Late-Quaternary Vegetation History at White Pond on the Inner Coastal Plain of South Carolina¹

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At White Pond near Columbia, South Carolina, a pollen assemblage of *Pinus banksiana* (jack pine), *Picea* (spruce), and herbs is dated between 19,100 and 12,800 ¹⁴C yr B.P. Plants of sandhill habitats are more prominent than at other sites of similar age, and pollen of deciduous trees is infrequent. The vegetation was probably a mosaic of pine and spruce stands with prairies and sand-dune vegetation. The climate may have been like that of the eastern boreal forest today. ¹⁴C dates of 12,800 and 9500 yr B.P. bracket a time when *Quercus* (oak), *Carya* (hickory), *Fagus* (beech), and *Ostrya-Carpinus* (ironwood) dominated the vegetation. It is estimated that beech and hickory made up at least 25% of the forest trees. Conifers were rare or absent. The environment is interpreted as hickory-rich mesic deciduous forest with a climate similar to but slightly warmer than that of the northern hardwoods region of western New York State. After 9500 yr B.P. oak and pine forest dominated the landscape, with pine becoming the most important tree genus in the later Holocene.

INTRODUCTION

The vegetation history of the southeastern United States during the last 25,000 yr is still incompletely known. The classic work of Buell (1945) and Frey (1951, 1953) first showed that jack pine (Pinus banksiana) and spruce (Picea spp.) were present at Jerome Bay and Singletary Lake, North Carolina before 10,500 yr B.P. Subsequently it was established that the jack pine/spruce flora was widespread in the Southeast. The southern limit of vegetation rich in jack pine and spruce has not yet been established, and the character of the vegetation lying immediately to the south is unknown. More information on these topics is necessary to gain insights into the origin and history of the rich present-day flora and fauna of the Southeast that contain "some of the most celebrated biogeographic puzzles on earth" (Deevey, 1965). The reconstruction of the late Pleistocene and Holocene climate of the Southeast is necessary to test postulated paleoclimates for the region (CLIMAP, 1976; Peterson et al.,

¹ Contribution No. 188, Limnological Research Center, Univ. of Minnesota, Minneapolis. 1979) and is an essential element in understanding its biotic history. The present investigation is one of a series of site studies addressed to these problems. The objective is to establish a transect of sites from North Carolina and northwest Georgia to link with Lake Annie in southern Florida (Fig. 1; Watts, 1975a) which is south of the Pleistocene limit of the boreal trees.

Frey's work at Singletary Lake was expanded by Whitehead (1965, 1967, 1973), who also (1973) recorded jack pine/spruce vegetation at Rockyhock Bay, North Carolina. Similar vegetation is known from Hack Pond, Virginia (Craig, 1970), Bob Black Pond in northwestern Georgia (Watts, 1970), and Anderson Pond, Tennessee (Delcourt, 1978). In the most northerly sites, Hack Pond and Rockyhock Bay, both spruce and pine were abundant. To the south at Singletary Lake, Bob Black Pond, and Anderson Pond, pine greatly exceeds spruce in the pollen diagrams. In the Tunica Hills, Louisiana, macroscopic Picea glauca (white spruce) with up to 30% spruce pollen is known from river-terrace sediments dating to the transition from the Wisconsin to the Holocene (Delcourt and





Fig. 1. Vegetation map of southeastern United States, showing location of sites mentioned in the text. Vegetation types generalized from Küchler (1964).

Delcourt, 1977). Picea glauca cones are also known from an exposure in a strip mine near Pennington, Georgia. They have been dated to 21,300 ± 400 yr B.P. (W-3944; T. Ager, personal communication, 1979). At Lake Annie in southern Florida, vegetation dated to before 13,010 yr B.P. is interpreted as rosemary (Ceratiola ericoides) scrub on dunes, with prairie-like vegetation and scrub oak (Quercus) (Watts, 1975a). South Carolina, the Piedmont and Coastal Plain of Georgia, and northern peninsular Florida are thus defined as the region where further investigations are desirable, although the data from Tunica Hills

and Pennington, Georgia, already suggest that spruce may well have penetrated to the Gulf Coast.

