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Pollen production and depositional behaviour of teak (*Tectona grandis* Linn. F.) and sal (*Shorea robusta* Gaertn. F.) in tropical deciduous forests of Madhya Pradesh, India: An overview

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A B S T R A C T

Teak (*Tectona grandis* Linn. F.) of the family Verbenaceae and Sal (*Shorea robusta* Gaertn. F.) of Dipterocarpaceae, are dominating as well as important constituents of tropical deciduous forests of India and Madhya Pradesh, constituting about 24–26% of the total forest flora of the country. These two taxa are high pollen producers, but their pollen grains are retrieved in lesser frequencies in the sediments (surface samples, moss cushions/polsters, samples of sediment profiles/cores). This peculiar behaviour in the representation of their pollen grains could be attributed to poor pollen preservation in the sediments as well as low dispersal efficiency. However, microbial as well as chemical degradation of their pollen in the sediments cannot be ruled out. The number of stamens, flowers, inflorescences on a plant, anther size, pollen grain size, and types and nature of pollination are also related with the abundance of pollen. Genotypes in association with the variations in environmental factors could also govern the pollen production of a particular taxon/variety. In addition to knowing the pollen productivity of the taxa, assessing the representation of the taxa in extant vegetation is helpful in establishing the modern pollen/vegetation relationships which serve as modern analogues for the appropriate explanation of fossil pollen diagrams.

1. Introduction

Reconstruction of the vegetation succession and climate of the past in a definite time-frame is achieved through pollen analysis (Seppa, 2007). The pollen records, however, retrieved from various preserving media, including surface soil/sediments, mud samples, moss cushions/polsters, spider web samples, and samples from sediment profiles/cores, do not directly reveal plant abundance around the study area (Prentice, 1988). Differences in pollen production, dispersal, and preservation of taxa are responsible for the over-representation of some taxa and under-representation of others in the pollen samples. The difference in pollen production, dispersal and surface deposition depends on plant species and climatic conditions (Hicks, 2001; Spieksma et al., 2003). Anemophilous species produce enormous pollen grains and are over-represented in palynoassemblages. Those having a zoophilous mode of pollination produce fewer pollen grains and are under-represented (Faegri and Iverson, 1989), because an increase in the production of pollen occurs in order to compensate for a reduction in efficiency (Faegri and van der Pijl, 1979). Very little work has been carried out in relation to pollen production and dispersal in India. Taxa studied include *Holoptelea integrifolia* (Nair and Sharma, 1965; Khandelwal and Vishnu-Mittre, 1973), *Mimosa rubicaulis* (Saxena and Vishnu-Mittre, 1977), some anemophilous angiosperms (Subba Reddi and Reddi, 1986) and *Shorea robusta* (Bera, 1990; Atluri et al., 2004). Pohl (1937) gave the figures of pollen production per anther, flower, inflorescence, and branch, revealing an annual production averaging many millions for square meter of ground covered. Similar work was carried out on anemophilous trees (Molina et al., 1996), on the Poaceae family (Prieto-Baena et al., 2003) and also on selected species of anemophilous plants (Piotrowska, 2008). In the present study, an attempt has been made to collate the data on teak and sal, the two dominant taxa of one of the core monsoon zones of the Indian subcontinent, regarding their pollen production, dispersal and deposition in the sediments. This would be of paramount significance in establishing the pollen rain/vegetation relationships as well as in reconstructing the past vegetation and climate in chronological order in the region as well as similar floristic regions of the tropics during the Quaternary.

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2. Regional setting

The present study is confined to the eastern (Sidhi, Shahdol and Umaria Districts) and western (Hoshangabad, Sehore and Harda Districts) parts of Madhya Pradesh, India, which lie between the latitudes of 21° 90' and 24° 85' N and the longitudes of 76° 20' and 83° E (Fig. 1). The area has almost undulating topography with linear valleys, plateaux, and hills, with gentle and steep slopes as the dominant physiographic units. Physiographically, the area can be divided into hilly and plain regions. The hilly regions (elevations varying from 250 to 350 m asl) are on the upper part of the Narmada basin and the forested areas are in the lower middle reaches. The topography of river bed is irregular because of rocky braided islands. The plain regions between the hilly tracts and in the lower reaches are broad and fertile areas, well suited for cultivation. The black soils are predominant, whereas alluvial clays with a layer of black soil on the top constitute the coastal plains. Most of the area is under cultivation of conventional crops such as wheat, paddy, pulses, and sugarcane, and is inhabited by the Gonds, Bhils, Oraons, Korkens, Kols, Baiga, Panika tribes (Quamar and Chauhan, 2012).

