Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses

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Abstract

Plants respond to Pleistocene climatic change as species, not as associations or biomes. This has been demonstrated unequivocally by paleobotanical data for temperate latitudes. In the far richer vegetations of the tropics species populations also fluctuated independently in response to climatic forcing, from their longlasting glacial states to the patterns of brief interglacials like the present and back again. We use pollen data to reconstruct the vegetation of the Amazon basin in oxygen isotope stages 3 and 2 of the last glaciation in order to measure how the plant populations of the Amazon responded to the global warming at the onset of the Holocene. We find that plant communities of the neotropics vent copious pollen to lake sediments and that this pollen yields powerful signals for community composition. Three continuous sedimentary records reaching through oxygen isotope stage 2 are available from the Amazon lowlands, those from Carajas, Lake Pata and marine deposits off the mouth of the Amazon River. All three records yield pollen histories of remarkable constancy and stability. By comparing them with deposits of equal antiquity from the cerrado (savanna) of central Brazil, we show that most of the Amazon lowlands remained under forest throughout a glacial cycle. This forest was never fragmented by open vegetation as postulated by the refugia hypothesis. Instead the intact forest of glacial times included significant populations of plants that are now montane, suggesting that the global warming of the early Holocene resulted in the expulsion of heat intolerant plants from the lowland forest. Pollen data from the Amazonian flank of the Andes and from Pacific Panama provide evidence that populations of these heat intolerant plants survive the heat of interglacials in part by maintaining large populations at cooler montane altitudes. Our conclusion that the Amazon lowlands were forested in glacial times specifically refutes the hypothesis of Amazonian glacial aridity. Accordingly we examine the geomorphological evidence for glacial aridity and find it wanting. Of the three paleodune systems reported for tropical South America, that of NE Brazil was active in the Holocene as well as the Pleistocene. Parts of NE Brazil were actually moister than now in late-glacial times. Paleodunes in the Pantanal have never been seen on the ground, and those in the Orinoco Llanos are undated and may be of any age since the Tertiary. Arkosic sands in the Amazon fan deposits came from the Andean foothills or from down cutting by rivers and cannot be evidence of a former arid land surface. White sands of Amazonia formed as podzols, not by aeolian activity. Such Amazonian stone lines as have received critical scrutiny are concretionary pisolites in stratigraphic formations that are more than ten million years old. Although the Amazon was never arid, modeling cooler glacial tropics gives plausibility to a somewhat drier Amazon in glacial times, a concept given substance by pollen data for the movement of ecotones in Rondonia, by stream histories in the Bolivian Andes, and by evidence for lowered lake levels at Carajas and Lake Pata. But this reduced precipitation was never enough to fragment the forest in the Amazon lowlands themselves. Pleistocene mammals of the Napo river valley in Ecuador were able to live along the river system in a forested landscape. Our data suggest that the Amazon forests have been stable since the start of the Pleistocene, a fact that has contributed to the storage of vast diversity. The coming anthropogenic global warming and CO_2 enrichment will add to the global warming already endured by Amazon biota in the Holocene. We think it possible that the expulsion from the lowland forests of heat intolerant species is already complete and that the forest property of maintaining its own microhabitat will allow the high species richness to survive more global warming, provided large enough tracts of forest are preserved. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

This is an ecological enquiry. We examine the response of the Amazon forest and associated vegetation types to the climatic changes of the last glacial cycle. In the process it is necessary to seek evidence of what those climatic changes truly were, and we cannot escape the fact that ecological data are also used to establish the history of climatic change in the first place. The risk of circular reasoning is obvious.

Nevertheless, the circle can be broken. A conclusion that air temperatures were lower in the tropics can be disentangled from the pollen evidence for cooling, and the evidence for CO_2 reduction is quite independent of ecological data. The contentious issue of the history of precipitation in the glacial age Amazon still confounds biological evidence for climatic change with ecological evidence for plant response to those changes but, even with the "Was the Amazon ever arid?" controversy, we should be able to record the main responses to any changes in precipitation that may have occurred, while acknowledging that quantifying those suspected precipitation changes is still not possible.

The thrust of this paper is to use pollen data to reconstruct the history of plant communities. It is an established principle of modern community ecology that the unit of response is the species population, not the community or association as a whole (Whittaker, 1962; Harper, 1977; Davis, 1986; Webb, 1986; Huntley and Birks, 1983; Prentice et al., 1991; Colinvaux, 1993a). There are no permanent plant associations, whether in lowlands or as belts on mountainsides. Thus ecological theory predicts that the response among plants to modest changes in climate should be changes in relative abundance of species within plant formations to produce associations more or less different from those with which we are familiar in modern vegetation.

Extreme changes in relative abundance can eliminate a life form, as in the removal of trees from parts of northern Europe in oxygen isotope stage 2 time, allowing the claim that one formation has been replaced by another (in this case forest by tundra). The most drastic vegetation change in the tropics would be removal of so many tree populations from a forest that the canopy is opened, the consequences being caatinga or the savanna/grassland known in Brazil as *cerrado sensu stricto* (Eiten, 1972). Such fragmentation of a canopy is classically attributed to limited precipitation, and has been demonstrated to have happened in the Peten of Central America in glacial times (Deevey et al., 1983; Leyden, 1984).

Closed forest in the Amazon basin exists under a very wide span of precipitation regimes, varying from > 5000 mm of rain a year to < 1500 mm and with from a negligible dry season to > 5 months without rain (Nimer, 1989). By far the greater part of the lowlands below 1000 m elevation are forested at present, though with a great diversity of forest communities across the enormous extent of the basin. Compared with this diversity of forest, the extent of open vegetation is very small. The massive plant species diversity in the Amazon is very largely a diversity of forest plants, most of which must be expected to have been in existence for far longer than a full glacial cycle. It is the possible reshuffling of this great diversity over the huge Amazon real estate in response to glacial climate forcing that we seek to reconstruct.

It is essential to realize the size and diversity of both the forest and the real estate on which it sits. As Fig. 1 shows, the Amazon drainage, nearly all of it forested, is spread over an area larger than Europe. At present, only two published pollen diagrams from within the basin offer a continuous pollen history since early in oxygen isotope stage 2, those from Carajas and Lake Pata (Absy et al., 1991; Colinvaux et al., 1996a). When seeking to describe the condition of the whole basin from the evidence of either site it is worth reflecting on the difficulty of using a pollen diagram from Moscow to reconstruct the environmental history of Paris, an enterprise that would involve extrapolating over a comparable east–west distance. The possibility for error in such an extrapolation should be obvious. Nevertheless, we consider that data so far accumulated are now sufficient to set aside some of the more extreme speculations of the past.

Fig. 1. The Amazon river system and Europe drawn to the same scale. Extrapolating details of climatic history from one part of so large a space to another invites error.

2. Modern Amazonian vegetation and pollen spectra

Pollen concentration and influx into Amazonian lakes are comparable to, or in excess of, concentrations and influx into lakes of temperate latitudes (Colinvaux et al., 1998), despite early worries that the predominance of zoophily in tropical forests should result in a depauperate pollen signal (Faegri and van der Pilj, 1979). The pollen of both the majority zoophilous trees and the minority of tropical plants that are anemophilous are well represented in sediments of the neotropics. This has been confirmed by airborn pollen trapping, particularly in the Panamanian forest reserve of Barro Colorado Island (BCI) but also in Amazon lowland forests at Cuyabeno, in Ecuador, and near Manaus, in Brazil (Bush and Rivera, 1998).

Widely dispersed, probably mostly anemophilous, pollen types in the neotropics, tend to come from broadly defined pollen taxa, typically identified only to family rank, that have genera or species adapted to many different habitats. Notable among these widespread taxa are Moraceae, Urticaceae, Ulmaceae, Melastomataceae and Myrtaceae that together make up a significant part of the pollen falling onto rain forest lakes. The tiny pollen of the moraceous weed tree *Cecropia*, for instance, can form 40% of the pollen rain in some Amazonian lakes (Bush and Colinvaux, 1988). *Cecropia* species are present across the whole range of reasonably moist vegetation types in the neotropics, from the lowlands to at least 2000 m elevation. Likewise the family Melastomataceae has representative shrubs and small trees throughout the moister parts of the neotropics, from the lowland tropical rain forest to forests high in the Andes. Nevertheless, multivariate analysis of pollen percentages of taxa present as $>2\%$ of the pollen sum distinguishes between facies of the neotropical forests (Bush, 1991).

Other anemophilous Amazon tree genera include *Ilex*, *Bursera*, and shrubs of the family Euphorbiaceae. More importantly, grasses (Poaceae [Gramineae]), together with other herbs such as Cyperaceae, are producers of copious quantities of wind-blown pollen in the Amazon basin as elsewhere. *Podocarpus* is another anemophilous taxon with bladdered pollen typical of many conifers, but our trapping data show that pollen of tropical *Podocarpus* species is not widely dispersed from the parent tree (pollen traps placed almost within sight of a montane population of *Podocarpus* in Cerro Campana, Panama, collected virtually no *Podocarpus* pollen in a year). This is quite contrary to what would be expected of temperate conifers, including high latitude species of *Podocarpus*.

Taken together, the anemophilous pollen taxa of the Amazon basin provide a signal for vegetation that appears comparable to the classical pollen signals of temperate latitudes. Yet the Amazon forests yield in addition a far more detailed signal with a diverse list of zoophilous pollen taxa. Most such pollen falls to the ground close to the parent tree, and yet many of these pollen types are found in lake sediments, presumably carried in the run-off water of the watershed. The pollen signal of these animal-pollinated plants, therefore, records only the community actually growing within the watershed or catchment of the local drainage, potentially providing a detailed history of a local flora.

A pollen signal for replacement of closed canopy forest by open vegetation as postulated by the arid Amazon and refugia hypotheses should be clear, as is illustrated by comparing pollen spectra from the cerrado of central Brazil (Fig. 2) with those from lowland tropical rain forest (Fig. 3).

Fig. 2 is a pollen percentage diagram of glacial and postglacial time from a *Mauritia* palm swamp in the cerrado phytopgeographical domain in the relatively dry central Brazilian highlands, outside the Amazon basin to the south at Crominia, State of Goias (Ferraz-Vicentini and Salgado-Labouriau, 1996). The region has a dry season so long and severe as to prevent the establishment of closed canopy forest except for gallery forests along streams. The present cerrado vegetation is described as "..savanna-like vegetation in which the low stratum is dominated by grasses and has scattered shrubs and low twisted trees, mainly Leguminosae"(Ferraz-Vicentini and Salgado-Labouriau, 1996).

This cerrado pollen diagram is characterized by 50% of grass [Gramineae] pollen in the Holocene samples. Surface samples of soil from the gallery forest and from lacustrine sediments and the swamp surface also had about 50% grass pollen. The main contributors to the pollen sum other than grass are herbs of the families Compositae and Cyperaceae. Input of tree pollen (even *Cecropia*) is little more than a trace, despite the nearby presence of gallery forests. A few percent of the ubiquitous Melastomataceae in the absence of other trees cannot represent forest and is probably accounted for by low melastome shrubs of lacustrine margins. The Cyperaceae record in this core probably emphasizes plants actually growing on the bog, as of course does the *Mauritia* pollen. Here *Mauritia* gives a local habitat (presence of a swamp) signal.

