The Holocene 17,5 (2007) pp. 599–611

Pollen representation in surface samples of the *Juniperus*, *Picea* and *Juglans* forest belts of Kyrgyzstan, central Asia

Ruth Beer,[1]* Willy Tinner,[1] Gabriele Carraro[2] and Ennio Grisa[3]

([1]Section of Palaeoecology, Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland; [2]Dionea SA, Lungolago Motta 8, CH-6600 Locarno, Switzerland; [3]Intercooperation KIRFOR (Kyrgyz-Swiss Forestry Support Programme), Kyrgyzstan, Karagashova Rosha 15 720000 Bishkek, Kyrgyz Republic)

Received 20 December 2006; revised manuscript accepted 29 January 2007

A HOLOCENE RESEARCH PAPER

Abstract: Surface pollen deposition at five sites (Kichikol, Karakol, Nishneye and Verkhneye Ozero, and Bakaly) in four different forest types (*Juniperus*, *Picea*, *Juglans* and mixed forests) in Kyrgyzstan have been investigated to assess the relationship between modern vegetation and pollen composition in order to calibrate the pollen representation. Vegetation surveys with an estimation of the tree-crown cover (%) were made in 10 m × 10 m plots to relate the vegetation to surface pollen of moss polsters. Correlation calculations show a close relationship between vegetation (tree-crown cover) and pollen for the *Juniperus* site (eg, $r^2 = 0.76$ between crown cover and arboreal pollen, AP) and the *Picea* site ($r^2 = 0.85$), whereas the linkage is weaker at the *Juglans* site ($r^2 = 0.35$) and in mixed forests ($r^2 = 0.32$). The results of the surface samples of moss polsters are compared and discussed with surface samples of lake sediments that were taken at the same locations. We use vegetational maps from around the lakes to discuss the link between vegetation and pollen at extra-local scales (800 m around the sites). These comparisons show that AP underestimates the effective tree cover around all sites, with in extreme cases densely forested areas corresponding to AP values as low as <60; 30%. We explain this finding by the prevalent background pollen load that derives from the dry lowland and slope steppes (*Artemisia*, Chenopodiaceae, Poaceae). Our investigation may improve the reconstruction of Quaternary vegetation and climate history of these forest belts in Kyrgyzstan (Central Asia) on the basis of fossil pollen assemblages from mire and lake sediments. It provides new insights into the pollen reflection of forest isles (eg, on humid slopes or mountain tops) that are surrounded by continental steppes; a vegetational situation that may be used as an analogue for the conditions during the full glacial in Eurasia and Northern America.

Key words: Surface samples, tree-crown cover, palynology, Kyrgyzstan, juniper forests, *Juniperus*, *Picea*, *Juglans*, mixed forest, central Asia.

Introduction

Much of the uncertainty in the interpretation of late Quaternary pollen assemblages can be removed by the judicious use of pollen surface samples from a variety of vegetation formations. The technique is especially useful in new regions of investigation, where not much is known of the vegetation imprint on the pollen sequence (Wright, 1967). A special focus is the separation of pollen sources from local to regional scales (Wright, 1967). In Europe such efforts were undertaken more than 50 years ago to better understand the linkages between vegetation and pollen (eg, in treeline situations; Firbas, 1934; Welten, 1950). More recently, several studies on pollen source area, pollen productivity estimates and pollen dispersal have been carried out in America (Janssen, 1967; Calcote, 1995; Jackson and Kearsley, 1998) and in Scandinavia, where modelling studies are used to calibrate vegetation cover and pollen (Sugita, 1994; Sugita *et al.*, 1999; Broström *et al.*, 2004, 2005; Bunting *et al.*, 2004). Near our study region, Wright *et al.* (1967) studied the relationship between modern plant cover and pollen rain in western Iran. Bottema and Barkoudah (1979) studied the modern pollen rain and its relation to vegetation in Syria and Lebanon. El-Moslimany (1990) investigated sites in the Middle East. Kvavadze and Stuchlik (1990) studied the subrecent spore and pollen spectra and their relation to recent vegetation belts in northwestern Georgia. Liu *et al.* (1999) made a study of the woodland ecotone in relationship to surface pollen in the Inner Mongolian Plateau, China. Recently a study was made on the

*Author for correspondence (e-mail: ruth.beer@ips.unibe.ch)

© 2007 SAGE Publications

10.1177/0959683607078984

quantitative relationship between modern pollen rain and climate in Tibet (Shen *et al.*, 2006).

However, so far no investigation on modern pollen rain in relation to vegetation has been made in Kyrgyzstan, Central Asia. The pollen sequences available from Kyrgyzstan (data not yet published) are made from mire and lake sediments in the different vegetation belts. Surface samples of lake sediments are presented here in comparison with the data obtained by surface samples of moss polsters. The results may prove useful to improve the interpretation of the Quaternary vegetation and climate history of this region.

Material and methods

Study sites

Kichikol (39°59′ N, 73°33′ E) is a lake located at 2554 m a.s.l. on the northern slope of the Alay range (Figure 1). The surface of the lake is 10 ha; it has no major inlet or outlet. The present-day forests of *Juniperus turkestanica* Kom. and *J. semiglobosa* Rgl. are restricted to north-facing slopes and are rather open. Pastures and meadows occur in open patches of the forest and on south-facing slopes. Karakol (42°50′ N, 77°23′ E) is a subalpine lake located at 2353 m a.s.l. on the south-facing slope of the Kungey Alatau (Figure 1). It has a surface of 5 ha and has an outlet at its eastern border. Dense stands of *Picea schrenkiana* F. et M. form the forests in this area. Pastures and meadows extend around the lake. The nearest climatic station at a comparable altitude for these two sites is located at Naryn (41°43′ N, 76°00′ E, 2039 m a.s.l.), where mean January and July temperatures of −15.8 and 17.3°C and a mean annual temperature of 3.65°C are recorded. The mean annual precipitation is 285.5 mm (World Climate, 2006 http://www.worldclimate.com (last accessed 2 April 2007)). Bakaly lake (41°52′ N, 71°58′ E) lies south of Chatkal Range at 1880 m a.s.l. in the Sary Chelek Reserve (Figure 1) at the upper altitudinal limit of *Juglans regia* L. It has a surface of approximately 1 ha with no major inlet or outlet. The forests consist of a mosaic of *Juglans regia*, *Juniperus turkestanica*, *J. semiglobosa*, *Picea schrenkiana*, *Abies semenovii* Hill., *Acer turkestanica* Pax., *Malus kirghisorum* Al. et An. Theod., *Prunus* spp. and *Crataegus* spp. and are rather open. Nishneye (41°18′ N, 72°57′ E; 1371 m a.s.l.) and Verkhneye Ozero (41°18′ N, 72°57′ E; 1440 m a.s.l.) are two lakes located in the Arslan-Bob region on the south-facing slope of the Fergana Range (Figure 1). Both lakes have a surface of 3 ha and have no major inlet or outlet. They lie in the core-region of the so-called walnut-fruit forests. The local forests around the lakes are dense (Figure 2). Forests with *Juglans regia*, *Crataegus turkestanica* A. Pojark., *Malus kirghisorum, Prunus mahaleb* L., and *Prunus sogdiana* Vass. are dominant on north-facing slopes. Stands of *Acer turkestanica* together with the above-mentioned tree species are found on south-facing slopes, while *Pistacia vera* L. forms thickets on the driest patches. For a thorough description of the walnut-fruit forests see Blaser *et al.* (1998) and Epple (2001). At Ak Terek Gava (1748 m a.s.l.; 41°17′ N, 72°5′ E, the nearest climatic station to Bakaly, Nishneye and Verkhneye Ozero, mean January and July temperatures are −3.1 and 20.5°C and mean annual temperature is 8.9°C. The mean annual precipitation is 1020 mm (data provided by Intercooperation).

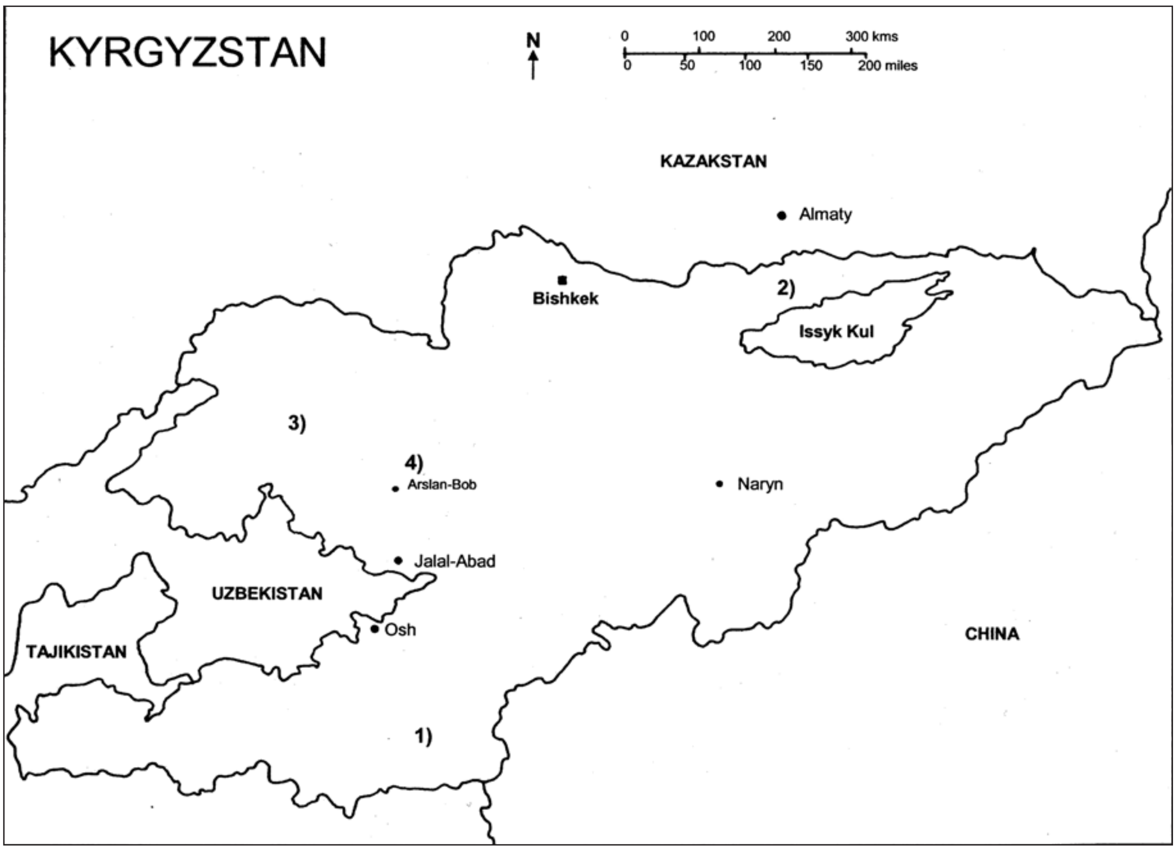

Figure 1 Map of Kyrgyzstan and location of the four studied sites: 1, Kichikol (KKO1, KKO2); 2, Karakol (KAO); 3, Bakaly (BAO2, BAO); 4, Nishneye and Verkhneye Ozero (NOVO)

