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Taxon-related pollen source areas for lake basins in the southern Alps: an empirical approach

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Abstract The pollen/vegetation relationship in broadleaved forests dominated by *Castanea sativa* was analysed using an empirical approach. The pollen content of surface sediments of three lake basins of different sizes (6.3, 22.2, and 101.2 ha) in Ticino (southern Switzerland) was used for a comparison with the surrounding vegetation. We surveyed the vegetation around the two small lakes, Lago di Origlio and Lago di Muzzano, and estimated the relative crown coverage of tree species. The regional vegetation outside the lake catchment (ca. >1 km) was determined with the data from the first Swiss National Forest Inventory. For the third large lake, basin of Ponte Tresa, we used only this latter approach for comparison with pollen data. We compare uncorrected and corrected pollen percentages with vegetational data that were processed with distance-weighting functions. To assess the degree of correspondence between pollen and vegetation data we define a ratio pollen/vegetation, which allows a comparison at the taxon level. The best fit between total pollen load and vegetation is reached for a distance from the lake shore of ca. 300 m for Lago di Origlio (150 × 350 m in size) and of ca. 600 m for Lago di Muzzano (300 × 750 m in size). Beside these general patterns, our analysis reveals taxon-specific pollen dispersal patterns

that are in agreement with results from previous studies in northern Europe. Ratios of species with local (proximal) and long-distance (distal) pollen dispersal provide evidence that pollen dispersal mechanisms can influence the size of the taxon-related pollen source area, from small (100–400 m) to large (>5 km) for the same lake. The proportion of distal species increases with increasing lake size, highlighting the predominance of atmospheric pollen transport. We conclude that the large species-related differences in pollen source areas have to be taken into account when the provenance at a site is estimated and discussed.

Keywords Pollen representation · Pollen correction factors · Vegetation-pollen link · Vegetation history · Southern Switzerland

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Introduction

The reconstruction of past vegetational changes is important for understanding ecosystem dynamics as well as the impact of changing climate and land-use. Fossil pollen records have been an important source of information about changes in vegetation composition, but only a few palynological studies provide the spatial information and the resolution necessary to estimate pollen source areas (Bunting et al. 2004). Pollen percentages do not correspond to vegetation abundance directly, being systematically affected by production and dispersal biases (Prentice 1985). In addition, significant water-borne pollen transport may occur at lakes where permanent inflowing streams drain large watersheds (Jackson 1994). According to Sugita (1994), the relevant source area of pollen (RSAP) is defined as the distance from a deposition point beyond which the relationship between vegetation composition and pollen assemblage does not improve.

The concept of the pollen source area and the need to understand pollen dispersal mechanisms have led to different research efforts. Dispersal distances of pollen grains were estimated empirically or simulated by means of

quantitative modelling (for a historical overview, see Jackson 1994). Both empirical and simulation studies demonstrate a correlation between the size of the lake and the relevant source area of pollen. According to Jacobson and Bradshaw (1981), for lakes less than 1 ha in size, pollen assemblages will be dominated by pollen deriving from within a few hundred metres. When a lake size increases, the proportion of pollen transported from a long distance increases as well (Broström et al. 2004; Jackson 1990). In addition, open water bodies display different pollen-collecting properties in comparison with moss polsters and humus samples, capturing a substantial influx of regional pollen from the atmosphere above the tree canopy (Prentice 1985; Sugita 1993). Thus pollen records from large lakes represent a good estimate of the background pollen input (regional vegetation). Furthermore, the modelling approach (Sugita 1994; Sugita et al. 1999; Bunting et al. 2004) suggests that the pattern of vegetation within the landscape, patch size in particular, affects the spatial sensing properties of pollen assemblages, for example the greater the vegetation units, the larger the relevant source area of pollen. The relative proportion of landscape elements, such as size and distribution pattern of openness, has also some effects on the estimates of the relevant source area of pollen, while the number of taxa as well as variations in the properties of a single taxon, such as altering pollen fall speed or relative pollen productivity, does not appear to affect the relevant source area of pollen. In general, the estimated relevant source area of pollen reflects the minimum distance at which regional vegetation composition is reached. As a consequence, the relevant source area of pollen tends to be larger in the case of the presence of larger vegetation patches (Bunting et al. 2004). Similarly, the presence of rare communities increases the relevant source area of pollen, by causing the regional vegetation composition to be reached at greater distance from the deposition point of the pollen (Sugita et al. 1999). According to Bunting et al. (2004), the best estimate of the relevant pollen source area corresponds to the area in which the distribution of the taxa is more or less even.