This cerrado pollen record should be compared with the signal for closed forest given by the Lake Pata pollen percentage diagram in Fig. 3 (discussed in detail below). In the rain forest pollen spectra, grass and herb pollen is little more than a trace. The bulk of the pollen is divided between a few anemophilous tree pollen taxa and a large flux of diverse zoophilous taxa, most present as only one or two grains. A total of 169 pollen taxa were identified. Obviously the pollen signal for closed forest is utterly different from that of cerrado or savanna. If there had been an historical replacement of one plant formation by the other, this should be self-evident in a pollen diagram.
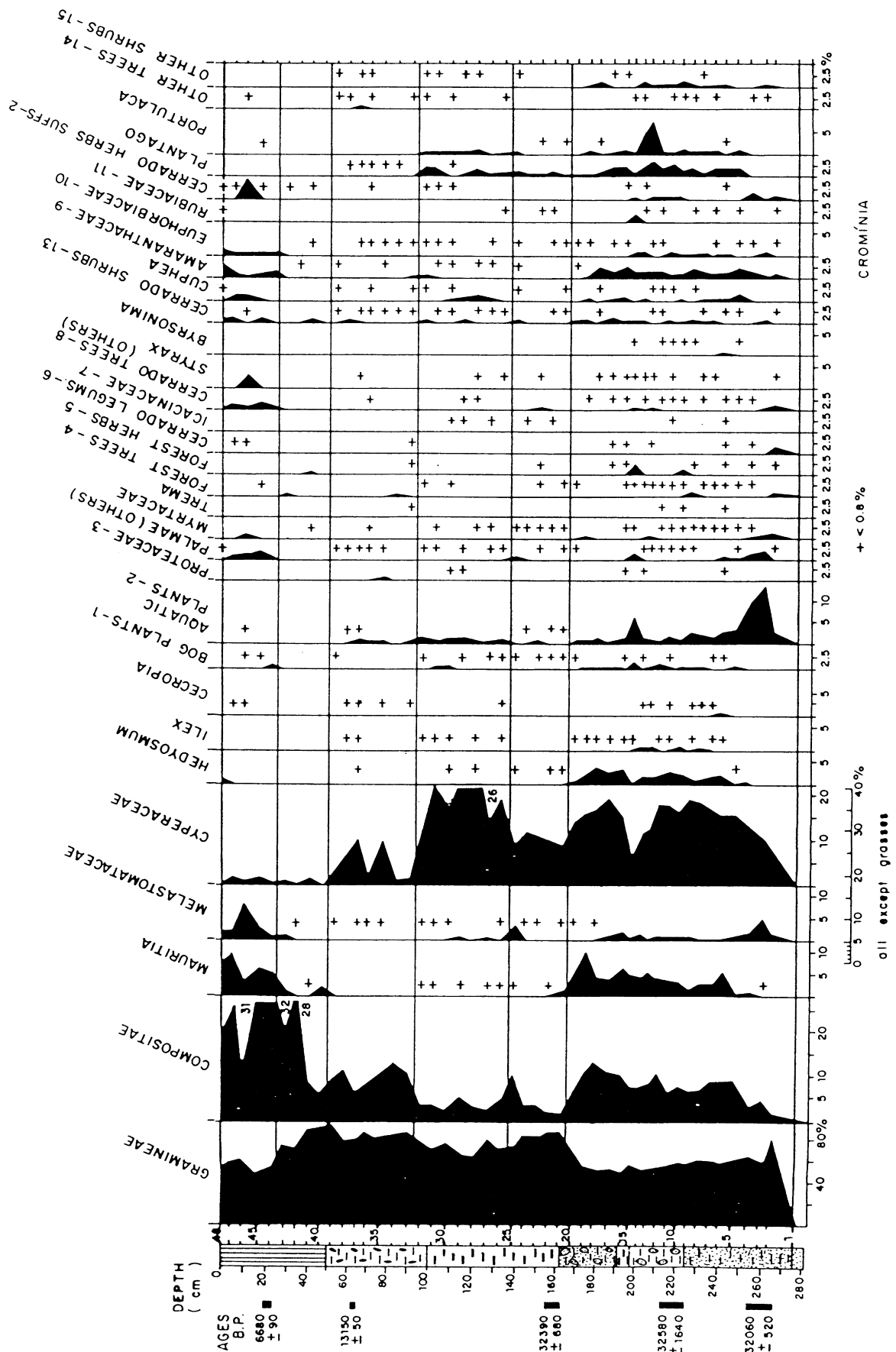
Fig. 2. Pollen percentage diagram from swamp deposits in *cerrado sensu stricto* from the central Brazilian highlands (from Ferraz-Vicentini and Salgado-Labouriau, 1996).
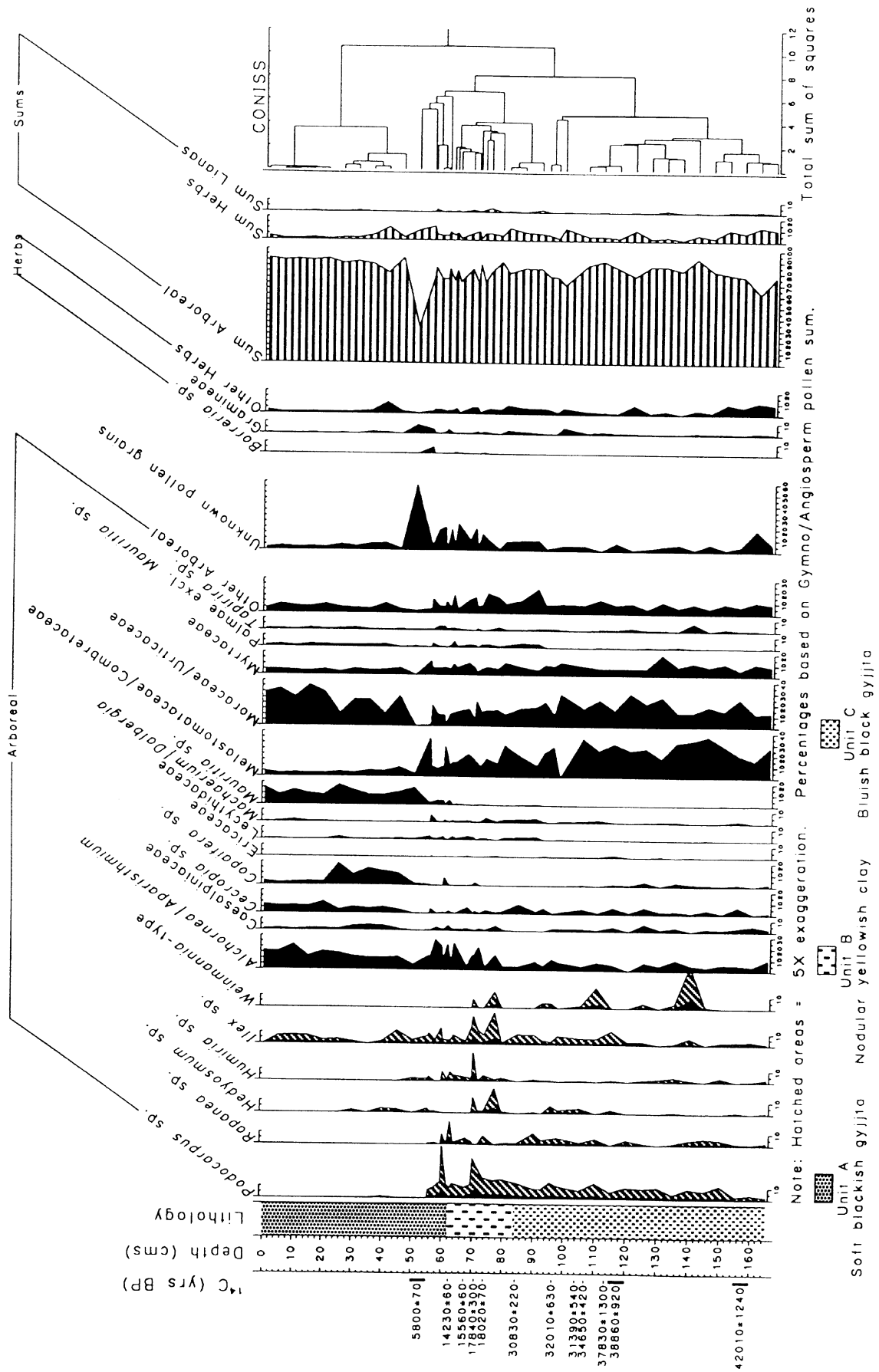
Fig. 3. Pollen percentage diagram from lowland tropical rain forest at Lake Pata (from Colinvaux et al., 1996b).

A general property of Amazonian pollen taxa is that they cannot safely be assigned to vegetation types. Broadly defined taxa such as Melastomataceae, Moraceae, Ulmaceae, Gramineae, Cyperaceae, Urticaceae etc. include species that occur in virtually any habitat. This redounds particularly on identifying dry vegetation types. Dry facies of neotropical vegetation all have thick ground covers of grass and all yield pollen spectra in which Gramineae pollen is predominant, possibly at 50% or more. Thus any Amazon pollen spectrum without large Gramineae percentages cannot represent dry habitats or climates. The converse proposition, however, that high Gramineae always means drying, is unfortunately not true. Grasses form floating mats in the Amazon system, and other grasses are seasonal colonists on *varzeas* or mud-bank islands. Emergent aquatic grasses grow as dense stands in many shallow lakes, and other grasses colonize the surface of drying bogs.

Thus grasses, although always associated with open vegetation, are not index fossils for savannas and cerrado. Similar interpretational difficulties plague reliance on herbs such as *Borreria* and Compositae. These taxa contain many weed species, particularly prominent on bog surfaces and lake margins. Even the genus *Cuphea*, known to be present in savannas and beautifully distinctive to pollen analysts, provides common understory shrubs in moist forests, has species that colonize stream banks or drying bogs and even has species that are rooted aquatics (data from collections at the Chicago Field Museum and the NY Botanic Gardens). Despite claims to the contrary (Van der Hammen and Absy, 1994), *Cuphea* pollen cannot be used as an indicator of savanna. As potential index fossils of Amazonian climate change, *Cuphea*, *Borreria*, and Compositae, the most commonly identified neotropical herbs, are useless.

Two woody plant genera, *Curatella* and *Stryphnodendron* appear to have only obligate savanna species and could be indicators of savanna, when considered in the context of the rest of the pollen spectra in which they appear. A third genus, *Caryocar*, has to be used with more caution, despite being prominent in savannas, because the genus also provides some of the largest trees in lowland tropical rain forest.

Subjective grouping of pollen taxa by habitat or community as practiced in the pollen analysis of temperate latitudes is, therefore, unwise and likely to lead to error. Is Melastomataceae pollen to be allocated to lake margin shrubs so small that they are part of the forb layer, to high elevation bushes, to understory trees of the wettest rain forest? When seeking to identify plant formations (is it savanna, forest or shrubland?) Amazon pollen taxa must be judged by the company they keep. Extended discussions of the interpretation of Amazonian and neotropical pollen diagrams can be found in Colinvaux et al. (1999) and Bush and Rivera (1998).

3. Tropical cooling, lowered CO_2, and Amazonian plant response

We have reviewed elsewhere the pollen and other evidence for significant cooling of the neotropics at low elevations during oxygen isotope stages 3 and 2 (Colinvaux et al., 1996b). The pollen evidence is for large changes in the altitudinal range of plant populations thought to be sensitive to temperature in Ecuador and Panama, together with the northward advance of *Araucaria* forests in southeastern Brazil (Liu and Colinvaux, 1985; Bush et al., 1990,1992; Piperno et al., 1990; Bush and Colinvaux, 1990; Ledru, 1993; De Oliveira, 1992). These data, together with other pollen data from Africa and tropical Asia, provided increasingly persuasive evidence for significant cooling in glacial times. But paleoecologists were freed from having to use the pollen data to infer temperature depression when independent measures of sea surface temperature (SST) in the tropics and noble gas concentration measures in fossil groundwater of eastern Brazil both suggested cooling (Guilderson et al., 1994; Stute et al., 1995). Since then the lowering of surface temperatures in the tropics in glacial times has been shown by climate models to be plausible letting it be reasonable to accept glacial cooling of low latitudes as a working hypothesis (Webb et al., 1997; Ganopolski et al., 1998; Gasse and Van Campo, 1998; Stute and Talma, 1998; Bush et al., 1999; Still et al., 1999). This frees the pollen data of the neotropics from its role as thermometer, and we can address the pollen data to identify the response of Amazonian plant populations to cooling in the order of $6°C$ in glacial times.

Both the Ecuadorian and Panamanian records are from lacustrine deposits of glacial age at mid-elevations in tropical forests. The Ecuadorian sections are 160 km apart at Mera and San Juan Bosco (SJB) in the Amazon lowland forest near its upper reaches between 900 and 1100 m (Liu and Colinvaux, 1985; Bush et al., 1990; Colinvaux et al., 1997). Radiocarbon dates on wood samples of between 26,000 and 33,000 yr BP assign the deposits to oxygen isotope stage 3 (Imbrie et al., 1984). Within this interval pollen, phytolith, and macrofossil data together demonstrate that significant populations of plants now restricted to above 2000 – 3000 m were growing at about 1000 m above present sea level (say 1100 m above the eustatic low sealevel of glacial times. Among these plant taxa were *Podocarpus*, *Drimys* and *Alnus* none of which occur on the lower slopes of the Andes today.

A clear distinction needs to be drawn between the general altitudinal descent of species and the movement of whole plant communities *sensu* Van der Hammen (1974). In the former, species respond individualistically, according to their physiological constraints, invade new areas, and die out or are reduced in portions of their former range. Because no two species have precisely the same ecological tolerances, climatic change induces

constantly changing assortments of species. Thus the Mera and SJB pollen spectra do not imply the descent of whole plant communities, as required by the hypothesis of descending belts of vegetation down mountainsides proposed by Van der Hammen (1974). At Mera and SJB many taxa of the lowland tropical forest remained (see particularly Bush et al. (1990) for a discussion of forest taxa and for an analysis of why these assemblagies of pollen, phytoliths, and macrofossils cannot be the result of post-depositional mixing of floras from different elevations). What is implied is changed forest communities so that *Podocarpus* and *Drimys* grew in the lowland forest of those times, while *Alnus* grew on the banks of the forest stream. A parallel descent of temperature sensitive taxa is shown even more unequivocally in the Panamanian records at La Yeguada and El Valle.

The sediments at Lake La Yeguada (700 m) yield a continuous pollen record from > 14,000 BP, thus spanning from isotope stage 2 until the present (Piperno et al., 1990; Bush et al., 1992). The 55 m long core from the El Valle basin (500 m) extends from well before radiocarbon infinity until shortly after 8000 BP, when the lake drained, thus spanning at least isotope stages 3 and 2 as well as the early Holocene (Bush and Colinvaux, 1990). Both sites are on the Pacific (southern) side of the cordillera as it passes through Panama, both sites are forested today, though La Yeguada is drier because partly in rain shadow from the Pacific. As at the Ecuadorian sites, pollen and phytolith data show population descents of some taxa in the order of 1000 m in glacial times. Both pollen records demonstrate extensive populations of *Quercus* growing as low as the rim of the El Valle caldera (600 m). Phytoliths demonstrate low altitude populations of *Magnolia* and of what are now alpine grasses. Other taxa more typical of cooler or montane environments included *Ilex*, *Thalictrum*, *Symplocus*, *Ranunculus*, *Valeriana*, *Rumex* and *Gunnera*. As in Ecuadorian Amazonia, however, the pollen data also demonstrate continuing presence of tropical forest taxa, including *Luehea*, *Mortoniodendron*, *Bocconia*, *Erythrina*, *Dipteryx*, *Bursera*, *Warszewiczia*, *Trichanthera gigantea* and *Bombacopsis quinata*. This was a reassortment of plant communities, not a descent of vegetation belts.

These results are best understood by considering the order in which the reassortments actually took place. The beginning was the relatively cool glacial times of oxygen isotope stages 3 and 2, when lowland forests of coastal Panama and the western Amazon basin were the habitat of both the plants of the modern tropical forests and of extensive populations of a few plants that we now think of as montane. The decisive environmental event was warming at the onset of the Holocene, when temperature was raised in the order of 6°C, a condition not experienced since the time of isotope substage 5e nearly an hundred thousand years earlier. This warmth was within the tolerances of most of the plants of the lowland tropi-

cal forest, which accordingly maintained viable populations. But a minority of taxa came under thermal stress in the lowlands while expanding their populations at higher elevations to yield the modern patterns of distribution and abundance.

Evidence for reassortment of plant communities with postglacial warming is also present in the scant pollen records so far available from the Amazon lowlands. At Lake Pata (Figs. 3 and 4) pollen data show that a significant population of *Podocarpus* was present in isotope stage 2 but disappeared in the early post glacial (Colinvaux et al., 1996a). One species of *Podocarpus* (*P. lambertii*) is currently found in the lowlands of Amazonia, though at low population densities. Nevertheless, the *Podocarpus* in the Lake Pata pollen record can confidently be attributed to species at present restricted to high elevations because three pollen types, apparently representing different species of *Podocarpus* compatible with the array of species known from high on Pica da Neblina, but not with the modern species whose range extends to the lowlands, were identified in the Pata sediments.