The Vindhyan Group and Deccan Trap in the central sector of the Narmada Valley form the basement for the Quaternary deposits in the area of investigation. The lithostratigraphy of the Quaternary deposits is divided into seven formations on the basis of critical appraisal of multiple parameters of i) order of superposition; ii) erosional unconformity; iii) nature of sediments; iv) sedimentary structures; v) pedologic characters; and vi) palaeomagnetic signature (Tiwari and Bhai, 1997). In order of decreasing age, these are: i) Pilikarar Formation, ii) Dhansi Formation, iii) Surajkund Formation, iv) Baneta Formation, v) Hirdepur Formation, vi) Bauras Formation, and vii) Ramnagar Formation.

The conglomerate bed, between older alluvium and the glacio-fluvial boulder bed, predominantly consists of sub-rounded to well-rounded boulders, cobbles, and pebbles of quartzite, gneiss, sandstone, basalt, agate, jasper, chert, and chalcedony. The fine sediments include different grades of brown and maroon sand and silt, commonly laminated and cross-laminated.

Black soil, red soil and alluvial soil are chiefly found in most of the areas of present investigation. However, black cotton soil, derived by weathering from Deccan Trap, is the predominant soil type. It is clay with patches of loams and sandy loams. The black soil is rich in soil nutrients such as calcium carbonate, magnesium, and potassium, and has a high water retaining capacity. These soils are generally poor in phosphoric contents. Laterite soils of different grades are also found, especially well developed on the summits of hills which are red and ferruginous. Erosion occurs considerably every year in different areas, especially of the laterite. Laterite is usually found to have a slag like crust and to be quite soft below it. Its composition varies between two extremes, limonite rich in iron, and bauxite rich in aluminium. The black cotton and laterite soils are very poor in calcium carbonate and magnesium and deficient in nitrogen. They are also poor in available phosphorus and

