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Research paper

Pollen–vegetation relationships in the central Caspian (Hyrcanian) forests of northern Iran

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ABSTRACT

We studied pollen–vegetation relationships along an altitudinal transect in the Caspian (Hyrcanian) forests of northern Iran. We collected surface samples from 20 plots of 400 or 625 m² in the major forest communities and compared pollen percentages of the most abundant plant taxa with the vegetation abundances (cover and basal areas) in the pollen plots and in areas of different radii (100, 250, 500 and 1000 m) around the pollen plots using both linear regression and qualitative methods. The results show that anemophilous taxa (i.e. *Quercus*, *Fagus*, and *Carpinus*) in general produce more pollen relative to entomophilous taxa (i.e. *Acer*, *Parrotia*, *Diospyros*, and *Hedera*). Taxa with light pollen grains, such as *Quercus* and *Carpinus*, show large positive intercepts in linear regression analysis, while heavier pollen grains or those possessing a patterned exine, such as *Diospyros*, *Parrotia*, *Acer*, and *Hedera* show small or even negative intercepts. Larger intercepts indicate that a higher proportion of pollen in the samples arrives from outside the area covered by the vegetation analysis. Our findings indicate that light pollen grains are deposited more slowly than heavy pollen grains. Dissimilarity matrices using the Bray–Curtis index showed that the overall relationship between species composition of vegetation plots and pollen assemblages is better for the areas with 100 m radius than for the pollen plots.

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1. Introduction

Reconstruction of vegetation history through pollen analysis requires thorough knowledge of how vegetation composition and pattern are reflected by pollen assemblages (Wright et al., 1967; Bottema, 1974; Jackson, 1990). Due to differences in pollen production and dispersal between taxa, pollen percentages do not unequivocally reflect the abundance of corresponding plant species in the vegetation around the pollen sample site (Prentice, 1985; Prentice et al., 1987). Since the inception of palynology (von Post, 1918), the link between vegetation coverage and pollen rain has been explored both theoretically and empirically (e.g. Davis, 1963; Andersen, 1970; Prentice, 1985; Prentice et al., 1987; Jackson, 1990, 1991; Jackson and Smith, 1994; Sugita, 1994; Hicks and Birks, 1996; Jackson and Kearsley, 1998; Broström, 2002; Bunting et al., 2005; Theuerkauf et al., 2012; for a review of theoretical models see Broström, 2002). An important tool to interpreting fossil records is the study of the relationship between extant vegetation and its

contemporary pollen rain, especially in regions where little is known about pollen production and dispersal (Wright, 1967).

Pollen rain studies in mountainous areas are an extra challenge, since atmospheric temperature stratification and resulting wind patterns are complex and strong temperature and moisture gradients define a spatially condensed geographic distribution of plant communities (Solomon and Silkworth, 1986). In such areas, a sampling design of surface samples along altitudinal transects crossing the main forest belts, in combination with a detailed analysis of the major vegetation units, has been proven useful (Wright, 1967; Janssen, 1981).

The first pollen–vegetation calibration study in the Caspian (Hyrcanian) forests of northern Iran, using both multivariate and descriptive approaches, was performed over a forest–steppe transect in Golestan National Park, in the extreme northeastern part of the forests (Djamali et al., 2008). Wright et al. (1967) studied pollen–vegetation relationships along terrestrial surface sample transects in the Zagros Mountains of western Iran in order to interpret the regional vegetation and climate history since the late Pleistocene from a sediment core from Lake Zeribar. The latter study is the only survey of regional pollen rain for western Iran and one of the most extensive for semi-arid areas (Wright, 1967). Yazvenko's study of the forests of Azerbaijan provides information on pollen source area and pollen dispersal of both insect- and wind-pollinated taxa from the southeast Caucasus (Yazvenko,

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1991). Analyzing surface lake and wetland sediments along an altitudinal transect in southern Georgia (Caucasus), Connor et al. (2004) pointed out the importance of indicator pollen types to detect tree-line variation and deforestation in the Holocene. A review of pollen–vegetation relationship studies performed in neighboring regions is provided by Beer et al. (2007).

The main objectives of our study are (1) to explore how contemporary vegetation is represented in surface sample pollen assemblages along an altitudinal transect in the central Caspian forests, (2) to examine the relationship between pollen deposition and plant abundance, and (3) to estimate the source area of various pollen types. By pollen source area we mean the area that shows the best pollen type–taxon abundance relationship.

2. Study area

The broad-leaved deciduous Hyrcanian forests form a 20–70 km wide and 800 km long belt parallel to the southern coast of the Caspian Sea. These forests cover the northern slopes of the Alborz¹ Mountains of northern Iran and extend from the Caspian lowlands up to 2500 m (or occasionally 2800 m) elevation covering an area of ca. 1.9 million ha (Sabeti, 1994; Sagheb-Talebi et al., 2004). Because of the occurrence of many Arcto-Tertiary relict plant species such as *Zelkova carpinifolia*, *Parrotia persica*, and *Pterocarya fraxinifolia*, the Caspian forests are considered to have been an important refugium of summer-green trees during the Quaternary glaciations (Zohary, 1973; Leroy and Roiron, 1996; Leroy and Arpe, 2007; Ramezani et al., 2008).

Differences in forest composition and structure reflect the gradients in climatic and edaphic conditions (Zohary, 1973; Sabeti, 1994; Ramezani et al., 2008). Mean annual precipitation decreases from 2000 mm in the west to ca. 600 mm in the east (Sabeti, 1994; Sagheb-Talebi et al., 2004). From north to south forest communities change as a consequence of rapid changes in temperature and moisture along the strong altitudinal gradient. We investigated an altitudinal transect running in a north–south direction in the Mashalak forests, south of Nowshahr (= Noshahr) (Fig. 1).

The meteorological station nearest to the studied transect is Nowshahr (20.9 m below sea level), situated at the coast of the Caspian Sea, with a mean annual precipitation of 1310 mm, a mean annual temperature of 16.1 °C, and mean temperatures of the coldest month (February) and warmest month (August) of 2.3 and 29.2 °C, respectively.

The bedrock of the highest part of the transect consists predominantly of sandstone and siltstone, over which rendzine and brown earth soils have developed. In mid- to low-elevations, brown earth and occasionally pseudogley soils have formed over limestone (Forest, Range and Watershed Organization of Iran FRWO (1997a,b, 2002)).

3. Materials and methods

3.1. Vegetation survey

In 2004 and 2005 we studied vegetation composition, structure, and distribution of forest communities along a 20 km long altitudinal transect. The transect extends from the uppermost natural forest at Djamand peak (2400 masl) down to the Caspian lowlands, where human impact has removed the forests below 50 masl. The clear vegetation zonation along the transect was described on the basis of characteristic and dominant tree species (Fig. 2) and served as a guide for our sampling strategy (see below).

Vascular plant nomenclature follows Mozaffarian (1998).

3.2. Pollen sampling, preparation, and counting

Palynological samples were taken as moss polsters every 100–150 m of elevation change in representative closed-canopy stands so that the transect of 20 sample points covered all vegetation zones (Figs. 1 and 2, Table 1).