Physical models (e.g. Prentice 1985; Sugita 1993) and empirical studies (e.g. Jackson 1990), however, suggest that pollen size and pollination biology play a role in determining the dispersal behaviour of single taxa: for a given lake, pollen with small sized grains usually originate from a larger area than those with large grains, while wind-pollinated taxa tend to have a better pollen dispersion than insect-pollinated ones. These authors highlight the fact that the dispersal characteristics of pollen have a distance-weighted influence on the pollen assemblage, giving more influence to nearby plants (Prentice 1985). Thus the abundance of each pollen type in a pollen assemblage may carry a unique message with respect to size, location, and the area covered by the plant populations (Jackson 1994).

Most studies dealing with the quantification of the pollen-vegetation relationship have been carried out in northern Europe (Scandinavian peninsula) and North America. To our knowledge, no attempts exist for the temperate broadleaved forests of the southern Alps, where *Castanea sativa* (sweet chestnut) is dominant. As suggested by differ-

ent authors, additional studies are needed in different types of vegetation, landscapes, and regions that refer to pollen assemblages in which the deposition is integrated over several years, in order to assess the possible differences in pollen productivity and dispersal caused by various environmental factors (Jackson and Wong 1994; Broström et al. 2004).

In this paper we discuss the results of the comparison between pollen and vegetation for lakes located in the *Castanea sativa* broadleaved woodlands of southern Switzerland. In particular, we address the question whether the results and models from northern Europe and North America do apply to the temperate broadleaved forests of the southern Alps. In addition, we investigate whether taxon-specific patterns are relevant for the definition of the source area of pollen.

Study area

The study area is situated in the southern part of the Canton Ticino (Sottoceneri) in southern Switzerland (Fig. 1). The climate is warm-temperate and rainy, with a mean annual precipitation of 1600–1700 mm and a mean annual temperature of about 12 °C (Spinedi and Isotta 2004). The predominance of summer rain (June–September, ca. 800 mm of precipitation) contrasts with that of Mediterranean climates. The geology is mainly formed

Fig. 1 The Sottoceneri (whole area) and the three study sites

Table 1 Main characteristics of the considered lakes

	Origlio	Muzzano	Ponte Tresa
Lake	Lago di Origlio	Lago di Muzzano	Lago Ceresio
Greenwich longitude	8° 56' 30" E	8° 55' 30" E	8° 52' 00" E
Greenwich latitude	46° 02' 54" N	45° 59' 57" N	45° 58' 00" N
Elevation (m a.s.l.)	416	337	271
Size (ha)	6.34	22.22	101.24*
*the size of entire Lago Ceresio is 4890 ha	Watershed size (ha)	123.0	164.0
**including isolated tree	Open area (%)	33	83
***not considering the inflow of the Lago Ceresio outside of the Ponte Tresa basin	Mean size of the vegetation units (m ²)	2904 (1079)**	1857 (340)**
	Inlets	1	0
	Surface geology	Crystalline	Crystalline

by Late-glacial siliceous deposits and metamorphic crystalline rocks (gneiss) with a small spot of limestone in the southeastern part (Fig. 1). The forests are dominated by *Castanea sativa* up to 900 m a.s.l. Cultivation of the sweet chestnut was initiated in the southern Alps by the Romans nearly 2000 years ago (Conedera et al. 2004) and was systematically favoured until the 1950s. Since then, chestnut stands have tended to be invaded by other trees, giving way to post-cultural successional dynamics. At present other important trees in former pure chestnut stands are *Quercus petraea*, *Q. pubescens*, *Alnus glutinosa*, *Fraxinus excelsior*, *Betula pendula*, *Fagus sylvatica*, and *Tilia cordata* (Conedera et al. 2001). Forest stands of *Ostrya carpinifolia* are confined to limestone areas (Fig. 1).