THE SITE

White Pond is a small natural lake 500 m in diameter that lies about 40 km northeast of Columbia, South Carolina, (80°46′30″W, 34°10′N) at an elevation of 90 m above sea level; it is located on the Elgin 7-1/2 minute topographic sheet of the U.S. Geological Survey. The pond lies on the innermost edge of the coastal plain, where outliers of Cretaceous sands overlap the crystalline rocks of the Piedmont (Ridgeway et al.,

1966). The area has more relief than the outer Coastal Plain. Large swamps are absent. The depression is of unknown origin, but the presence of windblown sands in the area suggests origin by deflation. The lake may overflow at times of high water through a channel at the southwest corner of the basin. The water level is reputed locally to show strong fluctuations.

The main vegetation type around White Pond is commercially managed pine forest, so that it is now difficult to imagine the original vegetation. Pinus taeda (loblolly pine) is abundant, and P. echinata (shortleaf pine) also occurs (nomenclature follows Radford et al., 1968), Pinus palustris (long-leaf pine) may have been more abundant before logging. Quercus falcata (southern red oak), Carva sp. (hickory), and Liquidambar styraciflua (sweet gum) are common on low ground near the lake. Cornus florida (flowering dogwood) and other "mesic" trees and shrubs also occur. A stand of vegetation of very arid aspect occurs on the eastern shore of the lake on white sand. It is dominated by Ceratiola ericoides (rosemary) with Ouercus laevis (turkey oak). Selaginella arenicola (sand spikemoss), Opuntia sp. (prickly pear), and Cladonia spp. (lichens). A similar assemblage appears to have been a dominant element in the vegetation of south-central Florida during the Wisconsin Glaciation (Watts, 1975a). The vegetation of the pond itself is predominantly large water lilies (Nymphaea sp.). There is a stand of Betula nigra (river birch) on the southeast shore.

In March 1977 a core 390 cm long was obtained from the middle of the lake in 170 cm of water with a Livingstone piston sampler 5 cm in diameter. This core was used for the pollen and macrofossil analyses described here.

THE POLLEN DIAGRAM AND PLANT MACROFOSSILS

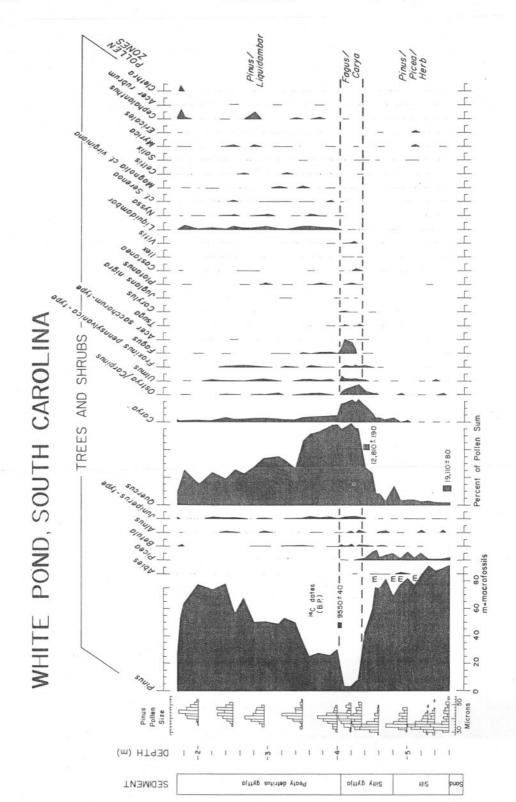
Pinus/Picea/Herb Zone (19,100 to 12,810 yr B.P.)

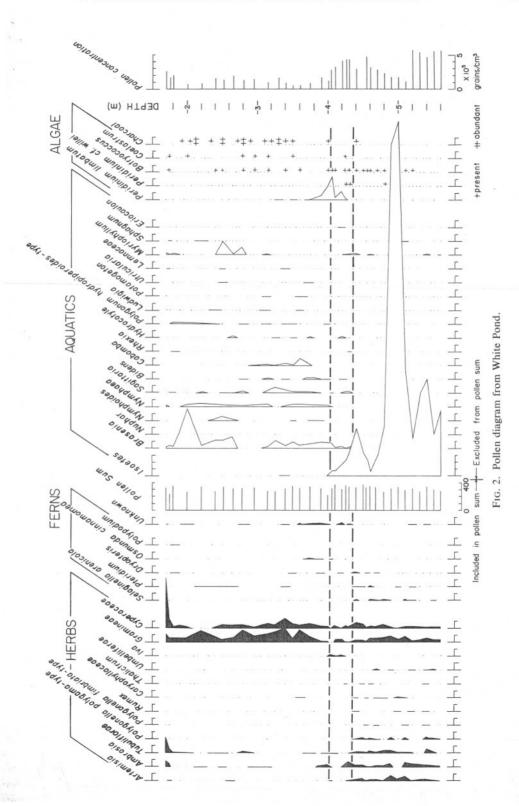
The base of the pollen diagram (Fig. 2) is dominated by pine, which contributes up to 90% of the upland pollen at some levels.