Within quadrates of 25×25 or 20×20 m ('pollen plots'), about 10 moss polsters were randomly collected (without differentiating for moss species) from rock outcrops or tree bases located between 0.1 and 0.5 m above the forest floor and pooled into one sample of 4–5 cm³ (cf. Räsänen et al., 2004). We collected both green and brown tissues of mosses to obtain samples covering several years.

Sample preparation followed Fægri and Iversen (1989) and included treatment with HCl and KOH, sieving (120 µm), treatment with HF, acetolysis (7 min) and mounting in silicon oil (2000 cSt).

Pollen and spore counts were made using a Zeiss Axiolab microscope with 400× magnification. Larger magnification was used to identify problematic pollen grains. Calculation of pollen and spore frequencies was based on the sum of all arboreal pollen types (AP) (average per sample 922, min. 613, and max. 1725 grains), as such sum – because of the general better dispersal of arboreal pollen – provides a more stable calculation base than one also including non-arboreal pollen types (NAP).

Pollen-morphological types are displayed in the text and in the pollen diagrams by SMALL CAPITALS to clearly distinguish them from plant taxa (Joosten and de Klerk, 2002). Pollen and spores were identified and named after (M): Moore et al. (1991), (B): Beug (2004), (P): the Northwest European Pollen Flora (Punt et al., 1976–2003), and the reference collection of the Institute of Botany and Landscape Ecology at Greifswald University. PTERIS CRITICA was identified with help of figures of (R): Reille (1992) and the reference collection.

For calculation and presentation of the palynological data we used the computer program Tilia 1.7.16 (Grimm, 2011).

3.3. Forest inventory data

Vegetation data were collected as (1) percentage of cover of trees, shrubs, lianas, and herbs within the pollen plots and within a circle with a 100 m radius from the center of each pollen plot and as (2) percentage of basal area of tree species within circles with a 250 m, 500 m, and 1000 m radius from the pollen plots. The crown cover of each tree species in a pollen plot was determined by measuring each crown in two perpendicular directions and expressed as a proportion of the plot area. For the calculation of the crown cover within the circles of 100 m radius, the number of trees from each species was multiplied by the average crown area of that species in the pollen plots. The cover of other vascular plant species (shrubs, lianas, and forest floor vegetation) within the pollen plots and 100 m circles was estimated visually using the Braun–Blanquet scale (cf. Mueller-Dombois and Ellenberg, 2002). For the 250 m, 500 m, and 1000 m circles the FRWO (1997a,b, 2002) 150×200 m grid was used, which provides the diameter at breast height (dbh) of all trees (> 12.5 cm dbh) within a 1000 m² circular plot around each grid point. The abundance of each species was expressed as the mean abundance of all grid plots within the respective radii, whereby tree species producing similar pollen types (e.g. all species of *Acer*) were pooled (cf. Jackson, 1990).

3.4. Data analysis

We used both qualitative and quantitative approaches to explore pollen–vegetation relationships.

In a first step we investigated the overall relationship between the species composition of vegetation plots at two spatial scales (pollen plots and 100 m plots) and the pollen assemblages, after square root transformation of the relative abundances of both species and pollen types. For the three resulting plot×species/pollen type abundance

¹ Also spelled "Alburz", or "Elburz".

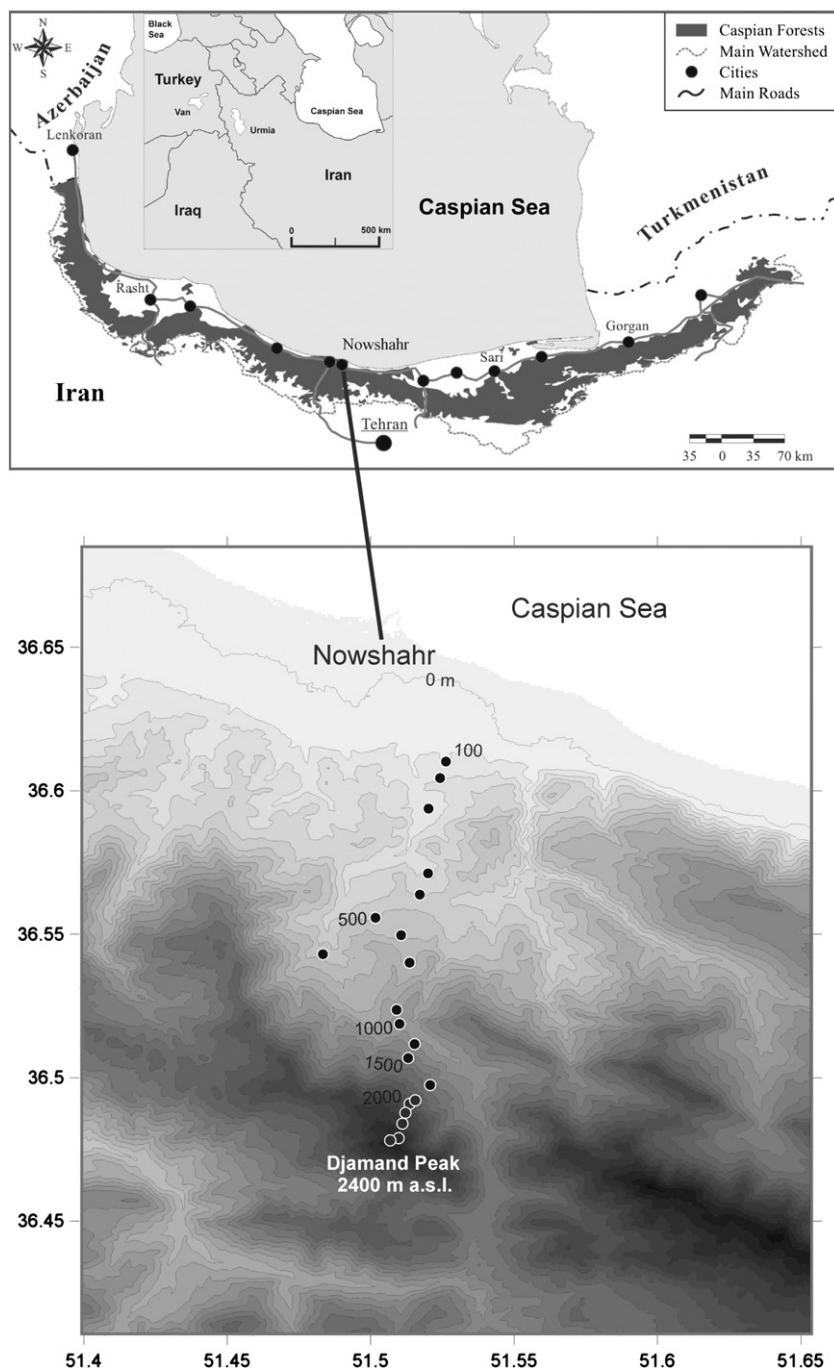


Fig. 1. The study area and the locations of the surface sample plots.

matrices we calculated dissimilarity matrices using the Bray–Curtis index as a robust quantitative measure of compositional dissimilarity between sites (Faith et al., 1987). To describe the correlation between dissimilarities in species and pollen type space we used Pearson correlation coefficients. To remove the effect of elevation on dissimilarities ('distance decay', cf. Nekola and White, 1999; Soininen et al., 2007), we also calculated partial correlations between pollen and vegetation dissimilarities, while controlling for the distance matrix of elevation distances between sites. Partial correlation allows detecting potentially spurious correlations between two vectors X and Y that are the result of the correlation of a third vector Z with X and Y (Cox and Wermuth, 1996).

