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On the interpretation of fossil Poaceae pollen in the lowland humid neotropics

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Abstract

Poaceae pollen is abundant in fossil records and is often used as a paleoclimatic indicator. A common interpretation is to link increases in Poaceae pollen abundance to increased regional aridity. However, the representation of Poaceae pollen is influenced by a number of factors, such as the proportion of other plants in the flora that are anemophilous, the size of local marshes, and the influence of humans on the landscape. Abundant anemophilous trees are likely to mask the contribution of Poaceae pollen, whereas floras that are primarily entomophilous are likely to produce a pollen spectrum containing an over-representation of Poaceae. As most fossil pollen data are drawn from flooded settings, it is critically important that palynologists recognize the Poaceae pollen contribution derived from floating grasses and marshes that surround their coring site. Interpretations that ignore changes in effective lake size and assume that Poaceae percentage is a simple indicator of regional vegetation change are likely to overstate 'dry' episodes and transitions from wet forest to scrub environments. Human occupation of a site is sometimes manifested in increased Poaceae pollen abundance in lake sediments. The duration, intensity and land-use associated with occupation are all variables that influence Poaceae pollen representation. Very high (50–90%) abundances of Poaceae pollen provide a strong indicator of savanna habitats, but trying to determine transitional vegetation types between savanna and wet forest is best determined using other taxa. Indeed, reliance on Poaceae abundance as an indicator of paleoprecipitation is potentially very misleading when it is in the fossil record at moderate abundances. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Poaceae; rain forest; pollen; anemophily; grassland; glacial; aridity; disturbance; openness

1. Introduction

Poaceae pollen is one of the most ubiquitous and readily recognized pollen types found in lake sediments. Although these monoporate

grains differ in size, surface texture and annular width, these features do not permit reliable recognition at the subfamily level (with the notable exception of some crops, e.g. *Zea* and *Cerealia*). In most palynological records, Poaceae are treated as a single unit and, in the absence of other information, are taken as indicators of openness. Undoubtedly, it is true that the pollen rain of grasslands is characterized by high abundances of Poaceae. In true cerrado, Poaceae commonly account for 50–90% of the pollen rain (Salgado-

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Labouriau, 1979), whereas the pollen spectrum of a mature closed-canopy lowland neotropical forest rarely contains more than 2–3% Poaceae pollen (Bush, 1991). Because under natural conditions, mesic lowlands usually go through a succession in which grasses are outcompeted by trees, finding increased abundances of Poaceae pollen is a reliable indicator of a greater proportion of the source area being relatively open. However, what does this openness mean?

It is a common inference that higher Poaceae pollen abundance in a fossil pollen spectrum is due to increased openness induced by aridity (e.g. Absy, 1979; Absy et al., 1991; van der Hammen and Absy, 1994; Hooghiemstra and van der Hammen, 1998; Ledru, 1999). In the absence of human activity, openness and high Poaceae pollen abundances are likely consequences of strong aridity. Nevertheless, it does not follow that high Poaceae percentages in a pollen rain necessarily reflect open, dry vegetation. Poaceae are found in most lowland neotropical habitats ranging from bamboo forests and savanna to swamp. Thus the assumption that a change in Poaceae pollen is indicative of a regional replacement of trees with grasses is simplistic.

Without losing sight of the possibility that an increase in Poaceae pollen abundance in a fossil sediment can indicate decreased forest cover, alternative interpretations often provide more parsimonious explanations of the change.

2. Poaceae in modern pollen spectra

Poaceae pollen is present in most modern pollen samples from the neotropics, but its representation varies dramatically according to local vegetation types. The principal factors that determine the abundance of Poaceae in a flora are annual precipitation, seasonality, the effects of human occupation, the frequency and severity of fire, edaphic conditions, and hydrology. Additionally, the abundance of Poaceae pollen in a modern pollen rain is also influenced by the pollination strategies of the specific grass species and the other members of their community.

2.1. Pollination biology

Poaceae are wind-pollinated (anemophilous) taxa and necessarily produce a huge quantity of pollen compared with insect-pollinated (entomophilous) plants. Only 2–3% of lowland neotropical rain forest tree species are anemophilous, compared with ca. 70% in a temperate forest (Bawa et al., 1985). Faegri (1966) suggested that anemophilous taxa in the lowland tropical forests would be massively over-represented due to the relatively small pollen production of the entomophilous species. In essence he was correct, the rare anemophilous species are heavily over-represented in neotropical pollen rain (i.e. they contribute a disproportionately high percentage of pollen compared with their % basal area in surrounding forest). Quantitative studies have compared tree pollen deposition to basal area (which is a fair proxy for biomass) of trees (Grabandt, 1980; Bush and Rivera, 1998), but these studies did not estimate the biomass of grasses in the study areas. In the mature forest stands of Barro Colorado Island or La Selva the biomass of Poaceae is trivially small, certainly much less than 1% of the total. Yet, though so rare, Poaceae contribute 1–3% of pollen trapped within the forest (Bush and Rivera, 1998) and are thus clearly over-represented in the pollen rain.

