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Research paper

Pollen as nutrient source in Holocene ombrotrophic bogs

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ABSTRACT

Several laboratory experiments and field observations demonstrate that saprotrophic and ectomycorrhizal fungi effectively use pollen cytoplasm and suggest pollen produced by wind-pollinated trees as a crucial nutrient source for fungi and their plant hosts in nutrient-limited environments. However, the role of such interactions is still underestimated or neglected in ecology and paleoecology. Here, we consider pollen attacked by fungi in palynological records from Holocene raised peat bogs as a nutrient source for ecosystems in the past. The attacks occurred through the pollen germination areas by a variety of saprotrophic, ericoid mycorrhizal, ectomycorrhizal or dark septate endophyte fungi. Large amounts of attacked pollen in phases rich in *Calluna vulgaris* highlight the importance of Ericaceae shrubs, hosting ericoid mycorrhizal fungi and forming hotspots of decomposition in nutrient-deficit bogs. Applying estimations of pollen rain from literature, and based on own observed pollen infection rates we estimate the annual release of nitrogen, phosphate and potassium from pollen, and highlight their significance in pushing the ecosystem nutrient cycle in early spring time, when several species release their pollen. We highlight the significant role of anthropogenic changes in pollen deposition for pre-industrial bogs and hypothesize about the consequences of the pollen-based interrelation between wind-pollinated plants and their mycorrhizal fungi in paleoecology and evolution.

1. Introduction

In northern terrestrial ecosystems and especially in organic-rich soils, nutrients are present mostly in organic forms that are not directly available to plant roots, what makes the decaying activities in the soil and presence of easily degradable organic matter critical for the functioning of the entire ecosystem (e.g. Michelsen et al., 1998; Read et al., 2004; Vohník et al., 2011).

Pollen cytoplasm contains important nutrients such as N, P and K (Knight et al., 1972). The N content makes up about 2–4% of pollen dry weight and 60% of this N is water-soluble, making it a high quality and readily degradable nutrient-rich material for organisms (Greenfield, 1999). By entering terrestrial ecosystems, all the pollen that was not used for reproduction turns to a nutritional source. The total annual pollen deposition estimations reported vary from 16–25 kg/ha in the boreal forest in Canada (Lee et al., 1996) to 55–96 kg/ha in temperate forests in Japan (Saito and Takeoka, 1985). For boreal forests in Canada, this pollen input corresponds to nutrient inputs of 0.34–0.49 kgN/ha, 0.04–0.07 kgP/ha and 0.11–0.2 kgK/ha (Lee et al., 1996). Although these values appear relatively small compared with boreal forest nutrient uptake rates, pollen fallen to ground provides a rapid pulse of easily available nutrients and energy to soil microbes in the spring (Stark, 1972; Lee et al., 1996; Greenfield, 1999). Lee et al. (1996) concluded that pollen-mediated "nutrient cascades" operate in boreal forest ecosystems and are important in ombrotrophic bogs and oligotrophic lakes, where atmospheric deposition is the principal form of nutrient input.

Several groups of soil microorganisms are able to use nutrients from pollen cytoplasm. Microscopic observations (Goldstein, 1960; Stark, 1972; Greenfield, 1999) demonstrated that the contents of pollen grains are susceptible to decomposition by bacteria, actinomycetes, chytrids, and hyphal fungi. Laboratory experiments with *Pinus* pollen as single nutrient source for filamentous fungi (Hutchison and Barron, 1997a) and observations in the ectomycorrhizal association between *Paxillus*

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involutus and *Betula pendula* (Perez-Moreno and Read, 2001a) show that the fungal hyphae attack pollen grains and utilize their cytoplasm for nutrients. Moreover, mycorrhizal fungi pass a significant proportion of pollen nutrients to their autotrophic host, and therefore, to one of the producers of pollen.

Experienced Quaternary palynologists are familiar with the occurrence of fungal growth inside pollen grains. Although laboratory experiments and field observation highlight pollen as an important nutrient provider for the recent boreal ecosystem, there are no systematic studies available on the relationships between pollen deposition, fungal activities and nutrient cycling. This paper presents the records of pollen attacked by dark-colored fungal hyphae found in the Holocene peat sediments from several raised bogs in northern Germany; thereafter, we discuss in detail about the importance of pollen as a nutritional source for ecosystems in the past, including mechanisms of fungal attack on pollen, taxonomic groups of fungi involved, and estimates of nutrient loading on the boreal bog ecosystem via pollen deposition.

2. Material and methods

As part of a dendroecological study, six peat profiles from four *Sphagnum* raised bogs in Northern Germany (Fig. 1) were investigated for palynological analyses, using a standard procedure including treatments with HCl, KOH, HF and acetolysis. All records prove the presence of pollen attacked by fungi (further details to each site in Achterberg, 2010; Eckstein et al., 2010; Bauerochse et al., in press; Shumilovskikh et al., 2015). In order to discuss the relation of such pollen to vegetation and environmental changes, we present the most relevant palynological taxa as diagrams (Fig. 2). Changes in the pollen frequency of *Pinus diploxylon*-type (further *Pinus*), *Quercus robur-type* (further *Quercus*), *Corylus*, *Alnus*, *Betula*, and *Calluna vulgaris* reflect vegetation changes in the surrounding forests and dwarf shrubs on the bog, *Sphagnum* together with the thecamoebes *Amphitrema*, *Arcella* and *Assulina* indicate hydrological changes within the bog while charcoal fragments document fire influence. Taxa percentages in the pollen diagrams are based on the total sum of identified pollen grains of 600–1200.

