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ORIGINAL ARTICLE

The development of composite dispersal functions for estimating absolute pollen productivity in the Swiss Alps

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Abstract Considering the complexity of real-world pollen dispersal, a single set of parameters may be inadequate to model pollen dispersal, especially as dispersal occurs on both local and regional scales. Here we combine more than one dispersal function into a composite dispersal function (CDF). The function incorporates multiple parameters and different modes of pollen transportation, and thus has the potential to better simulate the relationship between deposited pollen and the surrounding vegetation than would otherwise be possible. CDFs based on different dispersal functions and combinations of dispersal functions were evaluated using a pollen-trap dataset from the Swiss Alps. Absolute pollen productivity (APP) was estimated at 7,700 ± 2,000 grains $\mathrm{cm}^{-2}\ \mathrm{year}^{-1}$ for *Larix decidua*, 13,500 ± 1,900 grains $\mathrm{cm}^{-2}\ \mathrm{year}^{-1}$ for *Picea abies* and 95,600 ± 17,700 grains $\mathrm{cm}^{-2}\ \mathrm{year}^{-1}$ for *Pinus cembra* (with 95% confidence level). The results are consistent with previous APP estimates made from the same dataset using different methods.

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Introduction

Pollen production and dispersal are key factors for the interpretation of fossil pollen spectra, as well as being important ecological processes in themselves. They form the basis for the 'intuitive' interpretation behind most palynological investigations, as well as for more objective, quantitative vegetation reconstructions (e.g. Sugita 2007a, b). At the very beginning of quantitative palynology it was pointed out that pollen productivity and dispersal properties vary between taxa (Hesselman 1916). Although many palynologists developed an intuitive understanding of the relationship between the amount of deposited pollen and surrounding vegetation, it was not until the 1960s that pioneering attempts were made to formalize this relationship mathematically. Influential among these pioneers is Margaret Davis (1963), whose *R*-value model still forms the conceptual basis for almost all current mathematical models. With thorough investigation and theoretical development by Andersen (1970), the mathematical relationship between deposited pollen and vegetation obtained its modern form. Andersen's 'correction factors' remain a useful tool in the interpretation of pollen data, although today mostly as a support for intuitive interpretations. Further development stagnated because of the limitations of relative data and a lack of absolute pollen data. This problem was first overcome in the early 1980s with the introduction of the extended *R*-value model (ERV-model; Parsons and Prentice 1981; Prentice and Parsons 1983). The model enabled the calculation of relative pollen productivity on the basis of relative pollen data. The application of the method remained nonetheless rather limited until user-friendly computer programs were developed and made available in the late 1990s and early 2000s (Sugita et al. 1999; cf. Broström et al. 2008). About the same time, annual pollen-trap series started to provide reliable mean pollen accumulation rates (PAR) (e.g. Hicks 2001; van der Knaap et al. 2001; cf. Giesecke et al. 2010), allowing the calculation of absolute pollen productivity (APP) (Sjögren et al. 2008a; Sugita et al. 2009; Filipova-Marinova et al. 2010). APP of a taxon is in the current context the total amount of pollen that a taxon releases in the air per unit of horizontal coverage. In practice this means the pollen accumulation rate (PAR; grains cm^{-2} year^{-1}) at a study site divided by the vegetation cover of that taxon weighted according to a pollen-dispersal function (distance-weighted plant abundance = DWPA; cf. Sugita 1994, 2007a, b).

The use of absolute, instead of relative, pollen data facilitates the use of pollen dispersal as a quantitative parameter in pollen-productivity models, as it is free of the inter-dependence of relative data. In addition, it makes comparison of results between investigations easier, even if these were obtained from different areas or using different methods. The absolute value of a taxon obtained from one study is directly comparable with values for the same taxon in other studies, irrespective of other taxa in the investigations (cf. Sugita et al 2009). APP also opens the way to absolute vegetation reconstructions, which may be especially important in areas with sparse vegetation cover such as alpine or arctic regions (Sjögren et al 2008a; Sugita et al. 2009), although this requires data of a very high quality.