However, we cannot assume that Poaceae will always be over-represented in local pollen rain. In the permanently wet cloud forests of Panama and Colombia, bamboos such as *Chusquea* are an important component of the understory. In some cloud forests these woody grasses virtually fill the space from ground to the lower tree canopy. However, a combination of factors lead to bamboos being under-represented in the pollen rain of these forests (e.g. Salomans, 1986). The bamboos flower infrequently and unlike most grasses have a massive investment in body size compared with flower production. Also, they often live amid anemophilous trees, e.g. *Quercus*, *Ulmus*, *Myrica*, and *Alnus*, that produce massive amounts of pollen, swamping the output of the bamboos. These anemophilous arboreal taxa migrated from Central America to South America in the mid- to late Quaternary. Clearly, the arrival of these trees

would have had an impact on local pollen records that goes beyond a simple turnover in canopy species. Therefore, inferred climate change from deposits that span the Quaternary requires careful consideration of whether observed changes in entomophilous taxa or ‘low’ pollen producers such as bamboos are primarily the consequence of climate change or the result of arrival of a new balance in pollination strategies.

An excellent example of the arrival of anemophilous taxa changing the pollen yield of a community is the two-step migration of *Alnus* and *Quercus* into the 3 Myr long record from the Sabana de Bogotá, Colombia (Hooghiemstra et al., 1993). During each of the glacial episodes of the past 3 Myr the vegetation around the Sabana de Bogotá is a grassland. During the interglacials forest elements return to dominate the pollen spectrum, and Poaceae pollen are probably contributed (primarily) by forest bamboos. The Poaceae component of the pollen spectra during the grassland episodes is consistently 50–70%. However, the interglacials reveal a pattern of declining Poaceae pollen percentages that reflects the arrival of an increasingly anemophilous component that dilutes the pollen production of bamboos (Table 1).

For the first 2 Myr of the record, each interglacial phase is dominated by entomophilous tree taxa such as *Hedyosmum*, Melastomataceae and *Myrsine*, yet Poaceae still account for ~50% of the pollen sum. About 1 Myr ago *Alnus* migrated from Central America into Colombia and appears to have become a fairly common forest component (Hooghiemstra and Cleef, 1995). The arrival of this anemophilous genus into a primarily entomophilous forest system would have boosted the amount of pollen being liberated into the air and falling on lake surfaces. Whereas the representa-

tion of entomophilous forest trees in pollen spectra generally provides R-rel (sensu Davis et al., 1973) values within the range of 0–1.3 (Bush and Rivera, 1998), *Alnus* is strongly over-represented, probably by a factor in excess of 5 (obtained in a study of the Colombian Cordillera – Grabandt, 1985). Consequently, the presence of *Alnus* at the Sabana de Bogotá leads to a lower proportional representation of other species. When *Alnus* is present, the interglacial proportion of Poaceae pollen falls from ~50% to ~20% of the pollen sum (Table 1). This pattern of reduced Poaceae representation is repeated when at ~423 000 yr ago another anemophilous genus, *Quercus*, established a permanent presence in the Sabana de Bogotá record (Van’t Veer and Hooghiemstra, 2000). Thereafter Poaceae pollen abundances fall as low as 10% during interglacial episodes (Table 1) (Hooghiemstra, 1984). The changes in Poaceae abundance probably do not represent a transition to a more closed forest, but are purely the result of changes in the pollination biology of the forests. A logical extension of this analysis is to consider the effect of changes in the balance of pollination syndromes on the interpretation of the downslope migrations of forests that accompany glacial cooling (van der Hammen and Gonzalez, 1960; Hooghiemstra, 1984). Since the arrival of *Quercus* and *Alnus* in the Andes, these downslope movements have introduced abundant anemophilous trees into the lowland forests. Until now, changes in lowland Poaceae pollen abundance during glacial intervals had been interpreted as due to new precipitation regimes resulting in species turnover and the establishment of novel plant communities (Bush and Colinvaux, 1990; Bush et al., 1990; Hooghiemstra and van der Hammen, 1998). However, it would be prudent to consider not only the ef-

Table 1

Typical percentages of Poaceae in the pollen spectra of the Sabana de Bogotá, Colombia, during glacial and interglacial episodes over the last 3 Myr

	Pre- <i>Alnus</i> arrival	<i>Alnus</i> present	<i>Alnus</i> and <i>Quercus</i> present
Glacial	50	65–70	50
Interglacial	50	20	10

Alnus arrived at the site ~1 Myr ago, *Quercus* arrived ~423 000 yr ago. Interglacial Poaceae pollen percentages are lowered by the successive arrival of the anemophilous genera *Alnus* and *Quercus*.

fects of climate change, but also the effects of changing balances of pollination strategies in the community. Some of the apparent novelty of assemblages that form as species respond individually to the climate change (Bush and Colinvaux, 1990; Bush et al., 1990), may be exaggerated by a trend toward, or away from, anemophily. In other words, an unknown portion of the observed Poaceae pollen differences may result from a shift in the balance of pollination strategies. Poaceae will be over-represented when the surrounding forest is one comprising primarily entomophilous taxa, e.g. almost all lowland neotropical floras, but will become increasingly under-represented as montane anemophilous elements invade.