Pollen size measurements for pine were carried out on the maximum internal diameter of the body cell, following the procedures described by Whitehead (1964) and Watts (1970). Fifty grains were measured at each level; results are recorded as histograms on the pollen diagram. The small size of the pollen grains, most commonly 34 µm, suggests that jack pine may have been the predominant species (Whitehead, 1964, 1973: Watts, 1970). A few small and poorly preserved fragments of a two-needle pine are consistent in external morphology with a determination of Pinus banksiana, Pinus resinosa (red pine), the other species with small pollen grains, has morphologically very distinct needles. Occurrences of fossil pine needles are recorded by the letter M on the pollen diagram. Unlike northwest Georgia (Watts, 1970) and North Carolina (Whitehead, 1964) at least one other pine species with larger pollen grains also occurs, but in much lower frequency. On grounds of size and morphology this is a "southern" pine species. Unfortunately pollen size is not diagnostic for "southern" species, and no conifer macrofossils occur other than the needle fragments referred to Pinus banksiana.

On pollen-morphological grounds (Richard, 1970; Watts, 1980) the spruce species was mainly Picea rubens (red spruce), with traces of P. glauca (white spruce). This contrasts with Whitehead's (1980) opinion, based on size measurements, that the spruce present in North Carolina was largely P. mariana (black spruce). There is no necessary conflict, for the Wisconsin-age forests were probably richer in tree species than has been supposed. Picea rubens was not present in the forest near the glacial front at the Wisconsin maximum (Watts, 1980) but appeared as a migrant in southern Pennsylvania shortly before the invasion of white pine at the beginning of the Holocene.

Quercus pollen is present throughout, but it becomes frequent at the end of the zone for the first time, as does Carya. A crude estimate, based on the assumption of a con-





stant sedimentation rate, suggests that oak and hickory populations began to expand or invade for the first time about 15,000 yr B.P., long before the final decline and disappearance of spruce and jack pine, dated to $12,810 \pm 190 \text{ yr}$ (QL-1170). A similar expansion of deciduous forest trees beginning at 16,300 yr B.P. is noted by H. Delcourt (1978) at Anderson Pond, but no comparable event took place in northwestern Georgia (Watts, 1970), where oak was constantly present and provided up to 9% of the upland pollen influx between 23,000 and 13,000 yr B.P.

The most frequent herbs are Artemisia (wormwood), Ambrosia (ragweed), other Compositae, Polygonella spp. (jointweeds), Umbelliferae, and Selaginella arenicola. Two types of Polygonella pollen occur, polygama type and fimbriata type. Polygonella species are very characteristic of deep sandy soils and fossil dunes. A very similar assemblage of herbs, including both Polygonella types, occurs in sediments of Wisconsin age at Lake Annie in southcentral Florida (Watts, 1975a). Lake Annie is now surrounded by a fossil dune field, and it is believed that the herb assemblage was present in a drier climate than now, perhaps when the dunes were active.

The macrofossils from this zone are rather limited in both numbers and diversity (Table 1). The association of Isoetes (quillwort) with abundant Nitella and Chara (charophytes) and with Potamogeton berchtoldii (P. pusillus, pondweed) indicates an acid unproductive lake with clear or brown water. Elatine minima, which belongs with the group ecologically, has its southern limit in Virginia today.

Fagus-Carya Zone (12,810 to 9550 yr B.P.)

At 12,810 yr B.P. *Pinus* declines steeply in the pollen diagram, and *Picea* disappears soon after. *Quercus* and other deciduous tree genera rise to replace them. The character of the vegetation is indicated by the high percentage values reached by *Carya*, *Fagus* (beech), and *Ostrya*/