In a second step, we examined the relationship of frequently occurring pollen types and associated tree taxa for all plot sizes using linear

regression (cf. Andersen, 1970; Bradshaw, 1981; Webb et al., 1981; Heide and Bradshaw, 1982; Bradshaw and Webb, 1985; Prentice and Webb, 1986; Jackson, 1990, 1991; Yazvenko, 1991; Jackson and Wong, 1994; Beer et al., 2007).

To estimate regression parameters, we used the geometric-mean method, which assumes that error in measurement occurs in both the dependent and independent variables (Riggs et al., 1978; Webb et al., 1981). When both variables are subject to error, the ordinary least squares method is inappropriate because it tends to underestimate the true slopes of regression lines (Riggs et al., 1978). We used scatter plots for approaching pollen productivity and dispersal properties of a plant species (cf. Seppä, 2007).

For taxa without linear relationship between pollen and plant abundances or for which the values did not justify numerical analysis,

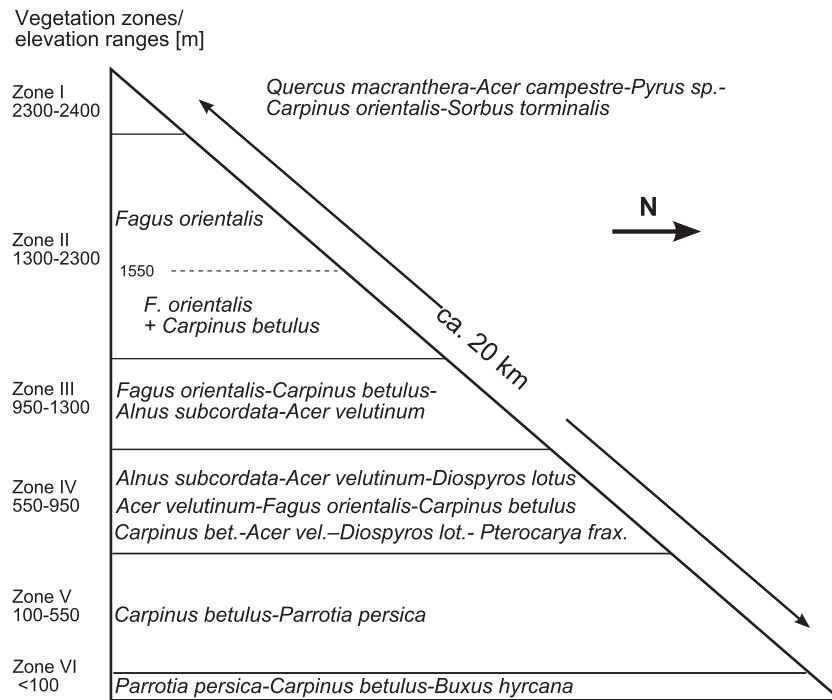


Fig. 2. Main forest types along the altitudinal transect in the central Caspian forest of northern Iran. Vegetation zone IV consists of a variety of forest types, of which the most common ones are mentioned.

we divided the aggregate abundances of a pollen type of all pollen plots (A) with the aggregate vegetation abundances in both pollen (B) and 100 m plots (C) (cf. Bradshaw, 1981). Pollen diagrams furthermore allow visual inspection of the pollen-vegetation relationships in the study area.

Calculations were performed in Microsoft Excel, Minitab 14 (Minitab Inc., State College PA, USA), and the R statistical environment (R Development Core Team, 2011). For calculating dissimilarity matrices we used the function `vegdist` of the package `vegan` (Oksanen et al., 2010) and for calculating partial correlations the function `pcor` of the package `ggm` (Marchetti and Drton, 2010).

4. Results

Fig. 2 shows the zonation of forest communities along the altitudinal transect. A total of 220 plant taxa (30 tree species, 18 shrub species, and 172 species of herbs, lianas, epiphytes, etc., excluding mosses) were identified.

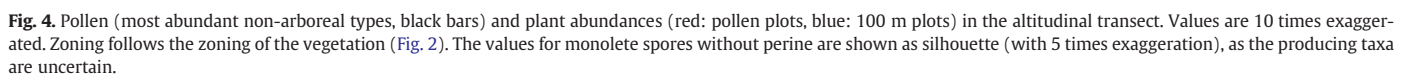
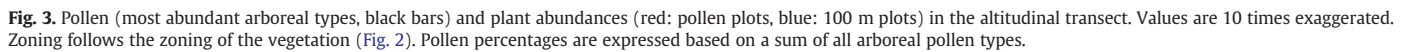
Pollen assemblages of the surface samples are shown in Figs. 3 and 4.

The correlation coefficient for the relation between vegetation and pollen assemblages is higher for the 100 m plots than for the pollen plots (pollen plots: $r=0.682$, $P<0.001$; 100 m plots: $r=0.775$, $P<0.001$, Fig. 5).

Table 1

Forest communities and site characteristics of the surface sample plots.

Site no.	Vegetation zone	Extralocal to regional forest community	Slope (%)	Exposition	Altitude (m)	Latitude (N)	Longitude (E)
1	VI	<i>Carpinus betulus</i> – <i>Parrotia persica</i> – <i>Buxus hyrcana</i>	5–35	NW	75	36° 36′ 39″	51° 31′ 35″
2	V	<i>Carpinus betulus</i> – <i>Parrotia persica</i>	0	–	150	36° 35′ 40″	51° 31′ 13″
3	V	<i>Carpinus betulus</i> – <i>Parrotia persica</i>	20	NW	180	36° 36′ 18″	51° 31′ 27″
4	V	<i>Carpinus betulus</i> – <i>Parrotia persica</i>	25	N–NE	300	36° 34′ 18″	51° 31′ 12″
5	V	<i>Carpinus betulus</i> – <i>Parrotia persica</i>	15	N–NW	400	36° 33′ 51″	51° 31′ 02″
6	V	<i>Carpinus betulus</i> – <i>Parrotia persica</i>	20	E–SE	520	36° 33′ 22″	51° 30′ 06″
7	IV	<i>Carpinus betulus</i> – <i>Acer velutinum</i> – <i>Diospyros lotus</i>	5	NW	560	36° 32′ 36″	51° 29′
8	IV	<i>Carpinus betulus</i> – <i>Acer velutinum</i> – <i>Pterocarya fraxinifolia</i> – <i>Diospyros lotus</i>	3	N	600	36° 33′	51° 30′ 38″
9	IV	<i>Carpinus betulus</i> – <i>Acer velutinum</i> – <i>Alnus subcordata</i>	15	N	700	36° 32′ 25″	51° 30′ 49″
10	IV	<i>Carpinus betulus</i> – <i>Acer velutinum</i> – <i>Alnus subcordata</i>	5	N–NW	940	36° 31′ 26″	51° 30′ 32″
11	III	<i>Fagus orientalis</i> – <i>Carpinus betulus</i> – <i>Acer velutinum</i> – <i>Alnus subcordata</i>	10	N	1030	36° 31′ 08″	51° 30′ 36″
12	III	<i>Fagus orientalis</i> – <i>Alnus subcordata</i> – <i>Acer velutinum</i>	46	N	1140	36° 30′ 43″	51° 30′ 55″
13	II	<i>Fagus orientalis</i> – <i>Acer velutinum</i> – <i>Carpinus betulus</i> – <i>Alnus subcordata</i>	30	NE	1320	36° 30′ 25″	51° 30′ 47″
14	II	<i>Fagus orientalis</i> – <i>Alnus subcordata</i> – <i>Carpinus betulus</i>	24	NE	1470	36° 29′ 51″	51° 31′ 15″
15	II	<i>Fagus orientalis</i> – <i>Carpinus betulus</i>	24	N	1690	36° 29′ 32″	51° 30′ 56″
16	II	<i>Fagus orientalis</i> – <i>Carpinus betulus</i> – <i>Acer velutinum</i>	12	NE	1810	36° 29′ 27″	51° 30′ 49″
17	II	<i>Fagus orientalis</i> – <i>Sorbus torminalis</i>	43	E	2010	36° 29′ 16″	51° 30′ 44″
18	II	<i>Fagus orientalis</i>	37	E	2130	36° 29′ 02″	51° 30′ 40″
19	I	<i>Fagus orientalis</i> – <i>Acer campestre</i> – <i>Quercus macranthera</i> – <i>Carpinus betulus</i> – <i>Sorbus torminalis</i>	45	N–NE	2300	36° 28′ 44″	51° 30′ 35″
20	I	<i>Quercus macranthera</i> – <i>Acer campestre</i> – <i>Pyrus sp.</i> – <i>Carpinus orientalis</i> – <i>Sorbus torminalis</i>	0	–	2400	36° 28′ 41″	51° 30′ 24″