With the disappearance of *Podocarpus* pollen at Pata came changes in other pollen percentages also suggestive of loss of population by other heat intolerant taxa. Reduction of *Podocarpus* in the lowland Amazon forest in the early Holocene is also suggested by a pollen diagram spanning the late glacial to early Holocene transition at Lake Curuca, NE of Belem near the mouth of the Amazon River (Behling, 1996 Fig. 4). At Carajas (Figs. 4 and 7), the long pollen record is notable for remarkably large percentages of *Ilex* in glacial time but near absence in the Holocene (Absy et al., 1991). *Ilex* is one of the taxa withdrawn from the Lake Pata record in the early Holocene, along with *Podocarpus*. Thus the few pollen data we have from glacial times in the Amazon suggest that a number of heat-intolerant species were noticeably diminished, or actually removed, from lowland forest communities by Holocene warming.

3.1. The effects of changing carbon dioxide concentration

CO_2 concentration in the global atmosphere is known to have fluctuated in synchrony with glacial cycles, being lower in the prolonged glacial intervals than in the brief interglacials (Leuenberger et al., 1992). With postglacial warming CO_2 concentration rose from 0.02% to the preindustrial Holocene level of 0.03%. Because CO_2 is the raw material of plant production, and because in bright light CO_2 concentration sets the limits to productivity, when water, nutrients, or temperature do not, it seems inescapable that the rise in CO_2 in the early Holocene should have altered, if only subtly, previous patterns of distribution and abundance.

The most obvious possibility is that plants with C4, or crassulacean acid metabolism (CAM), should have had a competitive advantage at glacial times of low CO_2 over
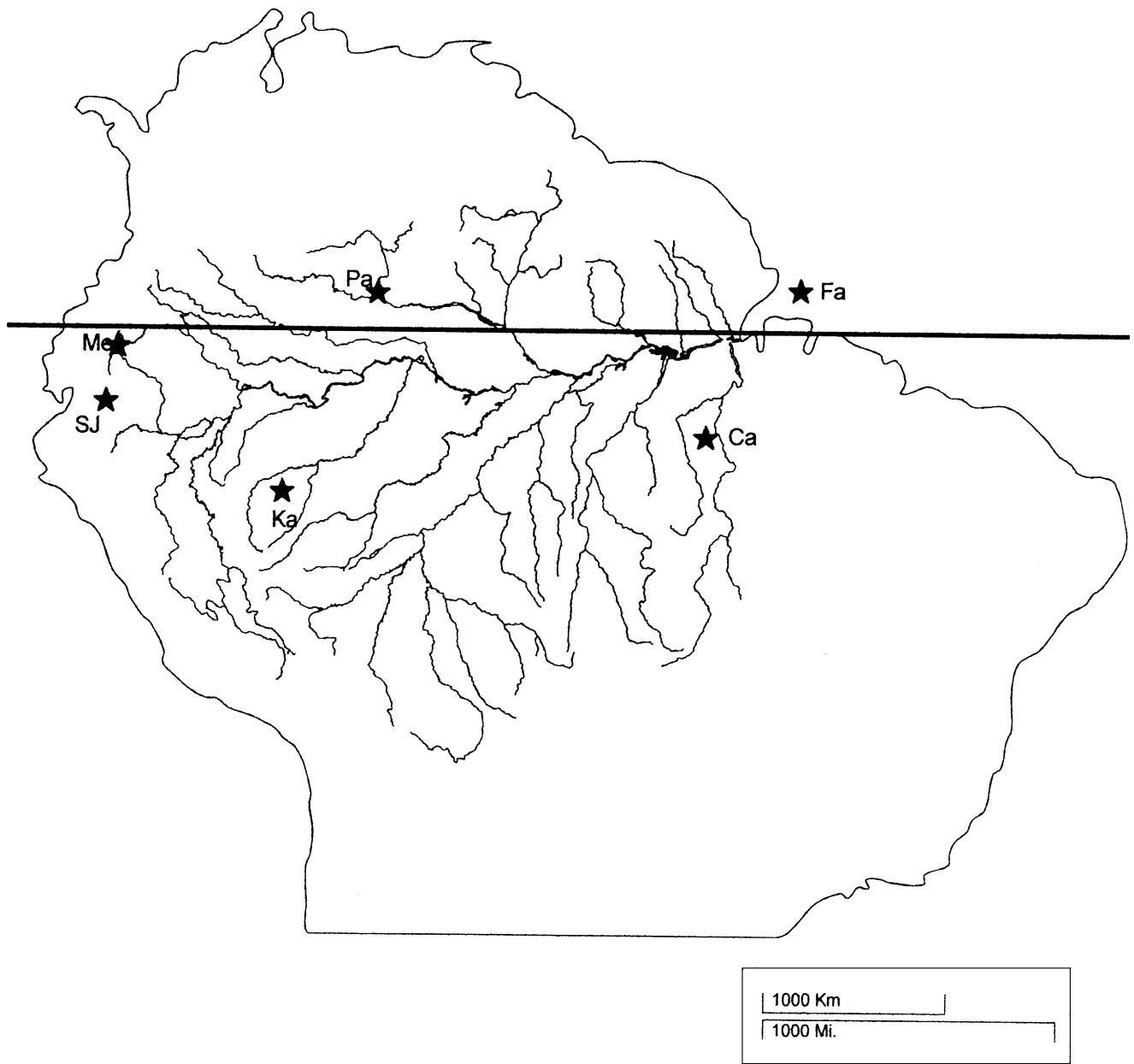
Fig. 4. Sketchmap showing principal Amazonian sites mentioned in text. Me = Mera, Sj = San Juan Bosco, Ka = Katira (Rondonia), Pa = Lake Pata, Ca = Carajas, Fa = Amazon fan.

C3 plants because the reaction constant of the enzyme PEP Carboxylase used for carbon uptake by these plants appears to extract CO_2 against a steeper concentration gradient than does the rubisco enzyme used by C3 plants. A prime objection to this argument, however, is that most of the worlds plants, and essentially all trees, are C3. These C3 plants, including the vast majority of the plants of the Amazon basin, apparently did well enough in the Amazon, as over the rest of the earth, in the last prolonged ice age because they are still with us, still the dominant life forms. Then, as now, the C4 and CAM plants – bromeliads, cactus and opportunistically CAM plants like *Clusia* — would have had their advantage confined to habits or habitats of unusual water stress; to life as epiphytes or on thin soils on rocks (Winter and Smith, 1996). Savanna grasses tend to be C4 (because also adapted to dry habitats), but if grasslands replaced forest the evidence should be clear in the pollen record, which is examined below.

The expectation that C4 and CAM should have had a compelling competitive advantage in glacial times of low CO_2 has echoes of an earlier debate when, shortly after the discovery of the C4 pathway in sugar cane by Hatch and Slack (1979), C4 plants were dubbed "efficient" plants (as opposed to the "inefficient" C3 plants), generating expectations of evolutionary change

from C3 to C4 to be in progress that were, however, soon refuted (Burris and Black, 1976). The manner of carbon uptake is but one of the many properties that adapt a plant species to its microhabitat, or its niche, so that a change in CO_2 concentration should have a limited impact on relative success. Whether significant changes in relative abundance in the hugely diverse Amazon flora followed the carbon enrichment of the early Holocene would depend on the plasticity of physiological responses of the members of this diverse array, responses which are still essentially unknown.

Recent research has concentrated on effect of reduced CO_2 at high altitudes when the low partial pressure of all gasses might be presumed to make the problems of carbon uptake most serious. All trees are C3: might not, therefore, the C3 treeline be depressed from shortage of carbon alone (Street-Perrott et al., 1997). Modern tree-lines constitute the formation boundary for which we have the most satisfactory mechanistic explanation, that they are set by temperature acting through heat budgets of erect plants, or through susceptibility to freezing of young shoots, or both (Gates, 1968; Tranquilini, 1979). The suggestion that treelines in glacial times should have been set by CO_2 concentration rather than, as now, by temperature, is certainly intriguing, but it violates both the principles of parsimony and uniformity, particularly with the accumulation of evidence from lower elevations that cooling was severe in glacial times.

None of the arguments of this paper rest on movements of tree-lines. The reassortments shown by our pollen data are all between lowland and montane forests and within plant communities dominated then as now with plants using C3 photosynthesis. Even the grasses associated with the reassorted plant communities at Mera and SJB were of C3 genera, as shown with phytolith data by D. Piperno (Bush et al., 1990). It remains parsimonious to conclude that the reassortments we find in our pollen data are responses to temperature, with the largest changes being expulsion of heat-intolerant plants from the lowland forest at the onset of the Holocene.

4. Ice-age vegetation of the Amazon lowlands

The only direct evidence for the vegetation of the Amazon lowlands in glacial times comes from pollen analysis of sediments, either from catchment basins in the Amazon lowlands themselves or from sediments deposited by the river system on the on the off-shore Amazon fan (Fig. 4).

4.1. Forests of the western Amazon: Pata, Mera, and San Juan Bosco

Lake Pata occupies a closed basin without significant inlet or outlet streams, probably a pseudokarst basin formed by the slow solution of silicates from the parent plutonic rocks. The lake lies at about 300 m elevation on a low inselberg rising above an immense stretch of lowland plains, at roughly 100 m elevation and covered with lowland tropical rain forest. From a vantage point near Lake Pata one can look out over unbroken forest as far as the eye can see. The inselberg itself is also covered with tropical forest, though somewhat stunted and modified in places because of shallow soils on the hard rocks that have resisted weathering, forming a forest that is edaphically constrained. A Livingstone piston core shows the sediments to be nearly 7 m thick, the top 1.7 m spanning the last 40,000 radiocarbon years. Pollen analysis of this top section provides the first history from within the lowland Amazon forest through the last glacial cycle (Colinvaux et al., 1996a).

The upper pollen spectra of Fig. 3 are of Holocene age and illustrate the pollen signal for lowland Amazon forest of the kind now present in the area. Four things are apparent about this part of the diagram:

1. The prominence of wind dispersed taxa, for instance Moraceae, Urticaceae and Euphorbiaceae (*Alchornea*).
2. The presence of significant amounts of animal-pollinated trees, such as *Caryocar* (Caryocaraceae), *Mauritia* (Arecaceae/Palmae); *Copaifera* (Caesalpinaceae/Leguminosae) and many others.
3. When all the tree pollen, including the low counts of grains found as a trace (listed as "other arboreal") are added together, the total tree (arboreal) pollen is in the vicinity of 90%.
4. The very low count of herb pollen, particularly the almost complete absence of Gramineae.

These four pollen characteristics of the Holocene rain forests of the L. Pata watershed also define pollen spectra of glacial times, as they are present in sediments directly dated to the CLIMAP last glacial maximum (LGM) at 18,000 BP and on to the limit of radiocarbon at 40,000 BP. A watershed record of pollen from zoophilous trees delivered to the lake by surface run-off is also present, including such tropical forest genera as *Tapirira Copaifera*, Caesalpiniaceae, Lecythidaceae, and *Tapirira* [Anacardiaceae]. Of these *Tapirira* is a genus only of lowland forest trees. *Copaifera*, which attains 10% of the pollen sum in the mid-Holocene, is a genus of large forest trees in the family Caesalpiniaceae [Leguminosea-Caesalpinioideae]. Twenty-five species are known from the neotropics, any one of which might be represented in the Lake Pata pollen diagram. Our pollen data suggest a local *Copaifera* population event in the watershed lasting many tree lifetimes and starting about 6000 yr ago. We have not yet been able to identify the pollen from most Caesalpiniaceae and Lecythidaceae below family rank but both families are well-represented among trees of the lowland rain forest, and Caesalpiniaceae includes

forest lianas. Together with *Tapirira* the presence of these familial taxa demonstrates the presence of lowland rainforest trees actually growing within the small Lake Pata watershed from whence their pollen could be washed into the lake.

The taxon *Mauritia* is prominent in the Holocene portion of the section, but not earlier. *Mauritia* is a palm of wet or marshy ground, as well as being a principal tree of gallery forests in savanna areas. It appears to be zoophilous but stands of the trees are very common in marshy areas at the edges of lakes so that their pollen tends to be present in most Amazonian lacustrine pollen diagrams. There is an extensive stand of *Mauritia* beside modern Lake Pata and the pollen diagram suggests that this has been a feature of the Holocene. In glacial times, however, the *Mauritia* stand was not present. This is a purely local record of a patch of wetland within the watershed that might or might not record changed climate: increased precipitation could create a swamp for *Mauritia*, but so could impoundment of drainage or rising of the water table. The apparent coincidence of the *Mauritia* rise at Lake Pata with a stratigraphic change in the sediments and the onset of postglacial time gives strength to the hypothesis that this particular swamp was associated with the end of the last glaciation as increased precipitation raised the water level creating the swamp beside the lake. Persistence of tropical forest both before and after the establishment of the *Mauritia* swamp shows that any change in the rainfall regime cannot have been major. Thus the record of *Mauritia* pollen suggests that mean lake level rose at the end of glacial time to flood the

shallow portion of the basin now occupied by the *Mauritia* swamp, but, of itself, it gives no indication of the cause of lake level rise.