2.2. Precipitation and seasonality

Modern pollen rain studies of a wide variety of sites in lower Central and South America reveal that Poaceae pollen does not respond as strongly

to changes in precipitation and seasonality as might be expected, and certainly not in a linear manner (Bush, 2000). Although Poaceae are often used as an indicator of openness, they actually prove to be rather insensitive indicators of changes in vegetation community and structure. For example, the gradient of seasonal canopy openness between a minimally seasonal forest such as La Selva, to a forest such as Barro Colorado Island in which many of the canopy trees are deciduous, is not reflected in Poaceae pollen abundance (Tables 2 and 3). Furthermore, it is not until annual precipitation falls below 2000 mm that sensitivity in Poaceae pollen percentages to seasonal and total precipitation input becomes apparent. In these dry settings, e.g. savanna and cerrado, Poaceae abundance increases as soil moisture deficit increases. However, in moist forest, where annual precipitation exceeds 2000 mm, unless edaphic or anthropogenic conditions supersede moisture availability as determinants of local vegetation structure, substantial changes in pre-

Table 2

Representative samples of modern pollen spectra showing the proportion of Poaceae pollen relative to vegetation, precipitation, and seasonality

Habitat type	Location	Precip. (mm)	Dry season length (months)	Poaceae pollen (%)	Data type (<i>n</i> =)	Collection period (yr)	Citation
Evergreen rain forest	Ecuador						
	Cuyabeno	3000	2	1–2	Trap (39)	3	Bush et al., 2001a,b
	Brazil						
	Hill of Six Lakes	3000	2	1–2	Polster (6)	N/A	Bush (new datum)
	Dimona	2700	3	1–2	Trap (20)	2	Bush et al., 2001a,b
	Campo 41	2700	3	0–2	Trap (20)	2	Ibid.
Semi-deciduous forest	Caixuanã	2500	0	0–2	Trap (5)		Behling and Da Costa, 2000
	Costa Rica						
	La Selva	4000	2	0–2	Trap (36)	2	Bush, 2000
	Panama						
Deciduous forest	Barro Colorado Island	2200	5	0–1	Trap (56)	3	Bush and Rivera, 1998
	Pipeline Rd.	2200	5	1–2	Trap (12)	2	Bush, 2000
Natural cerrado	Costa Rica						
Xeric caatinga	Santa Rosa	1500	6	2–5	Trap (6)	2	Ibid.
	Brazil						
Xeric caatinga	Aparecida	1500	6	90	Trap (3)	1	Salgado-Labouriau, 1973, 1979
	Costa Rica						
	Santa Rosa	1500	6	90	Soil pinch	N/A	Rodgers and Horn, 1996

Data are drawn from pollen trap, soil pinch, or polster samples that are typical of the habitat type.

Table 3

Representative mud–water interface samples from lakes showing the proportion of Poaceae pollen relative to vegetation, precipitation, presence of fringing herbaceous swamp, and seasonality

Habitat type	Location	Precip. (mm)	Dry season length (months)	Poaceae pollen (%)	Extensive fringing herbaceous swamp (Y/N)	Citation
Wet evergreen	Peru					
	Cocha Cashu	2500	2	1–2	N	Bush (n.d.)
	Ecuador					
	Cuyabeno	3000	2	1–2	N	Bush, 1991
	Ayauch ¹	3000	2	1–2	N	Bush and Colinvaux, 1988
	Kumpak ^a	3000	2	1–2	N	Liu and Colinvaux, 1988
	Maxus 5	3300	0	0	N	Athens and Ward, 1999
	Brazil					
	Hill of Six Lakes	3000	2	1–2	N	Colinvaux et al., 1996
	Rio Curuá	2500	0	2	N	Behling and Da Costa, 2000
Semi-deciduous forest	Panama					Bush and Colinvaux, 1994
	Wodehouse	2200	4	25	Y	
	Cana	2200	4	1	N	Ibid.
	Costa Rica					Rodgers and Horn, 1996
	La Selva	4000	0	1–2	Y (shaded)	
Savanna	Brazil					Bush et al., 2000
	Geral	2200	5–6	8	N	
	Comprida	2200	5–6	12	N	Ibid.
Caatinga/semi-deciduous forest	Colombia					Behling and Hooghiemstra, 1999; <i>ibid.</i>
	Carimagua	2000	4–5	80	N	
	El Pinal	2000	4–5	70	N	
Derived savanna	Brazil					De Oliveira et al., 1999
	Icatu River Valley	400–800	7–8	15	N	
Derived savanna	Panama					Bush et al., 1992
	La Yeguada	3300	5	20	N	
	Costa Rica					Rodgers and Horn, 1996
	Santa Rosa	1500	5	33–35	N	

precipitation availability and seasonality could take place without significantly altering Poaceae pollen abundance.