A previously published dataset of absolute pollen accumulation data from the Swiss Alps is used for evaluation. This allows a direct comparison between the present results and published results based on other methods (van der Knaap et al. 2001; Sjögren et al. 2008a). Sjögren et al. (2008a) tested different dispersal functions on the data set, namely Sutton's equation at different wind-speeds, logarithmic down-weighting, and a fixed-area function, both on individual pollen traps and on regional means for each trapping area. Andersen's (1970) *P*-value model (Eq. 1) was used, and the results subsequently corrected for 'regional pollen productivity'. This ad hoc approach produces correct pollen productivity estimates, but it does not provide a specific dispersal function, and is thus of limited applicability and explanatory value. In the present investigation we combine different dispersal functions into a single composite dispersal function (CDF). This function has the potential to explain both the local and regional pollen–vegetation relationship in itself, without the need for any subsequent corrections.

The pollen dispersal model

There is a wide range of pollen dispersal models (cf. Fægri and Iversen 1975; Jackson 1994), although by far the most commonly used are wind dispersal models (cf. Tauber 1965; Prentice 1985; Jackson and Lyford 1999). The most widely used model for pollen dispersal is the *P*-value model introduced by Andersen (1970), where a 'background' or 'regional' component was included in the equation describing the pollen–vegetation relationship. It can be described as:

$$C_\text{t} = P * f(V_\text{l}) + C_\text{r} \tag{1}$$

where C_t is the total pollen deposited, P is the pollen productivity, $f(V_\text{l})$ is the investigated local vegetation weighted according to a pollen-dispersal function, i.e. the distance-weighted plant abundance (DWPA). If a linear regression is applied to a set of pollen/vegetation data points, the *y*-intercept will be a good estimation of the regional component, or, in this case, more correctly labelled as the background component (C_r). One of the basic assumptions of the model is that the pollen dispersal function applied to the investigation area is equally valid for more distant vegetation. Hence the model can be described as:

$$C_\text{t} = P * f(V_\text{l}) + P * f(V_\text{r}) \tag{2}$$

where V_r is the regional vegetation outside the investigation area. If the dispersal function is correct and the investigation area is increased, the background component should decrease and approach zero as a very large area is considered. For a large investigation area the model can then also be described as:

$$C_\text{t} = P * f(V_{\text{l+r}}) \tag{3}$$

where $V_{\text{l+r}}$ includes both the local and regional vegetation. In its mathematical form the dispersal model is identical to the absolute form of the *R*-value model (cf. Davis (1963); i.e. the basic version of the *P*-value model by Andersen (1970, p. 46)). The requirements that separate it from the *R*-value model are thus that it is only applicable to absolute data and the investigated vegetation area needs to be very large (although not very detailed on a regional scale).

The composite dispersal function

Pollen deposition from a local source (0–5 km) has been successfully modelled using Sutton's (1953) dispersal function with no or very low injection height (e.g. Sugita et al. 1999; Broström et al. 2008; Sjögren et al. 2008a, b). There are two main reasons for choosing a low injection height. The first is to avoid the 'skip distance' in which no pollen deposition is modelled to occur when Sutton's equation is applied to an elevated source. Some empirical investigations of pollen deposition suggest, on the contrary, that pollen deposition is highest close to the plant and then declines with distance (e.g. Wright 1953; Janssen 1966; Lanner 1966; Pidek et al. 2010), so the skip distance seems false when applied to pollen dispersal. Rempe (1937) does, on the other hand, report the highest pollen deposition rate at some distance from the tree, after which it declines. This means that a skip distance for tree pollen cannot be disregarded, although it is not as clear-cut as predicted by Sutton's equation. Considering that Sutton's equation assumes a point source with fixed parameters, while pollen in reality is shed from a voluminous source during shifting atmospheric conditions, this also seems reasonable from a theoretical point of view. The second reason for choosing a low injection height is that the effective dispersal height for a tree should not be measured from the ground but from the mean canopy height of the forest, which in practice means a height of zero (Prentice 1985). It could be debated whether a forest canopy can really be simplified to a flat surface with no dispersal below it, but the argument is at least valid in the sense that a forest tree cannot simply be treated as a smokestack of the same height. A low injection height, i.e. 0–1 m, gives little or no 'skip distance', and thus seems reasonable for modelling local pollen dispersal.