The history of the local *Mauritia* population is not the only evidence for fluctuating water table of Lake Pata because a sedimentary unit spanning the LGM is consistent with low water level or even intermittant drying of the basin (Fig. 3). Because of the extremely slow sedimentation rate of this interval it has even been suggested that that there is a "gap" in the sediment column between about 18,000 and 30,000 yr BP, with the implication that this "gap" represents a time of drought (Ledru et al., 1998). However, dating of a sample in the short length of core spanning this interval has now yielded an age of 22,600 ± 90 yr BP and a depth–age plot using the entire data set shows that sedimentation has been continuous over this interval, although slowed (Table 1, Fig. 5). Pollen concentration rises over this interval by a factor of up to 4, suggesting that pollen influx was roughly constant despite the reduced accumulation of other sedimentary materials (Fig. 5). With continuous sedimentation demonstrated, it is convenient to replot the Lake Pata pollen diagram with age as the *y*-axis instead of depth in core (Fig. 6). This presentation of the data shows clearly that there are no significant changes in plant associations across unit B other than the intrusion into the forest of the few taxa that we now associate with montane forest. Sediment unit B, spanning as it does for roughly 30,000 BP to 15,000 BP, closely approximates oxygen isotope stage 2 (Imbrie et al., 1984). The percentage composition of pollen over this interval is similar to that

Table 1
Radiocarbon dates from the Lake Pata inselberg (The Hill of six Lakes)

Lake Dragão			Lake Pata			Lake Verde		
DEPTH (cm)	AGE		DEPTH (cm)	AGE		DEPTH (cm)	AGE	
2.0	1800 ± 60	AMS	4.0	2420 ± 60	AMS	2.0	12,050 ± 50	AMS
3.0	5370 ± 50	AMS	14.0	2810 ± 50	AMS	7.5	2790 ± 50	AMS
18.0	2290 ± 60	AMS	50–55	5800 ± 70	BULK	12.0	12,480 ± 60	AMS
20.0	8050 ± 60	AMS	62.5	14,230 ± 60	AMS	26.0	17,100 ± 70	AMS
33.0	22,630 ± 120	AMS	67.5	15,560 ± 60	AMS	52.5	16,410 ± 70	AMS
37.0	12,020 ± 60	AMS	72–77	17,840 ± 300	BULK	57.0	18,430 ± 100	AMS
49.0	35,200 ± 240	AMS	73.5	18,020 ± 70	AMS	84.5	19,740 ± 70	AMS
55.0	34,300 ± 590	AMS	76.5	17,850 ± 60	AMS	90.0	19,170 ± 120	AMS
57–62	37,540 ± 680	BULK	81.5	22,600 ± 90	AMS	135.0	18,680 ± 130	AMS
108–113	39,780 ± 990	BULK	84.5	30,830 ± 220	AMS	193.0	23,600 ± 450	AMS
183.5	> 46,200	AMS	96.5	32,010 ± 630	AMS	393.0	> 43,800	AMS
			105–110	31,390 ± 540	BULK			
			106.5	34,650 ± 420	AMS			
			113.5	37,830 ± 130	AMS			
			115–120	38,860 ± 920	BULK			
			155–160	42,010 ± 124	BULK			

Radiocarbon ages of approximately 23,000 BP have now been obtained from all three lakes on the inselberg for which we have cores. This age is in the middle of the epriod for which Ledru et al. (1997) suggested that there were no records from the Amazon. In all three cores, pollen spectra from this interval is of closed lowland tropical forest as published for Lake Pata (Colinvaux et al., 1996a). The effects of repeated drying of Lake Dragão through leakage, as witness by our field party, is apparent in a disturbed record of Holocene dates.
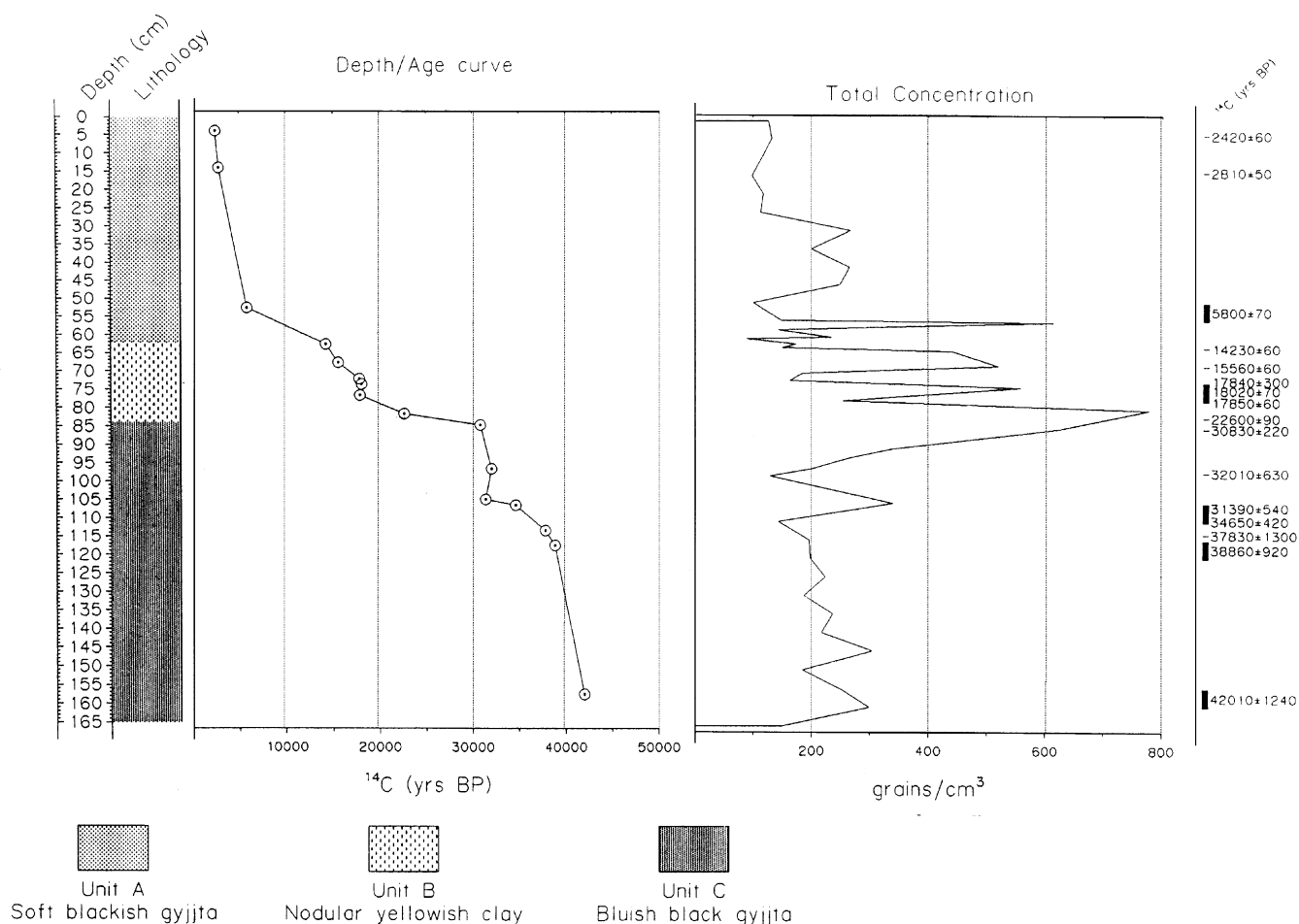
Fig. 5. Depth–age plot and pollen concentration in sediments of Lake Pata. Increased pollen concentration in sediments spanning the last glacial maximum shows that pollen deposition was continuous even though total sedimentation accumulation was slowed. The record is without significant gaps.

of the Holocene sediments and of those directly dated to the 18,000 y LGM, showing that occupancy of the Lake Pata watershed by tropical rain forest was unbroken throughout the Last Glacial Maximum, contrary to the assertion of Ledru et al. (1998). Dates spanning the LGM are now also available for our cores from neighboring Lakes Verde and Dragão, where the pollen signals are also all of closed tropical forest (Table 1). We conclude that the Lake Pata pollen record demonstrates that closed tropical forest was present in the western Amazon lowlands throughout the times of oxygen isotope stages 3 and 2 as well as in stage 1 (the Holocene).

The Mera and SJB lacustrine sections (dated between 26,000 and 33,000 BP) describe only late oxygen isotope stage 3 times but demonstrate closed forest for this interval (Liu and Colinvaux, 1985; Bush et al., 1990; Colinvaux et al., 1997). The details of the forest community have no modern analogs, as discussed earlier, but they retain many of the taxa prominent in Holocene pollen diagrams from Amazonian Ecuador (Frost, 1988; Liu and Colinvaux, 1988; Bush and Colinvaux, 1987). Pollen

from the western equatorial Amazon lowlands so far available, therefore, all show the continuence of closed tropical forest from glacial times through the Holocene, with only species reassortments to accommodate Holocene warming. There is no hint of savanna.

4.2. Pollen from valley fill in Rondonia

Five pollen spectra are available from one of a series of drill cores of valley fill in Rondonia (Absy and van der Hammen, 1976; Van der Hammen and Absy, 1994). All five spectra are dominated by grass pollen, except that the bottom sample has about 45% of pollen of the marsh palm *Mauritia*. The 5 samples represent a 13 m accumulation of colluvium. Two radiocarbon dates at 7 m and 13 m are in the 40,000-50,000 yr BP range, though a separate alkaline extract of organic matter from the upper sample had an age in the 18,000 BP range, possibly representing postdeposition humic compounds introduced in groundwater. In the published analysis, the *Mauritia* pollen at the bottom is taken to represent
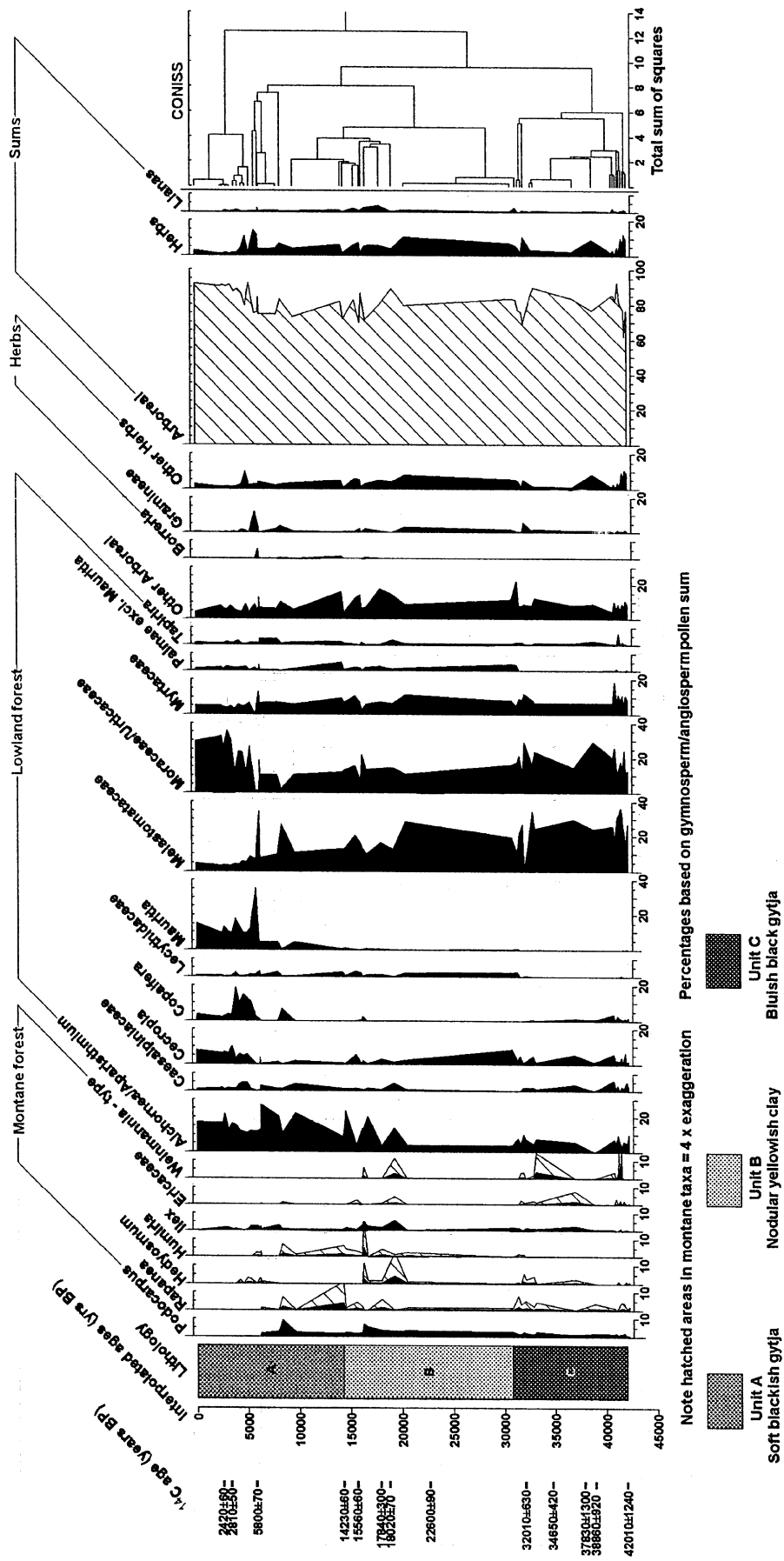
Fig. 6. Pollen percentage diagram of Lake Pata plotted against years before present. Sediment unit B apparently defines oxygen isotope stage 2. Pollen spectra within and bounding unit B demonstrate that closed tropical forest occupied the site throughout the last glacial maximum.

tropical rain forest and the grass dominated pollen of the upper samples to represent a savanna that replaced the presumed forest. But the base spectrum with *Mauritia* is in fact nothing like the pollen spectra of rain forest (compare with Fig. 3); it actually almost certainly represents ponding in the valley fill which produced an habitat for a *Mauritia* stand like that offered by ponding even in the cerrado of the Central Brazilian Highlands (see Fig. 2). Apparently the pollen analysts were not able to visit the site themselves, with the result that no surface samples were taken. No description of the current vegetation of the site is offered, beyond what is obtainable from the regional literature. This shows that the site has probably been forested in the recent past but is within 100–200 km of the forest/savanna ecotone in modern southwest Amazonia.

Valley fill is a difficult material for pollen analysis. Pollen is initially trapped on the soil surface, where it is much subject to differential destruction. The pollen spectra are very liable to local overrepresentation of plants actually growing on the colluvium, and the colluvium itself defines a disturbed habitat likely to be occupied by pioneer herbs. Thus a first hypothesis must be that the high grass and weed percentages represent local overabundance of pioneer plants on the colluvium.

Nevertheless these five pollen spectra (including that with the *Mauritia* palm prominent) are strikingly like the pollen spectra from cerrado (Fig. 2). Although they do not include any index taxa suggestive of savanna, the massive predominance of grass pollen does allow the working hypothesis of extensive movement of the forest/savanna ecotone early in glacial times > 40,000 yr BP. This is consistent with pollen evidence from a long lake sedimentary record from close to the forest/savanna ecotonal boundary in Amazonian Bolivia for the local spread of savanna early in Isotope Stage 2 times (F. Mayle, personal communication).

South-western Rondonia is on the periphery of the Amazon basin at between 10° and 12°S, and has one of the more extreme dry seasons in Amazonia, hence its situation astride the forest/savanna boundary. This dry climate is reflected in the properties of lakes in the region. An extensive survey of Rondonia lakes by our field parties in 1997 found them to be universally shallow (typically no more than 1–2 m deep) and prone to dry completely every year. Typically they hold no organic sediment, suggesting that the carbon cycle is closed annually. This finding is consistent with the presence of ecotones and the findings of the Rondonian and Bolivian pollen studies that, at different times during the last glaciation, savanna encroached on forest. Very little change in precipitation would be required for this.