Study sites

Three coring sites were selected in the study area, with attention to the closeness of the studied lake (minimum and maximum linear distance of 5.9 and 11.1 km respectively, see Fig. 1), so that the background pollen rain can be assumed to be similar for all selected sites. Table 1 summarizes the main characteristics of the three selected lakes.

The basin of Ponte Tresa (PT; 271 m a.s.l.) is a sub-basin of Lago Ceresio and has an inlet from the south in Italy and a connection with the main lake body through the straits of Monte Caslano on the east. This strait is very narrow (<100 m), so that the basin of Ponte Tresa can be considered as an independent lacustrine unit with a size of 101.24 ha. The main outlet of the “lake” of Ponte Tresa (river Tresa) flows to the Lago Verbano. Lago di Origlio (O; 416 m a.s.l.; 6.34 ha) has a minor inlet on the east and an outlet on the north. Lago di Muzzano (M; 337 m a.s.l.; 22.22 ha) has no permanent inlet and only a minor outlet to the Lago Ceresio.

Material and methods

Coring and sediments

The core of Lago di Origlio was taken in May 1994 from a rubber boat in the northern deepest part of the lake, where

the water depth was 5.65 m (Tinner et al. 1998). The sediment was frozen in place around an aluminium box containing dry ice and alcohol. A sediment column 60 cm long was recovered, and the topmost 47 cm were analysed contiguously every 0.5 cm (Tinner et al. 1998). For this study we selected nine samples from 11.75 to 7.25 cm sediment depth, dated to ca. A.D. 1978–1984 (± 4 years; Tinner et al. 1998). The core of Lago di Muzzano was taken in July 2002 with a HTH-Teknik Kajak-sampler from a rubber boat. We analysed seven samples between 6.5 and 0.5 cm depth. The precise age is not known, but the biostratigraphical comparison with Origlio shows that the samples are later than A.D. 1965 due to the regular presence of *Ambrosia* pollen. The core of Ponte Tresa was taken in 1998 with a surface gravity corer developed by the ETH Zürich. The sediments were annually laminated (C. Ohlendorf 2002, pers. comm.) and we analysed the sediments of seven varves dated A.D. 1982–1988. Pollen analysis was carried out by W. Tinner at Lago di Origlio and Lago di Muzzano and by M. Gugisberg at Ponte Tresa.

Palynological data

Inter-annual variation in pollen productivity (masting years, climatic variability) and dispersal (meteorological conditions at time of pollen release) are well documented for tree taxa. According to Hicks (2001), it is imperative that a surface sample represents a period of at least 5 years to avoid extreme annual variations. In our case, in order to smooth this variability, 7–9 levels of pollen samples were taken into account for each lake.

Pollen data are expressed as percentage values, which are sensitive to special vegetational characteristics and thus the most promising method for providing detailed, quantitative reconstruction of forest composition (Jackson 1994). The pollen sum is adapted to the main question of the study, including only tree taxa. *Pinus sylvestris* and *P. cembra* were summarized under *Pinus*; *Fraxinus excelsior* and *F. ornus* under *Fraxinus*; and *Quercus ilex*, *Q. robur*, *Q. petraea*, *Q. pubescens*, *Q. cerris* under *Quercus*, and *Alnus incana* and *A. glutinosa* under *Alnus glutinosa*-type (*A. incana* is very rare in the area, but cannot be excluded). Because of the high resolution of the study, insect-pollinated and consistently underrepresented taxa such as *Robinia* were

Table 2 Correction factors used. For taxa without information about correction factors (*Juglans regia*, *Ostrya carpinifolia*, *Populus*, *Salix*) raw values were not changed (i.e. correction factor = 1)