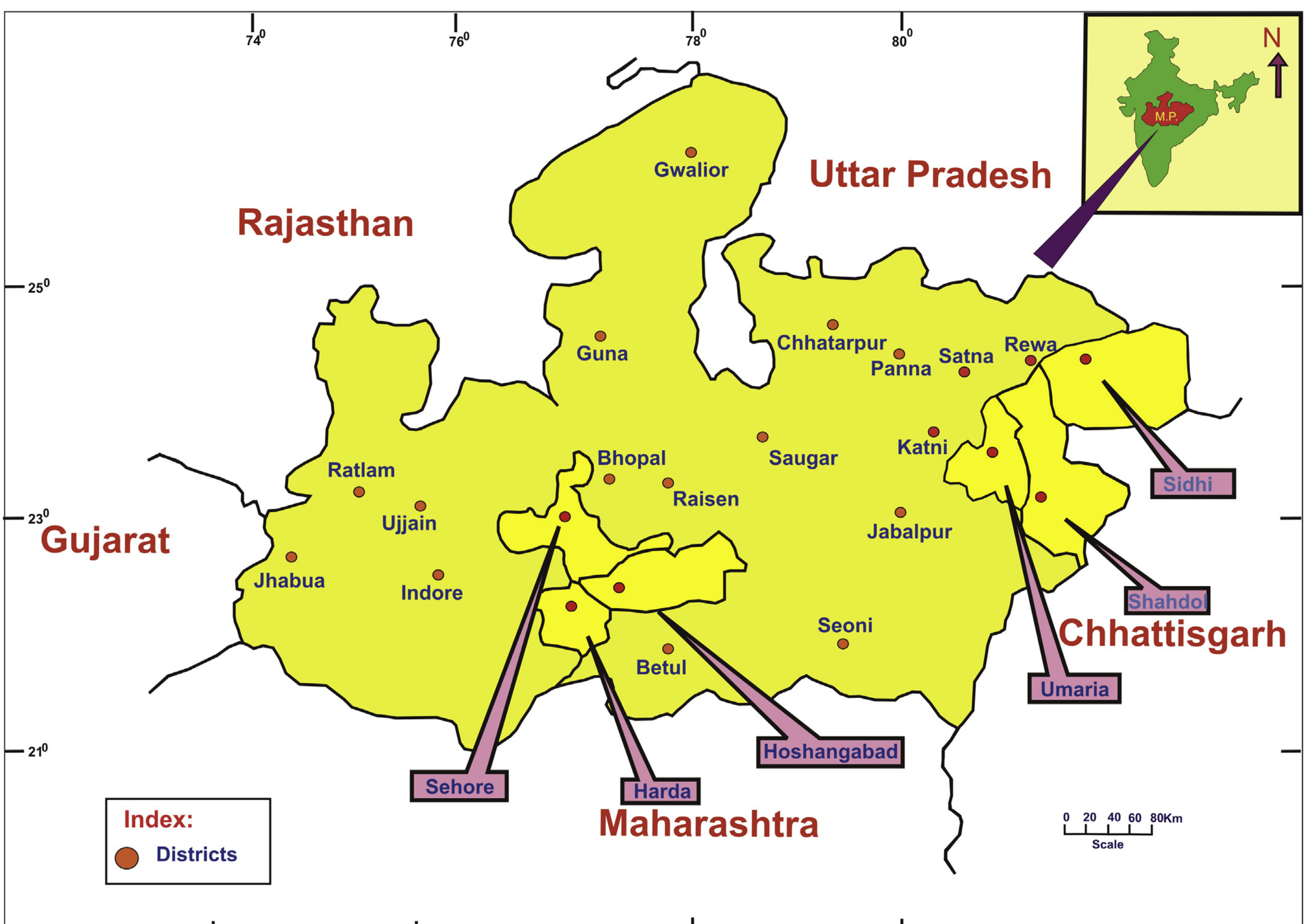

Fig. 1. Map showing the areas of the present investigation.

potassium. Occasionally the phosphate content may be high, probably present in the form of iron-phosphate, but potash is always deficient.

2.1. Vegetation

The vegetation of the study area is characterised by the presence of tropical deciduous forests dominated by *Tectona grandis* (teak) and *Shorea robusta* (sal) (Champion and Seth, 1968). The other associates of teak and sal in the forest are *Diospyros melanoxylon*, *Madhuca indica*, *Aegle marmelos*, *Terminalia arjuna*, *Terminalia bellerica*, *T.* spp., *Schleichera oleosa*, *Emblica officinalis*, *Lannea coromandelica*, *Buchanania lanzan*, *Semecarpus anacardium*, *Boswellia serrata*, *Lagerstroemia parviflora*, *H. integrifolia*, *Flacourtia indica*, *Ailanthus excelsa*, *Sterculia urens*, *Syzygium cumini*, *Wrightia tinctoria*, *Kydia calycina*, *Bridelia retusa*, *Bauhinia retusa*, *Bauhinia integrifolia*, *Bauhinia malabarica*, *Bauhinia racemosa*, *Bauhinia purpurea*, *Elaeodendron glaucum*, *Ficus infectoria*, *Chloroxylon sweitenia*, *Melia azedarach*, and *Anogeissus latifolia*. The shrubs are few and comprise *Ziziphus mauritiana*, *Adhatoda vasica*, *Carissa opaca*, *Vitex negundo*, *Rungia repens*, *Rungia elegans*, *Ricinus communis* and *Calotropis procera*.

The herbaceous flora on the forest floor mainly comprises grasses, together with the presence of *Xanthium strumarium* as well as *Ageratum conyzoides*, *Sida rhombifolia*, *Justicia simplex*, *Artemisia*, *Portulaca*, *Alternanthera*, *Chenopodium album*, *Amaranthus viridis*, *Euphorbia hirta*, *Euphorbia thymifolia*, *Trigonella foenum*, *Trigonella occulata*, *Achyranthes aspara*, *Mazus japonicus*, *Cynoglossum meeboldii*, *Viola suffruticosa*, *Nepeta indica*, *Leucas aspara*, and *Coolebrokia oppositifolia*. *Cynodon dactylon*, *Polygonum plebeium*, *Rotala rotundifolia*, *Ammania baccifera*, *Cyperus rotundus*, *Scirpus articulatus*, *Fimbristylis ferruginea*, *Gnaphalium polycaulon*, *Gnaphalium luteo-album*, *Gnaphalium pensylvanicum* also grow profusely. *Hydrilla verticillata* grows very preponderantly in the lake together with *Nymphaea stellata* and *Nelumbo nucifera*. *Trapa* spp., *Typha* spp., *Lemna* spp., *Potamogeton* spp., and *Nymphoides* spp. are the other aquatic plants. The pteridophytic taxa growing in damp and shady situations include *Adiantum philippensis*, *Dryopteris prolifera*, *Ceratopteris thelictroides*, *Ophioglossum reticulatum*, *Equisetum debile*, *Selaginella lepidophylla*, and *Lycopodium clavatum*.