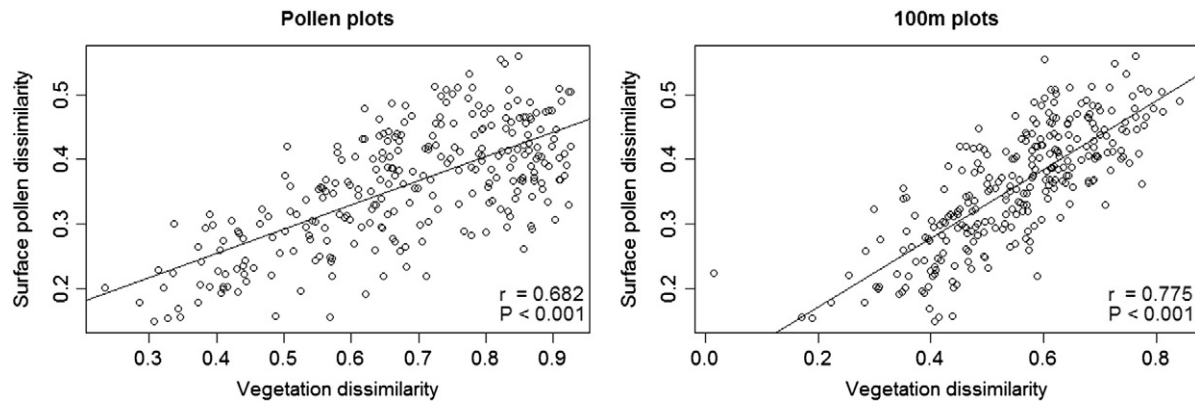


Fig. 5. Overall modern pollen–vegetation relationships at two spatial scales, expressed as Bray–Curtis dissimilarity matrices for the surface pollen samples and the vegetation data sets. Left: correlation between the vegetation at pollen plot scale and surface pollen; right: correlation between the vegetation assemblages in 100 m plots and surface pollen. Each point in the graphs represents the Bray–Curtis dissimilarity between two given plots, either in species space (x axis) or in pollen type space (y axis).

When applying partial correlation to correct for the possible influence of altitudinal differences, the overall strength of the correlation between pollen and vegetation data is only slightly weaker. Contrasting to the first correlations the relation is now stronger at the smaller scale (pollen plots: $r = 0.616$; 100 m plots: $r = 0.583$).

The scatter plots show that the scatter of points for insect-pollinated taxa (*Tilia*, *Acer*, *Parrotia*, *Diospyros*, *Ilex*, and *Hedera*) is concentrated mainly along the horizontal x- or tree-axis (Figs. 6–10), while for obviously wind-pollinated plants, such as *Alnus*, they are largely situated along the vertical y- or pollen-axis (Fig. 8). The points for *Fagus* and *Carpinus* are mainly scattered along the line $y = x$ (Fig. 7). For *Ulmus* no clear pattern is detectable (Fig. 10).

The correlation coefficients (Table 2) and regression parameters (Tables 3 and 4) reveal that for several taxa a significant linear relationship exists between paired pollen and plant abundances. Still, for many cases the relationship is insignificant (cf. *P*-values in Table 2). For other taxa, the limited vegetation and/or pollen data prohibit further statistical analysis. *y*-Intercepts (Table 3) and slope coefficients (Table 4) are

generally higher for *Quercus*, *Fagus* and *Carpinus* (anemophilous taxa) compared to *Parrotia*, *Acer*, *Ilex*, and *Hedera* (entomophilous taxa).

5. Discussion

Pollen–vegetation calibration studies have substantially evolved over the past decades. New methods, i.e. extended R-values (ERV) models initiated by Colin Prentice and colleagues in the 1980s and progressed since 1993 by Shinya Sugita, have increased our insight into the complex relationships between vegetation and pollen assemblages. We refrained, however, from applying ERV models because:

- the ERV method requires species-specific pollen dispersal functions (Jackson and Lyford, 1999), which so far are not available for the species in the Caspian forests of N Iran.
- ERV models assume a constant background component (Sugita, 1994), which is unattainable in our study area due to strong vegetation zonation.

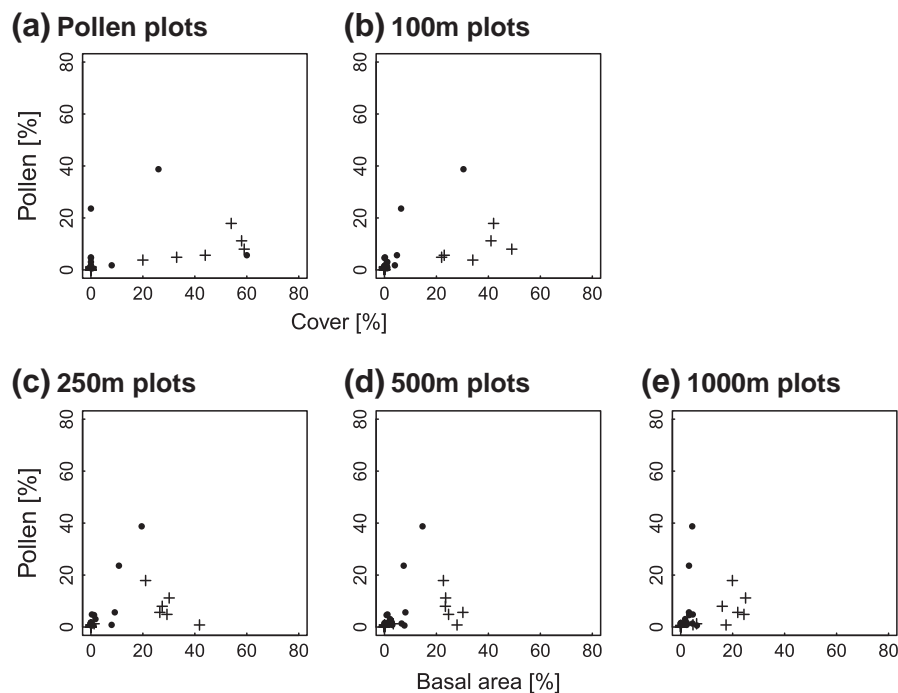


Fig. 6. Scatter diagrams for *Quercus* (●) and *Parrotia* (+) showing pollen percentage versus plant cover percentage (a, b) and pollen percentage versus percentage of basal area (c–e) of the respective taxon within areas with different radii from the center of the sampling plots.