	<i>Picea abies</i>	<i>Abies alba</i>	<i>Pinus</i>	<i>Larix decidua</i>	<i>Castanea sativa</i>	<i>Fagus sylvatica</i>	<i>Alnus glutinosa</i> -type	<i>Acer</i>	<i>Fraxinus</i>	<i>Quercus</i>	<i>Betula</i>	<i>Tilia</i>	<i>Carpinus betulus</i>	<i>Ulmus</i>
Andersen (1970)	0.5	1	0.25	(1)	(1)	1	0.25	2	2	0.25	0.25	2	0.33	0.5
Lang (1994)	1	1	0.25	4	4	1	0.25	4	1	1	0.25	4	1	1

also considered, but grouped under “other taxa”. Further attributed to the group of “other taxa” are the pollen of *Aesculus hippocastanum*, *Arecaceae*, *Buxus sempervirens*, *Carpinus betulus*, *Cedrus*, *Chamaerops humilis*, *Hedera helix*, *Ilex aquifolium*, *Juniperus*, *Liquidambar styraciflua*, *Parthenocissus*, *Phillyrea*, *Pistacia*, *Platanus*, *Myrtus communis*, *Oleaceae*, *Olea*-type, *Rosaceae*, *Sorbus aucuparia*, *S. aria*, *Taxus baccata*, *Trachycarpus fortunei*, *Tsuga* and *Vitis*.

Correction factors

Fagerlind (1952) demonstrated that differences in pollen productivity among taxa can give rise to a non linear relationship between pollen and tree percentages (Fagerlind effect). Wind-pollinated taxa producing a large amount of small pollen grains are usually overrepresented in the pollen assemblages. Zoophilous and amphiphilous (both wind- and insect-pollinated) taxa such as *Tilia*, *Acer*, and *Salix* occur in temperate zone pollen assemblages, but they are consistently underrepresented if compared to their abundance in vegetation (Bradshaw 1981; Jackson 1994). In our study we therefore applied correction factors for each single taxon as proposed by Andersen (1970) and Lang (1994), who modified the correction factors of Fægri and Iversen (1950) for the situation in central Europe (see also Table 2). The correction factors were applied to the pollen counts in order to avoid non-linearity effects in the corrected percentage values (Jackson 1994).

Vegetation survey

According to Jacobson and Bradshaw (1981), local pollen is defined as originating from plants growing within 20 m of the edge of the sampled lake, extra-local pollen as coming from plants growing between 20 and several hundred metres from the lake, and regional pollen as derived from plants at a greater distance. For the two small lakes Lago di Origlio and Lago di Muzzano, the local and extralocal vegetation as thereby defined by Jacobson and Bradshaw (1981) was surveyed in the field as the relative crown coverage of the tree species according to Andersen (1970). At Lago di Origlio the surveyed area corresponds to the watershed (Fig. 2a), at Lago di Muzzano to a mean distance around of the lake shore of 600 m (Fig. 2b). It was assumed that the pollen-source strength of a given taxon is directly related to

the flower density on distal buds, which are in turn related to the crown area (Jackson 1994). Each forest stand was considered as a homogeneous vegetation unit and for each tree species the percentage of the crown coverage was estimated (mapping threshold 5%), giving in total 100%. Single trees in open areas were also mapped, and their crown projection was assumed to be 25 m² for broadleaved species and 50 m² for coniferous species, which corresponds to average values in our study area.

For the large-scale survey of the regional vegetation, we used the data from the first Swiss National Forest Inventory (NFI), where permanent plots were created as sample units on a 1 × 1 km² square grid for the whole forest area (EAFV 1988). The DBH (diameter at breast height) of all surveyed trees in the plots were used to calculate the basal areas (cross-sectional area of the stem 1.3 m above the ground), there being generally assumed a close linear correspondence between basal area and crown coverage of trees (Andersen 1970; Jackson 1994).