In some investigations, a rather high injection height has been used (e.g. Kabailiene 1969; Peters and Higuera 2007). Empirical studies (Sjögren et al. 2008a; Filipova-Marinova et al. 2010) also suggest that dispersal functions that work well for distances up to a few kilometres consequently underestimate the regional input. A high injection height, or some alternative function, thus better explains long-distance pollen transport. It thus seems that a low injection height is required to explain local dispersal, while a high injection height or some other function is required to explain regional dispersal. We incorporate both these aspects by creating a composite dispersal function (CDF). This method weights the vegetation data according to both local dispersal ($\mathrm{DWPA_{loc}}$) and regional dispersal ($\mathrm{DWPA_{reg}}$). Locally and regionally weighted vegetation is then combined to obtain the total weighted vegetation ($\mathrm{DWPA_{tot}}$) according to the following equation:

$$\mathrm{DWPA_{tot}} = \mathrm{DWPA_{loc}} * X + \mathrm{DWPA_{reg}} * (1 - X) \qquad (4)$$

where X is the fraction of pollen dispersed according to a local dispersal function. It should be noted that this is the simplest possible form of a CDF, and one could just as well combine three, four or any number of different dispersal functions (cf. Filipova-Marinova et al. 2010). A higher number of dispersal functions might result in more realistic CDF, but its complexity would make it more difficult to evaluate.

Dispersal parameters and vectors

For the specific parameters of pollen dispersal we follow Tauber (1965). He suggested a wind-speed of 2–6 m s^{-1} for the local (canopy) component. As explained above, there are fairly good reasons for using a low injection height and moderate wind-speed as parameters for local pollen dispersal. In this paper we use an injection height of 1 m and a wind speed of 4 m s^{-1} to model the local component. For the regional component, Tauber (1965) suggested a wind speed of 4–10 m s^{-1}, and here we use the average value of 7 m s^{-1}. For the injection height of regional pollen, we apply the approximate height of the tree concerned, i.e. 20 m for *Larix* and *Picea*, and 10 m for *Pinus cembra*. An alternative mode of transportation for the regional pollen component would be the 'pollen rain' model. It has been suggested that pollen rises up with the wind during warm days, mixes in the atmosphere and then settles during the night (Fægri and Iversen 1975). A different scenario, but with the same effect when it comes to dispersal, is that pollen is carried high up in the atmosphere by turbulent winds and subsequently washed out by rain. This would mean that 'regional' pollen is evenly distributed over the entire region. An assumption for this function is that there is no net pollen exchange between the regional area and any area beyond, or alternatively, that the regional vegetation extends indefinitely. This mode of regional pollen dispersal has previously been used by Sjögren et al. (2008a) and the published APP values we use for comparison are primarily based on it. Here we refer to it as 'rain' dispersal when the pollen is evenly mixed in the atmosphere and subsequently settles during rainy or still conditions.

Determining the CDF composition

In the present investigation we include only two different dispersal functions in any specific CDF, one for local dispersal and another for regional dispersal. Two different approaches were used to determine the exact fractions of local and regional pollen dispersal. The first, a fixed function (FF) approach, assumes a fixed ratio for all taxa. This is similar to the common use of dispersal functions, where the function is considered a physical process that is equally valid for all taxa. A problem is, of course, determining the correct function. In the present investigation we use ratios that seem realistic and give reasonable results in respect of this specific dataset, but further research on different datasets is required to assess whether the ratios have general validity. In the second approach, termed zero *y*-intercept (ZI), the ratio between local and regional dispersal is determined so that a linear regression will give a *y*-intercept of zero. A correct CDF applied to a large investigation area should give a background component of zero, so the ZI approach should, theoretically, provide the most accurate ratio. The drawback of the ZI approach is that the CDF will depend on the specific dataset, and any error or inaccuracy will propagate into the CDF with little or no chance of detection. This kind of approach was first adopted by Prentice et al. (1987, p. 53), where he used an ERV-model on a Swedish dataset, stating 'Approximate *R*-values can be obtained by choosing a forest sampling radius just large enough to reduce each taxon's intercept to near zero'. The difference between this model and the ZI approach is simply that the latter uses a CDF instead of a fixed-area function. The major theoretical difference between the FF and ZI approaches is that the FF approach emphasizes universal physical properties, while the ZI approach emphasizes the empirical result from the specific dataset. Our two approaches are briefly described below:

Fixed-function approach (*FF*): For wind dispersal the ratio between local and regional pollen dispersal is set to 1:1 (FF wind), assuming that both are of equal importance. The down-weighting by distance for rain is normally much lower, so a 3:1 ratio is applied (FF rain).

Zero y-intercept approach (*ZI*): The ratio between local and regional pollen dispersal is set so that the *y*-intercept equals zero (see Table 1). This ratio provides the best fit to any specific dataset. The ZI approach is tested using both wind and rain as the main vectors for regional pollen dispersal (ZI wind, ZI rain).