2.3. Anthropogenic landscapes and fire

Because neotropical modern pollen rain studies have targeted mature forest (e.g. Rodgers and Horn, 1996; Behling et al., 1997; Bush and Rivera, 1998; Bush, 2000; Bush et al., 2001a,b), empirical data are lacking on the Poaceae signal induced by various scales of human disturbance. In an ideal pollen record, human disturbance is in-

dicated by abrupt increases in pollen of Poaceae, weedy trees, e.g. *Cecropia*, the regular presence of a crop such as *Zea mays*, and charcoal. In such a scenario, the Poaceae pollen curve probably reflects increased open ground as a result of land clearance and it should behave independently of marshland indicators such as Cyperaceae. Such tidy records are available from relatively few sites, but have been documented from steep-sided explosion maars or solution basins in humid forest environments (Bush and Colinvaux, 1988; Liu and Colinvaux, 1988). Unfortunately, most neotropical pollen records are not this clear-cut as it

is more common to find a situation where the pre-disturbance proportion of Poaceae is not the 0–3% of a closed forest setting, but is 5–25% (e.g. Bush et al., 1992). From this elevated baseline the additional disturbance accompanying human activities may only add an extra 5–10% Poaceae pollen. The high initial abundance of Poaceae found in many records reflects either existing openness in the forest or the presence of a fringing marsh. Indeed, in some recently analyzed samples from Amazonian Peru, even when agriculture is established, Poaceae pollen does not increase significantly in abundance (C. Listopad, new data). In most Amazonian settings, consistently high abundances of charcoal are the best single indicator of cultivation (Bush et al., 2000). Studies in Mexico and Central America demonstrate that subtle chains of events induced by human activities can also increase pollen representation (Binford et al., 1987; Metcalfe et al., 1989). Farming, particularly the overexploitation of an area, can lead to increased erosional rates that in turn lead to higher rates of sedimentation and infilling of a basin. The infilling accelerates hydarch succession and thus increases the ratio of area of marsh fringe to open water. The effect of such events on the pollen record is to increase Poaceae representation in pollen spectra (below).

Even within forested settings it is possible to find regions that would produce a high percentage of Poaceae pollen. It is possible that human disturbance underlies a long-term change in vegetation structure. In South and Central America, many areas of low to mid-elevation forests have been cleared for grazing. Especially if overstocked, the erosion of soil leads to the formation of anthropogenic cerrados. The Poaceae contribution to the pollen spectra from such habitats is similar to that of natural cerrados in Brazil (Bush, 1991). Within Amazonia large tracts of nutrient-poor, white sands support a range of vegetation from cerrado to savanna. Biogeographic affiliations with grasslands outside the Amazon basin have been used to suggest that these are ancient grasslands that have been a long-term component of the Amazonian landscape (Eiten, 1972; Prado and Gibbs, 1993; Pennington et al.,

2000). An alternate hypothesis is that these areas are another example of an anthropogenic landscape. Prance and Schubart (1977) suggested that early human colonists edaphically altered these areas by repeatedly setting fires on poor sand soils. They hypothesize that with the loss of organic material and leaching of nutrients, these systems were permanently altered. No data exist on the modern pollen rain of these environments, although given their floristic composition (Prance and Schubart, 1977), they may have a spectrum similar to that of cerrados in central Brazil in which Poaceae contribute ca. 80–90% of the local pollen (Salgado-Labouriau, 1973, 1979). Other grasslands, particularly extensive stands of bamboos in Peruvian Amazonia, may result from local soil conditions or an arrested succession (M. Silman, personal communication), but no pollen analyses have been conducted on such areas.

2.4. *Hydrology and basin size*

Special care in interpreting Poaceae pollen must be exercised when lake size is variable or seasonal flooding of a marsh occurs. Because the area of open water determines the proportion of pollen that is derived from local versus regional vegetation, a reduced surface area of open water results in an increased abundance of the locally derived component (Jacobson and Bradshaw, 1981; Prentice, 1985; Sugita, 1993, 1994). Thus, for example, as hydarch succession proceeds, observed increases in Poaceae pollen may derive from marsh inputs rather than from the adjacent uplands. This effect of changing lake surface area through time on the balance between local and regional pollen source inputs is a critical but often ignored variable in interpreting neotropical pollen records. A trend of decreasing lake size, and the formation of a marsh that floods seasonally may be an inherent part of habitat maturation, but this process does not induce a linear response in Poaceae pollen abundance. For example, the 4000-yr-long record from Lake Wodehouse, Panama, contains several high water episodes that correspond to times of low Poaceae representation ~4–6% (Fig. 1) (Bush and Colinvaux, 1994). During these

