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# Pollen dispersal properties of Poaceae and Cyperaceae: First estimates of their absolute pollen productivities

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ABSTRACT

Pollen-trap results from the Swiss Alps 1996–2009 were used to assess the pollen dispersal–deposition properties of Poaceae (grasses) and Cyperaceae (sedges). Dispersal parameter values were investigated for a modified version of the Prentice–Sugita pollen dispersal–deposition model. Appropriate values (i.e. realistic in the field and allowing realistic modelling results) for wind speed are suggested to be in the range of 3–7 m $s^{-1}$ and for pollen an injection height of 0.03–0.1 m above the ground. The appropriate range of pollen injection height values for grasses and sedges differs from that of trees in the same area, suggesting different pollen dispersal properties between herbs and trees. In addition, logarithmic weighting of the vegetation was tested as an alternative to the modified Prentice–Sugita model. This yielded very similar results, suggesting that the use of such much simpler approximations of the pollen–vegetation relationship is a plausible alternative. Based on the modified Prentice–Sugita model, absolute pollen productivity for Poaceae was estimated to 7300 ± 400 grains $cm^{-2}$ $year^{-1}$ (1 SE). The data basis for Cyperaceae is smaller than for Poaceae, but the dispersal parameter values determined as appropriate for Poaceae yield good results. Absolute pollen productivity for Cyperaceae was estimated to 6300 ± 1100 grains $cm^{-2}$ $year^{-1}$ (1 SE).

## 1. Introduction

Quantitative vegetation reconstruction and evaluation of dynamic vegetation models are becoming increasingly important applications of fossil pollen data (e.g. Gaillard et al., 2010; Nielsen and Odgaard, 2010; Mazier et al., 2012; Nielsen et al., 2012; Sjögren et al., 2014). For such applications an understanding of the pollen–vegetation relationship is crucial, and the topic has attracted a substantial amount of research (e.g. Eisenhut, 1961; Tauber, 1965; Janssen, 1966, 1973; Andersen, 1970; Prentice, 1985; Okubo and Levin, 1989; Sugita, 1993; Jackson, 1994; Jackson and Lyford, 1999; Matthias and Giesecke, 2014). In the last decade most pollen–vegetation investigations have focused on estimating relative pollen productivities using extended R-value models (sensu Prentice, 1985) coupled with the Prentice–Sugita pollen dispersal–deposition model (sensu Sugita, 1994; c.f. Broström et al., 2008; Gaillard et al., 2008), while little or no effort has been directed towards a better assessment of the applied dispersal models, functions and parameters themselves. Recently Theuerkauf et al. (2013) have shown that pollen productivity estimates strongly depend on the assumed mode of pollen dispersal, and that the Prentice–Sugita model strongly underestimates the pollen deposition arriving from distances of over 10 km as well as the dispersal capabilities of pollen grains with higher fall speed. They achieved better results using a Lagrangian stochastic model. One reason for this may be that the Prentice–Sugita model assumes that the pollen is released at ground level (Sugita, 1994). If an elevated rather than ground-level injection height for the release of pollen is applied in the Prentice–Sugita model, the modelled deposition of pollen from distant tree vegetation as well as from trees producing heavy pollen grains such as *Larix decidua* have been shown to increase substantially (Filipova-Marinova et al., 2010; Sjögren et al., 2010). However, the taxon-specific height of pollen release applied by Filipova-Marinova et al. (2010) and Sjögren et al. (2010) is in the range of tree heights (1–20 m) and thus not applicable to lower-growing plants as herbs, sedges and grasses, leaving the potential effect of pollen release height applied to the Prentice–Sugita model fairly unknown for low-growing taxa.

Long-term pollen influx data (or PAR = pollen accumulation rates; grains $cm^{-2}$ $year^{-1}$) from pollen traps (Kvavadze, 1999; van der Knaap et al., 2001) have allowed the study of single-taxon dispersal parameters (Filipova-Marinova et al., 2010; Sjögren et al., 2010). These studies have as mentioned been confined to tree taxa, avoiding the presumably more problematic herbs and grasses (cf. van der Knaap et al., 2001). Still, Poaceae (grasses) constitute a very important taxon as it is in many regions the main indicator of open landscape elements, both in present vegetation surveys and in fossil pollen assemblages.

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In addition, Poaceae is often used as a reference taxon for relative pollen productivity estimates (e.g. Broström et al., 2008), which makes realistic estimates of absolute Poaceae pollen productivity (APP) highly desirable.

In the present investigation we explore the Poaceae pollen–vegetation relationship by varying the dispersal parameter values in a modified Prentice–Sugita model using Sutton's (1953) equation for dispersal of small particles, and we endeavour to resolve the problems that arise. As a result, we present an absolute pollen productivity estimate for Poaceae, which can then be compared with the estimates for trees in earlier studies. Although the present investigation does not consider stand-scale gravitational or water-borne pollen dispersal (cf. Tauber, 1965; Prentice, 1985; Jackson, 1994), a better understanding of the local and regional wind dispersal may improve the interpretation of many pollen assemblages. For better applicability to fossil pollen assemblages, this study uses long-term averages (14 years of pollen influx) rather than focussing on year-to-year variation.

In addition to Sutton's (1953) equation for dispersal of small particles we also test a simpler mathematical distance-weighting of vegetation based on logarithmically $10^{1/3}$ increasing vegetation rings. Such simpler weighting allows a more "intuitive" understanding of the pollen–vegetation relationship, is dependent on less parameters and assumptions, and is easier to compute. If the results are similar, this would allow a simpler but sufficiently accurate alternative to approximate the pollen–vegetation relationship.