Dispersal functions for FF wind and ZI wind are provided in Fig. 1. The relationship between the PAR and DWPA was analysed with least-squares linear regression. When the FF-approach is used to calculate APP the *y*-intercept has been fixed to zero, because the dispersal model applied (function 3) assumes no background component. Pollen productivity was also calculated directly for each trap by dividing the PAR by DWPA.

The Swiss pollen–vegetation dataset

The dataset comprises pollen-trap data collected in the Swiss Alps between 1997 and 2005 from four different regions: Aletsch, Grindelwald, Simplon and Zermatt (Fig. 2; van der Knaap et al. 2001; Sjögren et al. 2008a). Each region contained 5–8 traps (A8, G7, S5, Z5), providing a total dataset of 25 traps. Three taxa were well enough represented in both the pollen and vegetation to provide robust datasets: *Larix decidua*, *Picea abies* and *Pinus cembra* (the genus names *Larix* and *Picea* will be used to indicate these species throughout the text). *Picea* data from one trap in Aletsch was disregarded as it had a much higher pollen/vegetation ratio than the other traps

Table 1 The effect of percentage local dispersal ($DWPA_{loc}\%$) on pollen productivity (*P*), *y*-intercept (C_r) and the coefficient of determination of the linear regression (R^2; *Larix* 20 data points, *Picea* 24 and *Pinus cembra* 25) when using a composite dispersal function (CDF)

Regional vector wind

$DWPA_{loc}\%$	P	C_r	R^2
Larix			
100%	7,100	+55	0.83
75%	8,300	+18	0.82
$64\%^{ZI}$	8,800	0	0.81
$50\%^{FF}$	9,500	-22	0.79
25%	10,300	-51	0.69
0%	9,900	-37	0.49
Picea			
100%	9,000	+339	0.76
75%	10,500	+238	0.81
$50\%^{FF}$	12,300	+116	0.84
$28.5\%^{ZI}$	13,900	0	0.86
25%	14,100	-19	0.86
0%	15,600	-135	0.82
Pinus cembra			
100%	61,600	+165	0.78
75%	73,700	+97	0.78
$50\%^{FF}$	91,100	+7	0.78
$48.5\%^{ZI}$	92,300	0	0.78
25%	117,000	-112	0.75
0%	154,800	-224	0.68

Regional vector rain

$DWPA_{loc}\%$	P	C_r	R^2
Larix			
100%	7,100	+55	0.83
$78.5\%^{ZI}$	9,100	0	0.83
$75\ \%^{FF}$	9,500	-12	0.83
50%	14,300	-145	0.83
25%	28,500	-544	0.83
Picea			
100%	9,000	+339	0.76
$75.2\%^{ZI}$	12,000	0	0.76
$75\%^{FF}$	12,000	-3	0.76
50%	18,000	-688	0.76
25%	36,000	-2741	0.76
Pinus cembra			
100%	61,600	+165	0.78
$75\%^{FF}$	82,200	+21	0.78
$72.3\%^{ZI}$	85,300	0	0.78
50%	123,300	-267	0.78
25%	246,600	-1130	0.78