Figure 2 Verkhneye Ozira. The site is situated in the *Juglans-Acer* forests of Kyrgyzstan. Closed forests are reflected by 59.8% of arboreal pollen. The lowlands in this area are dominated by treeless dry steppes

Selection of sampling sites and vegetation maps

The collection of samples of moss polsters was made along transects laid around five lakes located in forests that are characteristic for Kyrgyzstan, ie, *Juniperus* forests around Kichikol, *Picea* forests around Karakol, *Juglans* forests around Nishneye and Verkhneye Ozero, and mixed forest stands around Bakaly. Vegetation maps were made by the vegetation typology group of Intercooperation Bishkek and allow definition of characteristic vegetation units on the basis of local conditions (topography, geomorphology, soils) and vegetational relevés that were made to determine the tree-crown cover and the forest structure (Typology group KIRFOR, 2004). The following standard methodology was applied at the four sites Kichikol, Karakol, Nishneye and Verkhneye Ozero. An overview survey in the field allowed the identification of the main vegetational complex of a site. Subsequently, detailed field surveys were used to delimit polygons of homogenous vegetation types on the basis of the local physiognomy and morphology of the vegetation, (coloured) aerial photographs, overview pictures of the landscape and/or topographic maps. A vegetational relevé 10 m × 10 m (including, eg, species composition, tree cover, slope aspect, inclination, degradation, coordinates) was then made in a representative part of the vegetational unit (polygon). The same was repeated for all polygons at a site. Polygons representing the same vegetation type (see Table 1) were assigned to already mapped vegetational units. Topographic maps at scale 1:10 000 were used at Kichikol and Karakol to map the vegetation. At the latter site aerial photographs provided additional information. The vegetation maps of Nishneye and Verkhneye Ozero were made by using Quick bird satellite images (1 m pixel definition). The vegetation map of Bakaly dates back to 2002 and was made by the State Forest Service of the Kyrgyz Republic. This map is part of the forest management documentation for the Sary Chelek Zapavednic (= protected territory) and similarly to the other maps delimits units of characteristic vegetation types (State Forest Service of the Kyrgyz Republic, 2002).

Sampling of surface samples

Moss polsters have been found to be effective natural pollen traps. A recent comparison between pollen collected in Tauber traps and moss polsters in Finland showed that pollen assemblages in the green part of the moss polsters represent only one year, or possibly two years of deposition (Broström *et al.*, 2004). A total of 43 surface samples of moss polsters or the top 2 cm of Ah soil horizons were collected during coring expeditions in 2003 and 2005 on a radius of 0.5 m. Sugita (1994) states that the relevant source area of pollen (ie, the area beyond which the correlation between pollen loading and plant abundance in the surrounding vegetation does not improve) in lakes in simulated landscapes is within 50–100 m from the lake edge for forest hollows (Radius (R) = 2 m), 300–400 m for small lakes (R = 50 m) and 600–800 m for medium-sized lakes (R = 250 m). This is in agreement with empirical studies (eg, Conedera *et al.*, 2006). Among these, moss polsters correspond most to forest hollows where much of the pollen derives from vegetation close to the sampling spot. Therefore vegetation relevés were made in plots of 10 m × 10 m around the surface sample (Mazier *et al.*, 2006). Distance weighting was not applied for the vegetation data, because detailed spatial information of species distribution in the plots was not available. Tree-crown cover was estimated by means of percentages. Surface samples of lake sediments have been analysed for the five lakes from cores taken during the coring campaigns in 2003 and 2005.

Laboratory work and analysis

Surface samples were treated with KOH and sieved with a mesh of 1 mm, then treated with HCL, HF and acetolysis (Moore *et al.*, 1991), and suspended in glycerine. In each sample at least 600 pollen grains were identified with pollen keys (Moore *et al.*, 1991; Beug, 2004), pollen atlases (Reille, 1992, 1998) and the reference collection of the Institute of Plant Sciences of the University of Bern. Spores and Cyperaceae pollen were excluded from the pollen sum. Pollen diagrams were

Table 1 Spatial area covered by vegetation units represented by surface samples within a radius of approximately 800 m around the lakes

Locality	Plot numbers	Vegetation units	Area (ha) of units	Area (%) of units
Kichikol	1; 2	*Juniperus* on steep slopes, with shrubs	12	9.5
	3; 4; 5	meadows and pastures	84	68
		Juniperus on stony debris	8.5	7
		Juniperus wide apart, with shrubs	11.5	9
		meadows with a few *Juniperus*	8	6.5
Karakol	1; 2	*Picea* dense forest	26.5	20
	3	meadows and pastures	78	60
	4; 5; 6	*Picea* forest	17.5	14
		Juniperus stands (single trees)	8	6
Bakaly[a]	4a; 5a; 6b; 8b; 9b; 10b	Mixed forest (*Juniperus*, *Picea*, *Juglans*, *Acer*, *Malus*)	11	7
	1b	Broadleafed forest (*Juglans*, *Acer*, *Crataegus*)	24.5	15.5
		Coniferous forest (*Picea*, *Abies*, *Juniperus*)	6	4
	1a; 3a; 7b	Shrub forest (*Malus*, *Prunus*, *Crataegus*, *Juniperus*)	31	19.5
		Pasture	68	43
	2a; 2b; 3b	Other, non-forested area	18.5	11
Nishneye Ozero	1; 3	*Juglans* on steep northern slopes	35	51
	(2)	*Malus* with *Juglans*	7.5	11.5
	4	Mixed shrub forest with *Malus* and *Acer* on very steep slopes	8	11.5
		Juglans, Malus, Crataegus on northern slopes	3.5	5
		Juglans on northern slopes	2	3
		Juglans with *Crataegus*	3.5	5
		Juglans with *Malus*	3.5	5
		Malus with *Crataegus*	5.5	8
Verkhneye Ozero	5; 8	Mixed shrub forest with *Malus* and *Acer* on very steep slopes	12	18
	6; 9	*Juglans, Malus, Crataegus* on northern slopes	22	33.5
	7	*Juglans* on northern slopes	4.5	7
	10	*Juglans*	2.5	4
	11	*Malus* with scattered *Juglans*	7	10.5
		Juglans and *Malus*	3	4
		Juglans with *Crataegus*	5	7.5
		Juglans with *Malus*	7.5	11.5
		Juglans	2.5	4

[a]Bakaly plot numbers: a, N–W transect (BAO2); b, W–E transect (BAO).
Numbers of samples that were taken in the marsh vegetation around the lakes are not recorded in this table.

made including all the important pollen types for each site. Sketches of the sites were drawn according to the vegetation surveys along the axis of the pollen diagrams to visualize the landscape and the vegetation. Altitudinal variation was integrated, but the distance to the lake is approximated. Correlation coefficients (r) and determination coefficients (r^2) were calculated to asses the relationship between pollen representation (AP) and vegetation cover (tree-crown cover and forest cover).

Results

Kichikol: *Juniperus* forests, tree-crown cover (KKO1): Figure 3

Five samples were taken from sites ranging from a single *Juniperus* tree (sample 1, crown cover 10%) to closed *Juniperus* forest (sample 5, crown cover 100%). The results (Table 2, Figures 3 and 4) show that vegetation and pollen are in very good agreement, eg, AP values increase with increasing tree-crown cover. The linear correlation between AP (*Juniperus*) and tree cover (Figure 4) attains a determination coefficient of 0.76. Samples 1 and 2, from sites with *Juniperus* tree-crown covers of 10 and 20%, both show *Juniperus* pollen values around 25%, in association with low stomata finds. Sample 3 represents a crown cover of 45% and yields 35% of *Juniperus* pollen. Only a few *Juniperus* stomata were found. In sample 4 a crown cover of 80% is reflected by 80% *Juniperus* pollen and many stomata. In vegetation plot 5 dense stands of *Juniperus turkestanica* and *J. semiglobosa* form a closed canopy. They are represented by 65% *Juniperus* pollen in association with numerous stomata. Single pollen grains of *Prunus*- and *Sorbus*-type pollen cannot be related to trees growing in the vegetation plots. *Artemisia* pollen shows increasing values up to 45% with diminishing tree-crown covers of the *Juniperus* forest, although not present locally in the relevés. Chenopodiaceae pollen reaches 10% only in sample 1. Poaceae pollen reaches 15% in sample 2 and 10% in samples 1 and 3. High percentages of Cyperaceae pollen recorded in samples 1 to 3 may be related in part to the riparian vegetation around the lake.

Transect of *Juniperus* forest to meadows (KKO2): Figure 5

Five samples were taken along a transect from dense *Juniperus* stands (samples 1 and 2) on the west-facing slope of the lake to the meadows on the east-facing slopes (samples 3, 4 and 5). Figure 5 shows decreasing *Juniperus* pollen percentages with increasing distance to the forest. In vegetation plot 1 *Juniperus turkestanica* and *J. semiglobosa* form dense stands with a crown cover of 75% on the steep slope above Kichikol. *Juniperus* pollen reaches 35%, and numerous stomata were found. In plot 2 *Juniperus* trees form open stands with 30% crown cover. Here the values of *Juniperus* pollen drop to 20%, without any stomata finds. In samples 3 to 5 *Juniperus* pollen reaches 10%.