4.3. The Amazon fan and continental shelf

In interglacial times like the present, the sediment load of the entire Amazon river system is dropped on the broad continental shelf, but with eustatic lowering of sea level in glacial times sediment-laden water flows across the then shallow shelf as a turbidity current in a submarine canyon, after which the sediment load is dropped into the deep sea to contribute to an immense deposit known as the Amazon fan (Milliman et al., 1975; Meade et al., 1985). Sediment cores from fan and shelf should yield traces from every part of the Amazon system, though skewed towards mineral contributions from the west where the flanks of the Andes erode under heavy rains. Multiple analyses of drill cores taken by Leg 155 of the International Drilling Program (ODP) confirm these expectations (Flood et al., 1997). But pollen input to the rivers should be less skewed by local relative erosion than by the mineral inputs; so vegetation of the entire Amazon basin is represented by pollen in the marine deposits of the Amazon fan.

Pollen studies of offshore marine sediments elsewhere show that they provide convincing broad-brush descriptions of vegetation change in continental interiors (Heusser and Shackleton, 1994; Hooghiemstra et al., 1992; Kershaw et al., 1993). Sediments from the Amazon system should be particularly revealing of the vegetation of the broad Amazon lowlands because all the major tributaries flow into and through the Amazon tropical rainforest. If, for instance, the lowland forest were to be replaced by open vegetation at any time an unmistakable signal should result as pollen spectra like those of Fig. 2 replaced spectra like those of Fig. 3 in the Amazon lowlands.

The first pollen results from the Amazon fan by two independent investigators revealed a striking constancy of the pollen signal throughout the last two glacial cycles of isotope stages 1 through 6 (Haberle, 1997; Hoorn, 1997). In particular, pollen spectra of glacial times had no more grass pollen than is found in Holocene samples from the shelf or from the modern sediment load of the Amazon River (Fig. 7). Both investigators reached the inevitable conclusion that the modern forests of the Amazon lowlands cannot have been replaced by savanna in glacial times.

The pollen data did, however, record lesser floristic changes synchronous with glacial rythmns. Each interglacial was marked by an increase in mangrove (*Rhizophora*) pollen, apparently signalling increased mangrove habitat with the coastal flooding that accompanied raised sea level. More interesting were increased percentages in glacial times of *Alnus*, *Podocarpus* and *Hedyosmum* pollen, thus recording at the Amazon mouth the increased populations of these taxa in the western lowlands observed at the Mera, SJB, and Lake Pata sites. These pollen data from the fan, therefore, seem uncompromising in declaring that the Amazon lowlands, taken as a whole, remained forested throughout glacial cycles, but that forest associations were slightly reassorted in glacial periods in response to cooling.

Fig. 7. Summary pollen percentage diagram from sediment samples from the Amazon fan and continental shelf. The chronology is reconstructed from portions of several different cores (from Haberle, 1997).

One uncertainty remained about these data, however, in that the chronologies were not secure. Most of the sediments were beyond the reach of radiocarbon dating, nor could sedimentation be assumed to be constant. Use of delta ^{18}O and paleomagnetic measurements was handicapped by post depositional displacement of sediment masses within the fan, one of the achievements of ODP Leg 155 being to demonstrate the relocation of sediment bodies on the fan by turbidity currents and channel meander (Flood et al., 1997). But Haberle and Maslin (1999) overcame this problem for the last 50,000 yr in one core by using the paleomagnetic record calibrated by ams radiocarbon dates, both to date the deposits and to demonstrated continuous deposition at this core site (Fig. 8).

In Fig. 8, eight magnetic intensity horizons (crossed circles) were aged by correlation with a dated sequence elsewhere, and the resulting chronology was confirmed by identification of the Lake Mungo excursion, directly dated by ams radiocarbon, and by a second ams date near the surface of the core. As expected, sediments from the later Holocene were not present in the core from the fan, the upper part of the record in Fig. 8 being supplied from piston core samples from the continental shelf, independently dated by ams, and by samples of the sediment load of the modern river.

Pollen percentages in Fig. 8 are as uncompromising as those in the earlier Haberle (1997) and Hoorn (1997) studies. Pollen percentages of grass or other indicators of open vegetation during the last glacial maximum were not noticeably different from those of the Holocene. The only special property of the glacial age was a modest incursion of tree taxa now prominent only at higher elevations, sugesting minor reassortment of forest associations in response to cooling. To anticipate those who might attempt the tendentious argument that the pollen evidence for savanna had been hidden by lines of trees on the river banks, Haberle and Maslin (1999) appeal to carbon isotope studies that show that gallery forests do not prevent signals from lowland savannas from reaching Amazon river sediments. This conclusion is, of course, also inherent in the pollen data themselves because the grass pollen remains roughly between 10% and 15% in glacial and interglacials alike, thus being far removed from the 50% to 80% found in open vegetation like the cerrado of Central Brazil (Fig. 2). Grass percentages in fan and shelf sediments are comparable to the 6% to 17% found in suspended sediment load of the Amazon river over a 2000 km traverse (Haberle, 1997). This grass pollen of the modern Amazon system cannot be attributed to agricultural clearing because the percentage remained roughly constant throughout the Holocene sediments from the continental shelf. Its source is almost certainly the non-savanna grasses of the river system itself: floating mats, pioneer communities on sedimentary islands, and *varzeas*. Some portion of the total could

originate from savanna patches at the periphery of the basin (e.g. from near the savanna/forest ecotone in Rondonia and Bolivia), but the extensive non-savanna grass communities of the lower Amazon itself seem more likely as the source.

A property of the fan sediments remarked by Hoorn (1997) is that they are enriched with fern spores. These, like the arkosic sands in the fan, are probably the product of deep weathering of ancient sediments from which all palynomorphs but fern spores have been removed, a common condition of ancient sediments. A phytolith study by Piperno (1997) found that the ratio of phytoliths from C4 and C3 grasses was higher in the glacial fan deposits. This might be the first actual evidence that within the grass community the lowered CO_2 of glacial times had caused a dominance switch from C3 grasses to C4. Or it might merely be due to the fact that the gorge through which the lower Amazon flowed in times of eustatic lowering of sea level afforded more habitat to the C4 grasses that still colonize open ground in the flood plain.

But the real importance of the fan and shelf pollen is to demonstrate that savanna was never wide-spread in the Amazon lowlands. If extensive grasslands of cerrado or savanna had existed in place of what are now lowland rain forests, the immense flux of wind-blown grass pollen would have yielded a clear signal in the pollen rain, just as changes in continental vegetation in other regions have been signaled in marine sediments delivered by major river systems (Heusser and Shackleton, 1994). Thus the pollen from the Amazon fan and shelf allows the strong inference that the lowland Amazon forests were not fragmented by open vegetation at any time in a glacial cycle.

4.4. The pollen record at Carajas

The plateau at Carajas is part of an inselberg system comparable in structure to that on which Lake Pata lies, but of much larger extent, at higher elevation, and in the east central lowlands of Brazilian Amazonia, > 1000 km east of Lake Pata (Fig. 4). Both inselbergs have outcrops of ironstone rocks, areas with thin soils, and a number of pseudokarst solution basins holding marshes or lakes. Cores of sediment from a shallow lake on the Carajas Plateau have yielded both pollen and limnochemical data for the local environment for more than 30,000 radiocarbon years (Soubies et al., 1991; Absy et al., 1991; Fig. 9).

The Carajas Plateau differs from the Lake Pata inselberg in being larger and much more elevated, rising to 900 m. The sampled lake is at about 700 m as opposed to the 300 m of Lake Pata. Mean annual precipitation at Carajas (2000 mm) is ample for closed forest yet much of the plateau surface has open vegetation, variously described as "wet savanna", "altitudinal savanna" or *campo rupestre*. This savanna-like vegetation apparently results from a combination of edaphic control by the thin iron-stone soils and altitude. The sampled lake is situated
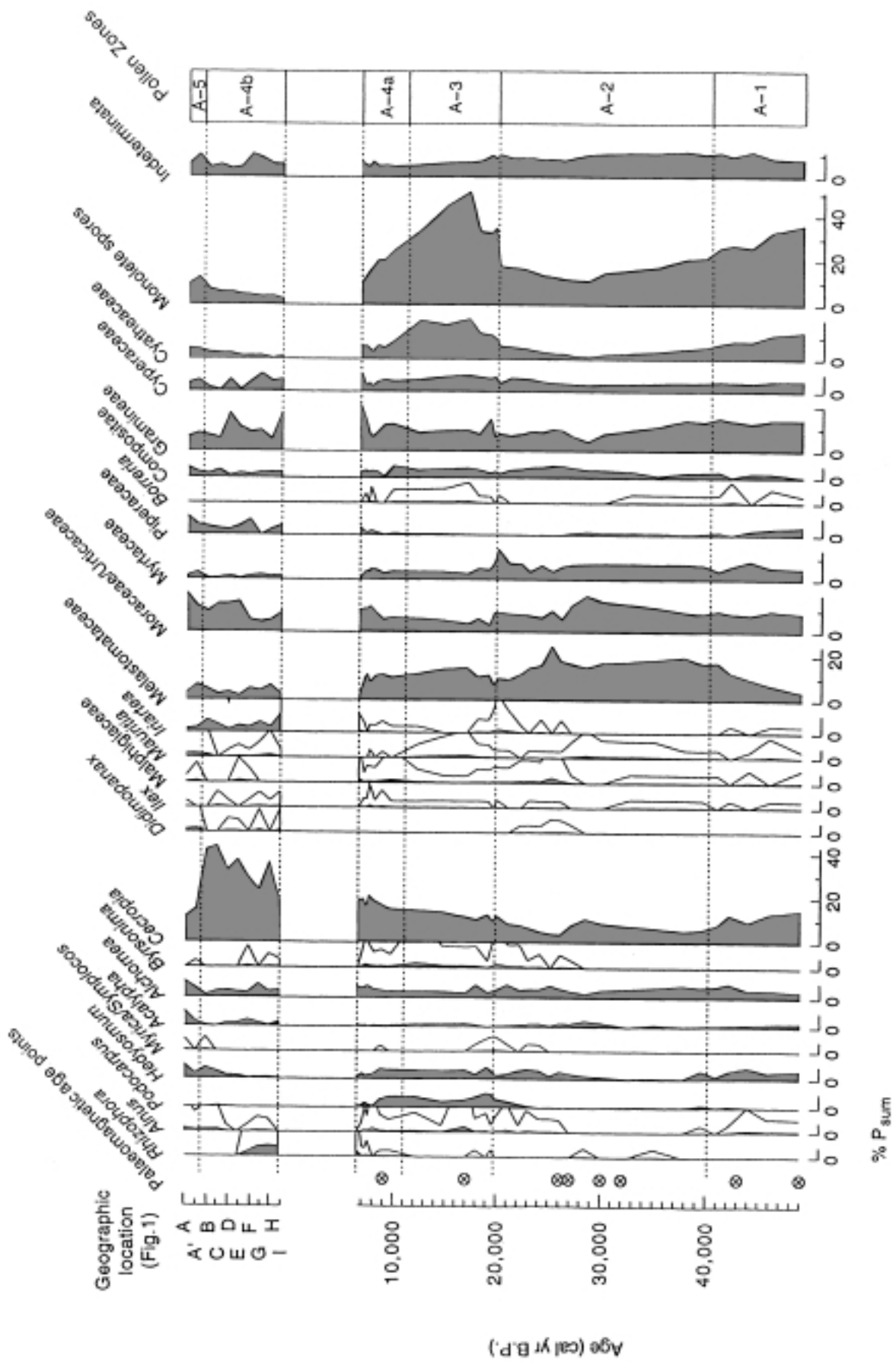
Fig. 8. Continuous pollen percentage diagram from core ODP 932 compared with Holocene and modern pollen percentage data from the continental shelf and surface samples. Dating of core ODP 932 is by magnetic intensity (crossed circles), bracketted by ams dates, and by placement of the Lake Mungo paleomagnetic excursion (from Haberle and Maslin, 1999).

in, and surrounded by, *campo rupestre* (Absy et al., 1991). Closed tropical forest occupies the lower flanks of the inselberg, but tapers out across an ecocline between 600 and 650 m. We have reports from an aircharter company serving settlements in the region of patches of woodland growing on the plateau itself.

A collection of Carajas plants in the herbarium of the Field Museum in Chicago lets us amplify the description of the *campo rupestre*, which is shown to include stands of such bromeliads as *Dyckia*, *Pitcairnia*, and *Tillandsia*. Common weed species include *Borreria* sp. and *Cuphea* sp. The two *Cuphea* species in the Field Museum Carajas collections are *C. antisypyhillitica* and *C. carthagenensis*, both typical of wet sites from savannas, flooded soils, and lake and river margins: these *Cuphea* species, therefore, are wetland indicators. Grasses are prominent in this vegetation type, both as part of the open vegetation and as rooted aquatics. Short shrubs of the Melastomataceae are also characteristic.

The partial pollen diagram so far published lists only taxa that are consistent with what is known of vegetation in the immediate vicinity of the lake, the most prominent taxa being Gramineae and Melastomataceae (Fig. 9). Of three herb taxa listed, *Borreria* and Compositae are prominent in rocky shore communities on inselbergs and the Carajas *Cuphea* species are common on lake or marsh margins. Of the few woody plant taxa listed *Celtis*, *Trema* (both Ulmaceae) and *Cecropia* have anemophilous pollen and all three taxa are to be expected in forest patches on the plateau, or indeed as plants of the *campo rupestre* itself. We have collected *Byrsonima*, which is present in low percentages throughout, growing and flowering on boggy ground at the edge of similar basins on the Maicuru inselberg 300–400 km to the NW of Carajas. Thus *Byrsonima*, although a genus known from lowland savannas, is also a plant characteristic of this "wet savanna". The taxa *Aparisthmium* and *Piper* are present throughout in low percentages, w ith single sample peaks in the later Holocene. *Aparisthmium* was formerly included in the genus *Alchornea*, and pollen of the two genera are so similar or overlapping that we combined both into one pollen taxon in the Lake Pata diagram (Fig. 2). While *Alchornia* includes mostly forest trees of mid-elevations, *Aparisthmium* includes mostly small trees or shrubs of poor soils, suggesting that the *Aparisthmium* pollen at Carajas is contributed by shrubs of the *campos rupestre* itself (Gentry, 1993). Most species of the very large genus *Piper* are small shrubs, the pollen again being consistent with plants growing in the immediate vicinity of the lake. The persistently present pollen taxa at Carajas, therefore, are all accounted for by plants prominent in the modern vegetation surrounding the lake.