FF fixed function; *ZI* zero *y*-intercept—see text

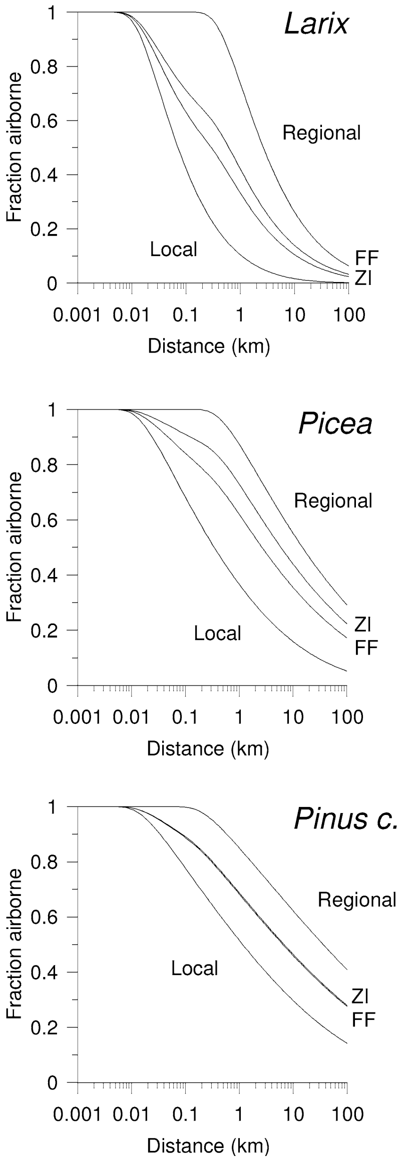

Fig. 1 Composite dispersal functions for *Larix*, *Picea* and *Pinus cembra*, comparing fixed function (FF) and zero y-intercept (ZI) approaches to wind dispersal. Local pollen dispersal is modelled using Sutton's equation (1953) with a pollen injection height of 1 m and wind speed of 4 m s^{-1}. Regional pollen dispersal is based on a pollen injection height of 20 m and wind speed of 7 m s^{-1}. For the FF approach, total pollen dispersal comprises 50% local and 50% regional components. For the ZI approach, the ratio between local and regional dispersal is set so that the y-intercept of a linear regression equals zero (see Table 1). Note the logarithmic scale of the x-axis

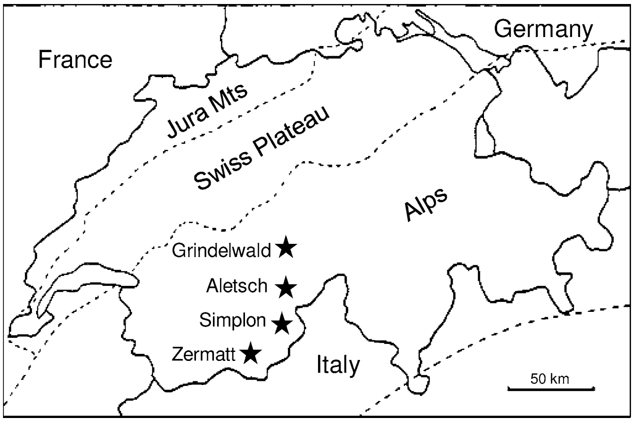

Fig. 2 Pollen trapping areas in the Swiss Alps

and some error or unexplained process probably affected it. For *Larix*, an entire region, Simplon, was removed from the final analysis as these data-points consistently showed lower pollen/vegetation ratios than in the other regions. The effect of the inclusion of data from this region was studied separately. The *Picea* outlier was also removed in the investigation by Sjögren et al. (2008a), so this will not affect the comparison between the two studies. The removal of the Simplon data points for *Larix* will on the other hand slightly increase the present APP compared to earlier results based on the entire dataset.

Large, bi-saccate grains, such as those studied in the present investigation, may be underrepresented in traps compared to moss samples (Pardoe et al. 2010). Although large regional differences are reported, this implies that the resulting APP here may be too low, especially if compared to fossil pollen assemblages from mires. Future research will hopefully give more accurate knowledge about the effect of different depositional environments, but for the present we assume that pollen traps provide a more controlled environment than lakes or mires.

The vegetation around the traps was estimated as percentage of surface cover in rings of logarithmically increasing size (van der Knaap et al. 2001). Visual estimations were made in the field and from 1:25,000 scale maps. In addition to the directly estimated vegetation in rings as used by Sjögren et al. (2008a), average vegetation cover was estimated for rings from 4.64 to 21.5 km radius in each trapping region (based on the Swiss National Forest Inventory—LFI; cf. van der Knaap et al. 2001) and the vegetation cover for the Swiss Alps from 21 to 464 km radius (Brändli et al. 2004; cf. Sjögren et al. 2008a). Pollen-dispersal/vegetation weighting was calculated with an Excel version (by Antti Huusko, see Sjögren et al. 2008a) of Sutton's equation (sensu Prentice 1985) using the xnumb55 add-in (Foxes Team 2007).

Results

The effect of changing the ratio between local and regional pollen dispersal is shown in Table 1 and illustrated in Fig. 3. A larger proportion of local dispersal results in a higher y-intercept, or in other words, in a larger amount of regional pollen that cannot be explained by the dispersal function. For regional wind dispersal, the y-intercept equals zero when the fraction of local pollen dispersal is set to 64% for *Larix*, 28.5% for *Picea* and 48.5% for *Pinus cembra*. For rain dispersal, the fraction of local pollen dispersal required for a ZI is considerably higher: 78.5% for *Larix*, 75.2% for *Picea* and 72.3% for *Pinus cembra*. Good correlations of pollen/vegetation data were found for both FF and ZI. Correlations for ZI are given in Table 1, and scatterplots in Fig. 3. Note that all R^2 values for ZI rain are identical (as all traps are equally affected by the regional pollen rain and the R^2 measurements are relative to the scale).