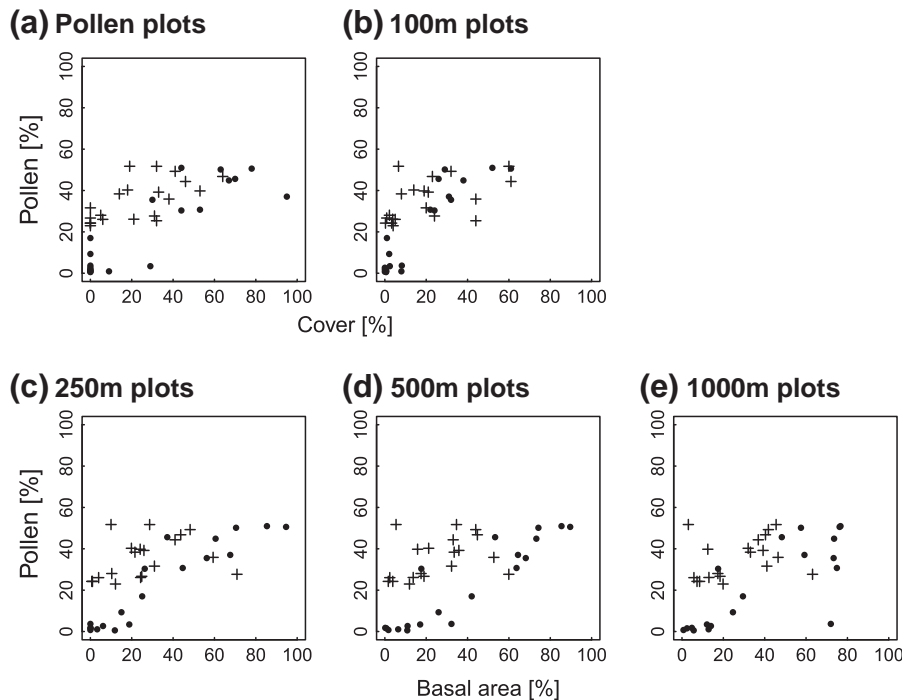


Fig. 7. Scatter diagrams for *Fagus* (•) and *Carpinus* (+). Legend: see Fig. 6.

- the Sutton equation used in the existing ERV software has been shown to be inappropriate in describing pollen dispersal in lowland situations (Kuparinen et al., 2007; Theuerkauf et al., 2012), whereas pollen dispersal in mountains is even more complicated.

Therefore we used linear regression as a first approximation of the relationship between pollen percentages and vegetation abundance. Davis (2001) considers this method as appropriate in mountainous regions, where vegetation patterns are fine scaled.

In regressions between pollen percentages and species abundances, the slope (r_i) value of the curve expresses the over-, equal- or under-representation of pollen compared to species abundance as influenced by pollen production and dispersal. A vertical scatter of points along the y- or pollen axis identifies a pollen type that over-represents the percentages of trees producing its pollen (cf. *ALNUS* in Fig. 8). The scatter of points for an under-represented type is near the horizontal x- or tree-axis (cf. *ACER* in Fig. 8). A scatter diagram with points along the line $y = x$ is characteristic of a taxon for which

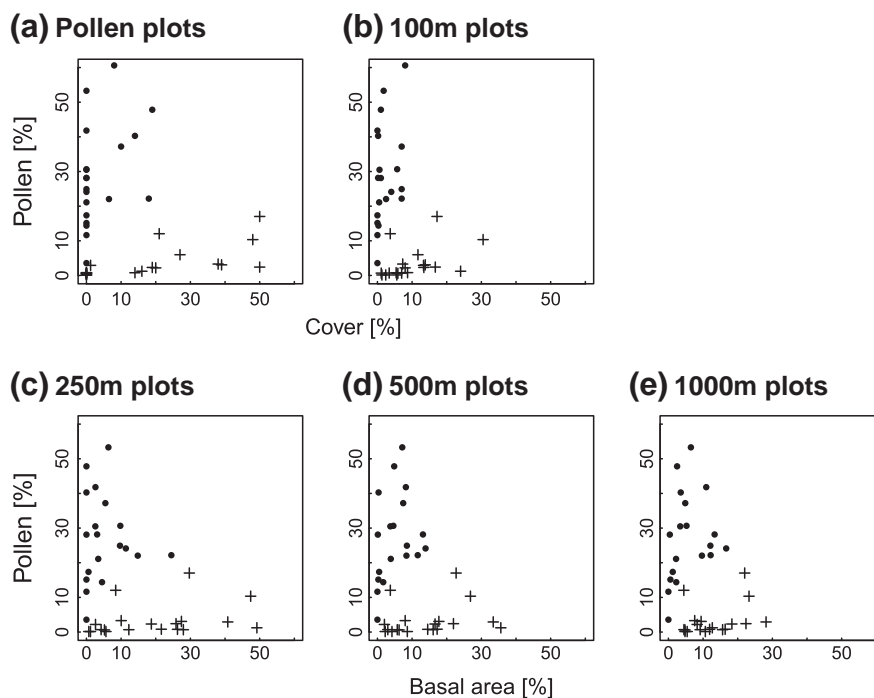


Fig. 8. Scatter diagrams for *Alnus* (•) and *Acer* (+). Legend: see Fig. 6.

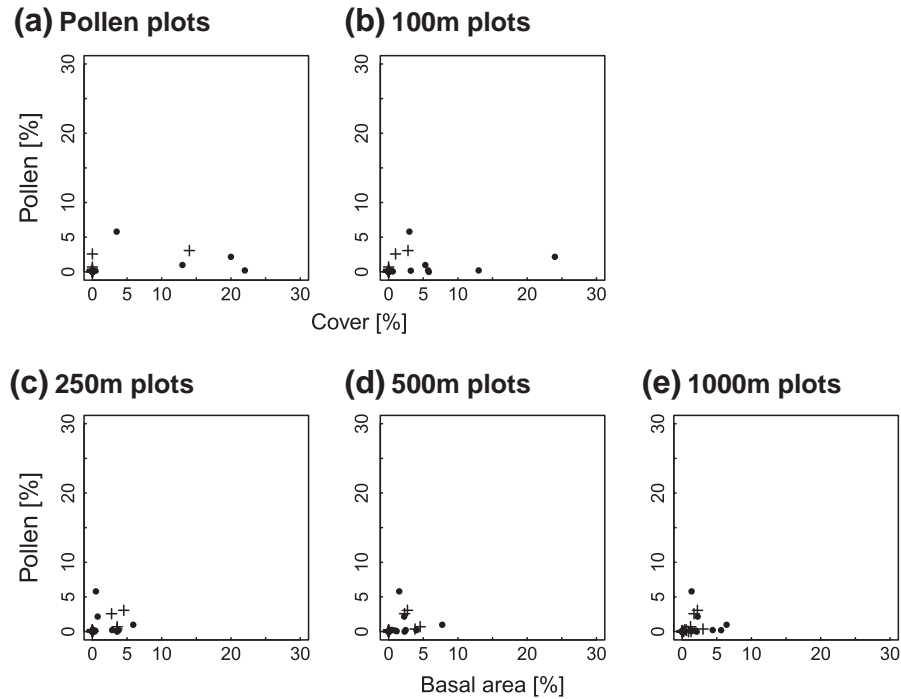


Fig. 9. Scatter diagrams for *Diospyros* (•) and *Fraxinus* (+). Legend: see Fig. 6.