Lake Wodehouse: fossil pollen

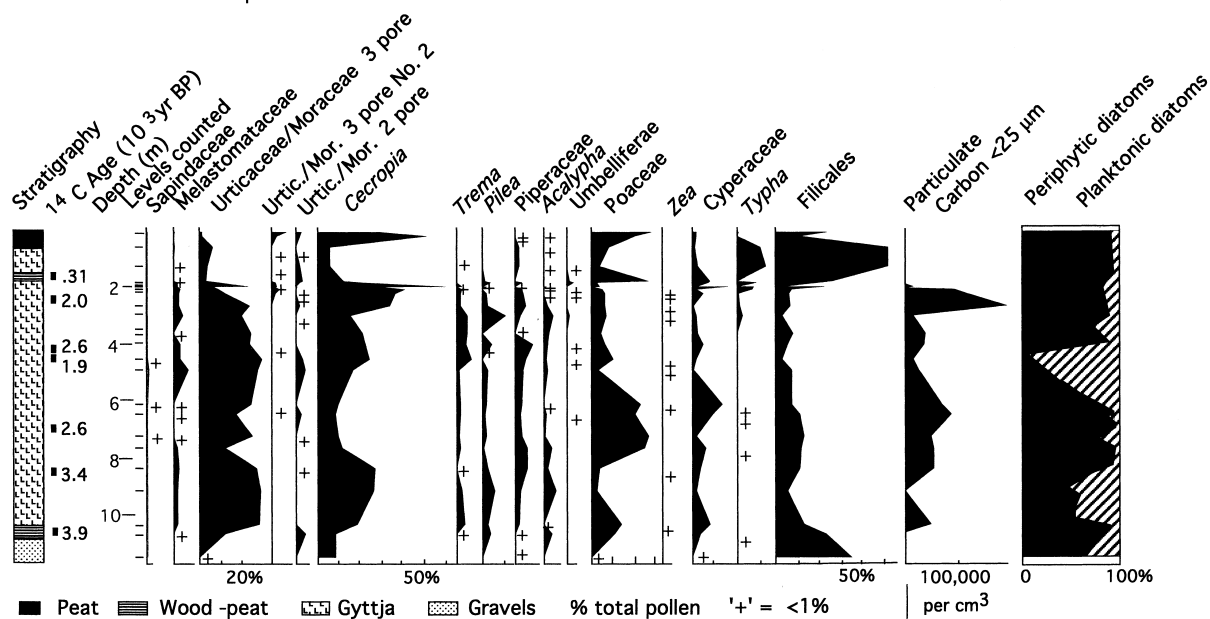


Fig. 1. Percentage pollen diagram for selected taxa and summary of diatom data from Lake Wodehouse, Panama (Bush and Colinvaux, 1994).

high stands the lake may have occupied the entire basin, an area of ca. 9 km², and had a shoreline edged with forest and cultivated land. As the lake contracted, indicated by a decrease in planktonic diatoms, Poaceae increase in abundance to a peak of 26%. However, during the driest period, about 200 yr ago, the lake may have been entirely seasonal and the lake bed was filled with a fern and *Typha* swamp. Under these conditions, Poaceae contributed only 3% of the pollen rain. A modern pollen analog for this site at this time is the nearby Cana Swamp, which is covered in ferns and during the dry season has no open water (Bush and Colinvaux, 1994).

Although Cana Swamp retains its fern swamp today, Lake Wodehouse appears to have re-flooded relatively recently. The uppermost sample from Lake Wodehouse contains 28% Poaceae pollen and is consistent with our field observation of a small lake with floating grass islands, surrounded by a broad grassy swamp. In this instance, an increase in available soil moisture results in an increased proportion of Poaceae pollen. Clearly, using Poaceae pollen abundance

as a proxy for dryness without due regard to local hydrology is perilous.

That Poaceae and other wetland taxa respond to hydrological changes can become a powerful paleoecological indicator of climate change. However, once again it requires us to abandon the idea that high Poaceae abundance equals aridity. The ancient crater lake of El Valle, Panama, provides an excellent example of information hidden in the Poaceae record. At this site, Bush and Colinvaux (1990) document the descent of cloud forest (indicated by *Quercus*, *Myrica*, and other upland taxa) to 500 m elevation during the last ice-age. Throughout the last glacial period, Poaceae pollen fluctuated synchronously with Cyperaceae, consequently, the increased abundance of Poaceae was interpreted to represent an expansion of marsh elements (Fig. 2). However, throughout this interval, both the Poaceae and Cyperaceae pollen records suggest repeated fluctuations in marsh area that probably reflect short-term changes in precipitation. During wet episodes, a larger lake catches a more regional pollen component, and flooding of the marsh area results in a reduction in the