Table 2 Dominant plants and tree-crown cover (%) in the vegetation plots studied for pollen of surface samples

Juniperus forest, *Juglans* forest				*Picea* forest, Mixed forest			
Locality	Plot number	Dominant plant species	TCC[a] (%)	Locality	Plot	Dominant plant species number	TCC[a] (%)
KKO1	1	*Juniperus turkestanica*, *J. semiglobosa*	10	KAO	1	*Picea schrenkiana*	100
	2	*Juniperus turkestanica, J. semiglobosa*	20		2	*Picea schrenkiana*	50
	3	*Juniperus turkestanica*, *J. semiglobosa*	45		3	Poaceae, upland herbs	0
	4	*Juniperus turkestanica*, *J. semiglobosa*	80		4	*Picea schrenkiana*, *Juniperus*	25
	5	*Juniperus turkestanica, J. semiglobosa*	100		5	*Picea schrenkiana*	75
KKO2	1	*Juniperus turkestanica*, *J. semiglobosa*	75		6	*Picea schrenkiana*	100
	2	*Juniperus turkestanica*, *J. semiglobosa*	30	BAO2	1	*Crataegus turkestanica*, *Malus kirghisorum*, *Juniperus turkestanica, J. semiglobosa*, *Prunus mahaleb*	70
	3	*Artemisia*, Poaceae, upland herbs	0		2	*Exochorda tianschanica*, *Lonicera nummularifolia*, *Malus kirghisorum*	0
	4	*Artemisia*, Poaceae, upland herbs	0		3	Cyperaceae	0
	5	*Artemisia*, Poaceae, upland herbs	0		4	*Malus kirghisorum*, *Crataegus turkestanica*	50
NOVO	1	*Juglans regia*	50		5	*Picea schrenkiana*, *Crataegus turkestanica*	70
	2	*Acer turkestanica*, *Crataegus turkestanica*, *Malus kirghisorum*, *Prunus sogdiana*	30		6	*Picea schrenkiana*, *Acer turkestanica, Prunus mahaleb*, *Juniperus turkestanica*	80
	3	*Juglans regia*	60	BAO	1	*Juglans regia, Prunus mahaleb, Acer turkestanica, Juniperus turkestanica*	60
	4	*Acer turkestanica*, *Crataegus turkestanica, Malus kirghisorum, Prunus mahaleb*	30		2	*Cotoneaster multiflora*, *Rubus caesius*, *Spiraea hypericifolia*	0
	5	*Prunus mahaleb*, *Juglans regia*, *Prunus sogdiana Crataegus turkestanica*	40		3	*Juniperus turkestanica*, *Acer turkestanica*,	50
	6	*Juglans regia*, *Prunus mahaleb*, *Crataegus*, *Prunus sogdiana*	80		4	*Betula alba*	80
	7	*Acer turkestanica*, *Juglans regia*, *Crataegus*	40		5	Cyperaceae	0
	8	*Acer turkestanica*, *Crataegus turkestanica, Malus kirghisorum*	50		6	*Juniperus turkestanica, J. semiglobosa*, *Malus kirghisorum*	40
	9	*Prunus mahaleb*, *Crataegus turkestanica, Juglans regia*, *Malus kirghisorum*, *Prunus sogdiana*	60		7	*Exochorda tianschanica*, *Berberis heteropoda*	0
	10	*Crataegus* sp., *Malus kirghisorum*	40		8	*Acer turkestanica*, *Juniperus turkestanica*, *Juglans regia*, *Malus kirghisorum*	40
	11	*Acer turkestanica*, *Crataegus turkestanica*, *Juglans regia*, *Malus kirghisorum*, *Prunus sogdiana*	60		9	*Juniperus turkestanica*, *Juglans regia*	30
					10	*Juniperus turkestanica*, *J. semiglobosa*, *Malus kirghisorum*	40

[a]TCC, tree-crown cover.

Artemisia pollen is present throughout the transect with 45–55%. The *Artemisia* pollen may originate from local plants in the meadows. Pollen of Chenopodiaceae is represented by low but constant values around 5–10%. Except for sample 1 the pollen of Poaceae shows constant values around 10%. Cichorioideae pollen shows a peak of 10% in sample 3, whereas *Mentha*-type pollen is found in high amounts in sample 4. Both types may mirror the meadows and pastures around the lake on the east-facing slopes. The pollen of Cyperaceae shows not only a peak in sample 3 near the lake but also in sample 5. This is easily explainable by the fact that Cyperaceae such as *Carex* are growing in both upland and wetland communities.

Karakol: *Picea* forest (KAO): Figure 6

Six samples were taken along a N–S transect at Karakol extending from closed *Picea* forest stands on the north-facing slope to

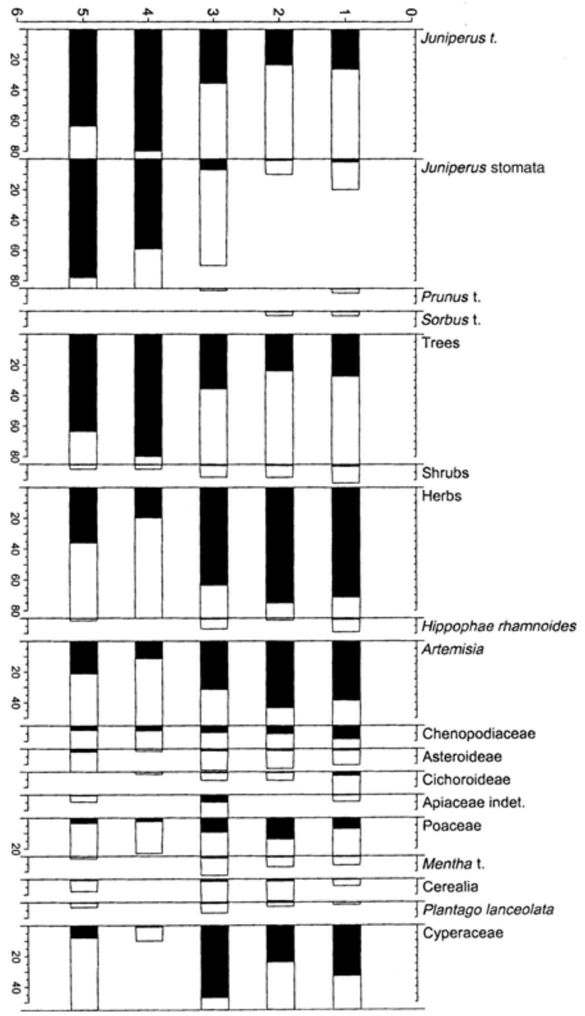

Figure 3 Pollen percentages of selected pollen types at Kichikol, sampled along a gradient of crown densities in a *Juniperus* forest. Tree-crown cover is 10% in plot 1, 20% in plot 2, 45% in plot 3, 80% in plot 4 and 100% in plot 5. Black bars are percentage values; white bars are ×10 exaggeration

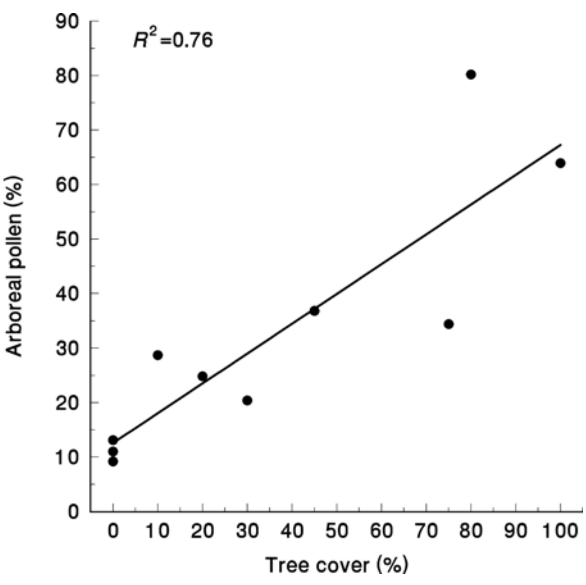

Figure 4 Correlation between tree-crown cover and pollen percentages of arboreal pollen (AP) in the *Juniperus* forest at Kichikol

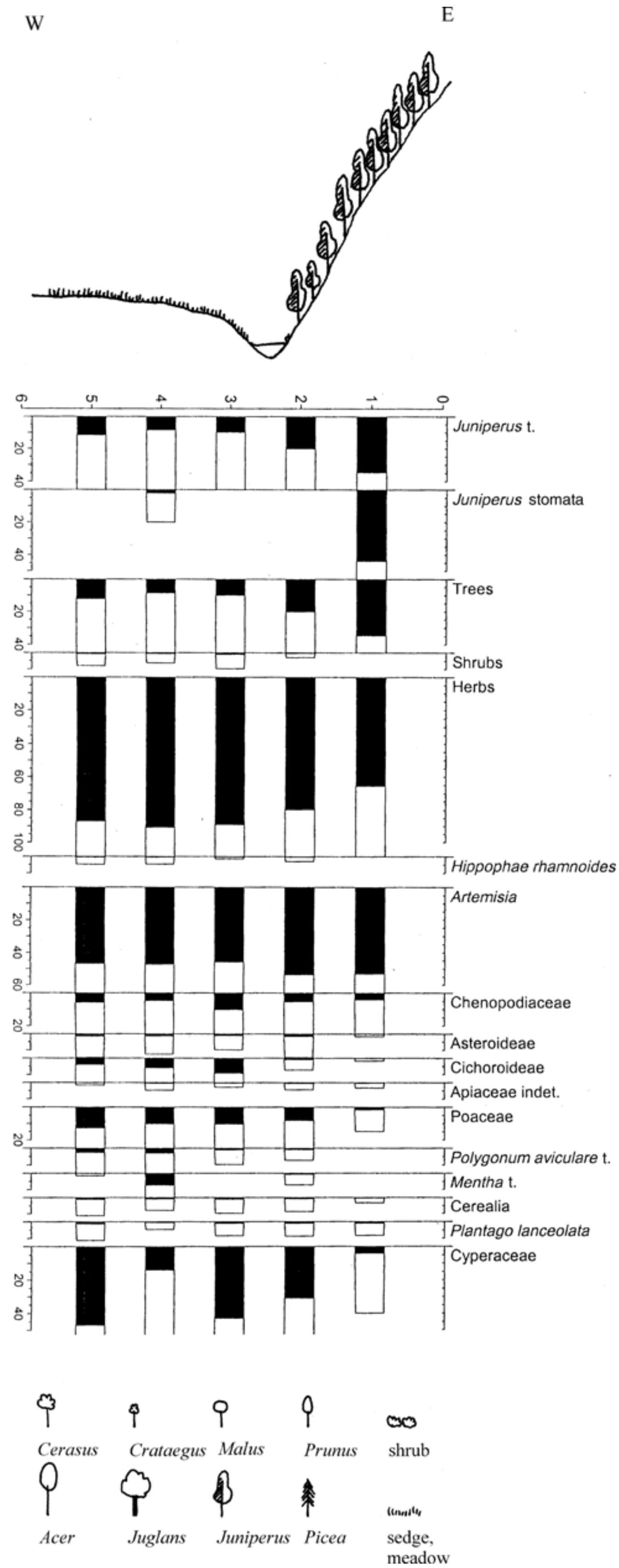

Figure 5 Vegetation transect and pollen percentages of selected pollen types at Kichikol, sampled along a W–E transect. Tree-crown cover of *Juniperus* is 75% in plot 1, 30% in plot 2, 0% in plots 3 to 5. Legend: symbols of the tree types used in Figures 5, 6, 8, 9 and 11