Two shortlived, but massive, peaks of *Ilex* pollen are shown in sediments more than 30,000 yr old (Fig. 9). *Ilex* in Amazonia is a genus now mostly associated with higher elevations (Gentry, 1993) so that the population

events recorded in glacial age sediments at Carajas are likely to be associated with glacial cooling and probably represent stands of *Ilex* in the shoreline community of the reduced lake.

This long pollen history suggests remarkable constancy of vegetation on the inselberg through a glacial/interglacial cycle, in which the only population events of note are the brief flourishing in glacial times of populations of *Ilex*, probably in response to cooling. Percentages of other taxa do oscillate from sample to sample, giving the diagram a rather jagged look compared with the cerrado and rain forest diagrams of Figs. 2 and 3, but this is probably inevitable when recording populations in so stressed an environment as an edaphically constrained open area. Most of the irregularities are from single sample peaks. No data on pollen sums or pollen concentration are given (Absy et al., 1991) so that the irregularity of the pollen spectra could reflect, in part, local or statistical over-representation (Faegri and Iversen, 1989). Despite this, the data show the reported diversity to be essentially constant. This constancy is all the more remarkable because an elegant use of data for sediment chemistry has demonstrated two prolonged intervals (roughly 20,000–35,000 and > 50,000 BP) when the lake/marsh system was drier than it has been in the later Holocene, yet the pollen data show that the same basic vegetation persisted (Soubies et al., 1991; Absy et al., 1991).

Contrary to some published commentary (Van der Hammen, 1991; Van der Hammen and Absy, 1994), the pollen record from the edaphic vegetation site at Carajas does not appear to record events in the more forested parts of the Carajas plateau nor of its surrounding lowlands. The self-evidental quality of this observation is easily seen by comparing the Carajas pollen diagram of Fig. 8 with those for rain forest or cerrado (Figs. 2 and 3), neither of which was available when the Carajas diagram was first published. That the woody-plant to weeds ratio is lowered in times of low lake level, as remarked by Van der Hammen and Absy (1994), is entirely consistent with the increased habitat for weed species on the exposed shoreline and drained lake surface, which provided a local increase in weed pollen without change in the more regional contribution of pollen from woody plants. We suggest that the true import of this splendid long record from Carajas is that the local pattern of Amazonian vegetation on the plateau can maintain itself throughout the vicissitudes of the climatic changes of a glacial cycle with no more than marginal changes in relative abundance of the more important taxa.

4.5. Summary of pollen conclusions: the vegetation of the Amazon basin through a complete glacial cycle

The pollen data, few as they are, reveal persistence of Amazonian vegetation in the face of the climatic changes
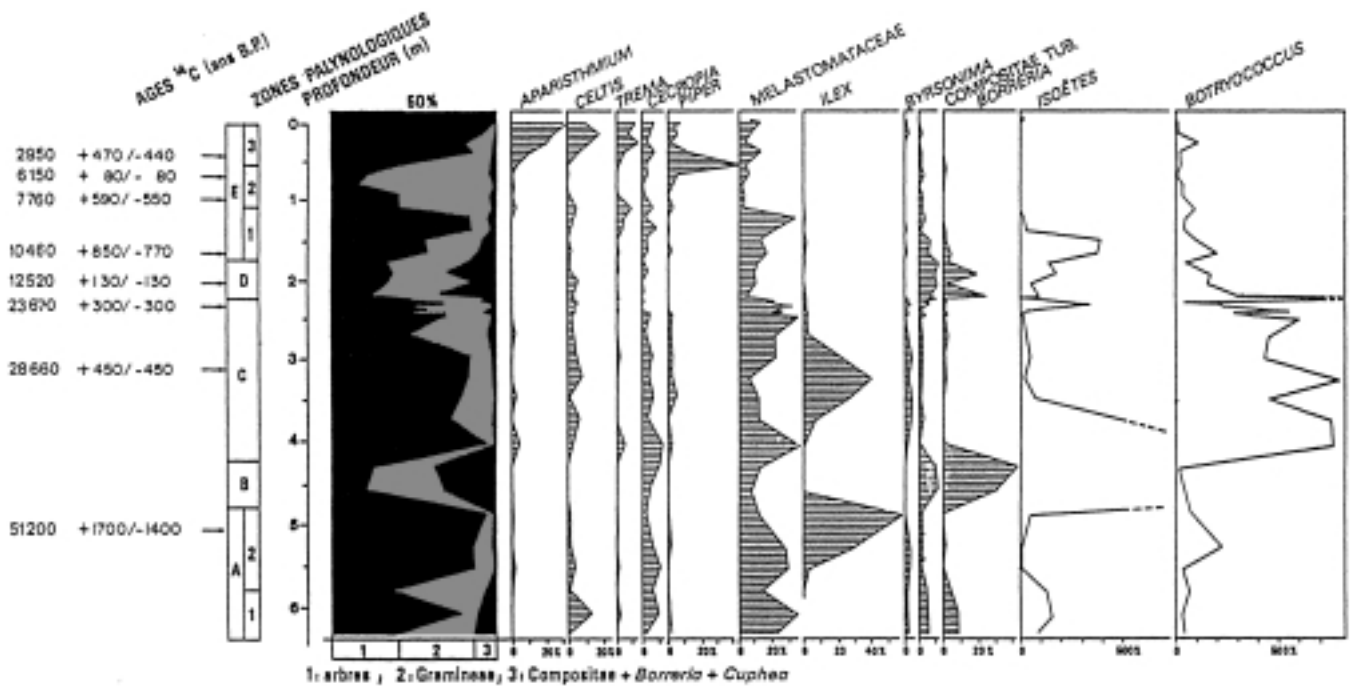
Fig. 9. Pollen percentage diagram from Carajas (from Absy et al., 1991).

of a glacial cycle. Only three published pollen diagrams span all the way from full glacial times (defined as oxygen isotope stages 3 and 2) to the present: Lake Pata, riverine marine deposits of the Amazon fan and continental shelf, and Carajas. Of these three, both Pata and riverine deposits show the persistence of closed tropical forest in the lowlands, while Carajas shows persistence of the local inselberg vegetation. It is true that pollen data from the southwest periphery of the Amazon basin suggest movement of the savanna/forest ecotone at the expense of forest, but even if more pollen data should show that similar movements of ecotones occurred at other sensitive parts of the basin periphery, such movements were too small or too local to have been registered in the mixture of pollen brought down to the sea by the river system.

Closed tropical forest covers most of the Amazon basin in modern times. We conclude that closed forest covered most of the basin in glacial times also, though community compositions in that diverse forest changed, particularly in response to changing temperature. The greatest community changes followed the warming at the onset of an interglacial as warm-temperature sensitive plants were expelled from the lowlands for the duration of the interglacial.

Such is the conclusion that we feel must be reached from the available pollen data. The forest has never been fragmented into "refuges" by tracts of savanna impassable to forest biota as required by the Haffer (1969) hypothesis, nor has the eastern half of the basin

been denuded of forests as has been postulated on the basis of geomorphological arguments (Clapperton, 1993). The data, of course, are still too few for a small scale mapping of forest boundaries in glacial times; even we three authors differ somewhat in our assessments of the forest boundaries. But that the forest persisted over most of the lowlands throughout glacial times seems inescapable.

5. Arguments or evidence for Amazonian ice-age aridity I: the biota

The pollen evidence that the Amazon lowlands remained forested throughout glacial cycles is a direct refutation of the hypothesis that the Amazonian glacial climate was so arid that open vegetation (typically called 'savanna' in the literature) occupied the lowlands in glacial times. Thus it is necessary to reexamine evidence or arguments cited in support of the aridity hypothesis. These are essentially of two kinds: biogeographic and geomorphological.

The biogeographic arguments mostly depend on the refuge hypothesis (Haffer, 1969,1974; Prance, 1982; Whitmore and Prance, 1987). The cited data are biogeographic discontinuities for which glacial age aridity separating forest isolates is postulated as a mechanism providing episodes of vicariance, thought necessary to produce these discontinuities. The refuge hypothesis, therefore, offers no direct evidence for past Amazonian

aridity, merely using aridity suggested on geomorphological grounds as a convenient explanation for observed distributions (Haffer, 1969). Denial of the required contraction of the Amazon forest into isolates ("refuges" in Hafferian terminology) by the pollen data should more easily be accepted if alternative explanations are offered for the biogeographic discontinuities.

We have severally argued elsewhere that if an appeal to Milankovitch time-scales is really needed for episodes of Amazonian vicariance, the isolates were the areas of change rather than the lowlands separating them (Bush, 1994; Colinvaux, 1993b,1998,1996). Reduced temperature and CO_2 made the elevated land of the isolates subtly different while the separating forest remained intact. This pattern is in accord with the pollen data, but as an explanation for endemicity is almost certainly also wrong. Speciation among Amazon birds and the rest is of far greater antiquity than is allowed for by Milankovitch cycles, as molecular phylogenies increasingly show that species separations usually require longer than a glaciation followed by an interglacial of a Milankovitch cycle (Patton et al., 1999).

This part of our argument can be concluded with the remark that an hypothesis is evidence for nothing. If the pollen data show that Amazon vegetation history does not fit the predictions of the refugial hypothesis, and if molecular data show that Milankovitch time-scales are too short for the required separations, so the hypothesis is falsified and should be abandoned.

One biological argument remains: that a Pleistocene mammalian fauna of the western Amazon basin required a savanna habitat. Radiocarbon dating of remains in river terraces of the upper Napo River in Ecuador led Webb and Rancy (1996) to conclude that a significant megafauna lived in the lowlands in glacial times, as well as in the inter Andean Plateau. On the basis of dentition, Webb and Rancy (1996) further interpret this fauna as of grazing animals requiring a savanna habitat. The Napo drainage is in the wettest part of the modern Amazon basin, with mean annual precipitation up to 5000 mm. It is also a region for which the Mera and SJB sections provide direct evidence of glacial forests. So how to explain the existence of a savanna fauna?

To our reconstruction of the vegetation of the region, the accuracy of the dating is largely irrelevant (provided the animals were of Pleistocene age), since the pollen data suggest continued forest cover at all stages of a glacial cycle. The parsimonious explanation of the presence of the fauna is that it did not require an open savanna habitat. To the extent that the animals really were obligatory grazers, rather than opportunistic grazers and browsers, the valley of the active river should have provided ample habitat in the grassy flats and disturbed areas characteristic of such systems, coupled perhaps with migratory behavior to graze above the lowered tree-line.

6. Arguments or evidence for Amazonian ice-age aridity II: the land surface

The geological hypothesis of Amazonian aridity rests on a number of disparate observations from across tropical and subtropical South America, chief among them being fossil dune systems outside the Amazon basin, the presence of white sands within the basin itself, buried stone lines, colluvial deposits in Amazon lowlands, arkosic sands in the deposits of the Amazon fan, and the apparent correlation of gaps in sedimentary records from the region (Clapperton, 1993; Ledru et al., 1998).

6.1. Fossil dune systems

Areas with reported fossil dune systems are the continental interior of Bahia State (NE Brazil), the Pantanal/Mato Grosso region of Central Brazil, and the Llanos region spanning the Orinoco drainage, providing a triangle of sites, all outside the Amazon basin but yet appearing to hold the whole basin in their grasp (Fig. 10). If these three extra-Amazonian features truly record active dunes of glacial age, then the suggestion that white sands in the Amazon basin itself are also aeolian becomes, by extrapolation, plausible. In fact the data do not support the postulate that these three sets of features record dune fields active in glacial times.

6.2. Paleodunes of NE Brazil

The best known system is that in the state of Bahia in northeastern Brazil (Fig. 10). The paleodunes are in the middle São Francisco River region, between 10–11°00 S and 40°30′–42°20′ W. So clearly recognizable are the dunes that the region was dubbed the "little Sahara" by Williams (1925). Modern vegetation of the dune fields ranges from caatinga woodland, through bush caatinga to xeric caatinga: being various facies of xerophytic communities of spiny, deciduous woody plants, with succulents, cacti and bromeliads (Kuhlmann, 1977). The sand deposit with its dunes has recently been investigated by core drilling and thermoluminescent dating by Barreto (Barreto, 1996; Barreto et al., 1997; AMF Barreto personal communication). There has been a long history of aeolian sedimentation, beginning in the late Tertiary or early Pleistocene and continuing to the recent past. The most recent period of dune activity was in the late Holocene, particularly from 4000 to 1700 BP. There was no discernable concentration of dune activity in the last glacial period as required by the arid Amazon hypothesis.