changes in pollen percentages approximately equal the changes in tree percentages (cf. *FAGUS* and *CARPINUS* in Fig. 7). The y-intercept value reflects the pollen component originating from outside the sampling plots and is determined by the overall forest composition and dispersal properties of different pollen types (Bradshaw, 1981; Webb et al., 1981; Bradshaw and Webb, 1985). Correlation coefficients (r) express the strength (cf. Jackson and Wong, 1994), while probability levels (P -values) evaluate the significance of the pollen-vegetation relationships.

Anemophilous taxa, such as *Quercus*, *Fagus*, *Carpinus*, and *Fraxinus* show medium to steep slopes (0.51 to 2.47); while entomophilous taxa such as *Acer*, *Parrotia*, *Ilex* and *Hedera*, show only gentle slopes (0.004 to 0.59). Apparently the former taxa generally produce more pollen than the latter ones. It seems that, among the wind-pollinated trees, oak produces more pollen than beech, hornbeam, and ash (cf. Table 4) and that its pollen values slightly over-represent its tree cover, especially for the 500 m plots. Good pollen representation of *Quercus* in moss polster pollen assemblages was also observed from

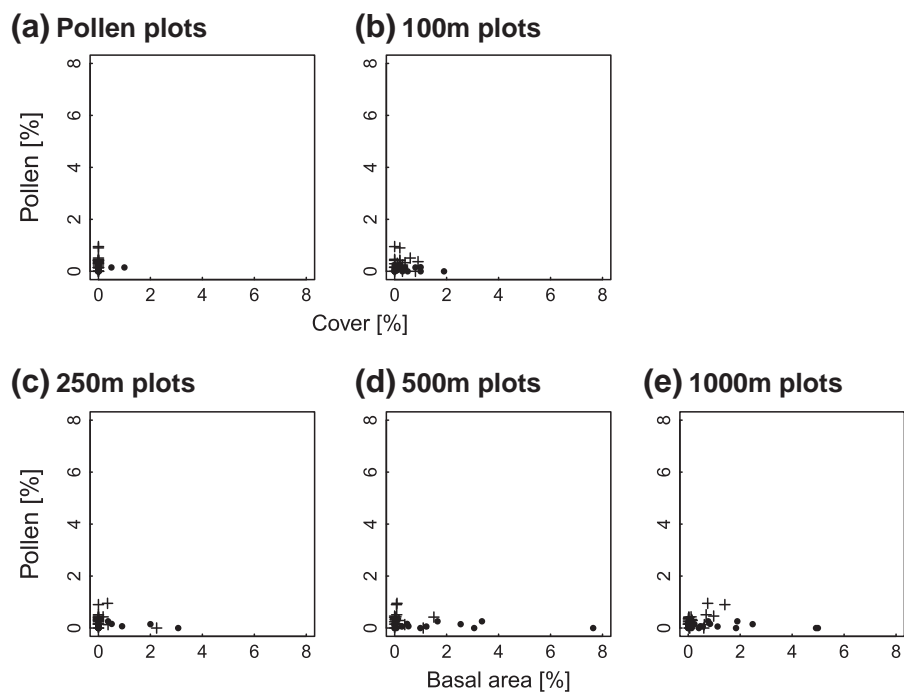


Fig. 10. Scatter diagrams for *Tilia* (•) and *Ulmus* (+). Legend: see Fig. 6.

Table 2

Correlation coefficients for the relationships between pollen percentage and plant cover/basal area percentage. “n” denotes number of plots. Dashes (–) refer to relationships for which correlation coefficients were not calculated because of insufficient pollen or vegetation observations. Values marked with one asterisk indicate significance of the relationship at $P < 0.05$, those with two at $P < 0.01$. Other relationships were insignificant ($P > 0.05$).

Taxon/pollen type	Pollen plots (n = 20)	100 m plots (n = 20)	250 m plots (n = 19)	500 m plots (n = 19)	1000 m plots (n = 19)
<i>Quercus</i>	0.35	0.92**	0.89**	0.77**	0.36
<i>Parrotia</i>	0.90**	0.88**	0.61**	0.70**	0.77**
<i>Fagus</i>	0.87**	0.92**	0.93**	0.92**	0.79**
<i>Carpinus</i>	0.64**	0.51*	0.32	0.38	0.34
<i>Fraxinus</i>	–	–	0.79**	0.59**	0.62**
<i>Diospyros</i>	0.29	0.31	0.05	0.22	0.14
<i>Alnus</i>	0.39	0.34	–0.02	0.30	0.23
<i>Acer</i>	0.66**	0.44*	0.30	0.24	0.34
<i>Ulmus</i>	–	–0.05	–0.23	–0.11	0.60**
<i>Tilia</i>	–	–0.13	–0.09	–0.07	–0.23
<i>Pterocarya</i>	–	0.84**	–	–	0.78**
<i>Ilex</i>	0.91**	0.66**	–	–	–
<i>Hedera</i>	0.96**	0.71**	–	–	–

the eastern part of the Caspian forests (Djamali et al., 2008). High pollen production of oak has been reported from the Caucasus (Connor et al., 2004), Denmark (Andersen, 1970), and the United States (Janssen, 1966). Contrary to our result which shows ash as a moderate pollen producer, Connor et al. (2004), for the Caucasus, and Janssen (1966), for Europe, report *Fraxinus* as a (very) poor pollen producer.

Based on the slope coefficients (Table 4), beech and hornbeam tree abundances appear to be moderately to poorly represented by their pollen abundances (except for *Fagus* pollen and the 100 m plots, where pollen abundance and tree cover are similar). *Fagus* has been characterized as a moderate pollen producer in the forests of the Caucasus (Connor et al., 2004), but as a low producer in Denmark (Andersen, 1970). In this context it should be noted that percentual pollen representation of a taxon is not only a function of its own pollen production and dispersal characteristics, but also from that of the other pollen types included in the pollen sum (Janssen, 1966). Both Connor et al. (2004) and Andersen (1970) report intermediate pollen production for *Carpinus*.

The slopes of the regression lines indicate that *Acer*, *Parrotia*, *Ilex*, and *Hedera* are extremely poor pollen producers and therefore severely under-represented in pollen assemblages even when these taxa grow in the immediate vicinity of the pollen plots. This observation is in agreement with the insect-pollinating nature of the taxa and implies that even very low pollen values of such taxon in deposits may indicate an appreciable share of the taxon in the nearby forest vegetation (Markgraf, 1980). The high (up to 20%) values of *Ilex* pollen in a late-Holocene La Bana 89-C pollen diagram from the Sierra Cabrera Baja, Spain can be ascribed to local overrepresentation of *Ilex* and to the extreme deforestation of the surrounding landscape producing few other upland pollen (Janssen, 1996; C.R. Janssen, personal communication, 2009). The large

Table 4

Geometric-mean linear regression estimates for the slopes and their standard errors. The parameter was not calculated for insignificant relationships (see text). “n” denotes number of plots.