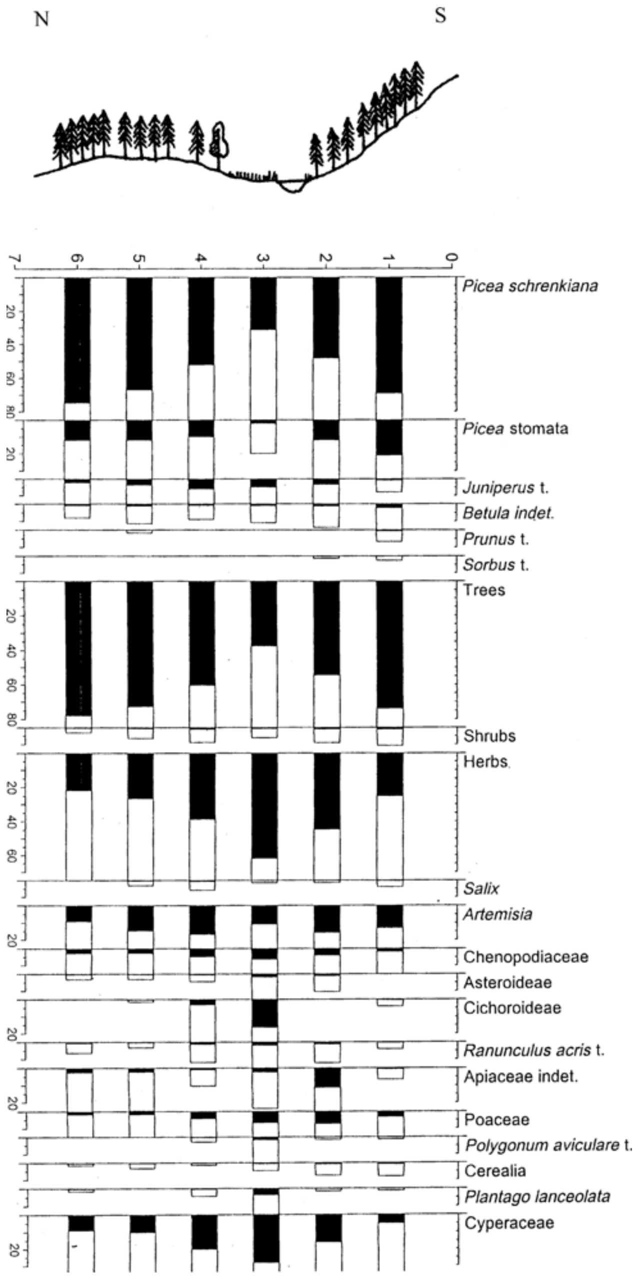

Figure 6 Vegetation transect and pollen percentages of selected pollen types at Karakol, sampled along a N–S transect. Tree-crown cover of *Picea schrenkiana* is 100% in plot 1, 50% in plot 2, 0% in plot 3, 25% in plot 4, 75% in plot 5, and 100% in plot 6

the meadows around the lake and into the forests of the south-facing slope (Figure 6). Figure 7 shows that a determination coefficient of 0.85 is reached, implying a very good agreement between the pollen percentages and the tree-crown cover. Closed forest stands of *Picea schrenkiana* with a crown cover of 100% are recorded in the vegetation plots 1 and 6. A crown cover of 75% is found in plot 5, whereas plots 4 and 2 represent semi-open stands. The pollen percentages in association with many *Picea* stomata reflect the density of the stands with 80, 70 and around 50% of tree-crown cover, respectively. Sample 3 was taken in a meadow without *Picea schrenkiana* trees. It still shows a value of 30% *Picea* pollen. *Juniperus* pollen is recorded throughout the transect, probably deriving from the *Juniperus* stands on the south-facing slopes in the area. A slightly higher percentage value is found in sample 4, where a single *Juniperus* tree is recorded. The steppe plants *Artemisia* and Chenopodiaceae are not

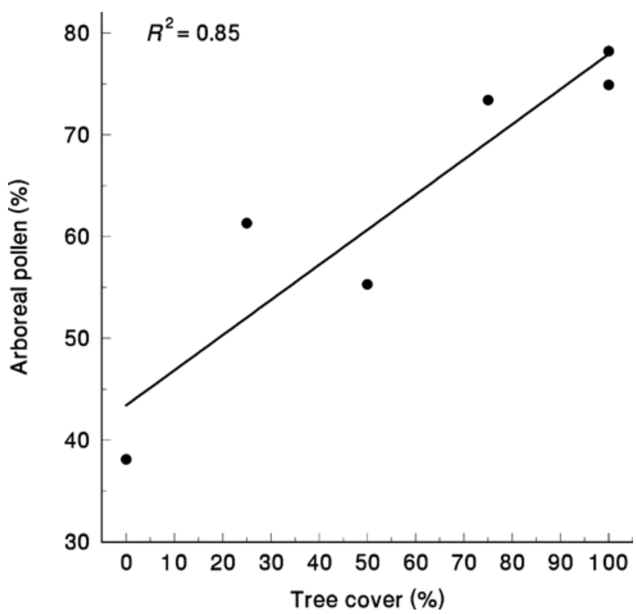

Figure 7 Correlation between tree-crown cover and pollen percentages of arboreal pollen (AP) in the *Picea* forest at Karakol

present in the local vegetation but they are represented by constant pollen values of 10–20 and <10%, respectively, probably again originating from the drier south-facing slopes. In sample 3 high percentage values of Asteroideae, Cichorioideae, *Ranunculus acris*-type and 10% Poaceae pollen reflect local meadows and pasturelands. The pollen of Cyperaceae may mirror both the meadows and the riparian vegetation.

Bakaly: mixed forests in a N–S transect (BAO2): Figure 8

Six samples were taken from a N–S transect in the mixed forests around Bakaly (Figure 8). Generally, more tree species form more complex woodland communities than in the southern *Juniperus* and the northern *Picea* forests. *Juniperus turkestanica* and *J. semiglobosa* are present in plot 1 together with *Crataegus turkestanica*, *Malus kirghisorum* and *Prunus mahaleb*. They build communities with a tree-crown cover of 70%, but AP reaches only 25% and is dominated by *Juniperus* pollen. Although no trees are recorded in vegetation plots 2 and 3, AP still accounts for 25% in sample 2, but then drops to 10% in sample 3. In plot 6, where *Juniperus turkestanica* grows together with *Picea schrenkiana*, AP reaches 30% and is dominated by *Juniperus* and *Picea. Picea schrenkiana* grows in plots 5 and 6, but high pollen values, associated with finds of *Picea* stomata, are only reached in sample 6, where the tree-crown cover attains 80%. *Juglans* pollen has low values in all the samples, although the tree does not grow in the vegetation plots. This pollen originates from the trees growing in the catchment (see W–E transect BAO, Figure 9). *Prunus mahaleb*, *Malus kirghisorum* and *Crataegus* grow in plot 1. *Malus kirghisorum* and *Crataegus turkestanica* are found in plot 4 as well as *Prunus mahaleb* in plot 6. Single grains of *Sorbus*-type may partly represent these trees. *Acer turkestanica* grows in plot 6, but no pollen is found. Single finds of *Acer* pollen occur in the samples 1 and 4. Pollen of taxa growing in the meadows and steppes, such as *Artemisia* and Chenopodiaceae, is present throughout the transect, with values around 15 and 10%, respectively, although these plants are locally missing in the vegetation plots. Poaceae pollen shows its lowest percentage (10%) in sample 6, where the crown cover of the forest stand with *Picea schrenkiana*, *Acer turkestanica*, *Prunus mahaleb* and *Juniperus turkestanica* reaches maximum

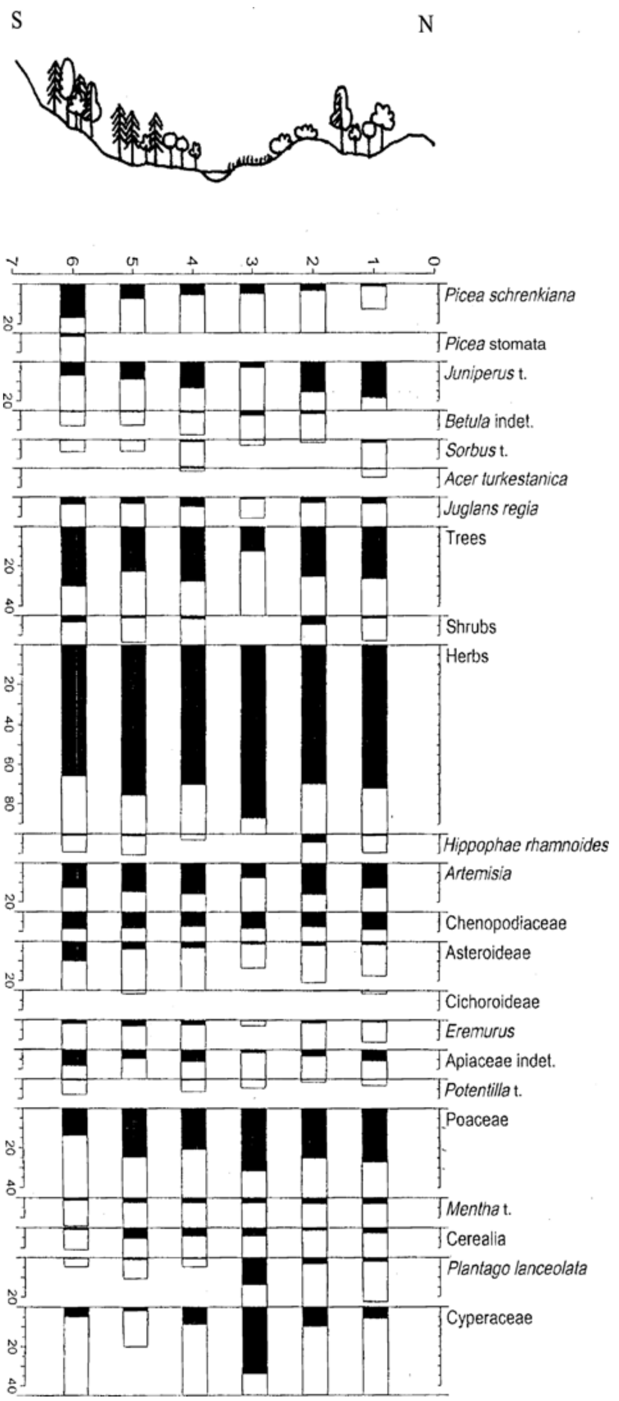

Figure 8 Vegetation transect and pollen percentages of selected pollen types at Bakaly along a N–S transect. Tree-crown cover is 70% in plot 1, 0% in plots 2 and 3, 50% in plot 4, 70% in plot 5 and 80% in plot 6