Regression, average and median statistical values for APP and descriptive statistics are provided in Table 2. Average and median are based on individual measurements from the 25 traps. With removal of outliers, the actual number of traps is 20 for *Larix*, 24 for *Picea* and 25 for *Pinus cembra* (24 for statistics related to mean APP, as one trap with extremely high APP was disregarded). APP estimates are very similar to those previously published (Sjögren et al. 2008a). Those were statistically determined by regression, so we use the regression values for comparison. In this comparison, the use of regional rain dispersal in the CDF produces 10–20% lower APP values than regional wind dispersal, but quite similar values compared to those in the earlier study (Sjögren et al. 2008a).

The variation between data points, i.e. between absolute pollen-productivity estimates of individual traps, is large, as shown in Fig. 4. Individual APP-values (ZI wind) for *Larix* range from 100–15,000 grains cm^{-2} year^{-1}, *Picea* 5,000–25,000 cm^{-2} year^{-1}, and *Pinus cembra* 30,000–170,000 cm^{-2} year^{-1} (300,000 if outliers are included). Data points with low PAR and DWPA values may cause a considerable degree of noise. Average values are sensitive to such noise and should be avoided or used carefully for such a dataset. A good example in the present dataset is the APP outlier for *Pinus cembra* (Fig. 4), which alone increases the average APP value by 9% when regional wind dispersal is applied (the difference is smaller for regional rain dispersal, only 2%). Standard deviation of the mean and other descriptive statistics are provided in Table 2. APP based on regression is more sensitive to data points with high PAR and DWPA values. This can be viewed positively as these probably contain less noise than low values, but a single data point may still have a large impact on the results. Median values may therefore provide the most robust results. Still, the different approaches give relatively similar values, and if a single approach were to be selected for comparison with other investigations, it would be prudent to choose the CDF using average values