Taxon/pollen type	Pollen plots (n = 20)	100 m plots (n = 20)	250 m plots (n = 19)	500 m plots (n = 19)	1000 m plots (n = 19)
<i>Quercus</i>	–	1.39 ± 0.12	1.81 ± 0.19	2.47 ± 0.36	–
<i>Parrotia</i>	0.21 ± 0.02	0.27 ± 0.03	0.34 ± 0.06	0.40 ± 0.07	0.49 ± 0.07
<i>Fagus</i>	0.63 ± 0.07	1.08 ± 0.09	0.65 ± 0.05	0.65 ± 0.06	0.68 ± 0.10
<i>Carpinus</i>	0.51 ± 0.09	0.52 ± 0.10	–	–	–
<i>Fraxinus</i>	–	–	0.57 ± 0.08	0.60 ± 0.11	1 ± 0.18
<i>Acer</i>	0.24 ± 0.04	0.59 ± 0.12	–	–	–
<i>Ulmus</i>	–	–	–	–	0.64 ± 0.12
<i>Pterocarya</i>	–	1.36 ± 0.17	–	–	3.76 ± 0.53
<i>Ilex</i>	0.007 ± 0.001	0.004 ± 0.001	–	–	–
<i>Hedera</i>	0.18 ± 0.01	0.13 ± 0.02	–	–	–

(up to 25 cm), showy inflorescences, prolific nectar production, small amounts of pollen, and the sculptured exine are evidences of the entomophilic nature of *Acer velutinum* (Yazvenko, 1991), one of the most abundant maple species in the Caspian forests. Strong under-representation of *Acer* and *Parrotia* has repeatedly been reported in modern pollen rain studies, also from adjacent areas (Wright et al., 1967; Yazvenko, 1991; Beer et al., 2007; Djamali et al., 2008).

Anemophilous plant taxa with light pollen grains (i.e. *Carpinus*) show large positive intercepts (Table 3) indicating that more pollen arrives from outside the area covered by the vegetation analysis, while taxa with heavier pollen grains or those possessing patterned exine, such as *Parrotia*, *Acer*, *Fraxinus*, *Ilex*, and *Hedera* reveal only small or even negative intercepts. For example, the constantly high y-intercept values of the scatter plots of all radii for *Carpinus* indicate that considerable amounts of pollen come from more than 1000 m away (cf. Fig. 7; Table 3). Our data thus suggest that *Carpinus* is a very good disperser but an intermediate to low producer of pollen. Good pollen dispersal of *Carpinus* has been reported from the eastern Caspian forests (Djamali et al., 2008) and Azerbaijan (Yazvenko, 1991). Comparable results were reported by the same authors for *Parrotia*.

The y-intercepts for *Fagus* (Table 3) suggest that little or no pollen originates from beech trees growing more than 100 m away, indicating that the dispersal capability of *Fagus* pollen is much weaker compared to the well-dispersed pollen grains, i.e. *ALNUS*, *CARPINUS*, and *QUERCUS* in the study area.

5.1. Qualitative approach

Visual inspection of the pollen diagrams (Figs. 3 and 4) shows that the main vegetation zones are well represented by the pollen assemblages, but that this relationship is biased as a consequence of different pollen production and dispersal between plant taxa, with pollen

Table 3

Geometric-mean linear regression estimates for the y-intercepts and their standard errors. The parameter was not calculated for insignificant relationships (see text). “n” denotes number of plots.

Taxon/pollen type	Pollen plots (n = 20)	100 m plots (n = 20)	250 m plots (n = 19)	500 m plots (n = 19)	1000 m plots (n = 19)
<i>Quercus</i>	–	1.35 ± 0.89	0.17 ± 1.17	–2.95 ± 1.91	–
<i>Parrotia</i>	–0.05 ± 0.55	–0.09 ± 0.61	–0.42 ± 1.14	–0.56 ± 1.01	–0.80 ± 0.92
<i>Fagus</i>	2.64 ± 3.02	2.74 ± 2.43	0.60 ± 2.49	–3.36 ± 2.93	–4.31 ± 4.80
<i>Carpinus</i>	23.58 ± 2.73	24.80 ± 2.95	–	–	–
<i>Fraxinus</i>	–	–	–0.03 ± 0.14	–0.02 ± 0.20	–0.24 ± 0.21
<i>Acer</i>	–0.79 ± 1.09	–2.58 ± 1.62	–	–	–
<i>Ulmus</i>	–	–	–	–	0.14 ± 0.06
<i>Pterocarya</i>	–	–0.10 ± 0.32	–	–	–0.35 ± 0.40
<i>Ilex</i>	–0.004 ± 0.008	–0.008 ± 0.02	–	–	–
<i>Hedera</i>	0.03 ± 0.04	–0.10 ± 0.11	–	–	–

of wind-pollinated taxa being equal- to over-represented and that of insect-pollinated taxa being weakly or not represented. Comparison of the abundance of pollen (A) and that of the corresponding taxa in the pollen (B) and 100 m plots (C) shows that for a strong pollen producer and/or disperser the A/B and A/C ratios are rather large; while for a weak producer or disperser the ratios are low (Table 5).

ALNUS was among the most ubiquitous pollen grains in all samples. Substantial values (ca. 40%) of ALNUS pollen were even recorded in sites where the nearest trees of *Alnus* (mainly *A. subcordata* and to a lesser extent *A. glutinosa*) grew in 500 m distance. Alder (*Alnus* spp.) thus appears to be a heavy pollen producer and disperser, which is also concluded by Djamali et al. (2008) from the northeastern Hyrcanian forest.

Being occasionally major canopy trees, various Rosaceae species like *Cerasus avium*, *Sorbus torminalis*, *Crataegus* spp., and *Pyrus* sp. were frequently encountered in the vegetation survey, but contributed exceptionally little to the pollen assemblages (Figs. 3 and 4). The maximum value (3%) of ROSACEAE type pollen was found in a sample plot (pollen/vegetation zone F/I in Fig. 3) where *S. torminalis* and *Pyrus* sp. cover 27% of the canopy within the pollen plot and 21% within the 100 m plot. Little pollen production and severely under-representation of Rosaceae pollen are reported from different geographical regions (e.g. Wright et al., 1967 and Djamali et al., 2008 from western and northern Iran, respectively).

Buxus and *Diospyros* appear to produce little pollen and are poorly represented in pollen assemblages. Even in sample plots where they were major components, their pollen values were extremely low. *Buxus hyrcana*, for instance, densely covered the understory of the lowermost sample plot but only 16.2% of the pollen assemblage consisted of *BUXUS* pollen (Fig. 3). It should also be taken into account that *Diospyros lotus* is dioecious and thus requires a correction of its percentage crown-cover.