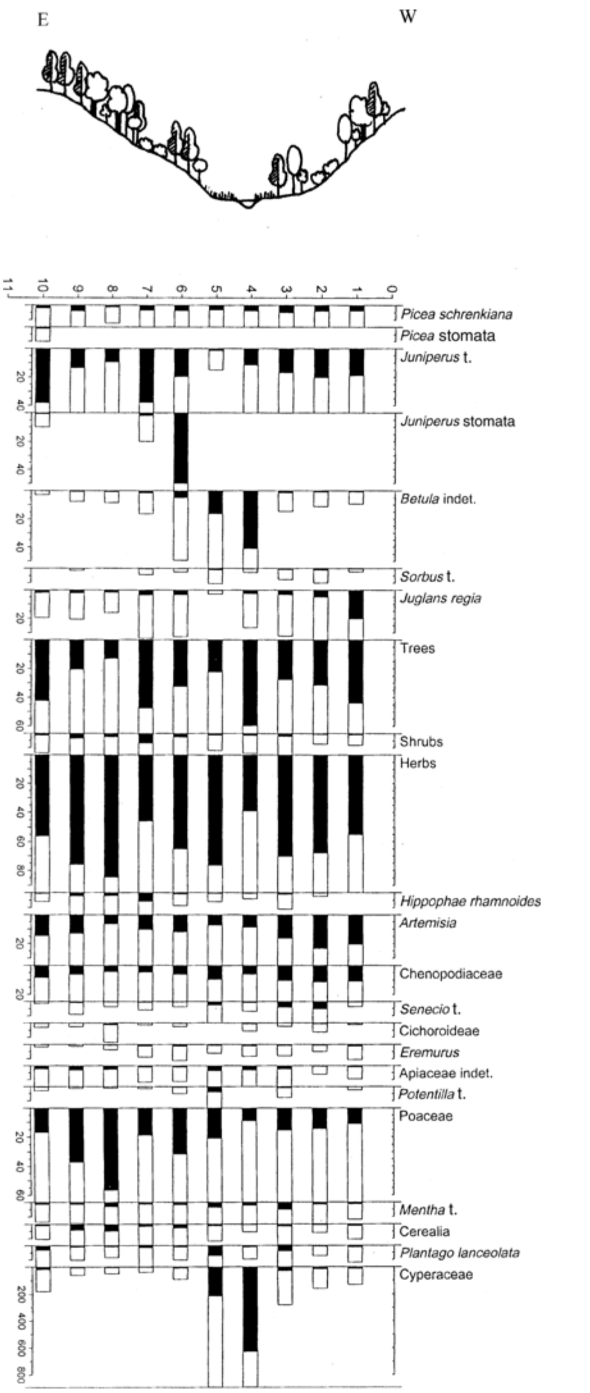

Figure 9 Vegetation transect and pollen percentages of selected pollen types at Bakaly, W–E transect. Tree-crown cover is 60% in plot 1, 0% in plot 2, 50% in plot 3, 80% in plot 4, 0% in plot 5, 40% in plot 6, 0% in plot 7, 40% in plot 8, 30% in plot 9 and 40% in plot 10

values of 80%. In plot 3 with open vegetation they reach 30% along with high values of Cyperaceae.

Mixed forests in a W–E transect (BAO): Figure 9

Ten samples were taken along a W–E transect at Bakaly, integrating the different types of mixed forests with different crown covers (Figure 9). *Juniperus turkestanica* and *J. semiglobosa* are present in the vegetation plots 1, 3, 6, 8, 9 and 10 where they form semi-open stands together with other tree species. Except for sample 5, the *Juniperus* trees are represented by percentage values from 10 to 40%. Although not present in the local vegetation relevés, the highest percentage of *Juniperus* pollen is found in sample 7 (40%). In sample 6 it reaches only 15% in association with many stomata. *Juniperus turkestanica* and *J. semiglobosa* form an open stand together with *Malus kirghisorum* in this vegetation plot. *Betula* pollen reaches 40% in sample 4 and 15% in sample 5 in association with high finds of Cyperaceae pollen. It mirrors a stand of *Betula alba* growing near the shore on upland soils at sampling site 4. *Juglans regia* is found in plots 1, 8 and 9, but only in sample 1 does it reach higher values (20%). As the forest stands are open (tree-crown cover 30–40%), with only single *Juglans regia* trees, a higher abundance of *Juglans* pollen in samples 8 and 9 might be masked by the conspicuous presence of Poaceae pollen (55 and 40%, respectively). *Picea* pollen is constantly found throughout the transect with rather low values (<10%), though the tree is not present in the vegetation relevés. *Sorbus*-type pollen is found in all samples except 8 and 10. Rosaceae shrub and tree species are found throughout the transect, except for those samples near the lake shore (samples 4 and 5). *Acer turkestanica* is found in vegetation plots 1, 3 and 8, but doesn't show up in the pollen samples. Pollen of *Artemisia* and Chenopodiaceae is constantly represented with 10–20% and 3–10%, respectively, although locally not recorded in the vegetation plots. Combining the plots of both Bakaly transects into a linear correlation attains a correlation coefficient of 0.56 and a determination coefficient of 0.32 (Figure 10).

Nishneye and Verkhneye Ozero: *Juglans* forests (NOVO): Figure 11

Eleven samples were taken around the two lakes with the aim to cover the different local vegetation types. *Juglans regia* dominates the forests in this region, but thickets of several species of Rosaceae and stands of *Acer* are also interspersed (Table 2; Figure 2). Figure 11 shows that *Juglans regia* pollen dominates the AP throughout the transect. The highest percentage (85%) of the species is found in sample 3, where the tree constitutes a monospecific stand in the vegetation plot. Samples 3, 6, 9 and 11 show *Juglans* pollen values around 70%, where *Juglans regia* forms mixed stands. In samples 2, 4, 5 and 7 the pollen percentages reach 35–40%, although *Juglans* is locally present only in plots 5 and 7. Sample 10 shows a value of 18% and sample 8 10%, with *Juglans regia* being absent in both plots. *Juniperus* pollen is present throughout the pollen spectrum with values from 5% to 12%, although lacking in the local vegetation relevés. Single pollen grains of *Acer* were found in samples 2, 4, 5, 7, 9 and 11, whereas the tree was recorded in the vegetation plots 2, 4, 7, 8 and 11. Trees of *Crataegus turkestanica* and *Crataegus* spp., *Malus kirghisorum*, *Prunus sogdiana* and *Prunus mahaleb* were found in all the vegetation plots except in plot 1. The corresponding *Prunus*- and *Sorbus*-type pollen occurs as single finds in samples 4, 5 and 11. *Hippophaë rhamnoides* reaches 5% in plot 4. Except for sample 1, *Artemisia* shows constant values around

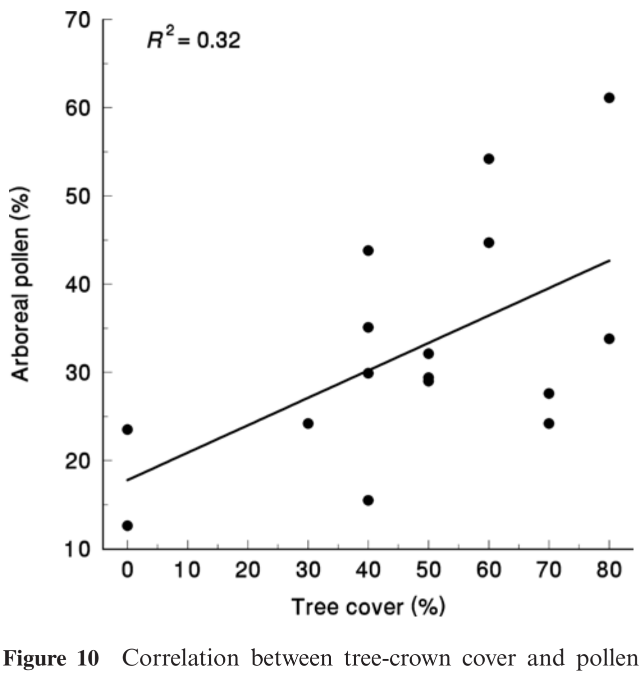

Figure 10 Correlation between tree-crown cover and pollen percentages of arboreal pollen (AP) in the mixed forest at Bakaly

10%. Pollen of Chenopodiaceae has values of 8–15% throughout the diagram. The highest percentage is recorded in sample 8, where it reaches 25%. Pollen of Poaceae consistently shows values of 5–10%. A slightly higher value (18%) is recorded in sample 10. Pollen of Asteraceae (Asteroideae and Cichorioideae) shows values up to 5% in samples 2, 8 and 10, probably reflecting grazed meadows. Very high values of Cyperaceae are found in samples 8 and 10. A correlation coefficient of 0.59 and a determination coefficient of 0.35 are attained when AP is correlated with tree-crown cover (Figure 12). When correlating the AP with tree-crown cover over all the samples a determination coefficient of 0.44 is recorded (Figure 13).