Carpinus (ironwood), which are far more abundant in this period than in the later Holocene. Betula (birch), Ulmus (elm), Acer saccharum (sugar maple). Juglans nigra (black walnut), Tsuga (hemlock), and Corylus (hazelnut) are exclusive to the zone or infrequent outside it. This group of "mesic" trees makes up to 30% of the upland pollen influx in the zone. It does not reach more than 8% in the later Holocene. Data from Lower Michigan (Webb, 1974) compare pollen percentages in surface mud samples from lakes with percentage basal area of the main tree genera in the surrounding forests. Of the relevant genera Ouercus, Tsuga, and Betula are strongly overrepresented in the pollen rain, Fagus is slightly overrepresented, and Carya is somewhat underrepresented. Acer, primarily Acer saccharum, is seriously underrepresented. Even with the crudity of such a comparison, the high pollen percentages for Fagus (to 10%) and Carya (to 15%) suggest that these two genera may have made up at least 25% of the forest around White Pond. Ostrya-Carpinus also has very high values and must have been abundant. Very high percentages and influx values for Ostrya-Carpinus are characteristic of the transition from the Wisconsin to the Holocene in the northeastern United States, where up to 17% of the pollen sum has been recorded (Maxwell and Davis, 1972). The same phenomenon has been observed at Anderson Pond, Tennessee (H. Delcourt, 1978) and in other southern localities. Such high percentages lack a modern analog. Today hickory makes up 4.2% of the hardwoods of South Carolina (Staff of Forest Resources Research work unit, 1976), and Fagus does not occur in large stands in the South Carolina Coastal Plain today (Hedlund and Knight, 1969). Acer saccharum, Corylus, and Juglans nigra may have been present in the forest with small populations. The pollen of Tsuga can be attributed to longdistance transport or, less probably, to very low local frequency of trees. Davis et al. (1973) show in Michigan that hemlock disperses pollen well beyond its range limit.

450-455 455-460 465-470 470-475 485-490 485-490 490-495 500-525 515-520 525-530 535-540 545-550 555-560	405-410 415-420 420-425 425-430 430-435	200-205 210-215 250-255 260-265 270-275 280-285 270-275 280-285 320-325 330-335 340-345 350-355 360-365 385-390 395-398	Depth (cm)
15 6 62		-	Isoetes sp.
_			Elatine minima
41 2 1 31	-	3 4 8	Juncus sp.
1 32			Potamogeton berchtoldii
1 111231	-		Cyperus sp.
+ + + +	+ +	+ +	Chara
++++++	+ +	+ + + + +	Nitella
+ + + +		8	Pinus banksiana needles
2	252 6	30 411 7 7 7 7 1	Nymphoides cordata
	221 6	20 3 3 9 9 11 13 13 14 4 4 1 1	Brasenia schreberi
CA CA	6 6 26 7	1 2 1 1	Naias gracillima
	2	2000 4-30 1	Potamogeton spirillus
	3 5 1	-	Myriophyllum humile
	7	2 262 1	Sagittaria spp.
		231 222622452	Nymphaea sp.
		2 8 9 2	Myriophyllum cf. heterophyllum
		w 12	Potamogeton diversifolius
		- · · ·	Potamogeton cf. pulcher
		2	Sagittaria latifolia
		2	Sagittaria cf. longirostris
		23 5	Ludwigia sp.
	-	7 3 51	Hydrocotyle sp.
		us us	Hypericum virginicum
		1 5	Scrophulariaceae cf. Agalinis
		61 1 1	Polygonum pensylvanicum
			Polygonum sp.
		27 2 2 1 1 1 1 17 17 17	Eupatorium sp.
,		- 2 3	Panicum sp.
		10 1 1 1 1 1 5 1 17 8 8	Fuirena cf. squarrosa
	_	10 15	Psilocarya nitens
		151200 9 12 1 3 1 1 10 54 10 54	Cyperus cf. engelmanni
		18	Scirpus purshianus
1		3 1 8	Scirpus atrovirens
		4	Scirpus sp.
		-	Rhynchospora sp.
			Rubus sp.
-			Geum sp.
_			Mollugo verticillata
-			Eleocharis acicularis
-			Typha sp.
1 2 1			Unknown or poorly preserved
P_i	F	P_i	Pc
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Pinus/Picea/Herb	Fagus –Carya	Pinus-Liquidambar	Pollen assemblage zones
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The low pollen percentages for pine and birch suggest that these two genera may also have been absent locally. The vegetation can be interpreted as mesic oak—hick-ory—beech forest. The herb percentages in the assemblage are very low, although *Iva* is exclusive to it.

Macrofossils of Brasenia schreberi, Nymphoides aquatica, Naias gracillima, Myriophyllum humile, Sagittaria spp., Chara, and Nitella provide evidence for a diverse aquatic vegetation, with floatingleaved, submerged, and emergent macrophytes. The sediments are fine algal gyttia with silt, indicating a lake with a high and relatively stable water level. Myriophyllum humile and Potamogeton spirillus do not occur in the Carolinas today, and Naias gracillima reaches its southern limit in North Carolina. All three are widespread in New England and the Great Lakes region. Similarly diverse northern aquatics were found in Wisconsin-age sediments in northwest Georgia (Watts, 1970).