This record has been enlarged by pollen analysis of a core of peat deposits formed in the flood plain of the Icatu River, which dissects the caatinga dune landscape in its passage from inland mountains to the São Francisco River, and hence to the sea 500 km down stream (De Oliveira et al., 1999). The 3 m peat core is shown by
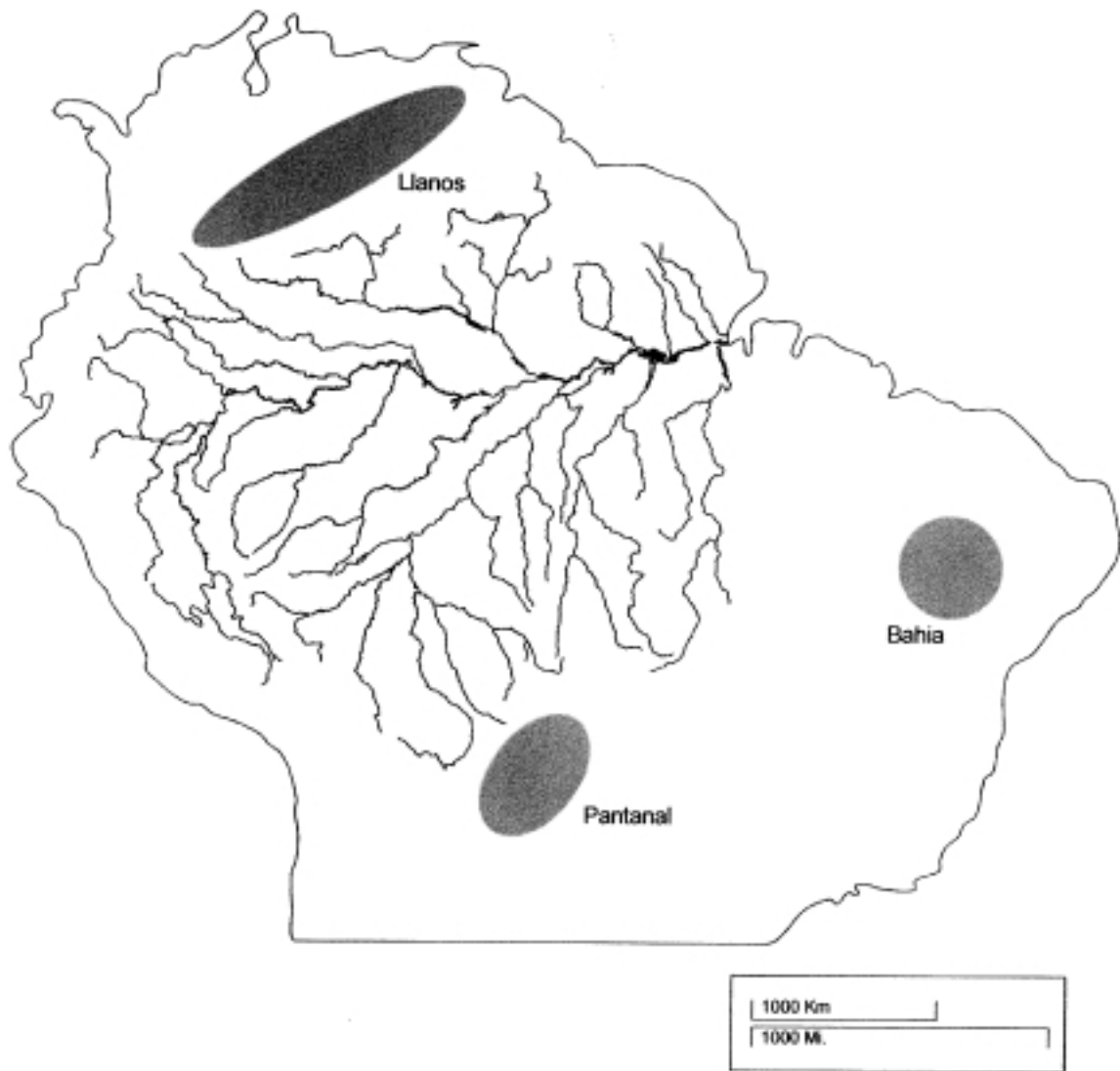
Fig. 10. Sketch map showing the approximate positions of three areas outside the Amazon basin described in the literature as having paleodune morphology.

6 internally consistent beta-decay radiocarbon dates to span the last 11,000 yr. The earliest part of the pollen history is of diverse, moist, probably riverain forest, with later establishment of increasingly xeric caatinga. The driest part of the pollen record correlates well with the reactivation of the dune system in the late Holocene. Thus this paleodune site was actually moister in lateglacial times than it has been for most of the Holocene.

The moist forest of lateglacial times along the Icatu River is consistent with other data for a moister climate in the later Pleistocene, among which is the recent discovery in the area of a complete skeleton of a large bodied *Protopithecus* primate (Cartelle and Hartwig, 1996; Hartwig and Cartelle, 1996), disjunct populations of *Podocarpus lambertii* and other indications of former continuous moist forest in the region (Jolly, 1976; Lorenzi, 1992; Andrade-Lima, 1982). Thus the fossil sand

dune system of the State of Bahia cannot be taken as evidence for ice-age aridity, either in the region itself or over the height of land into the Amazon basin.

6.3. Reported paleodunes in the Pantanal

The Pantanal is a large tectonic basin formed by the continuous uplift of the Brazilian central highlands, beginning in the Cretaceous (Freitas, 1951; Almeida, 1945). Infilling of the basin by gigantic alluvial fans from rivers draining the Mato Grosso has roughly kept base with subsidence, resulting in an alluvial plain of 110,000 km^2 (Braun, 1977; Ab'Saber, 1988). Unlike the "little Sahara" region of the State of Bahia, the area is not arid to-day.

Published reports of paleodunes are based entirely on interpretations of remote sensing data and are without

ground truth. Klammer (1982), in a lengthy paper, interprets landforms seen on his remote sensing data as possibly fossil dunes, making his most definite statement to that effect in his English language abstract. Tricart (1982) and (Tricart et al., 1984) concur in identifying features on remote sensing images as probably aeolian but offers different reconstructions of both dune and alluvial histories to those of Klammer. Clapperton (1993) bases his account of the supposed Pantanal glacial aridity on these studies, particularly Klammer's work, accepting that a huge desert system occupied the whole Pantanal, probably in glacial times.

Recent geological studies in the region find no evidence for arid landforms. Shiraiwa (1996), for instance, describes drilling in the Pantanal at many sites by the Petrobras oil company that reveals no evidence of arid landforms in the top 500 m of alluvium. Boggiani and Coimbra (1995), from a study of the limestone Xaraies Formation of the Pantanal thought to be of uncertain Pleistocene age on account of its included megafauna (Almeida, 1945), concluded that their data allowed at most only a semi-arid climate with occasional heavy rains, not one in which dunes should be active. Despite extensive inquiries in Brazil, we have been unable to discover any report by Brazilian field geologists, whether written or oral, of dune landforms anywhere in Central Brazil, the Pantanal in particular. Geologists who have spent their entire working lives in Central Brazil assure us that they have seen nothing that could be construed as a paleodune. Thus the hypothesis that the Pantanal had an arid climate with active dunes during, and only during, times of northern glaciation is decidely non-proven.

6.4. Paleodunes of the Orinoco (llanos) region

The third dune field, on the Orinoco and llanos region of the Venezuelan and Colombian highlands northwest of the Amazon basin (Fig. 10), has been known to geographers since first remarked by von Humboldt, though little studied. The dunes, many of them kilometers long, are covered by open vegetation, described variously as grass or scrub in the geomorphological literature. Thus they are in a somewhat water-stressed environment even today. The dune fields extend in a great ark from north of the Guyana Highlands inland from the mouth of the Orinoco River, and along the eastern flank of the Andes to Colombia (Khobzin, 1981; Roa, 1980; Tricart, 1974). An active time for the dunes should have been when reduced precipitation was accompanied by deep penetration of the northeast trade winds, deflected to a more southerly course by the Andes mountains (Clapperton, 1993). The dating of this conjunction of circumstances is still highly uncertain. The only radiocarbon dates (of paleosols underlying dunes) are of lateglacial age, $12,300 \pm 500$ BP and $11,100 \pm 450$ BP (Roa, 1980). If these dates are true ages, they would require vegetation

cover in late glacial times and dune activity in the early Holocene.

The proximity of the llanos dune fields to the Caribbean coast of Venezuela invites a correlation of times of dune activity with the strong evidence for glacial age aridity in the Caribbean region, in particular with the well-documented history of vegetation and water level at Lake Valencia that showed what is now a deep lake reduced to a marsh 14,000 yr ago (Salgado-Laboriau, 1980; Bradbury et al., 1981). This record for Caribbean aridity is extended further back to at least the beginning of oxygen isotope stage 2 time for the Peten region of Guatemala by paleolimnological and pollen data from radiocarbon dated lake sediments for a savanna climate in a region that supported closed tropical forest in the late Holocene (Deevey et al., 1983; Leyden, 1984). This correlation of climate change across the Caribbean Sea, however, is scarcely a satisfactory dating tool. An alternative glacial history for the western edge of the Caribbean region is given by the long El Valle record from the Pacific coast of Panama, which demonstrates that closed forest was maintained in the Panama lowlands for what is probably most of the last glacial cycle (Bush and Colinvaux, 1990).

Thus activity in the immense paleodune fields of the llanos and Orinoco has not been satisfactorily dated by either direct or stratigraphic means. It should be parsimonious to expect that, like those other proven paleodune fields in the State of Bahia, they have been intermittently active in their basically dry climate since at least the Tertiary/Quaternary boundary. What is certain is that concentration of llanos dune activity in times of northern glaciations has not been demonstrated.

6.5. Summary: the uncertain history and significance of paleodunes in tropical South America

We conclude that paleodunes in tropical South America cannot be used as evidence for glacial aridity across the continent. Concurrence of dune activity across the region cannot be demonstrated, nor is there compelling evidence that paleodunes activity at any of the three regions was concentrated at times of northern glaciation.

Evidence from the "little Sahara" region of the State of Bahia in NE Brazil is that dunes were active in the Holocene, and that aeolian activity has been a feature of the region since the Tertiary/Quaternary boundary. Opposed to the hypothesis of dune activity in the NE Brazil being concentrated in glacial times is a growing body of evidence that the region was actually wetter in at least part of the late Pleistocene. The data from the Pantanal are too few, or too debatable, to allow satisfactory inference. The times of activity for the paleodunes of the llanos are unknown, but, since the region is semi-arid to-day, only a marginal increase in local aridity would be

required to disrupt the present xeric vegetation. The llanos dunes may plausibly be correlated with demonstrated glacial aridity in parts of the Caribbean basin, though no independent dating supports this correlation. Thus the scattered dune systems of South America offer at best only a perilous base for assuming drier times in the Amazon at some as yet undated past interval, and they offer no data at all for calibrating the degree of the supposed dryness.

6.6. Arkosic sands in the fan deposits

Short cores were raised from the Amazon fan more than twenty years before the recent leg 155 of the Ocean Drilling Program, one result being the discovery of significant amounts of feldspar minerals, the so-called arkosic sands. Because these feldspars weather rapidly, particularly in the humid tropics, it was evident that the arkosic sands in the fan deposits could not have been exposed to prolonged weathering of the kind experienced by soils and river banks of the modern Amazon lowlands. The fan deposits were of course of glacial age, a dating confirmed by radiocarbon, and Damuth and Fairbridge (1970) accordingly suggested that the arkosic sands were consistent with the surface soils of an arid Amazon without humid weathering. This conclusion is perhaps the most cited reference for an arid ice-age Amazon.

As Irion (1984) argues, the deeply weathered surface sediments of the Amazon lowlands should always be without feldspar minerals, even if humid weathering were to be restricted to interglacial times. The weathering of successive interglacials should make this certain. Thus the surface of the Amazon lowlands have been without feldspars throughout the Pleistocene and cannot have been the source of the arkosic sands in the fan. There are two alternative sources for the feldspars, both of which probably contributed to the accumulation found in the fan deposits: the Andes and deep dissection of old deposits. The Andes origin is favored by Milliman, who points out that the larger part (perhaps 80%) of the sediment load is derived from rapid erosion of young Andean rocks that are rich in arkosic sands (Milliman et al., 1975; Meade et al., 1985). Inclusion of the resulting large flux of arkosic sands from the Andes is alone sufficient to account for their concentration in the fan (J.D. Milliman, personal communication). The alternative explanation rests on the consequence of eustatic lowering of sea level that caused the lower Amazon to cut its own channel in the order of 100 m deeper, thus mining arkosic sands from rock formations that are now deeply buried (Irion, 1976; Irion et al., 1995). Probably both mechanisms have contributed to the fan deposits. Arkosic sands in the fan deposits, therefore, are not evidence that the Amazon was ever arid.

6.7. Stone lines

Stone lines can be seen in road cuts and stream banks in many parts of the world: a cliff face of fine material is interrupted by a layer of stones. These can have various origins: a flash flood to roll stones as the original deposit was laid down; an old thin gravel bed subsequently buried; frost-heave that lifts stones to form a pavement at the surface that is subsequently buried; mineral concretions along a line of water penetration; and desert pavements subsequently buried. There are doubtless others. In Brazil the prevailing paradigm has been the hypothesis of desert pavements (Ab'Saber, 1982; Clapperton, 1993).

This concept was taken up by Ab'Saber (1982) (see also Brown and Ab'Saber, 1979) and applied to such stone lines as could be found in tropical Brazil, particularly in the Amazon basin. Anecdotal reports describe stone lines from all over the region, including the Amazon lowlands near Manaus. The Ab'Saber hypothesis requires that Amazon stone lines are fossil relics of a former desert climate in which bare ground replaced forest from at least Manaus to the sea. No stone lines have been dated by radiocarbon, for there is no carbon in a stone line. A pre-Quaternary age was suggested by Journeaux (1975) but the Projeto Radambrasil, in accord with the prevailing expectation of an arid Amazon in an ice-age, accepted the last glacial period, essentially oxygen isotope stage 2, as the time of deposition (Radambrasil, 1978).

For Amazon stone lines truly to be relics of an arid landscape, it must be shown that they did not originate in others of the ways that stone lines commonly originate. Perhaps the only mechanism that can be rulled out *a priori* is frost heaving. Movements of gravel by fluvial process is an obvious mechanism in the Amazon, particularly as a large proportion of exposures in this great wilderness is on river banks. But one obvious alternative to desert pavements is concretions (pisolites), the result of slow chemistry in percolating waters, a process well-known to occur in lateritic soils elsewhere.

Stone lines in the Belterra clay of central Amazonia are critical to the aridity hypothesis (Brown and Ab'Saber, 1979). The Belterra clay, and its included stone lines was examined by Irion and his colleagues by minerology, geochemistry and sedimentology of cores from more than 20 exposures (Irion et al., 1995). They concluded that the stones are indeed pisolites deposited in situ within the clay matrix of the Belterra formation, which they calculated to be at least ten million years old. Similar studies near Manaus and along the Rio Trombetas find the enclosing formation to be even older, from 30–50 million years (Chauvel et al., 1987; Lucas, 1989).

The Amazon stone lines, therefore, have been misidentified. They are not the product of desert pavements and subsequent burial, nor is there any direct evidence that they are of Pleistocene age. Thus they cannot be

used to support the hypothesis of ice-age aridity in Amazonia.

6.8. White sands

In northwestern Brazil are large areas of white sand, particularly in the drainage of the Rio Negro, where shorelines exposed when the river is low are astonishingly white against the black water and the dark green of forest. Rivers have meandered and changed course through the sand unit, leaving an irregular land surface of mounds and channels, all fixed and covered with relatively depauperate and stunted forest. As Clapperton (1993) remarks, when referring to conclusions by Ab'Saber (1982), "if the primary origin [of the sands] was aeolian, then they indicate much more arid conditions formerly over some parts of the Amazon basin". In the place of this cautious statement, it has been our experience that the supposed aeolian origin of the white sands has been used in informal discussion as a reason for concluding that the Amazon basin was once arid, particularly by associating the white sands with paleodunes of other regions of South America (see above) to postulate synchronous, continent-wide aridity. But recent pedological field work suggests very strongly that the white sands actually formed as podzols on the Tertiary Barreiras formation, and were, like all podzols, formed under a humid climate (M.L. da Costa, personal communication to K. Suguio). They cannot therefore be used as evidence for glacial aridity in the Amazon basin.