3. Materials and methods

Teak (*Tectona grandis*) and Sal (*Shorea robusta*) have been selected for the present study in view of seeing their dominance and luxuriant growth (80–95% and 75–90% taxa), respectively out of the total flora growing in the southwestern (Teak) as well as northeastern and southeastern (Sal) Madhya Pradesh.

The methodology adopted here involves the treatment of the samples (sediments/surface samples/moss polsters) with 10% aqueous KOH solution for 5 min to deflocculate the pollen/spores from the sediments and to dissolve the humus, followed by treatment of the samples with 40% HF solution in order to remove the silica. Thereafter, the samples were acetolysed (Erdtman, 1943), using an acetolysing mixture (9:1 ratio of acetic anhydride and concentrated sulphuric acid, respectively). Finally, samples were prepared in 50% glycerine solution for microscopic examination.

4. Results

4.1. Teak (*Tectona grandis* Linn. F.) and its pollen production

Teak is a large tropical deciduous tree (up to 40 m in height) found in a variety of habitats and climatic conditions from arid areas with only 500 mm of rain/year to very moist forest with up to 5000 mm of rain/year. Typically, the annual rainfall in the areas where teak grows averages 1250–1650 mm with a 3–5 month dry season. Teak, belonging to the order Lamiales and family Verbenaceae, grows well in well-drained deep alluvial soil. It prefers the Deccan trap and the Crystalline rocks (granite, gneiss, schist) and avoids laterite soil and black cotton soil.

Tectona grandis is native to India, Indonesia, Malaysia, Myanmar, Northern Thailand and Northwestern Laos. However, the other two species, *Tectona hamiltoniana* and *Tectona philippinensis*, are endemics with relatively small native distribution in Myanmar and Philippines, respectively. In India, *T. grandis* is found in Western Ghats, Tamil Nadu, Madhya Pradesh (as a dominant tree in southwestern Madhya Pradesh with 80–95% of the total forest constituents), Odisha, Karnataka, and Bihar.

Teak is regarded as a high pollen producer with 7500 average number of absolute pollen/flower (Bhattacharya et al., 1999). However, its pollen grains are either untraced or retrieved in values ranging from 2.09% to 25.16% in the surface samples collected from the open areas at Nitaya and Itarsi-Nagpur Road. Its pollen grains were not detected in all the samples collected from the open areas at Nitaya and in one sample IN2 from Itarsi-Nagpur Road (Quamar and Chauhan, 2011a) in Hoshangabad District. They represented <0.5–1% in the profile samples collected from a lake (Quamar and Chauhan, 2012) at Nitaya village in Hoshangabad District. Its frequencies further shows variation from 1.5% to 1% and 19.5% in the surface samples picked up from the open area, edge of forest and within the forest areas, respectively at Kishanpur (Quamar and Chauhan, 2010), and <0.5% in the profile samples of Kachia Jhora (Lake) in Sehore District (Quamar and Chauhan, 2011b). In another case, its values range between 1 and 2% in the surface samples from Shahganj (Quamar and Chauhan, 2011b), and <0.5–1% in the profile samples from Kachhar Lake (Quamar and Chauhan, 2011c) in the Sehore District, southwestern Madhya Pradesh.