The data from the field survey of the local vegetation of Origlio and Muzzano were transferred to GIS, and the percentage cover of each species was calculated for concentric areas around the lakes, increasing the radius by 100 m at each step.

The data from the single plots of the first Swiss Forest National Inventory were also assembled to concentric areas around the lake, building radii of 10 and 15 km respectively and finally for the whole region of Sottoceneri (see Fig. 1). The Italian part of the watershed of the Basin of Ponte Tresa was not surveyed, but we assume a forest vegetation similar to that in the Swiss part of the lake catchment.

Data analysis

Distance-weighting of the vegetation data

Beside the absolute vegetation data, that is the sum of crown projections or basal areas for each concentric area, two weighting functions were applied: inverse distance weighting, $1/d$, where d is the distance in metres from a point at the centre of the pollen sampling area, and the inverse squared-distance weighting $1/d^2$, as described in Broström et al. (2004). For the calculation, a 10 × 10 m grid was calculated for the surveyed area around the lakes of Origlio and Muzzano, and the corresponding percentage in crown coverage of each species was attributed to each grid point. Similarly, for the sample plots of the Swiss National Forest

Fig. 2 Distribution of *Fagus sylvatica* according to the field survey of the vegetation in the lake catchments; **a** Lago Origlio; **b** Lago Muzzano

Inventory, the basal area of each species was transformed to percentages and the values were weighted 10,000 times in order to simulate a 10×10 m grid.

Ratio pollen:plants

We analysed the relationship between pollen and plants by calculating a ratio:

$$R_a = \frac{\text{pollen percentages of taxon } a}{\text{percentages of taxon } a \text{ for a given source area}}$$

If R_a is greater than 1, the taxon is over-represented in the pollen assemblage with respect to its presence in the area of reference. The R_a factors were then used for the empirical analysis of the quality of the fit of the different source areas considered.

Results and discussion

Pollen-vegetation relationship for a single taxon

Pollen and plant frequencies do not agree absolutely and the relationship among them is not constant (Fig. 3). Although all major taxa growing around the lakes are represented in the pollen record, there are substantial differences in representation among them. As already stated by previous

authors (Straka 1975), some species are over-represented in the pollen data, such as *Pinus*, *Alnus glutinosa*-type, *Ostrya carpinifolia*, and partially *Salix* and *Betula* as well, while others are slightly (*Castanea sativa*, *Quercus*, *Fraxinus*, *Larix decidua*) or clearly underrepresented such as *Fagus sylvatica*, *Tilia* and *Acer*.

The correction factors as proposed by Andersen (1970) and Fægri and Iversen (1950; modified by Lang 1994) generally mitigate these biases, with some important exceptions such as *Castanea sativa* and *Fraxinus* for Lang (1994) and *Ostrya carpinifolia* for Andersen (1970). Among the distance-weighting factors, the $1/d$ seems to perform better than $1/d^2$ (Figs. 3 and 4). The $1/d^2$ weighting function displays a flat behaviour, being strongly influenced by the values of the first 100 m around the lake, which is in agreement with the discussion by Broström et al. (2004). This makes the $1/d^2$ unsuitable for the southern Alps, where the lake shores are colonized in a narrow belt (a few decametres) by wetland taxa (see, for example *Alnus glutinosa*, *Salix*, and *Fraxinus* in Fig. 4). In contrast, tree species with a marked long-distance pollen dispersal that are absent near the lakes such as *Ostrya carpinifolia* and *Pinus sylvestris*, are not represented in the vegetational data when the $1/d^2$ is used (Fig. 4). Nielsen and Odgaard (2005) also found stronger correlations between distance-weighted land cover and pollen proportions with $1/d$ than with $1/d^2$. Our results therefore do not support the value of $1/d^2$ as reported by Calcote (1995), who estimated the relevant source area of pollen for seven North American tree taxa. Instead, in agreement with

Fig. 3 Pollen percentages and covered area percentages for selected tree taxa at the three study sites

Boström et al. (2004) we conclude that a taxon-specific distance-weighting is theoretically more satisfactory than a general distance-weighting with $1/d^2$ or $1/d$ functions. Unfortunately, there is still a lack of basic knowledge about physical features (e.g. dimensions, weight) and transport mechanisms of pollen of broadleaved species such as *Castanea sativa* and *Ostrya carpinifolia*, which at present impedes such a modelling in our study region.