It is reasonable to assume that the pollen dispersal properties of Poaceae are more similar to those of other low-growing plants with wind-dispersed pollen than to those of trees. Insights gained for Poaceae may thus also help increase our understanding of the pollen dispersal properties of herbs, sedges, and dwarf-shrubs. Cyperaceae (sedges) constitute another abundant, wind-dispersed pollen type. We therefore apply in a next step the pollen dispersal parameter values determined as appropriate for Poaceae to Cyperaceae from the same pollen traps, and so achieve an absolute pollen productivity estimate for Cyperaceae. Absolute pollen productivities of grasses and sedges have without doubt a large variation in space, because the two groups comprise many different species varying in size by an order of magnitude, and because management like mowing and grazing must have large direct impact on pollen production. Our results are therefore also intended to stimulate colleagues with pollen-trap data to make such estimates for their geographical and ecological settings.

## 2. Methods

### 2.1. The Swiss Alpine pollen-trap data-set

The Swiss pollen-trap programme started in 1992, today providing one of the longest data series of annually deposited pollen available (van der Knaap et al., 2001, 2010). The great length of this period allows both studies in annual variation of pollen influx (Pardoe et al., 2010; Pidek et al., 2010; van der Knaap et al., 2010) and studies that require robust mean values of pollen influx, as the present study. The pollen traps employed are modified Tauber traps (Tauber, 1974), i.e. a 6 l container sunken into the ground with a 5 cm diameter opening (20 $\text{cm}^2$) surrounded by an outward-sloping, 3.5-cm-wide collar, all in accordance with the EPMP/PMP guidelines (Hicks et al., 1996). Vegetation around each trap was estimated in the field by eye as percentage cover of the total surface and included for each taxon both fertile and sterile plants. The grasses and sedges were estimated as totals; the Swiss Alps harbour about 350 grass species in 79 genera and 150 sedge species in 17 genera. The distinction between grasses, sedges, and other graminoids (mostly Juncaceae) was unproblematic in the field.

Variations in fertility between species, between years and between trap surroundings were not recorded. Vegetation was estimated in logarithmically $10^{1/3}$ increasing concentric rings around the traps, so that that each ring has an area 4.64 times that of the largest smaller ring, or 3.64 times the sum of all smaller rings (innermost radius 0.46 m, then 1, 2.15, 4.64, 10, 21.5, 46.4 m and so on; van der Knaap et al., 2001). For detailed field recordings by eye, the largest outer diameter varied between 10 and 46 m. The area of at least 100 m around the traps, but mostly more, was unmanaged or lightly grazed, and the cover of grasses and sedges varied little between years. The percentage cover of plants between the area investigated in detail and 4640 m around the traps was estimated based on 1:25,000 scale maps, averaged values of the field surveys and general visual assessment in the field. The main field survey of vegetation around the traps was carried out in 1998, although annual collection and replacement of traps has allowed continuous control of any major changes in the surroundings. In the surrounding countries agricultural grassland covers approximately 26.1% of France, 22.3% of Germany, 22.6% of Austria and 15.9% of Italy, while the mean cover in the EU is 18.6% (Kasanko et al., 2011). Based on these national estimates and the general distribution in the NUTS2 regions (Kasanko et al., 2011) we assume that grassland covers about 20% of the areas neighbouring Switzerland. Assuming that Poaceae constitute about 50% of these grasslands we use an estimate of 10% Poaceae cover in the most distant rings between 4.6 and 464 km. For Cyperaceae we lack such large-scale vegetation data, but it should be considerably less than for Poaceae and we assume a cover of 2%. It should be noted that the large-scale Poaceae and especially Cyperaceae cover values are rough estimates, so future refinement of the large-scale vegetation cover data and possibly also other factors such as species, shade, aspect, soil, and grazing and mowing practices might improve the results.

The data-set includes a total of 24 traps in four different Alpine regions in Switzerland (Fig. 1). Due to problems during the first years, the average annual pollen influx values used here include only the 14 years 1996–2009. Some traps, however, lack years due to different kinds of accidents. In addition, seven single-trap years with anomalously high pollen influx had to be excluded (3 for Poaceae, 4 for Cyperaceae), because we strongly suspect that these resulted from flowering spikelets having fallen directly into the traps, so that the results are not representative of wind-dispersed pollen deposition. Trap S3 was excluded from the analysis of Poaceae because it consistently provided incongruously high pollen influx values without any explanation found, whereas the Cyperaceae values of that trap fall within the normal range. Trap A2 was excluded from the analysis of Cyperaceae as it is the only trap placed in a sedge mire with dense *Carex rostrata* whereas all other traps are on dry ground. Also the 11 traps that had no Cyperaceae cover within 46 m distance were excluded for the analysis of Cyperaceae APP. The final data-sets consist of 23 data points (traps) for Poaceae and 12 for Cyperaceae. The traps, including some general information, are listed in Table 1.

### 2.2. The pollen dispersal–deposition model

We apply the Prentice–Sugita model for pollen dispersal and deposition (sensu Sugita, 1994), with the following modifications:

1) Pollen grains are released from a ground-level and/or an elevated source.
2) The model is applied to a large area (464 km radius) and all pollen deposited is assumed to derive from within this area.
3) Taxon-specific pollen injection height and wind speed values are so calibrated that the background component becomes zero when applied to a large area (here 464 km radius).

The Prentice variant of the Prentice–Sugita model deals with pollen deposition at a point and is more suitable for deposition in mires, while the Sugita variant (1993) of the model deals with pollen loading on a surface, which better mimics the deposition of pollen in lakes. For pollen traps, having a very small deposition surface (20 $\text{cm}^2$) in relation to the measured vegetation units, the Prentice variant of model is considered more suitable (cf. Sugita et al., 2010), so this variant is applied in the