Comparison of pollen in surface lake sediments and vegetation maps

The comparison between AP in surface lake sediment samples and forest cover in a radius of 800 m around the site (Table 3) suggest a positive correlation between pollen and vegetation at an extra-local scale ($r = 0.48$; $r^2 = 0.23$; Figure 14). At

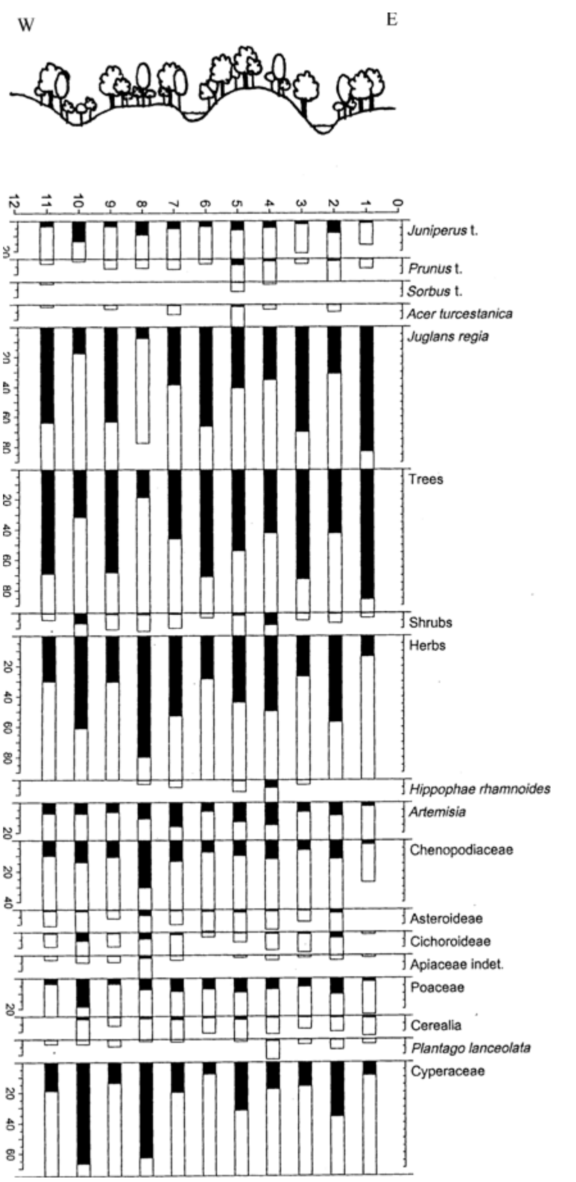

Figure 11 Vegetation transect and pollen percentages of selected pollen types at Nishneye- and Verkhneye Ozero. Tree-crown cover is 50% in plot 1, 30% in plot 2, 60% in plot 3, 30% in plot 4, 40% in plot 5, 80% in plot 6, 40% in plot 7, 50% in plot 8, 60% in plot 9, 40% in plot 10 and 60% in plot 11

Kichikol the area covered with *Juniperus* forest within a radius of 800 m around the lake is 25.5% (Table 1, Table 3) and 23.7% of *Juniperus* pollen is recorded. At Karakol 34% of the area is covered with forest of *Picea* but only 10.3% of *Picea* pollen is recorded. At Bakaly 46% of the area within a radius of 800 m of the lake is covered by open forest stands and 44.8% of AP is recorded. *Juniperus* yields the greatest share (32.2%), whereas *Picea* achieves only 1.3% and *Juglans* 2.8% (Table 3). At Nishneye and Verkhneye Ozero the forest cover reaches 100% (Figure 2) but only 25.5% AP is recorded at Nishneye Ozero, whereas for the same forest cover 59.8% AP is recorded at Verkhneye Ozero.

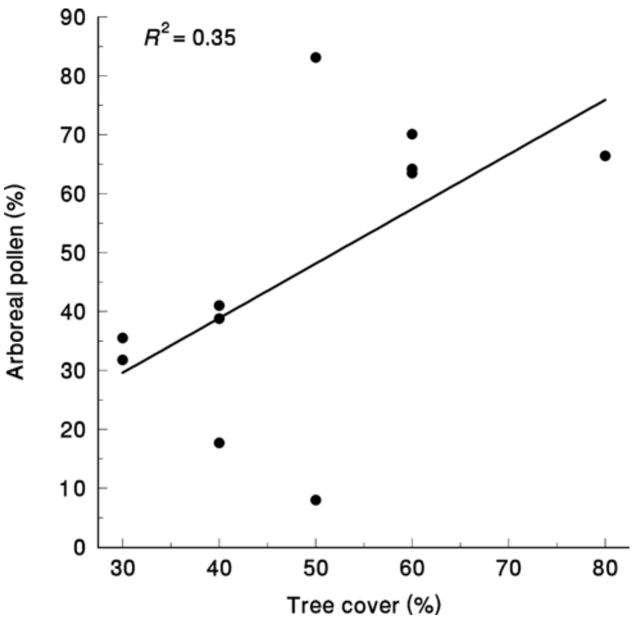

Figure 12 Correlation between tree-crown cover and pollen percentages of arboreal pollen (AP) in the *Juglans* forest at Nishneye- and Verkhneye Ozero

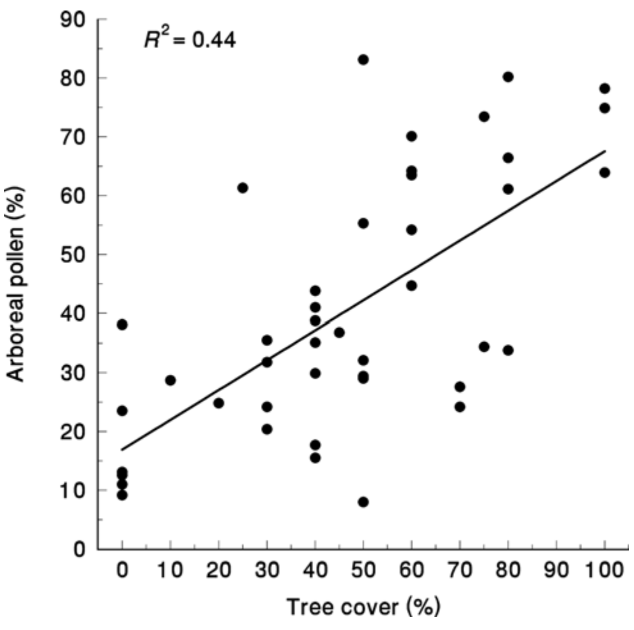

Figure 13 Correlation between tree-crown cover and pollen percentages of arboreal pollen (AP) of all four sites in Kyrgyzstan

Discussion

The different taxa growing in the Kyrgyz forest belts are represented very heterogeneously in the pollen data. Some taxa such as *Picea* are well represented, whereas others such as *Acer* are almost completely missing, though present in the local vegetation. Similar observations were made in previous studies from other areas of the world (Wright, 1967; Wright *et al.*, 1967) and emphasize that pollen does not mirror vegetation in a linear way (Wright, 1967; Prentice, 1985; 1986, Faegri and Iversen; 1989, Moore *et al.*, 1991).

The best fits between vegetation and pollen were obtained where the dominant tree taxa are wind-dispersed pollen producers such as *Picea* and *Juniperus*. In cases where insect-pollinated arboreal taxa were co-dominant or abundant (eg, Rosaceae, *Acer*) the linkage is blurred, probably because of the smaller quantities of pollen produced and to the selectivity of the dispersal vector (Prentice, 1985). The pollen percentages in our terrestrial surface samples can be compared with those in

Table 3 Forest cover and pollen representation of AP and corresponding tree species of surface lake samples

Locality	FC[a] (%)	AP[b] (%)	Tree species (%)
Kichikol	25.5	24.6	*Juniperus* (23.7)
Karakol	34	23.4	*Picea* (10.3); *Juniperus* (9.2)
Bakaly	46	44.8	*Juniperus* (32.2); *Juglans* (2.8); *Picea* (1.3)
Nishneye	100	25.5	*Juglans* (13.1); *Juniperus* (10.4); *Acer* (0); *Prunus*-type (0); *Sorbus*-type (0)
Verkhneye	100	59.8	*Juglans* (34.2); *Juniperus* (17.0) *Acer* (0.2); *Prunus*-type (0); *Sorbus*-type (0.2)

[a]FC, forest cover.
[b]AP, arboreal pollen.

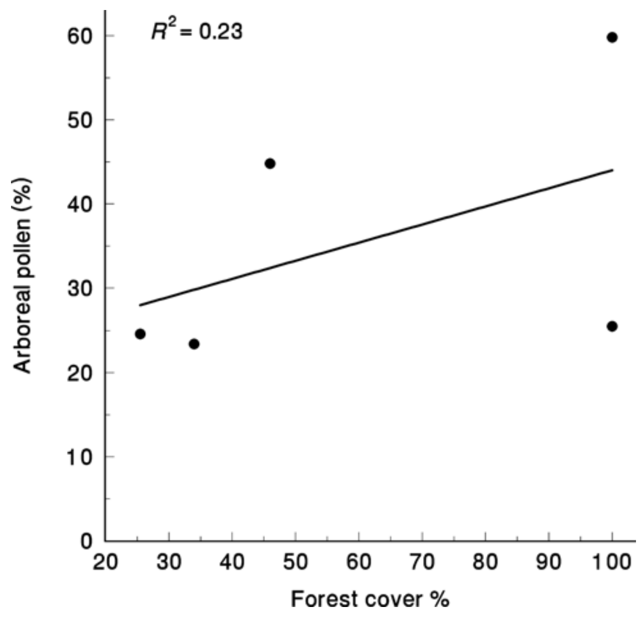

Figure 14 Correlation between foresty cover and pollen percentages of arboreal pollen (AP) from surface lake samples

the lake surface sediments if we take account of the difference in pollen catchment and the relative source area of pollen (Sugita, 1994). Much of the pollen in the terrestrial surface samples is of local and extra-local origin, ie, within tens of metres from the sampling point, which contrasts with the lake surface-sediment samples where most pollen has an extra-local to regional origin with a minor proportion of local pollen, especially from tree taxa that do not grow directly on the lake shores (Bradshaw and Webb, 1985; Prentice *et al.*, 1987). The pollen percentages of trees in lake surface-sediment samples will therefore be lower than in terrestrial surface samples. However, the vegetation plots (10 m × 10 m) on an average have the same tree-crown covers as the surroundings of the lakes (1–2 km). The relation between pollen percentages and tree-crown cover in the terrestrial surface samples is shown in Figures 4, 7, 10, 12 and 13.

Considering the huge differences of pollen representation in the surface samples among the taxa, we discuss the relationship between plant occurrence and pollen individually for each important taxon.

Juniperus spp.