Pinus-Liquidambar Zone (9550 B.P. to Present)

After 9550 \pm 40 yr (QL-1169) a sharp decline of Carya, Fagus, and Ostrya-Carpinus takes place in the pollen diagram. There is a new increase in pine, which morphologically and by size measurement is a "southern" pine. Oak maintains high values and is accompanied for the first time by Liquidambar (sweet gum) and Nyssa, probably N. sylvatica (black gum), the most abundant hardwoods in South Carolina today (Staff of Forest Resources research work unit, 1976). About 7000 yr B.P., assuming a constant sedimentation rate, pine again increases at the expense of oak, and a forest essentially like the modern forest was established.

The early abundance of oak justifies the recognition of two subzones within the *Pinus-Liquidambar* zone, an early oak subzone and a later pine subzone. An early oak-dominated zone with prairie plants followed by high pollen percentages of pine

in the later Holocene is also recorded from Mud Lake, Florida (Watts, 1969) and from Lake Louise, Georgia (Watts, 1971). A similar sequence has recently been recorded from Goshen Springs, Alabama (P. Delcourt, 1978). During the Holocene the pollen rain is overwhelmingly of pine and oak. The total for all other trees hardly ever exceeds 10% of the pollen rain. Carva and Liquidambar are the two most frequent genera after pine and oak. The presence of Magnolia cf. virginiana (sweet bay), Myrica (wax myrtle), Cephalanthus (button bush), and Acer rubrum (red maple) point to the development of modern swamp communities, but in this area of high relief the lowland swamp forest trees Taxodium and Nyssa, which dominate later Holocene pollen diagrams from such Coastal Plain sites as Dismal Swamp and Rockyhock Bay (Whitehead, 1972, 1973), are virtually absent. In this respect the pollen spectra also differ substantially from the modern pollen rain of the Singletary Lake area (Whitehead and Tan, 1969), where pocosins or bays are common and Taxodium. Cupressaceae, and Nyssa together contribute over 15% of the pollen rain. Pollen probably of Serenoa (saw palmetto) occurs in the middle Holocene. Unfortunately, preservation of the few pollen grains found does not permit a definitive identification. Serenoa does not now occur locally (Radford et al., 1968), although it is abundant farther south in the lower Coastal Plain. Herbs are insignificant in the Holocene assemblage, but their expansion following modern forest clearance can be seen at the top of the diagram. Lower in the diagram the frequency of grass and sedge pollen is probably attributable to shore communities, for macrofossils of both groups are frequent in the sediments.

The macrofossil record shows that the open-water communities of the Fagus/Carya assemblage were replaced at the transition to the Holocene, when northern aquatics disappeared, with the exception of Naias gracillima, which persisted until the middle Holocene. The sediment is coarse

detritus-gyttja, with some very fibrous layers virtually without seeds and fruits. and finer sediments with macrofossils. Charcoal at virtually all levels (Fig. 2) attests to the occurrence of fires. Floatingleaved and submerged aquatics (Nymphaea, Brasenia, Nymphoides, Cabomba, Potamogeton cf. pulcher, Myriophyllum cf. heterophyllum) show that a lake with open if shallow water was always present, while shore and marsh plants such as Fuirena cf. squarrosa, Psilocarya nitens, Cyperus spp., Eleocharis sp., Rhynchospora sp., Ludwigia sp., and Polygonum spp. suggest water-level fluctuations with unstable shore vegetation rich in weedy ephemerals. If extreme water-level fluctuations took place there may have been times when the sediment surface was exposed to the air, with loss of sediment by erosion and oxidation. If this took place, and the diversity of sediment type is consistent with that possibility, there may be hiatuses in the Holocene record. This would also be a partial explanation for the low values of pollen concentration (Fig. 2), from which very low influx values may be inferred. With only three radiocarbon dates and diverse sediments it was considered that a pollen influx curve would be of doubtful validity.