3. Results

3.1. Morphology

Fungal infection by dematiaceous (dark-colored) hyphae is documented in our material for pollen of gymnosperms and angiosperms as well as for spores of ferns and of *Sphagnum* (Plate I). From 17 pollen types attacked by fungi, 12 are wind-pollinated (i.e. *Pinus*, *Alnus*, *Betula*, *Corylus*) and 4 are (mostly) insect-pollinated (i.e. *Tilia*, *Calluna vulgaris*) (Table 1). The observed hyphae are concentrated in the aperture areas. In Angiosperm pollen, these are pores and/or colpi; thin regions in the pollen wall are supposed to be passed by the germination tube and therefore not entirely covered by the very inert sporopollenin layer of

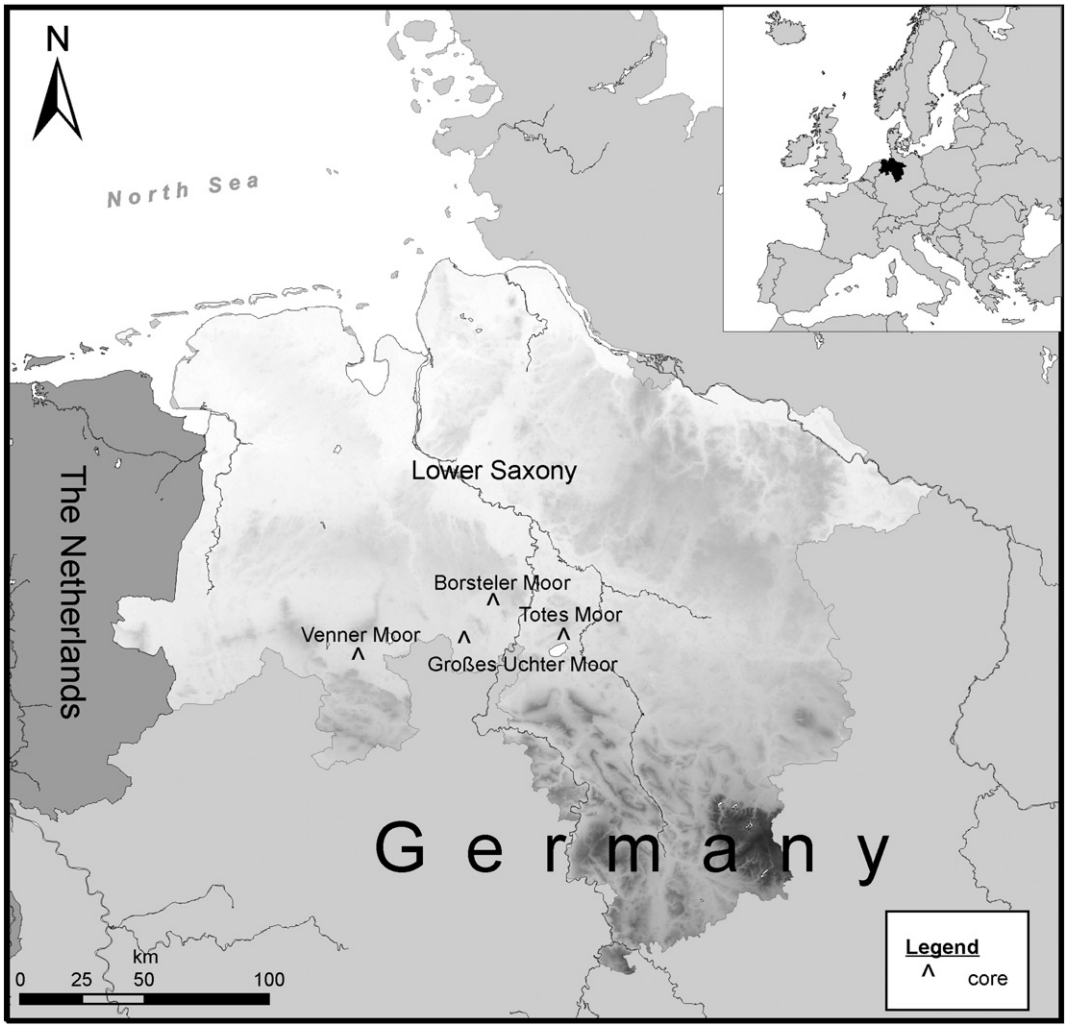

Fig. 1. Map of Lower Saxony (Germany) with locations of investigated pollen records: Borsteler Moor (Shumilovskikh et al., 2015), Venner Moor (Eckstein et al., 2010), Großes Uchter Moor (Bauerochse et al., in press), Totes Moor: M724 and M729 (Achterberg, 2010), M726 (Schlütz unpubl.).