7. On moderately reduced precipitation in glacial times

Our review leads to the conclusion that the Amazon basin was never arid at any time in a glacial cycle, and pollen data show that most of the basin was always forested. This is not to say that precipitation was constant, because there are excellent reasons for thinking that precipitation should have been reduced somewhat in glacial times. Reduced temperature alone should have moderated the cycle of '*evaporation followed by renewed precipitation*' thought to be responsible for heavy showers in parts of the Amazon lowlands (Nimer, 1989). Climate models that account for lowered temperature in the tropics also invoke comparative dryness of equatorial air (Webb et al., 1997), and even extrapolation from Africa or Lake Valencia may not be without merit.

At both the Carajas and Lake Pata sites gross stratigraphies of the sediment cores demonstrate episodes of lowered water levels in glacial times. At Carajas the hypothesis that color changes in the sediment reflect episodes of low water has been upheld by elegant use of sediment chemistry and minerology (Soubies et al., 1991; Absy et al., 1991). Radiocarbon dating demonstrates low water level prevailed over at least part of oxygen isotope

stage 2, although the two episodes of demonstrated low water do not correspond in other respects to glacial-interglacial chronology. At Lake Pata the evidence for low water has not yet been rigorously established, but it is a good working hypothesis that sediment unit B of yellowish, crumbly sediment that includes material spanning oxygen isotope stage 2 represents low water with occasional exposure to the air (Fig. 6; Colinvaux et al., 1996a).

That the lowered levels of these closed basin lakes at both sites represents reduced precipitation is a good working hypothesis. The two Amazon data points, however, are hardly definitive for the whole region, particularly as both lakes occupy pseudokarst basins in which water loss by seepage is inherently likely. This is illustrated by our experience at Lake Dragão, on the same inselberg as Lake Pata and within 5 km of it. The lake was 9 m deep when we set up our work camp on its bank in 1991, two weeks later the level had fallen by 2 m, and we learned that in 1997 a team of visiting geologists played soccer on the dried out lake bed. This modern history at Lake Dragão cannot be ascribed to changes in the precipitation/evaporation ratio: clearly the lake leaks. Yet our sediment cores from Lake Dragão show a long lacustrine history, with sedimentation rates comparable to those in Lake Pata and radiocarbon infinity reached in the second meter (Table 1). Thus lake level data from the two Amazon sites, Carajas and Lake Pata, are as plausibly explained by an hypothesis of leakage in intermittently sealed basins in the pseudokarst systems as they are by an hypothesis of climatic change.

Low lake levels at Lake Pata and Carajas have been correlated with low lake levels, or 'gaps' in sediment columns, of glacial age in other parts of Brazil (Ledru et al., 1998; Salgado-Labouriau et al., 1998). Among these sites are the *Mauritia* swamp at Crominia (Fig. 2; Salgado-Labouriau et al., 1997), the Salitre bog (Ledru, 1993), Serra Negra (De Oliveira, 1992) and Lake Valencia (Bradbury et al., 1981) as well as Carajas and Lake Pata. Apart from the difficulty of accurately dating "gaps" in cores, the conclusion that gaps represent arid episodes requires the assumption that each gap was caused by cessation of sedimentation through climatic change. This is often an hazardous assumption, particularly in bogs like Salitre or Crominia where sediment accumulation can potentially be drastically altered by such factors as changing direction of flow in the nourishing stream independent of climate. Some of the basins in this data set (particularly Serra Negra) apparently occupy pseudokarst basins like those of Carajas and Lake Pata and thus might be subject to the same possibilities of leakage (Gomes et al., 1990), so it is by no means certain that these correlations show synchronous reductions in precipitation across this vast region until alternative hypotheses for each "gap" are critically examined.

In SE Brazil a number of studies have demonstrated that stream flow and erosional processes have been

significantly different in the late Pleistocene, particularly in the Rio Doce region (Pflug, 1969a,b; Meis, 1977; Meis and Machado, 1978; Meis and Monteiro, 1979). A ready hypothesis has been that the old stream flows represented more seasonal rainfall in glacial times, with the result that this work has been some of the most persuasive for glacial aridity in at least southeastern Brazil (Clapperton, 1993). However, a recent study by Mello (1997) produces strong evidence that the patterns of change in stream flow in the Rio Doce region are more simply explained as the result of tectonic movements of the land surface. If Mello is correct, then evidence for reduced precipitation in southeastern Brazil in glacial times is much reduced.

Southeastern Brazil is a region that is climatically sensitive, e.g. to shifts in the position of the south Atlantic high pressure system, which gives plausibility to hypotheses of changed precipitation in glacial times. Not all the data from SE Brazil suggest drying in glacial times, however; some, like the northward advance of *Araucaria* populations are more consistent with precipitation maintained or even enhanced, alongside the cooling that made the *Araucaria* advance possible (De Oliveira, 1992; Ledru, 1993).

To the southwest, studies of stream deposits of the Bolivian Andes provide evidence that precipitation was reduced on the oriental flank of the Andes, with rainfall more seasonal and stormy in glacial times (Servant et al., 1981; Servant and Fontes, 1984). These data are consistent with the pollen evidence for movements of the forest/savanna ecotones of Rondonia and Bolivia (Van der Hammen and Absy, 1994).

Thus across the length and breadth of tropical South America it is possible to find data suggestive of local reductions in precipitation. It is important, however, to examine alternative hypotheses for local changes in water relationships. And it should also be salutary to examine examples of sites where precipitation appears to have increased (the *Araucaria* advance, for instance, or primate fossils and the forest corridor of NE Brazil). There is at least a suggestion in Amazon studies that climatic aridity has been the preferred hypothesis for any sediment gap, change in lake level, or altered stream flow as data have been fitted to the prevailing paradigm of tropical aridity.

8. The response of Amazon forests to past global change

The great global climatic change for which we have most data is the glacial to Holocene transition of ten thousand years ago. We conclude, contrary to the prevailing paradigm, that this change only minimally involved changes of precipitation in Amazonia: the paradigm that glacial cycles were oscillations between aridity and humidity is in error, and whatever changes in precipitation there may have been were too minor to disrupt the lowland forest. The real substantive climatic

changes at the Pleistocene/Holocene transition involved both warming and rising CO_2, thus letting this climatic event serve in some part as a model for the anthropogenic global changes that are to come.

The overwhelming property of the Amazon ecosystems in the face of this documented global change was stability. The closed tropical forests which, on the evidence of pollen analysis, occupied the Amazon lowlands in glacial times remained in their ancestral lowland habitats despite warming and CO_2 enrichment, and despite modest changes in the patterns of precipitation.

At Lake Pata, diverse, closed, tropical rain forest of glacial times persisted through the global change as an intact forest. On the Carajas Plateau to the east, the edaphically limited vegetation immediately round the lake remained distinctive and persisted. On the flanks of the Andes to the west, the data are less complete, but the moist forest of the Andean foothills gave way only to the moist forest of the Holocene.

Only where formation boundaries met at an ecotone in Rondonia and Bolivia have we evidence of one formation replacing another, as the forest/savanna ecotone moved out into what was formerly savanna at the time of global change.

This history of ecosystem stability is most graphically portrayed by the pollen data from the Amazon fan and continental shelf. But the fan data also hint at population responses within the ecosystem that were the real accommodations to global change. These data come from the far west of the Amazon.

Together with their 80% contribution of mineral sediment to the fan, the Andean forelands also contribute significantly to the pollen deposited at the river mouth. The fan pollen records the presence of sizable populations of *Podocarpus* and *Alnus* in the closed tropical forest of the western lowlands in glacial times as first reported in Ecuadorian pollen diagrams, and the shelf pollen their subsequent expulsion with the warming of global change. These population changes were the principal response of the Amazon ecosystems to the global change, when heat intolerant plant species found new distributions at higher elevations.

The expulsion from the lowland forests by global warming of *Podocarpus*, *Alnus*, *Hedyosmum*, *Drymis* and others, as recorded in the pollen data, reveal the principal plant responses to the global change. The plants responded as individual species populations, as should be expected. Those that found themselves at a competitive disadvantage because of the unaccustomed heat ceased to thrive in the forest, but were able to persist in the Amazon basin as a whole by expanding their populations in cooler montane areas.

The reduction of *Ilex* populations on the Carajas Plateau after the global warming probably represents a similar process. *Ilex* can still be found on the inselbergs of the region, even though the taxon disappears from the

Carajas pollen diagram in the Holocene (Fig. 9). Possibly most of the taxa whose lowland forest populations were largely reduced by Holocene warming linger on at low densities: *Podocarpus* (at least some species) has been recorded as lone individuals or small stands at widely separated places in the lowland forest, though never in sufficient numbers to let their pollen turn up in surface samples. Some of these victims of the early Holocene global warming did not become extinct in the lowland forest but instead occupy the tails of the log-normal distributions of species abundance (Preston, 1948).

The Amazon pattern of gross ecosystem stability, but population reassortment with Holocene global warming, seems to be mirrored for the cerrado of the central Brazilian highlands as illustrated by the Crominia pollen diagram (Fig. 2). Here too the local vegetation takes global warming in its stride, but with the interesting development of a population of the marsh palm *Mauritia* becoming established after the global change event (Fig. 2). It is possible that the *Mauritia* population thrived merely from increased ponding, either because precipitation was higher or from changes in the ponding mechanism, but this seems unlikely as a cause because the marsh was present even before the global change period (the sediments are marsh sediments). The alternative to increased ponding is that *Mauritia* was able to expand at what is an extreme southern latitude for the taxon because of the rise in temperature (Salgado-Labouriau, et al. 1998).

These population changes within Amazonian and Central Brazilian plant communities over the global change are most easily attributable to temperature, to the actual global warming of the time. It must always be possible that the rise in CO_2 was also involved, but we have no evidence for this. All the plants shown to experience population changes by the pollen data are C3, as are most of the populations for which we find no evidence of change. We have no evidence that changes in precipitation or seasons were involved. What is clear is that displaced plants now maintain their largest populations at elevated sites that are cooler.

9. Implications of the analysis for the maintenance of Amazon diversity

The view of the Amazon as a great museum of ancient species where extinction is rare is lent plausibility by these pollen data, because the forests are maintained throughout glacial cycles over most of the vast extent of the basin. Interruption of long periods of persistent ice-age climates by brief interglacials like the present results in no more than the expulsion of heat intolerant plants from the lowlands to the large areas of hospitable coolness at the elevated margins of the basin. To this extent the predictions of Sanders's (1968) time-stability

hypothesis, and the early arguments of Alfred Russel Wallace (1876), up upheld.

Our reconstruction is also consistent with Terborgh's (1973) latitude-area effect, the primary suggestion of which is that this large equatorial landmass offers so large an area with tolerable temperature that local habitats will be available for species to survive any likely climatic regime. The pollen data, using the example of *Podocarpus*, *Ilex* and the rest, show that even the heat and CO_2 enrichment of an interglacial can be escaped or endured by populations of sufficient size to ensure safety somewhere in the basin.

The shear size of the permanent forest cover enhances the opportunities for mechanisms of intermediate-disturbance and selective cropping to reduce extinction by excess competition (Connell, 1978; Janzen, 1970; Hubbel, 1979).

Only Haffer's (1969) postulated history of recurrent merging of forests isolates (called "refuges") in interglacials is removed as a possible diversity-inducing mechanism by the pollen data. What is left is the largest possible equatorial stage for an ancient evolutionary play (Hutchinson, 1965). Or, perhaps more trenchantly, Whittaker's (1969) "dance floor" on which species took their place until displaced by accident. Within the range of Pleistocene climates the chances of fatal accidents were minimized by the long duration of the forest over an immense expanse.

10. Possible responses to pending anthropogenic global changes

The coming anthropogenic "greenhouse" effect will imitate, and expand on, the great global change that began the Holocene. Temperature and CO_2 will again both rise. Patterns of precipitation will also change, though gross effects of differing rainfalls on the forest are likely to be confined to the ecotones as they were at the Pleistocene/Holocene boundary. The big changes we have to consider are in temperature and CO_2, coupled to the effect of the massive forest clearance now taking place.

The temperatures and CO_2 concentrations to come will be higher than any experienced by the Amazon species in the Pleistocene: it will be as if the climatic consequences of an interglacial were added to a preexisting interglacial, thus a doubling of the usual interglacial perturbation of the more usual ice-age climatic regimen. Unless some Amazon species encountered equivalent stresses in the late Tertiary, the coming temperatures and CO_2 concentrations will be without precedent in the history of modern Amazon species.

The effect of temperature, at least, on the biota of a great humid forest, might be moderated somewhat by the control of microclimate exercised by the forest itself.

Given enough water, trees thermoregulate, carrying the ambience of their habitat with them. Anyone who has walked from the hellish heat of an open space in the Amazon lowlands to the relative cool of the forest needs no thermometer to record the change in ambience. It is a reasonable expectation, therefore, that the effects of further increasing temperature *per se* on the relative abundance of Amazon taxa will be minimal. Possibly a few more genera will join *Podocarpus* and *Ilex* in becoming rarer except at higher elevation, but it is at least as likely that the thermal expulsions from the glacial age lowlands are already largely complete.

We have no data to asses the effect of further increases in CO_2 concentration on the relative abundance of Amazon biota. Most Amazon plants are C3, with C4 and CAM confined to habits and habitats of water stress. Their relative successes will continue to depend on the availability of water, not on changes of gas concentration.

To effects of whatever changes in precipitation that further global warming might bring, must be added the effects of forest clearance. If land is to be denied to forest by clearance, the prime safety valve of Amazon biota, dispersal over great, continuous distances, is removed for the first time in the Pleistocene. Thus preservation of the species richness of the Amazon lowlands will be a function of the sizes of forest reserves and their connectedness.

11. Concluding note

Quaternary scientists can offer Quaternary research. It is astonishing that we have so few data from this immense, and immensely interesting, real estate. This poverty of data has been the cause of mistaken paradigms about the Pleistocene history of the Amazon. In this paper we conclude that the Amazon was not arid at any time in the Pleistocene, that the lowlands were in the main always forested, that forest biota were never fragmented into isolates called refugia, and that the critical global changes in Amazon history were the warmings of interglacials that intermittently perturbed the great and persistent ice-age forests. Much or all of this needs testing with more data.

Acknowledgements

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