In the region of Kichikol *Juniperus* pollen percentages follow more or less the vegetation cover of *Juniperus* trees at the local level, ie, from within 20 m (*sensu* Prentice, 1985) (Figures 3, 5). Pollen values of 65–80% may indicate pure, dense stands of *Juniperus*. At KKO2 (Figure 5) pollen values of *Juniperus* as low as 35% indicate a tree-crown cover of 75%. Pollen values of 15–30% may reflect local stands of *Juniperus* trees, and pollen values around 10% may represent the pollen of extra-local (from within 20 m to 2 km, *sensu* Prentice, 1985) stands. Finds of stomata corroborate the proximity of the *Juniperus* stands, as they are only found regularly near the trees. The interpretation of *Juniperus* pollen percentages in mixed stands is less straightforward. *Juniperus* pollen percentages may be lowered by other pollen types, as in the case of Karakol (Figure 6) and the Bakaly N–S transect (Figure 8), or they may reach high values without being present in the local vegetation plots as seen at the Bakaly W–E transect (Figure 9). The surface sample of lake sediment (Table 3) shows that 23.7% *Juniperus* pollen represents the modern vegetation around Kichikol, where *Juniperus* forests cover 25.5% of the area within a radius of approx. 800 m (Table 1, Table 3; corresponding about to the relevant source area of pollen, *sensu* Sugita (1994) for a lake of this size). It seems therefore, that the pollen of *Juniperus* is moderately under-represented in the pollen rain. In agreement, in Europe shrubs of *Juniperus* produce relatively high amounts of pollen but are under-represented in the sediments. Values of 5% can represent an appreciable share in the vegetation (Burga and Perret, 1998).

Picea schrenkiana

In the almost monospecific stands around Karakol (Figure 6) the diminishing tree cover is correctly mirrored by reduced pollen percentages, whereby 80% pollen values represents a 100% tree-crown cover, and 50% pollen values a 50% tree-crown cover of the species. However, the plots with meadows and no *Picea* trees still show *Picea* pollen values of 30%; the intercept of the regression plot gives us a value of 42%. This gives us an estimate of the background value of the extra-local (20 m–2 km) and possibly regional (2–200 km) stands of *Picea* (*sensu* Prentice, 1985). Similar to *Juniperus*, stomata finds corroborate the density of the *Picea* stands. Minor values of *Picea* pollen (<10%) in the mixed forests around Bakaly (Figures 8, 9) reflect *Picea* trees in the vicinity and form a low background signal. In the surface sample of the Karakol lake sediment (Table 3) 10.3% of *Picea* pollen reflect the modern vegetation formed by dense stands of *Picea schrenkiana* covering 34% of the area (Table 1, Table 3). Applying the linear relationship between relevés and moss polsters a value of 50% pollen would be expected (Figure 7). This suggests that *Picea* forests are reflected in a weaker way in the lake sediments than in surface samples of moss polsters. From several studies of pollen and macrofossils it is known that *Picea abies*, a close relative of *Picea schrenkiana*, can be under-represented in the pollen rain, as it produces less pollen than pine, birch, alder or hazel, although it can also be over-represented because of long-distance transport (Latałowa and van der Knaap, 2006). Janssen (1967) calculated *R* values for several arboreal taxa at different sites in Minnesota and found that the pollen of *Picea* is moderately under-represented in the pollen rain. In the results presented here *Picea* pollen seems to represent the *Picea schrenkiana* forest accurately at a local scale (moss polster data). Yet the low percentage of *Picea* in the surface sample of the lake sediment suggests that, at extra-local to regional scales, the tree may be strongly under-represented in the fossil pollen records, especially in times of open to semi-open landscapes.

Juglans regia

In the closed stands around Nishneye- and Verkhneye lakes (Figure 11) *Juglans* pollen can reach percentages that reflect the density of the forest. Up to 85% was recorded in a closed monospecific stand. The anemophilous pollen is produced in rich amounts (Zoller, 1981), and our results suggest that it is transported rather well, as it is found in relatively high amounts in samples where the tree was not present locally. At Bakaly (Figures 8, 9), where *Juglans regia* is at its upper altitudinal limit, less abundant pollen is found. Pollen values as low as 1–2% may reflect the scattered distribution of the *Juglans* trees in the regional vegetation. In the surface samples of the lake sediments (Table 3) *Juglans regia* is represented by 13.1% pollen in Nishneye Ozero and 34.2% in Verkhneye Ozero although <50% of vegetation consists mostly of this tree (Table 1, Figure 2). We conclude that *Juglans regia* is under-represented in the pollen rain, especially at extra-local to regional scales.

Acer turkestanica

Acer pollen apparently does not reflect the occurrence of the species in the vegetation accurately, neither in surface samples of moss polsters nor in the lake sediment. Pollen is present where no *Acer* tree occurred in the vegetational surveys and *vice versa*. Generally, only single pollen grains were found. It is known that insect-pollinated trees such as *Acer* and Rosaceae are strongly under-represented in the pollen rain (Janssen, 1967; Wright *et al.*, 1967; Faegri and Iversen, 1989). Very low *Acer* percentages in pollen spectra may therefore point to an appreciable share of this tree in the forest vegetation (Wright *et al.*, 1967).

Rosaceae

Sorbus-type and *Prunus*-type were distinguished but could not yet be assigned to the various tree species of the Rosaceae family. It is striking to see that the trees play a considerable role in the vegetation although their pollen only occurs very rarely in the surface samples of moss polsters and in the lake sediment. For further discussion of the Sorbus-type see Faegri and Iversen (1989).

Artemisia

Though not regularly present in the local vegetational relevés around the lakes, *Artemisia* is an important pollen type at all sites. Its pollen shows high values up to 55% in the region of Kichikol (Figures 3, 5), increasing with diminishing abundance of *Juniperus* trees, ie, increasing with landscape openness. At Karakol (Figure 6) and at Bakaly (Figures 8, 9) percentages around 10–20% are found. Such values may therefore already reflect the background signal of the *Artemisia* steppes of the dry lowlands. The high pollen values at Kichikol probably also reflect the local regular occurrence of the taxon in the meadows near the lake, although the plant was not co-dominant there.

Chenopodiaceae

Pollen of Chenopodiaceae is present with rather low but constant values throughout the different transects. Since not regularly recorded in the vegetation relevés around the lakes its pollen signal may primarily reflect the background pollen signal of the *Artemisia*–Chenopodiaceae steppes of the lowlands. Our results support Liu *et al.* (1999), who found that *Artemisia* and Chenopodiaceae both are over-represented in the pollen spectra in Inner Mongolia and in western Iran. High *Artemisia* pollen values can indicate the existence of steppe, but the dominant species is not certain in regions where grass-dominated steppe co-occur, as Poaceae pollen is under-represented in the pollen spectra (Wright *et al.*, 1967; Liu *et al.*, 1999). In the Middle East El-Moslimany (1990) has shown that *Artemisia* dominates in the steppe vegetation in the semi-arid zone, while Chenopodiaceae and *Plantago* dominate in the arid zone. Both *Artemisia* and Chenopodiaceae are characteristic of highly continental climates with cold winters and dry summers. Because *Artemisia* pollen increases and Chenopodiaceae decreases with decreasing aridity the ratio of their pollen (C/A) is used as a moisture indicator within a narrow geographical range and within non-forested areas (El-Moslimany, 1990).

Poaceae

At Kichikol (Figures 3, 5) and Karakol (Figure 6) the pollen of Poaceae reaches only 10–15% in the meadows, where it is dominant in the herbaceous vegetation. Grass pollen is clearly under-represented in this type of vegetation and is probably masked by the high pollen representation of *Artemisia* and Chenopodiaceae. At Bakaly (Figures 8, 9) Poaceae pollen reaches 30 and 55% at its maximum, therefore providing strong evidence of the low tree-crown density (30–40%) on the spot. Poaceae pollen is consistently under-represented in percentage values (Wright *et al.*, 1967; Liu *et al.*, 1999). Broström *et al.* (2004) argue that landscape openness may be underestimated, as herb taxa (including Poaceae) produce 6–8 times less pollen than tree taxa.

Cyperaceae

The pollen of Cyperaceae is mostly found in high amounts closest to the lake shore, therefore mostly reflecting the wetland vegetation around the lake. But species belonging to the Cyperaceae family are also found in meadows and, to some extent, in the undergrowth of forests. As this pollen type cannot be broken down to the genus or species level it is difficult to interpret the pollen values, and we excluded it from the pollen sum, as is often done in palynology.

Sum of AP

Vegetation patterning can affect the pollen representation (Bunting *et al.*, 2004) and several factors, such as species composition, spatial pattern and structure of the vegetation influence the spatial scale of provenance of pollen (Sugita *et al.*, 1999). As trees with good pollen production (*Picea*, *Juniperus* and *Juglans*) are interspersed with low pollen producers (*Acer*, Rosaceae and *Pistacia*) these factors may come to play a more important role in vegetation types of mixed forest stands and semi-open landscapes. If all forest types are pooled together, the correlation coefficient (r) is 0.66, and 44% of the variability of AP is explained by the tree-crown density (Figure 13). We therefore conclude that AP percentage is a good proxy to estimate the tree-crown cover on the spot.

The correlation coefficient (r) of 0.48 and the determination coefficient (r^2) of 0.23 between AP in surface lake sediment and forest cover are rather low (Table 1, Table 3, Figure 14). Our data show that the forest cover is conspicuously and systematically under-represented in the pollen imprint of the Kyrgyz sites. This is in contradiction to the situation in forested biomes, such as the temperate or boreal forests of Eurasia. There 70–80% of AP may already indicate treeless conditions such as above treeline or forest openings (see discussion in eg, Zoller and Haas, 1995; Tinner and Theurillat, 2003). The seeming contradiction is explained by the fact that the forest stands of Kyrgyzstan are isolated isles surrounded by continental lowland and highland steppes. Here the overwhelming producers in the total pollen source area (10–50 km in radius around lakes of this size; eg, Bradshaw and Webb, 1985; Prentice *et al.*, 1987; Sugita, 1994; Conedera *et al.*, 2006) are non-arboreal steppic plants (eg, *Artemisia*, Chenopodiaceae, Poaceae). The local production of forests in rather narrow bands on the top of the mountains and on shady slopes is therefore partially masked by the regional pollen transport, indeed the contrary of the situation in temperate and boreal forests, where local production of non-arboreal plants is obscured by the pollen production of forests.