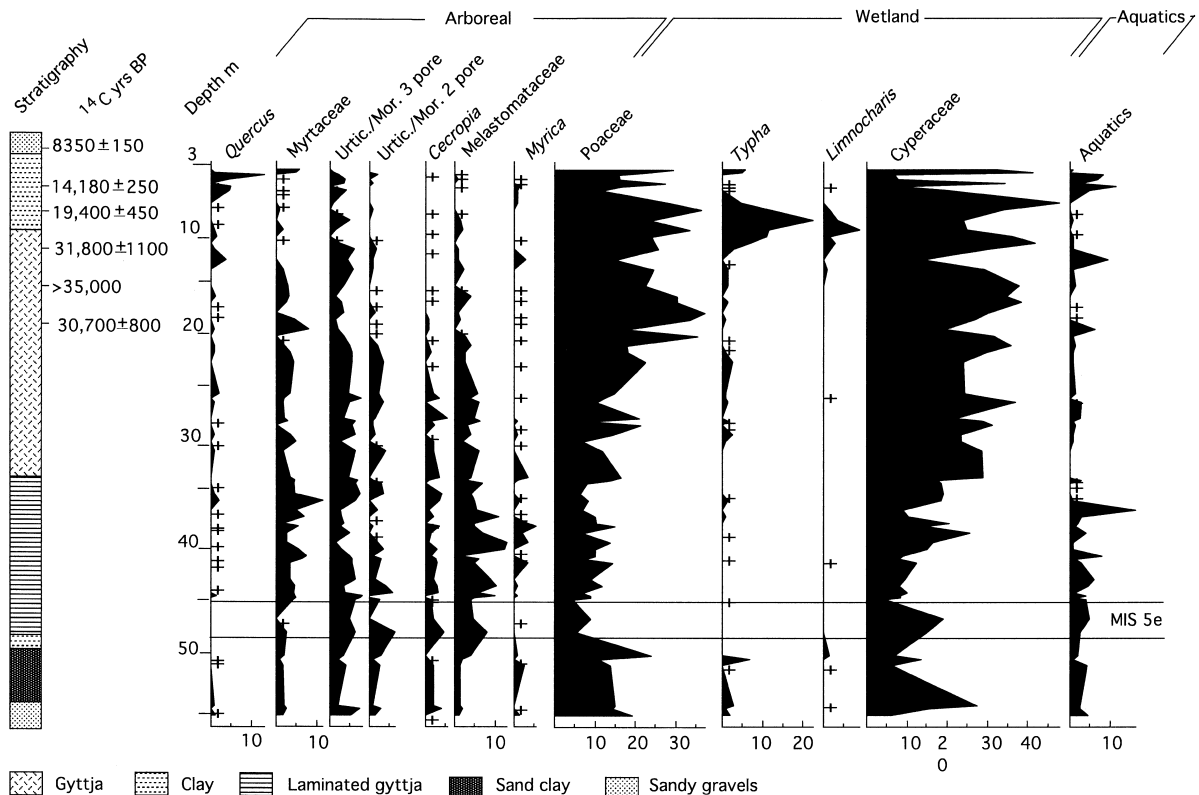


Fig. 2. Percentage pollen diagram for selected pollen taxa from El Valle, Panama (after Bush and Colinvaux, 1990).

abundance of swamp taxa. With reduced precipitation, lake level falls, the open water area contracts and the marsh edge expands, resulting in a higher proportion of locally derived swamp taxa. This reduction in precipitation is not reflected in the regional forest cover. Indeed, the presence of cloud forest elements from about 35 000 yr until 12 000 calibrated years BP at this site suggests that moisture was not limiting for plant growth, even when Poaceae pollen was most abundant.

New analysis of the El Valle pollen data allows a comparison of the pollen sum of the wetland elements, Poaceae, *Typha*, *Limnocharis*, and Cyperaceae, with the change in insolation received at 7°N (the latitude of El Valle) over the last 140 000 yr (Fig. 3a). First, the ^{14}C chronology of the pollen data within the range of radiocarbon dating was converted to calibrated years BP using Calib 4.3 (based on Stuiver and Reimer, 1993). Pollen samples associated with marine isotope stage 5e

(MIS 5e) were identified by the abundance of thermophilous species and lack of cold stenotherms in the arboreal pollen record (Bush and Colinvaux, 1990). The peak of this event was attributed an age of 125 000 yr BP (Martinson et al., 1987). A depth–age curve based on an assumed even rate of sedimentation was used to interpolate ages between 35 000 yr BP and 125 000 yr BP. This chronology was used to compare the El Valle wetland pollen data with the DJF insolation (Fig. 3a).

The wetland pollen data are also compared with the $\delta^{18}\text{O}$ record from the GISP2 ice core (Dansgaard et al., 1993). Because the resolution of the GISP2 record is much higher than that of the El Valle pollen, data from GISP2 were smoothed by taking a 3000-yr running mean at 1000-yr intervals, i.e. the data point for 10 500 reflects values from 9000 to 11 999 calendar years BP (Fig. 3b).