4.2. Sal (*Shorea robusta* Gaertn. F.) and its pollen production

Sal is one of the dominant trees (75–90%) in tropical deciduous forests (moist as well as dry types) in India and is presumed to be either entomophilous, as the flowers have mild fragrance and also visited by insects (Champion and Seth, 1968), or anemophilous (Bera, 1990). Sal is semi-evergreen physiognomically and extensively distributed in the tropics, from moist to the dry regions. Indian forests harbour four species: *Shorea assamica* Dyer., *S. robusta* Gaertn. F., *Shorea roxburghii* (*Shorea talura*) G. Don., and *Shorea tumbuggaia* Roxb.

S. robusta occurs extensively in parts of north, east and central India. The sal forests extend from the Himalayan foothills through central India, Madhya Pradesh, West Bengal, and Odisha to Vishakhapatnam in Andhra Pradesh, often forming pure stands over extensive areas. Besides India, it is widely distributed in Sri Lanka, Burma and other South-East Asian countries. Sal, belonging to the order Guttiferales and family Dipterocarpaceae, grows best in well-drained moist deep sandy loam soil. It also prefers laterite soil, alluvial soil, but absent on the Deccan Trap, where its place is taken by teak (Troup, 1921; Tewari, 1995; Oommachan and Srivastava, 1996). If present, as a rule, it is sparse and of short stature.

Sal is a high pollen producer with about 60,000 pollen grains/flower (Atluri et al., 2004). However, Bera (1990) reported the lowest average 61,020 pollen grains/flower and up to 94,600 pollen grains/flower. Its pollen grains are also recovered in lesser frequencies, ranging from 2% (in the surface soil collected from outside the forest) to average 4% (in samples from within the forest) in Sidhi District, northeastern Madhya Pradesh. However, its frequencies dwindled between an average of 10% (edge of forest) to 15% (within the forest) in the moss polsters taken from the same district (Bera, 1990). The frequency of sal pollen ranged between <0.5% and 1% in the samples gathered from Paundi (Quamar and Chauhan, 2007), Umaria District in southeastern Madhya Pradesh. Similarly, the value of sal pollen confined to an average value of 2% in the surface samples (moss polsters) collected from Shahdol District (Chauhan and Quamar, 2013) in southeastern Madhya Pradesh.

5. Discussion and conclusions

The following points should be taken under consideration in discussion of the pollen production, dispersal and depositional behaviour of a particular taxon:

1. Variation in the production of pollen has been noticed from plant to plant and also within different species of the same plant, which could be due to different anther length and size of pollen grains (Subba Reddi and Reddi, 1986; Bhattacharya et al., 1999). The total production of pollen grains by a flower depends upon the number of stamens and number of pollen grains produced per anther (Bera, 1990). The abundance of pollen is related to the number of pollen grains produced by the stamen and the flower. Levels of pollen production also depend on the number of flowers and inflorescences on a plant, as well as the conditions in which it grows (Piotrowska, 2008). The number of inflorescences, flowers, anthers, and pollen grains per anther varies considerably from one species to another (Molina et al., 1996).

Prominent dissimilarities in the production of pollen have been reported by various workers. The pollen production of *H. integrifolia*: 8500 (Nair and Rastogi, 1963), 2437 (Janaki Bai and Subba Reddi, 1980), 11,200 (Subba Reddi and Reddi, 1986); *S. robusta*: 61,020–94,600 (Bera, 1990), 60,000 (Atluri et al., 2004). However, some herbaceous elements also show such variations. The pollen production of *Cynodon dactylon* is 800 (Agnihotri and Singh, 1975), 582 (Janaki Bai and Subba Reddi, 1980), 1900 (Subba Reddi and Reddi, 1986); *Amaranthus spinosus*: 827 (Nair and Rastogi, 1963), 5076 (Janaki Bai and Subba Reddi, 1980), or 5310 (Subba Reddi and Reddi, 1986).

Variations in pollen production were also reported by others (Pohl, 1937; Smart et al., 1979). Smart et al. (1979) showed that such variations could be related to the mode of reproduction. Hevly et al. (1979), however, was of the view that changes in the production of pollen occur in response to physical (climatic or edaphic) and biotic alteration of the environment that could be either essentially permanent or short-term, resulting from climatic perturbations, fire, and biotic exploitation.

2. There is a direct relationship between the level of pollen production with the size of anther and inverse relationship with the pollen grain size i.e. the species possessing large anthers and small pollen grains have comparatively high pollen production (Agnihotri and Singh, 1975). The total pollen production of a plant is influenced by various factors (Stanley and Linskens, 1974) that also varies from year to year (Rogers, 1993). There is no association between high pollen production and mode of anther dehiscence, in general. Faegri and Iverson (1975) opined that climatic, edaphic, and biotic factors influence the production of pollen that varies from stand to stand and from year to year within a stand.