R_a -values

The R_a -values of the taxa (pollen: plant ratio) show clear fluctuations along the spatial gradient of all three lakes (Fig. 5). The underlying grey pattern represents the general linear trend that we assume to be characteristic for the given taxon. Trees with long-distance pollen dispersal such as *Ostrya carpinifolia*, *Pinus* sp., and *Betula* sp. are characterized by very high R_a -values in the vicinity of the lakes and a decreasing trend with increasing distance from the lake shore. This implies that the correspondence between pollen and plant abundances improves with increasing distance. R_a -values for *Ostrya carpinifolia* and *Pinus* remain high and unstable even when referred to the entire region of Sottoceneri, suggesting that a significant portion of the pollen of this taxon originates from extra-local sources (on

an average >5 km). Trees belonging to this group have pollen with very efficient dispersal mechanisms (light, wind transported pollen with low settling velocity).

Another group, represented in Fig. 5 by *Alnus glutinosa*-type and *Salix*, is characterized by low pollen dispersal and a biased spatial distribution of the trees related to wetlands around the lakes. Therefore the R_a -values increase with increasing distance from the lake edge, showing decreasing correspondence between pollen and vegetation abundance. Other tree species with a similar pattern are *Tilia*, *Fraxinus* (Fig. 5), and *Acer* (data not shown), but the R_a -values remain relatively low throughout the entire spatial gradient. An explanation is that these trees are more homogeneously distributed and not related to wetlands.

Castanea sativa and *Quercus* display a very homogeneous distribution (at least in the lowlands), as is reflected by almost constant R_a -values. In the case of *Quercus*, the R_a -values remain below 1, indicating a slight underrepresentation of the pollen. This applies especially to the smallest lake, Lago di Origlio (Fig. 5).

Fagus sylvatica has relatively heavy and rapidly falling pollen grains with a reduced dispersal radius (Moore et al. 1991). *F. sylvatica* pollen therefore usually originates from areas near the lake shore or mire edge and thus tends to be underrepresented in pollen assemblages (Straka 1975;

Fig. 4 Pollen percentages and distance-weighted covered area percentages for selected tree taxa at the three study sites. $1/d$ (small rhombic points) and $1/d^2$ (large square points)

Jacobson and Bradshaw 1981). The spatial distribution of the R_a -values (Fig. 5) confirms this effect: if the taxon is present near the lake, it is well represented as pollen. The effect increases with decreasing size of the lake, for example Origlio vs. Muzzano in Fig. 3. Regional *F. sylvatica* stands do not contribute much to the pollen deposition: beyond 400–600 m from the lake shore, R_a -values of *F. sylvatica* decrease abruptly, showing a strongly decreasing correspondence between pollen and vegetation. These examples show how much the area, from which the main pollen is dispersed, differs for each different taxon. *F. sylvatica* is weakly represented in the sediment record, though it is conspicuously present in the region of the Sottoceneri, where according to the first Swiss National Forest Inventory it represents $25.6 \pm 3.0\%$ of the total basal area (see e.g. Fig. 2a and b). Conversely, *Ostrya carpinifolia* is well-represented in the sediment record, although the nearest relevant stands, covering $3.5 \pm 0.8\%$ of the basal area of the Sottoceneri in the National Forest Inventory, are situated several km away, being the species confined to the limestone area for ecological reasons. An exception to this general pattern is represented by the limestone area with *Ostrya carpinifolia* on the southern slope of Monte Caslano (see Fig. 1). These small stands could to some extent be responsible for the conspicuous pollen values of the species at Ponte Tresa.