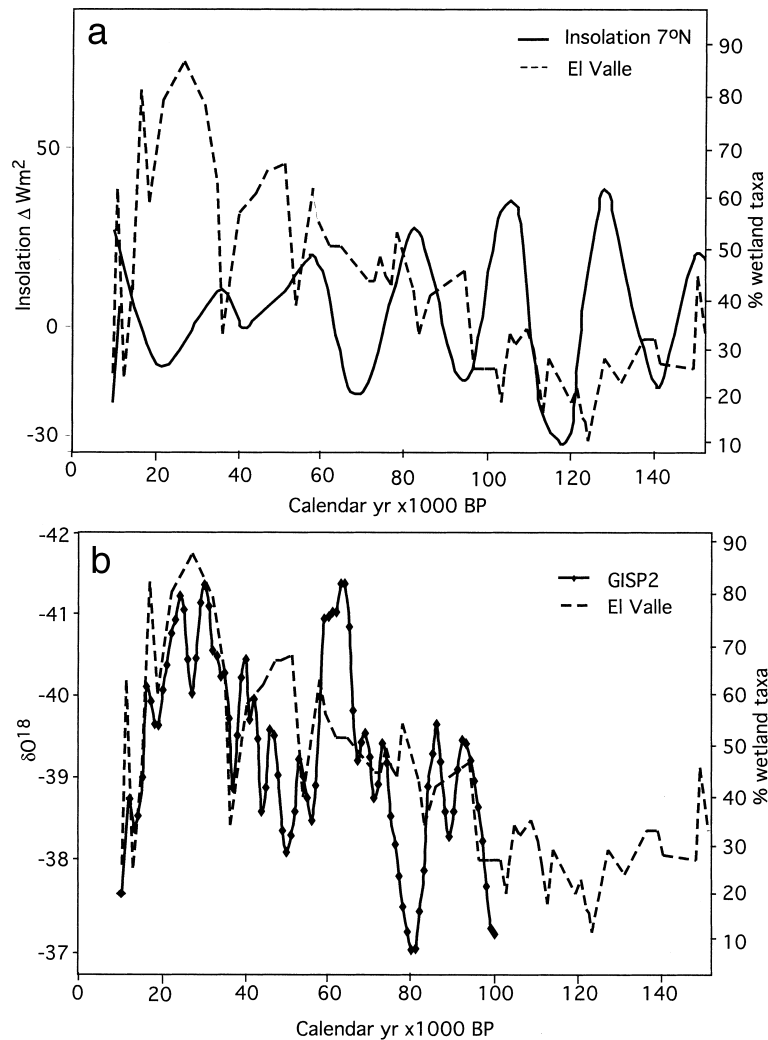


Fig. 3. (a) A comparison of the percentage pollen of swamp taxa in El Valle, Panama, with the insolation at 7°N for the last 140 000 yr. Insolation data generated using Analyseries 1.1 (Laskar, 1990; Paillard et al., 1996). The chronology of the pollen record was established using Calib 4.3 (Stuiver and Reimer, 1993) for the section of core within the range of ¹⁴C dating, and through the identification of MIS 5e based on the presence of thermophilous taxa (Bush and Colinvaux, 1990) in the El Valle record. All intervening points are assumed to have been deposited under a constant rate of sedimentation. (b) A comparison of the percentage pollen of swamp taxa in El Valle, Panama, with the GISP2 $\delta^{18}O$ record (Dansgaard et al., 1993). The GISP2 data were smoothed using a 3000-yr running mean.

From these two comparisons it becomes clear that a land–ocean–atmosphere linkage is manifested in wetland extent at El Valle. A causal linkage between changes in insolation and wetland extent is explained through invoking changes in the thermohaline circulation and the strength and location of the Inter-Tropical Convergence Zone (ITCZ). That thermohaline circulation mag-

nifies the effects of small changes in insolation is broadly accepted (Broecker, 1998). Thermohaline circulation is also an important agent in determining the position of the ITCZ, e.g. when North Atlantic Deep Water formation is reduced, the ITCZ shifts southward (Ganopolski et al., 1998). Another influence on the location of the ITCZ is the size of the Laurentide ice-sheet. At the last

glacial maximum when the Laurentide ice-sheet was largest, the increased polar–equatorial temperature gradient also caused the southward displacement of the northern boundary of the ITCZ (Ganopolski et al., 1998). The paleoecological data are consistent with models that predict that the areas influenced by the present northern limit of the ITCZ, e.g. El Valle, were drier during times of weakened thermohaline circulation or extensive northern hemispheric ice-cover (Fig. 3b) (Ganopolski et al., 1998; Hostetler and Mix, 1999; Whitlock et al., 2000).