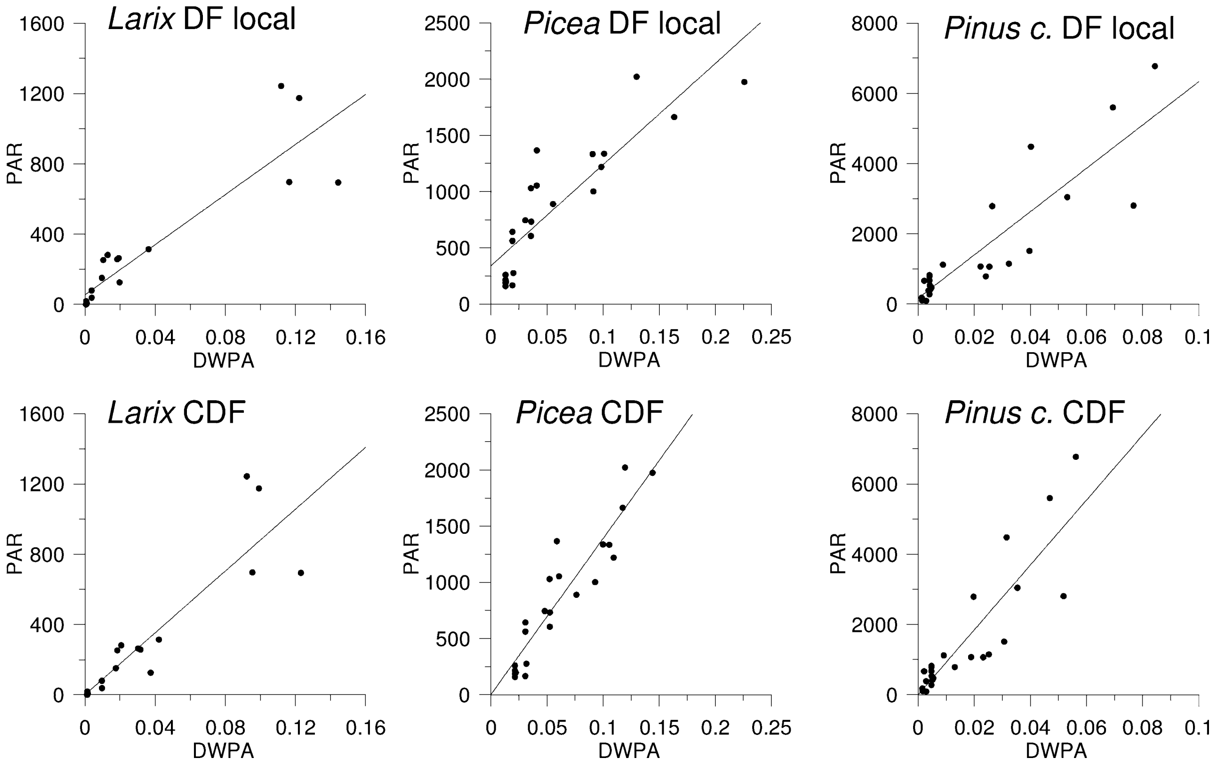

Fig. 3 Scatter for *Larix*, *Picea* and *Pinus cembra*, showing the modelled relationships between pollen accumulation rates (PAR, grains cm^{-2} year^{-1}) and distance-weighted plant abundance (DWPA, cm^{2}) for pollen traps in the Swiss Alps. The upper set of graphs indicate this relationship for a simple dispersal function based on an injection height of 1 m and wind speed of 4 m s^{-1}. The lower graphs show the improvement in model fit achieved by using a composite dispersal function (CDF) that combines the same dispersal function as above with a regional component injected at 20 m height into a wind speed of 7 m s^{-1}, i.e. CDF ZI wind, see Table 1. Both functions are based on the same vegetation area (0–464 km)

Table 2 Comparison between statistical estimates of absolute pollen productivity (APP; grains cm^{-2} year^{-1}) according to composite dispersal functions (CDF) using fixed function (FF) and zero *y*-intercept (ZI) approaches, assuming both wind and rain as the main vector of regional pollen dispersal

Composite dispersal function	*Local DWPA (%)*	*Regression APP**	*Mean APP***	*Median APP*	*Standard deviation***	*Standard error of the mean***	*Confidence level (95%)***	*Multiple R**	*R-square**
FF wind									
Larix	50	9,200	7,000	7,000	4,000	900	1,900	0.89	0.78
Picea	50	13,600	14,500	13,000	5,100	1,000	2,100	0.91	0.83
Pinus c.	50	91,300	95,400	87,200	42,000	8,600	17,700	0.88	0.78
ZI wind									
Larix	64	8,800	7,700	7,400	4,100	900	2,000	0.90	0.81
Picea	28.5	13,900	13,500	13,000	4,500	900	1,900	0.93	0.86
Pinus c.	48.5	92,300	95,600	86,800	41,900	8,600	17,700	0.88	0.78
FF rain									
Larix	75	9,300	7,400	7,400	5,600	1,300	2,700	0.91	0.83
Picea	75	12,000	11,400	12,300	5,000	1,000	2,100	0.87	0.76
Pinus c.	75	82,800	85,400	83,400	43,300	8,800	18,300	0.88	0.78
ZI rain									
Larix	78.5	9,100	7,600	7,100	5,700	1,300	2,700	0.91	0.83
Picea	75.2	12,000	11,500	12,300	5,000	1,000	2,100	0.87	0.76
Pinus c.	72.3	85,300	85,500	82,300	43,300	8,800	18,300	0.88	0.78

All values are in grains cm^{-2} year^{-1}

* *y*-intercept for FF fixed to zero; ** Outlier removed from *Pinus cembra*, mean APP value 8,800 higher if included

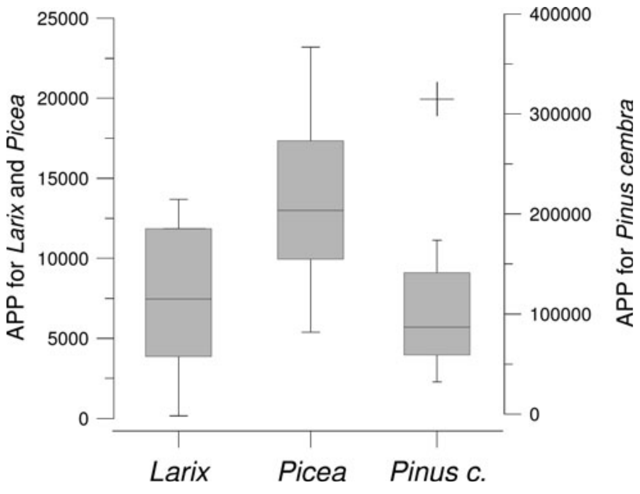

Fig. 4 The range of absolute pollen productivity (APP) values for *Larix*, *Picea* and *Pinus cembra* in the Swiss Alps, based on composite dispersal functions (CDF) using a zero *y*-intercept (ZI wind) approach—see text

of ZI wind. The reasons for this choice are that average values are the most commonly used, and that ZI wind provides the simplest and theoretically most plausible dispersal function. The results with a 95% confidence level are: 7,700 ± 2,000 grains cm^{-2} year^{-1} for *Larix*, 13,500 ± 4,500 grains cm^{-2} year^{-1} for *Picea*, and 95,600 ± 17,700 grains cm^{-2} year^{-1} for *Pinus cembra*.