Estimating the relevant source area of pollen

Our data indicate that the size of the lake significantly influences the pollen assemblages (Fig. 6). The over-representation of taxa that are easily dispersed and/or good pollen producers, such as *Pinus* or *Ostrya carpinifolia*, increases with increasing lake size. Conversely, tree taxa which are locally present near the shore, such as *Alnus glutinosa*, or trees with reduced pollen dispersal, such as *Castanea sativa* and *Tilia*, display lower percentages with increasing lake size. The ratio between the pollen sum of taxa with predominantly long-distance (distal) transported pollen (*Ostrya carpinifolia*, *Pinus*, *Betula*) and pollen with more local (proximal) pollen dispersal (*Alnus glutinosa*-type, *Salix*, *Fagus sylvatica*, *Fraxinus*, *Acer*, *Castanea sativa*) increases with increasing lake size (0.09 for Origlio, 0.14 for Muzzano, 0.29 for Ponte Tresa). We can thus confirm the general assumption that the proportion of pollen transported from long distance increases with increasing lake size (see Jackson 1990; Broström et al. 2004). As a result, assuming a similar vegetation pattern in the surrounding area of a site, the relevant source area of pollen should increase with increasing lake size. To test this hypothesis, we calculated average R_a -values for all trees considered for different concentric belts around the study sites (Fig. 7). R_a -values closest to 1 are reached at 300 m around

Fig. 5 Distance-unweighted R_a -values as a function of the different areas considered for selected tree taxa at the three study sites. The underlying grey pattern represents the general linear trend that we assume to be characteristic for the given taxon; grey bars represent outliers

Fig. 6 Pollen percentages (original uncorrected data) at the three study sites

the lake and the lake-catchment level for Lago di Origlio (6.34 ha, see also Fig. 2). For the larger Lago di Muzzano (22.22 ha) the best fit is at 600 m from the lake shore. No such estimates are possible for Ponte Tresa (Fig. 7), since the local and extra-local vegetation around the lake was not mapped in detail. Taken together, if referred to mean values (over all tree taxa), the studied lakes in south-

ern Switzerland seem to provide results very similar to those obtained by Sugita (1994), who estimated the relevant source area of pollen around lakes of different sizes by using quantitative approaches. According to this author, medium-sized lakes ($R = 250$ m), comparable to Lago di Muzzano ($R = 266$ m), display a relevant source area of pollen of 600–800 m, whereas source areas of pollen of

Fig. 7 Distance-unweighted mean R_a -values over all tree taxa as function of the different areas and the correction factors considered at the three study sites

larger lakes become unstable if the vegetation is distributed in small patches.

Conclusions

In this paper we analysed for the first time the pollen-vegetation relationships for lakes located in the *Castanea sativa*-dominated broadleaved forests of southern Switzerland by empirical means.

The results of our investigation are generally in good agreement with the main findings of empirical and modelling studies conducted in northern Europe and North America. Nevertheless, the great differences in pollen dispersal between species, the non homogeneous spatial distribution pattern of some species such as *Ostrya carpinifolia*, *Alnus glutinosa*, and *Fagus sylvatica*, and as a consequence the great differences in pollen source areas among the taxa have to be taken in account when trying to assess the total (taxa-independent) relevant source area of pollen *sensu* Sugita (1994). A grouping of trees according to pollen dispersal and pollen productivity seems a promising approach for the spatially and ecologically strongly differentiated vegetation types such as those of the southern Alps. Taxon-specific pollen dispersal patterns are clearly recognizable and are similar to those found in previous investigations in northern Europe (Fægri and Iversen 1950; Andersen 1970). In this context, the ratio between the total percentages of predominantly long-distance dispersed pollen and the to-

tal percentages of more locally dispersed pollen is a good indicator for the estimation of the background pollen load. At our sites the proportion of predominantly long-distance dispersed pollen increases with increasing lake size, highlighting the increasing role of long-distance atmospheric pollen transport for large sites. The results achieved in our study underline the necessity of extending this approach to other parts of southern Europe, since the relationships between pollen and vegetation has so far not been addressed in detail in some of the most important vegetation types of this area, such as *Ostrya carpinifolia* and *Castanea sativa* woodlands. A better knowledge of the spatial resolution of the pollen data is in fact a prerequisite for a correct ecological and palaeoecological interpretation of pollen records of sites in the Mediterranean region and elsewhere.