Our data suggest that *Tilia* is moderately to poorly represented in pollen assemblages. To our knowledge, no further data are available on pollen production and dispersal properties of *Tilia* in the Caspian forests and the neighboring Caucasus region. Hyde and Williams (1945) claim that pollen production in *Tilia* (insect-pollinated) is similar to that of wind-pollinated species (cf. Fægri and Iversen, 1989). In a pollen dispersal study in Switzerland, Markgraf (1980) found that *Tilia* is an extremely poor pollen disperser. She suggested that a value of several percents of *TILIA* pollen in sediments implies the existence of a rather dense *Tilia* population.

Trace values of *Juglans* pollen (not shown in Fig. 3) were encountered in several pollen sites whereas its corresponding tree (*Juglans regia*) was completely absent in the vegetation survey. Walnut is commonly cultivated for its fruit both in the Caspian lowlands and in the mountain villages of the region. A small (i.e. around 400–500 m² large) stand of this taxon, probably artificial in origin (cf. Sabeti,

1994), was observed a few kilometers away from the sites during field work in 2004. This clearly indicates the good dispersal of *Juglans* pollen, an observation also made in a surface sample study in Kyrgyzstan (Beer et al., 2007). Also Bottema (1974) assumed good pollen production and dispersal for *Juglans*.

Pollen of ARTEMISIA and CHENOPODIACEAE AND AMARANTHACEAE was present with low but constant values throughout the pollen assemblages. The contributing plants were completely absent in the vegetation survey. *Artemisia* and *Chenopods* occur in the Caspian lowlands and in the clearings or along forest roads in the mountains (personal observations, 2004, 2005) and their pollen in the surface samples must originate from extra-local or regional sources. Their over-representation has frequently been reported (Bottema, 1974; El-Moslimany, 1987; Connor et al., 2004; Court-Picon et al., 2005; Herzschuh et al., 2006; Leroy et al., 2007; Djamali et al., 2008). In deep sea cores from the south and middle basins of the Caspian Sea (Leroy et al., 2007), ARTEMISIA and CHENOPODIACEAE AND AMARANTHACEAE dominate the pollen assemblages, showing their long-distance transport capacity.

Several fern, Poaceae and Cyperaceae taxa were recorded in the vegetation, occasionally even as the major component of the forest ground cover. The aggregate percentages of pollen and fern abundances (Table 5) indicate that except for *Pteridium* and *Athyrium*, all taxa were (severely) under-represented in the pollen assemblages (Table 5). This can be due to the large size and sculptured exine of most fern spores, resulting in short distance transportation. Very short dispersal distances for MATTEUCCIA spores were observed in northeastern Minnesota (Janssen, 1966).

Similar to ferns, Poaceae and Cyperaceae are under-represented in the pollen assemblages (Table 5). With respect to POACEAE, this finding matches the results of Wright et al. (1967) and Beer et al. (2007) but contrasts those of Connor et al. (2004) who for an altitudinal transect in the southern Caucasus inferred that POACEAE pollen correctly represents the proportion of grasses in the vegetation, and those of Leroy et al. (2007) where POACEAE pollen dominated the pollen diagrams of all three deep Caspian Sea cores. The high values of POACEAE pollen in the Caspian Sea sediments may be attributable to water transported pollen of *Phragmites australis* that abounds in the wetlands in the catchment of the Caspian Sea. The under-representation of Poaceae in our study could be due to the fact that many grasses do not abundantly flower in the shade. The group of Poaceae species is actually too large and too diverse to arrive at general conclusions.

From our study, long (i.e. several kilometers)-distance transport must be concluded for PINUS, JUNIPERUS, EPHEDRA, JUGLANS, PTEROCARYA, BUXUS, ARTEMISIA, CHENOPODIACEAE AND AMARANTHACEAE, and PLANTAGO LANCEOLATA, all being anemophilous (except for *Buxus*, which is mainly insect-pollinated). Trace amounts of PINUS, JUNIPERUS and EPHEDRA pollen (mainly E. DYSTACHIA TYPE) were found in a number of pollen spectra, even though the corresponding taxa only occur outside the studied vegetation zones. The high pollen production of pine (an introduced taxon in the Hyrcanian region) and the excellent dispersal of its pollen are well-known (e.g. Court-Picon et al., 2005; Conedera et al., 2006; Leroy et al., 2007). Juniper is a rather large pollen producer in Europe (Beer et al., 2007) and its pollen disperses well (Jackson and Smith, 1994). EPHEDRA is supposedly one of the long-distance pollen types per se (Janssen, 1966; Markgraf, 1980; Connor et al., 2004; Herzschuh et al., 2006; Djamali et al., 2008). Long distance transport of PTEROCARYA and BUXUS pollen have also been reported from the Caucasus by Connor et al. (2004).

Markgraf (1980) showed that in mountain areas daytime upslope wind transports pollen from lower elevations into the uplands. The opposite, pollen transportation from upper elevations into the lowlands, is extremely rare. This phenomenon is, to some extent, illustrated in our study by *Parrotia persica*, *Pterocarya fraxinifolia*, and *Buxus hyrcana*, which grow in the Caspian forests below 1000 m elevation (Parrotia occasionally up to ca. 1500 m) (Sabeti, 1994; Ramezani et al., 2008), of which pollen grains were also found in samples of higher elevations.

Table 5

Aggregate percentages of pollen and vegetation (at two scales) and their ratios.

Plant taxa/pollen types	Aggregate pollen abundances	Aggregate vegetation abundances		A/B	A/C
	(A)	Pollen plots (B)	100 m plots (C)		
<i>Alnus</i>	575.2	75.5	46.8	7.6	12.3
<i>Tilia</i>	1.8	1.5	6.8	1.2	0.3
<i>Buxus</i>	19	76	80.2	0.3	0.2
<i>Diospyros</i>	10.29	58.90	61.05	0.17	0.17
Rosaceae	9.1	146.6	236.9	0.06	0.04
<i>Dryopteris filix-mas</i> /D. <i>affinis</i>	32.2	98.5	71.9	0.3	0.5
<i>Matteuccia struthiopteris</i>	2.4	31	106	0.08	0.02
<i>Athyrium filix-femina</i>	7	4.9	6.3	1.43	0.1
<i>Pteridium aquilinum</i>	0.9	0.3	15	3	0.06
<i>Pteris cretica</i>	0.9	4.8	23	0.2	0.4
Poaceae	16.9	366.6	349.7	0.05	0.05
Cyperaceae	10.7	252.5	88.6	0.05	0.1

6. Conclusion

This study provides first insights into pollen production and dispersal of a number of the most abundant and typical tree taxa in the central part of the Caspian/Hyrcanian forests of N Iran, such as *Fagus*, *Carpinus*, *Quercus*, *Parrotia*, *Acer*, and *Diospyros*. For some other taxa (e.g. *Alnus*) no relationship between pollen and vegetation abundances was found. In order to obtain better estimates, future studies must address larger areas, as light pollen grains may have optimal source areas of tens of kilometers radius (Theuerkauf and Joosten, 2009).

Our results can be used for interpreting fossil pollen sequences both from the Caspian forest region, where the relict *Parrotia persica* and *Pterocarya fraxinifolia* inhabit substantial areas and from Europe where these taxa occurred in the Pliocene (Leroy and Roiron, 1996) but got extinct during the Pleistocene (cf. de Beaulieu et al., 2001).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.revpalbo.2012.10.004>. These data include Google maps of the most important areas described in this article.

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