Conclusions

Quantitative reconstructions of past and present plant abundance and distribution from fossil and subfossil pollen records have been the goal of palynological research since the earliest days, yet they remain elusive (Bunting and Middleton, 2005). Empirical (Janssen, 1967; Calcote 1995; Jackson and Kearsley, 1998; Liu *et al.*, 1999; Shen *et al.*, 2006, and many others) and modelling studies (Sugita, 1994, Sugita *et al.*, 1999, Bunting *et al.*, 2004; Broström *et al.*, 2004, 2005, and many others) have shown that the relationship between vegetation and pollen imprint is not straightforward but is affected by pollen productivity, pollen dispersal, vegetation patterning, the degree of landscape openness and species composition (Prentice, 1985; Sugita *et al.*, 1999, Bunting *et al.*, 2004). The present work will help improve the reconstruction of the Quaternary history of Kyrgyzstan and central Asia by means of fossil pollen records. The specific spatial scale of vegetation represented by pollen will be critical for reconstruction of vegetation using fossil pollen from lakes with reference to the surface pollen data from moss polsters. The results presented in this paper can be used as a source of information for pollen representation for hollows and small bogs. Our estimates for lakes are only tentative, and more sites should be investigated to draw more reliable conclusions. Nonetheless, the results indicate that *Juniperus* spp. is under-represented in the pollen deposition, *Picea schrenkiana* pollen reflects the vegetation cover accurately in the moss polsters but is under-represented in the lake surface samples of Karakol, *Juglans regia* produces average pollen but is under-represented in the pollen rain, whereas *Acer* and tree species of Rosaceae (eg, *Prunus*-type and *Sorbus*-type) are strongly under-represented in the pollen spectra. Although AP and NAP percentages give only an approximation of the percentage of forest or open land, respectively (eg, Sugita *et al.*, 1999), we can state that one implication of the results presented in this paper is that in contrast to other previously investigated areas, forests (including parklands) are underestimated in the pollen representation at the Kyrgyz sites. This implies that isolated forests in steppic environments are not easy to trace by pollen records alone. In this sense, our results may be used to better understand the situation during the full glacial in Eurasia and Northern America. Owing to the climatic setting at that time, trees and possibly small forest patches were restricted to small micro-environmental 'oases' (Willis *et al.*, 2000; Willis and McElwain, 2002) in a steppe biome, a situation that is in part comparable with that in Kyrgyzstan.

Acknowledgements

We thank Brigitta Ammann, Marc Lehmann, Willi Tanner, Zakir Sarymsakov, Bronislav I. Venglovsky and all Kyrgyz friends who assisted in the extensive field trips in 2003 and 2005. Comments by H.E. Wright Jr., W.O. van der Knaap and two anonymous referees were helpful to improve the manuscript. We are very grateful to Intercooperation, Project KIRFOR (Kyrgyz-Swiss Forestry Support Programme), to the University of Bern, to the University of Bern Foundation (Hochschulstiftung) and to the Academy of Natural Sciences of Switzerland (scnat, Akademie der Naturwissenschaften Schweiz) for financially supporting this study.

References

Beug, H.-J. 2004: *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Dr Friedrich Pfeil Verlag.

Blaser, J., Carter, J. and **Gilmour, D.,** editors 1998: *Biodiversity and sustainable use of Kyrgyzstan's walnut-fruit forests*. English version. IUCN, Intercooperation.

Bradshaw, R.H.W. and **Webb, T.I.** 1985: Relationships between contemporary pollen and vegetation data from Wisconsin and Michigan, USA. *Ecology* 66, 721–37.

Bottema, S. and **Barkoudah, Y.** 1979: Modern pollen precipitation in Syria and Lebanon and its relation to vegetation. *Pollen et Spores* 21, 427–80.

Broström, A., Sugita, S. and **Gaillard, M.-J.** 2004: Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden. *The Holocene* 14, 368–81.

Broström, A., Sugita, S., Gaillard, M.-J. and **Pilesjö, P.** 2005: Estimating the spatial scale of pollen dispersal in the cultural landscape of southern Sweden. *The Holocene* 15, 252–62.

Bunting, M.J. and **Middleton, D.** 2005: Modelling pollen dispersal and deposition using HUMPOL software, including simulating windroses and irregular lakes. *Review of Palaeobotany and Palynology* 134, 185–96.

Bunting, M.J., Gaillard M.-J., Sugita, S., Middleton R. and **Broström, A.** 2004: Vegetation structure and pollen source area. *The Holocene* 14, 651–60.

Burga, C.A. and **Perret, R.** 1998: *Vegetation und Klima der Schweiz seit dem jüngeren Eiszeitalter*. (Vegetation and climate history in Switzerland during the later Pleistocene and Holocene.) Ott, Thun, 319–26.

Calcote, R. 1995: Pollen source area and pollen productivity: evidence from forest hollows. *Journal of Ecology* 83, 591–602.

Conedera, M., Tinner, W., Crameri, S., Torriani, D. and **Herold, A.** 2006: Taxon-related pollen source areas for lake basins in the southern Alps: and empirical approach. *Vegetation History and Archaeobotany* 15, 263–72.

El-Moslimany, A.P. 1990: Ecological significance of common nonarboreal pollen: examples from drylands of the Middle East. *Review of Palaeobotany and Palynology* 4, 343–50.

Epple, C. 2001: A vegetation study in the walnut and fruit-tree forests of Southern Kyrgyzstan. *Phytocoenologia* 31, 571–604.

Faegri, K. and **Iversen, J.** 1989: *Textbook of pollen analysis*. Fourth edition. John Wiley & Sons.

Firbas, F. 1934: Über die Bestimmung der Walddichte und der Vegetation waldloser Gebiete mit Hilfe der Pollenanalyse. *Planta* 22, 109–45.

Jackson, S.T. and **Kearsley, J.B.** 1998: Quantitative representation of local forest composition in forest-floor pollen assemblages. *Journal of Ecology* 86, 474–90.

Janssen, C.R. 1967: A comparison between the recent regional pollen rain and the sub-recent vegetation in four major vegetation types in Minnesota (U.S.A.). *Review of Palaeobotany and Palynology* 2, 331–42.

Kvavadze, E.V. and **Stuchlik, L.** 1990: Subrecent spore-pollen spectra and their relation to recent vegetation belts in Abkhazia (north-western Georgia, USSR). *Acta Palaeobotanica* 30, 227–57.

Latałowa, M. and **van der Knaap, W.O.** 2006: Late Quaternary expansion of Norway spruce *Picea abies* (L.) Karst. in Europe according to pollen data. *Quaternary Science Reviews* doi:10.1016/j.quascirev.2006.06.007.

Liu, H., Cui, H., Pott, R. and **Speier, M.** 1999: The surface pollen of the woodland-steppe ecotone in southeastern Inner Mongolia, China. *Review of Palaeobotany and Palynology* 105, 237–50.

Mazier, F., Galop, D., Brun, C. and **Buttler, A.** 2006: Modern pollen assemblages from grazed vegetation in the western Pyrenees, France: a numerical tool for more precise reconstruction of past cultural landscapes. *The Holocene* 16, 91–103.

Moore, P.D., Webb, J.A. and **Collinson, M.E.** 1991: *Pollen analysis*. Blackwell Scientific Publications.

Prentice, I.C. 1985: Pollen representation, source area and basin size: toward a unified theory of pollen analysis. *Quaternary Research* 23, 76–86.

—— 1986: Forest-composition calibration of pollen data. In Berglund, B.E., editor, *Handbook of Holocene palaeoecology and palaeohydrology*. John Wiley & Sons Ltd, 799–817.

Prentice, I.C., Berglund, B.E. and **Olsson, T.** 1987: Quantitative forest-composition sensing characteristics of pollen samples from Swedish lakes. *Boreas* 16 43–54.

Reille, M. 1992: *Pollen et spores d'Europe et d'Afrique du Nord*. Laboratoire de Botanique Historique et Palynologie.

—— 1998: *Pollen et spores d'Europe et d'Afrique du Nord. Supplément 2*. Laboratoire de Botanique Historique et Palynologie.

Shen, C., Kam-biu, L., Lingyu, T. and **Overpeck, J.T.** 2006: Quantitative relationships between modern pollen rain and climate in the Tibetan Plateau. *Review of Palaeobotany and Palynology* 140, 61–77.

State Forest Service of the Kyrgyz Republic 2002: *Instructions for the correct elaboration and reproduction of forest maps*.

Sugita, S. 1994: Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of Ecology* 82, 881–97.

Sugita, S., Gaillard, M.-J. and **Broström, A.** 1999: Landscape openness and pollen records: a simulation approach. *The Holocene* 9, 409–21.

Tinner, W. and **Theurillat, J.P.** 2003: Uppermost limit, extent, and fluctuation of the timperline and treeline ecocline in the Swiss Central Alps during the past 11,500 years. *Arctic, Antarctic, and Alpine Research* 35, 158–69.

Typology group KIRFOR 2004: Preliminary forest typology catalogue. (Internal document KIRFOR).

Welten, M. 1950: *Beobachtungen über den rezenten Pollenniederschlag in alpiner Vegetation*. Sonderdruck aus E. Rübel und W. Lüdi, Bericht über das Geobotanische Forschungsinstitut Rübel in Zürich für das Jahr 1949.

Willis, K.J. and **McElwain, J.C.** 2002: *The evolution of plants*. Oxford University Press.

Willis, K.J., Rudner, E. and **Sümegi, P.** 2000: The full-glacial forests of central and southeastern Europe. *Quaternary Research* 53, 203–13.

World Climate 2006: http://www.worldclimate.com (last accessed 2 April 2007).

Wright, H.E., Jr 1967: The use of surface samples in Quaternary pollen analysis. *Review of Palaeobotany and Palynology* 2, 321–30.

Wright, H.E., Jr, McAndrews, J.H. and **van Zeist, W.** 1967: Modern pollen rain in Western Iran and its relation to plant geography and Quaternary vegetational history. *Journal of Ecology* 55, 415 –43.

Zoller, H. 1981: Pteridophyta, Spermatophyta. In Hegi, G., editor, *Illustrierte Flora von Mitteleuropa, Band III Angiospermae, Dicotyledones 1, Teil 1*. Verlag Paul Parey, 3–15.

Zoller, H. and **Haas, J.N.** 1995: War Mitteleuropa ursprünglich eine halboffene Weidelandschaft oder von geschlossenen Wäldern bedeckt? *Schweizerische Zeitschrift für Forstwesen* 146 321–54.