3. High pollen producers are cross-pollinated and self-incompatible, whereas low pollen producers are either self-pollinated or apomictic (Fryxel, 1957). Perennial species produce large amounts of pollen per inflorescence in comparison to the annual species. This statement further substantiates the fact that in perennial plants, cross-fertilization is a must, as most perennial plants display marked self-incompatibility (Evans, 1964).

4. Genetics of the taxa/species/varieties could play a pivotal role in pollen production, and thus the quantity of pollen produced by a plant might be genetically fixed (Joppa et al., 1968). Diploid species produce more pollen compared to their corresponding tetraploid species (Scott and Longden, 1970; Sree Rangaswamy and Raman, 1973). It is the genotype that controls the intensity of pollen production in a particular variety and further variation, if any, could be due to the variations in environmental factors (Subba Reddi and Reddi, 1986). Thus, genetic and environmental factors act hand in hand and control the pollen production of the taxa.

5. Plants with an anemophilous mode of pollination are generally known to produce copious amounts of pollen. The capacity to produce huge amounts of pollen is primarily controlled by genetics and physiology (Stanley and Linskens, 1974). Subba Reddi and Reddi (1986) opined that the production capacity of anthers is genetically fixed. However, due to environmental factors, the real production per plant may vary significantly from year to year (Stanley and Linskens, 1974). Variations (about 20%) in pollen grains per anther of Poaceae species imply that the amount of pollen per anther is constant (Prieto-Baena et al., 2003). The variations, if any, could be ascribed to the differences among the varieties of a species (Beri and Anand, 1971). Subba Reddi and Reddi (1986) pointed out the lack of uniformity in the methodology by different workers could be another reason behind the variation.

6. The total production of pollen grains per tree is positively correlated with the diameter of the tree crown and not with the height, indicating that the amount of available light is a limiting factor in the production of inflorescences and flowers, suggesting that height might act in a negative way (Molina et al., 1996), as is indicated by the negative and significant correlation between the height and the number of flowers per tree.

7. Difference between various habitats also affects the total pollen production. This means that the total amount of pollen shed into the atmosphere varies from area-to-area (Prieto-Baena et al., 2003).

8. The seed production often depends on the production of pollen. Therefore, it is important to have an idea of the total production of pollen per plant (Cour and Van Campo, 1980; Faegri and Iverson, 1989). As for example, an increase in the quantity of seed can be obtained by adding an additional amount of pollen to *Betula* (Holm, 1994).

9. Age of flowering and forest structure also influence the estimates of pollen productivity (Matthias et al., 2012). Flowering age and forest structures play a crucial role in the calculation of pollen productivity estimates for some taxa. A gradual increase has been recorded in the amount of pollen produced in a single year in most trees with age. A free-standing tree produces more pollen compared to that growing within a dense stand (Abay, 1994).

10. Specific gravity, air current and pollen sinking speed are some of the factors that could also affect the preservation of pollen of teak and sal in the sediments (Curtis, 1930; Flenley, 1971; Hevly, 1981; Mildenhall, 2006).

11. High pH value of soil as well as the microbial and chemical degradation of the pollen grains of taxa in the sediments might have been detrimental factors for the scarcity of pollen of these plants (teak and sal) in the sediments (Sharma, 1985; Gupta and Yadav, 1992).

Thus, it can be said that knowing the total production of pollen per plant is useful in order to make estimation the number of pollen grains that could be in the air during a certain season, once the density of plants per surface unit is known. It can also be used as an estimate of the production of seeds (Allison, 1990; Campbell and Halama, 1993), as the efficiency of anemophilous pollination decreases with the reduction in the concentration of airborne pollen (Whitehead, 1983). The study could help understand the nature of pollen produced by these taxa, ultimately lead to the correct establishment of pollen rain/vegetation relationships that serve as modern analogues for the proper explanation of pollen diagrams from the region in terms of palaeovegetation and palaeoclimate during the Quaternary, culminating into understanding and modeling the present and future climate trends through which the society could be benefitted.

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