentioned that the pollen deposition of beech at an altitude of 1500 m a.s.l. is somewhat higher compared to that of hornbeam.

3. The comparison of pollen deposition of *Acer, Fraxinus* and *Ulmus* with equal participation in vegetation of sampling plot 2 (trap No. 2) showed that in spite of the fact that *Ulmus*, unlike *Acer* and *Fraxinus*, is a wind-pollinated taxon, the maximum deposition of its pollen (up to 2 900 grain/cm^2/year) is almost the same as for insect-pollinated *Acer* and *Fraxinus* (up to 3 000 grain/cm^2/year and 2 700 grain/cm^2/year, respectively).

4. Among shrubs *Corylus avellana* and *Hedera helix* are characterized by the highest, and *Rubus, Evonymus, Cornus* – by the lowest pollen deposition values.

5. Beech appeared most sensitive to climate drying, its pollen deposition reduced nearly seven times (trap No. 1). During the three years of investigations no cyclicity in the flowering of *Fagus* were observed. Maybe, farther investigations would give some detailed information on this problem.

6. There was nearly a threefold decrease in the hornbeam and oak pollen deposition and nearly a twofold decrease in the pollen deposition of *Ulmus*. The response of *Acer* and *Fraxinus* to climate drying was not very pronounced. Rather peculiar was the response of lime. In the arid year the pollen amount reduced only insignificantly, while next year the lime pollen deposition reduced more than six times. Climate drying and warming had positive influence only on the pollen deposition of *Pterocarya pterocarpa* and *Corylus avellana*.

ACKNOWLEDGEMENTS

I would like to thanks Professor Sheila Hicks (University of Oulu, Finland) for her constant care and consultations. Many thanks to Shota Eriashvili (Lagodekhi Reservation, Lagodekhi) for his help in the field, Marina Ashiyan (State University of Tbilisi) for the translation of my paper and Fati Kervalidze (Tbilisi) for help with some of the illustrations.

REFERENCES

ANDERSEN S.-T. 1974. Wind conditions and pollen deposition in a mixed deciduous forest. Seasonal and annual pollen deposition 1967–1972. Grana, 14: 64–77.

ANDERSEN S.-T. 1980. Influence of climatic variation on pollen season severity in wind-pollinated trees and herbs. Grana, 19: 47–52.

BERGLUND B.E. 1973. Pollen dispersal and deposition in an area of southwestern Sweden – some preliminary results: 117–129. In: Birks H.J. & West R.G. (eds). Quaternary plant ecology. Blackwell, Oxford.

BRAUN-BLANQUET J. 1951. Pflanzensoziologie. Grundzüge der Vegetationskunde. Springer Verlag, Wien.

CHIKOVANI T.G., GIGAURI G.I., DIDMANIDZE E.A., SIROECHKOVSKY E.E. & SHAVLIASHVILI I.A. 1990. Lagodekhsky zapovednik (The Lagodekhi Reservation): 210–226. In: Sokolov V.E. & Syroechkovsky E.E. (eds) Zapovedniki SSSR. Zapovedniki Kavkaza. Misl', Moskva. (in Russian).

DAVIS M.B. 1976. Pleistocene biogeography of temperature deciduous forest. Geoscience and Man, 13: 13–26.

DAVIS M.B., SPEAR R.W. & SHANE L.C.K. 1980. Holocene climate of New England. Quaternary Research, 14: 240–250.

DOLUKHANOV A.G. 1989. Lesnaya rastitel'nost' Gruzii, I (Forest vegetation of Georgia, I). Metsniereba, Tbilisi. (in Russian).

FREDSKILD B. 1973. Studies in the vegetational history of Greenland. Meddelelser om Grønland, 198(4): 1–245.

GULISASHVILI V.Z. 1964. Prirodnye zony i estestvenno-istoricheskie oblasti Kavkaza (Naturals zones and naturally-historical regions of Caucasus). Nauka. Moskva. (in Russian).

HICKS S. 1974. A method of using modern pollen rain values to provide a fimescale for pollen diagrams from peat depositions. Memoranda Soc. Fauna Flora Fenn. 49: 21–33.

HICKS S. 1996. The feasibility of using pollen deposition data as climate indices. Paläoklimaforschung, 20: 173–187.

HICKS S. 1999. The relationship between climate and annual pollen deposition at northem tree-lines. Chemosphere: Clobal Cange Science, 1: 403–416.

HICKS S., AMMANN B., LATAŁOWA M., PARDOE H. & TINSLEY H. 1996. European Pollen Monitoring Programme. Project description and guidelines. Oulu University Press, Oulu.

HICKS S., TINSLEY H., PARDOE H. & CUNDILL P. 1999. Europaen Pollen Monitoring Programme. Supplement to the guidelines. Oulu University Press, Oulu.

KVAVADZE E. 1999. The first results of the the Pollen Monitoring Programme in the Caucasus Mts. (Georgia). Acta Palaeobot., 39(1): 171–177.

KVAVADZE E. & STUCHLIK L. 1996. Recent pollen spectra of the mountain forests of the Lagodekhi Reservation (East Georgia). Acta Palaeobot., 36(1): 121–147.

LACHASHVILI I. & MAMUKELASHVILI G. 1986. Konspekt flory Lagodekhskovo Gosudarstvennovo zapovednika (The summary of the flora of Lagodekhi State Reservation). Metsniereba, Tbilisi. (in Georgian).

MAKASHVILI A. 1961. Lexicon Botanicum. Nomina plantarum. Sabchota Sakartvelo, Tbilisi.

MARKGRAF V. 1980. Pollen dispersal in a mountain area. Grana, 19: 127–146.

PECK R. 1973. Pollen budget studies in a small Yorkshire catchment.: 43–46. In: Birks J.H.B. & West R.G. (eds) Quaternary plant ecology. Blackwell, Oxford.

SPIEKSMA F.TH.M., EMBERLIN J., HJELMROOS M., JÄGER S. & LEUSCHNER R.M. 1995. Atmospheric birch (*Betula*) pollen in Europe: trends and fluctuations in annual quantities and the starting dates of the seasons. Grana, 34: 51–57.

STOCKMARR J. 1971. Tablets with spores used in absolute pollen analysis. Pollen et Spores, 13: 615–621.

STOCKMARR J. 1973. Determination of spore concentration with an electric particle counter. Danm. Geol. Unders., 1972: 87–89.

STUCHLIK L. & KVAVADZE E. 1998. Subfossil pollen spectra of flood-plain forest of *Pterocarya pterocarpa* in the Alazani Valley (East Georgia). Acta Palaeobot., 38(1): 217–222.

TAUBER H. 1967. Investigations of the mode of pollen transfer in forested areas. Review Palaeobot. Palyn., 3: 277–286.

VUORELA I. 1973. Relative pollen rain around cultivated field. Acta Bot. Fenn., 102: 1–27.