Discussion

The good linear relationship in the pollen/vegetation scatterplots, as well as the agreement of the estimates with values obtained by other models, suggests that the CDF-based dispersal modelling as applied here is both precise and robust. A much lower regional component was required for the ZI approach if a rain vector (here, evenly distributed regional pollen deposition) was used compared to a wind vector (here, a high pollen-injection height of 10–20 m, at high wind speed of 7 m s^{-1}). The regional component is 35–75% for ZI wind, while it is only 20–30% for ZI rain. The reason for the difference is probably that regional wind dispersal is relatively similar to local wind dispersal and that they partly overlap, whereas regional rain dispersal is more strictly a regional, not local, component.

APP values are 10–20% higher when wind is the regional vector instead of rain, both relative to the current and earlier results (cf. Sjögren et al. 2008a). One explanation for this discrepancy is that rain as a regional vector assumes no net pollen exchange between the regional area and any area beyond, or alternatively that the regional vegetation extends indefinitely. When applied to the real world, this may of course alter the calculated APP in both directions, but in most cases (as in the present dataset) there will be a net transport of pollen out of area, as the investigated taxa are mostly more common in the investigation area than beyond, especially if one considers that large part of the world is covered by water. The use of wind as a regional vector also has some properties that may modify the calculated APP compared to real-world situations. The most important of these is that wind as a regional vector does not directly account for the washing-out effect of rain, which could limit the range of dispersal. In summary, the potential error for rain as a regional vector is that it assumes no regional net loss of pollen, while a potential problem for the use of wind as a regional vector is that there is no washing out.

Larix data points from the Simplon region, when compared to the other regions, correspond better to a regional rain vector than a regional wind vector. If Simplon is included in the calculations for *Larix*, it reduces the APP-estimates by ca. 1,000–1,500 grains cm^{-2} $year^{-1}$ when the regional wind vector is used, but only 200–500 grains cm^{-2} $year^{-1}$ when the regional rain vector is used. *Larix* is relatively abundant in the trap region of Simplon (here applied between 4.64 and 21.5 km). Since the wind vector takes the trap region into account while the rain vector does not, it is likely that any potential errors are related to the wind factor. There are three possibilities: (1) the vegetation estimates are inaccurate; (2) the dispersal function for the regional wind component overestimates the pollen input from this distance (*Larix* is a very heavy pollen type); or (3) the area's topography affects pollen dispersal negatively (cf. Sjögren et al. 2008b). The latter is not unlikely, as the traps are placed in an open pass situation, whereas nearby *Larix* occurs mostly at a lower elevation on a sheltered, steep slope out of sight of the traps. Regional vegetation data from the individual trapping regions was not used for the determination of APP in Sjögren et al. (2008a), so if the problem is indeed related to the trap-area vegetation, the removal of the Simplon traps may in fact result in a more accurate comparison.

The main strength of the CDF method for modelling pollen dispersal, especially the fixed-function (FF) approach presented in this paper, is that it provides a robust and reasonably accurate relationship between deposited pollen and the surrounding landscape while remaining fairly simple. In some cases, the ZI approach to modelling CDFs provided a better fit to the empirical dataset, but this has the disadvantage that the parameters enforced by the ZI can be region-specific and therefore less generally valid. Even though many factors concerning pollen productivity, dispersal, deposition and reconstruction still remain obscure, we feel that the CDF explains a considerable part of the pollen dispersal by trees, and that it is helpful in understanding other aspects of pollen dispersal as well. The intuitive simplicity and utility of the model applied is underlined by the observation that it is conceptually identical to the *R*-value model (Davis 1963), and identical to the basic form of the *P*-value model (Andersen 1970) i.e. a simple linear relationship between pollen and vegetation where pollen productivity equals pollen deposition divided by vegetation. In absolute terms, this relationship can be translated to APP = PAR/DWPA (i.e. APP of a taxon equals its PAR divided by its DWPA).

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