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References

- Andersen ST (1970). The relative pollen productivity and pollen representation of north European trees, and correction factors for tree pollen spectra. Danmarks Geologiske Undersøgelse, Række 2 96:1–99
- Bradshaw RHW (1981). Modern pollen-representation factors for woods in south-east England. J Ecol 69:45–70
- Broström A, Sugita S, Gaillard M-J (2004) Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden. The Holocene 14:368–381
- Bunting MJ, Gaillard M-J, Sugita S, Middleton R, Broström A (2004) Vegetation structure and pollen source area. The Holocene 14:651–660
- Calcote R (1995). Pollen source area and pollen productivity: evidence from forest hollows. J Ecol 83:591–602
- Conedera M, Stanga P, Oester B, Bachmann P (2001). Different post-culture dynamics in abandoned chestnut orchards. Forest Snow Landscape Res 76:487–492
- Conedera M, Krebs P, Tinner W, Pradella M, Torriani D (2004) The cultivation of *Castanea sativa* (Mill.) in Europe: from its origin to its diffusion on a continental scale. Veget Hist Archaeobot 13:161–179
- EAFV (Eidgenössische Anstalt für das forstliche Versuchswesen) (1988). Schweizerisches Landesforstinventar. Ergebnisse der Erstaufnahme 1982–1986. EAFV Bericht 305:1–375
- Fægri K, Iversen J (1950) Textbook of modern pollen analysis. Munksgaard, Copenhagen
- Fagerlind F (1952). The real significance of pollen diagrams. Botaniska Notiser 105:185–224
- Hicks S (2001). The use of annual arboreal pollen deposition values for delimiting tree-lines in the landscape and exploring models of pollen dispersal. Rev Palaeobot Palynol 117:1–29

- Jackson ST (1990). Pollen source area and representation in small lakes of the northeastern United States. *Rev Palaeobotany Palynol* 63:53–76
- Jackson ST (1994) Pollen and spores in Quaternary lake sediments as sensors of vegetation composition: theoretical models and empirical evidence. In: *Sedimentation of organic particles*. Cambridge University Press, Cambridge, pp 253–286
- Jackson ST, Wong A (1994). Using forest patchiness to determine pollen source areas of closed-canopy pollen assemblages. *J Ecol* 1994:89–99
- Jacobson GL Jr, Bradshaw RHW (1981). The selection of sites for paleovegetational studies. *Quat Res* 16:80–96
- Lang G (1994) *Quartäre Vegetationsgeschichte Europas*. Fischer, Stuttgart
- Moore PD, Webb JA, Collinson ME (1991) *Pollen analysis*. Blackwell, Oxford
- Nielsen AB, Odgaard BV (2005) Reconstructing land cover from pollen assemblages from small lakes in Denmark. *Rev Palaeobot Palynol* 133:1–21
- Prentice IC (1985). Pollen representation, source area, and basin size: toward a unified theory of pollen analysis. *Quat Res* 23:76–86
- Spinedi F, Isotta F (2004) Il clima del Ticino. *Dati, statistiche e società* 4:5–39
- Straka H (1975) *Pollen und Sporenkunde*. Fischer, Stuttgart
- Sugita S (1993). A model of pollen source area for an entire lake surface. *Quat Res* 39:239–244
- Sugita S (1994). Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *J Ecol* 82:881–897
- Sugita S, Gaillard M-J, Broström A (1999). Landscape openness and pollen records: a simulation approach. *The Holocene* 9:409–421
- Tinner W, Conedera M, Ammann B, Gäggeler HW, Gedey S, Jones SR, Sägesser B (1998). Pollen and charcoal in lake sediments compared with historically documented wildfires in southern Switzerland since AD 1920. *The Holocene* 8:31–42