In addition to the general pattern of increased wetland extent during glacial periods, the El Valle pollen data record shorter-term cyclical variations throughout the last 125 000 yr presumably correlated with changes in insolation associated with the precessional orbital signal (Fig. 3a). Variation in insolation at 7°N may be reflected in precipitation, lake level, and hence the ratio of marsh: open water at El Valle. Consequently, the precessional orbital signal appears to be reflected in the percentage of wetland *Poaceae* pollen found at this site. For similar reasons, there is a correspondence between the percentage of wetland pollen and the $\delta^{18}\text{O}$ in the GISP2 ice core. Within the range of ^{14}C dating, a remarkably good concurrence exists between the pollen and isotopic data (Fig. 3b). In the section of core with an interpolated chronology, the broad trends are apparent, but without closer sampling for pollen it is not possible to determine if individual Heinrich events or Dansgaard–Oeschger cycles are represented in the pollen data.

The marsh expansion of El Valle is constrained by steep caldera walls, but in the great flat plains of South America a change in precipitation might induce an opposite signal in the abundance of swamp taxa. In these areas, an increase in rainfall causes more land to be flooded, which results in an expansion of swamp vegetation. The great swamplands of Amazonia, the Pantanal, and Orinoco may also have been driven by climate change that followed the 19 000- and 22 000-yr Milankovitch orbital cycles (Baker et al., 2001a,b; Bush et al., 2001a,b). In these locations, wet periods could cause these great swamps to expand, providing larger areas of *Poaceae*-domi-

nated systems, while dry periods would cause the contraction of these areas and the invasion of woody taxa. Thus, it can be argued that the proportion of *Poaceae* pollen in deltaic sediments of the Amazon and Orinoco would be expected to increase during wet periods and decrease during dry periods. Indeed, Behling et al. (2000) found the proportion of *Poaceae* pollen in continental shelf deposits increased during episodes of high river discharge.

3. Conclusions

Although it has been commonly assumed that *Poaceae* pollen abundance is an indicator of openness and aridity, this study suggests that much of the variation in *Poaceae* representation may be attributable to alternate factors. As fossil data are interpreted it is important to take into account shifts in the balance of pollination biology that might be contributing to apparent changes in pollen representation. Species-for-species replacements in which anemophilous tree taxa displace entomophilous tree taxa depress the representation of *Poaceae*. Consequently, *Poaceae* pollen percentages can change independently of a change in openness.

Poaceae pollen representation does not change linearly with changes in seasonality or total precipitation. Data from 300 modern samples studied from Panama, Costa Rica, Ecuador, and Brazil indicate that *Poaceae* pollen is a rather insensitive measure of precipitation and seasonality in forested settings. Indeed, *Poaceae* pollen is a rare component of the pollen rain of tropical moist, tropical deciduous and tropical semi-deciduous forests. Thus, local climates could vary a great deal before those changes are reflected in upland *Poaceae* pollen abundance.

Proportions of *Poaceae* pollen in lake or wetland sediment may be strongly influenced by the area of open water compared with that of the fringing marsh. Aquatic and marsh grasses are an important component of mud–water interface samples from many tropical lakes. Consequently, *Poaceae* representation is especially sensitive to relative changes in the size of marsh and open

water areas within. As discussed above, the ratio between the area of open water and the radius of the fringing marsh exerts a powerful influence over pollen representation in a sedimentary sequence. Factors that affect this ratio include changes in precipitation, seasonality, sedimentation rate, tectonic movement, human endeavors and hydrarch succession. Thus, explanations of changes in Poaceae abundance should first consider the influence of lake surface area and marsh extent, before considering possible changes in terrestrial biomes.

At El Valle, Panama, glacial age deposits reflect a linkage between land, atmosphere and ocean. The expansion and contraction of wetlands at that site appear to be driven by a chain of events in which moisture availability is influenced by the strength and position of the ITCZ. As the ITCZ is dependent on the thermohaline circulation and northern hemispheric ice volume, the overall driving factor is seen to be variation in insolation. A negative correlation is suggested between insolation and marsh extent at El Valle, Panama. At El Valle, the variations in precipitation induced changes in the extent of a marsh lying within a cloud forest. The increase in Poaceae pollen abundance throughout the last ice age reflects changes in the adjacent marsh ecosystem and not the replacement of forest with a grassland.

Human impacts on the landscape may be reflected in Poaceae pollen representation. Some of the pollen records in which early (i.e. pre-3000 BP) agriculture was taking place have a coincident increase in Poaceae, but others do not. A large clearance of forest would almost certainly result in an increased Poaceae pollen representation. However, more opportunist methods, such as planting the exposed lake margin during the dry season, or only occasional use of the site, may not result in an increase in Poaceae pollen.

When evidence for past peaks of Poaceae pollen abundance is found in sites within a modern forested setting, the most parsimonious explanation is a change in local Poaceae production, such as floating mats of grasses and marsh vegetation, or human occupation. These causes must be eliminated before accepting an explanation that changes in Poaceae pollen abundance reflect re-

gional vegetation change. The observation that there can be considerable change in both rainfall and seasonality without a corresponding increase in Poaceae pollen abundance means that Poaceae are a poor tool for assessing climate change in a forested landscape. In the light of these findings great caution must be used in allocating singular habitat characteristics to Poaceae in neotropical biome or habitat reconstructions.

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