DISCUSSION

The results from White Pond add another site, now in South Carolina, to the already documented occurrences of Wisconsin-age jack pine/spruce forest in northwest Georgia (Watts, 1970), Anderson Pond in middle Tennessee (H. Delcourt, 1978), and in North Carolina at Singletary Lake (Frey, 1953) and Rockyhock Bay (Whitehead, 1973). Jack pine and spruce were not recorded from Sheelar Lake in northern Florida (W. A. Watts, unpublished data) so that the southern limit of the boreal conifers may have been in the lower piedmont or coastal plain of Georgia. The superficial similarity of the sites to one another should not obscure important differences. In Georgia up to 9% oak, with constant presence of ironwood and hickory, characterizes the period between 23,000 and 13,000 yr B.P., when the dominant tree was jack pine. The sites in the Carolinas had few or no deciduous trees during most of the Wisconsin.

White Pond has a herb assemblage different from that of Rockyhock Bay (Whitehead, 1979). Polygonella is rare at Rockyhock Bay, and Selaginella arenicola is not recorded. This suggests that dune vegetation may have been more widespread in South Carolina than farther north. In contrast, Whitehead's (1963, 1973) "northern" elements in the herb flora-Schizaea pusilla, Lycopodium spp., and Sanguisorba canadensis-are completely absent from White Pond, suggesting that the more northerly site had a distinctly more boreal flora. The presence of Artemisia, Ambrosia, composites, grasses, sedges, and other herbs with up to 10% of the pollen sum at some levels is taken as evidence that herb-dominated prairie-like communities may also have been present. Webb's (1974) data from Michigan show that jack pine and red pine, which were not differentiated in his study, are markedly overrepresented in modern pollen surface samples from lakes. The very high jack pine percentages at White Pond may exaggerate the extent of forest cover. Whitehead and Tan (1969) argue that the full-glacial vegetation was extremely open pine-dominated forest, based on the abundance of pine pollen and generally low pollen accumulation rates. Possibly there were large areas of open herbaceous vegetation at White Pond, occurring as prairie or sandhill communities. There are no criteria by which the former patterns of the vegetation can be determined. Jack pine woods and herbaceous communities may have existed as a mosaic controlled by small edaphic and moisture differences, or the pines may have been widely spaced in a savannah-like community.

The climate of the jack pine/spruce period cannot be defined very precisely. There is no modern analog for the flora, because the conditions of competition, day

length, and soil type in South Carolina differed greatly from those of boreal forest with jack pine today. If the climate resembled that of central Maine or New Brunswick today, the nearest areas on the eastern seaboard where jack pine is widespread (Fowells, 1965; Little, 1971), then there would have been a greater average annual temperature range (about 30° instead of 20°C), lower temperatures at all seasons (January average of -10° instead of 7.7°C, July average of 19.8° instead of 27.1°C), a much shorter growing season (114 days without killing frost instead of 248), and slightly less precipitation (1050 instead of 1140 mm). The data compared are from Millinocket, Maine, and Columbia, South Carolina (U.S. Dept. Agriculture, 1941). Fowells (1965) notes that jack pine is confined to the boreal and northern forest regions except for its occurrence on sand dunes at the south end of Lake Michigan. Climatically, the Lake Michigan sites are intermediate between Maine and South Carolina, but a semi-maritime climate is created by the immediate proximity of a large body of water and, although this is the area with highest average annual temperatures and longest growing season in which jack pine now occurs, it may not provide a valid analog for central South Carolina. Lake Michigan and Maine are chosen for climatic comparison because they represent the climatically most favorable sites in which jack pine flourishes today, and they can be used to estimate the minimum climatic difference between the Pleistocene and modern climates of South Carolina. The difference may, of course, have been greater. Maine seems particularly appropriate for comparison because of evidence (Watts, 1980) that large populations of jack pine migrated northward on the Coastal Plain at the transition to the Holocene. The Maine and other jack pine populations in New England may be genetically derived from Pleistocene populations on the southern Coastal Plain.

It may be undesirable to deduce climate

from the occurrence of jack pine only. Other species present, including red spruce, grow in much less continental climates. Nevertheless, the dominance of jack pine in the woody flora suggests that its modern occurrences and climatic tolerance may provide the best analog for the Wisconsin age in South Carolina, even though that analog should be viewed with caution.

The herbaceous plants at White Pond are consistent with the cold climate inferred from the presence of jack pine and spruce. The climate may have been very dry and was probably very windy, as evidence from North Carolina and Florida suggests (Thom, 1970; Watts, 1975a). Thom (1970) has presented evidence that Carolina Bays formed under the influence of strong southwesterly winds. He has also shown that dune and bay formation were contemporary at Bull Creek, North Carolina, where dune formation was taking place after 17,000 vr B.P. Whitehead (1980) also considers that the climate was drier than at present, consistent with the assumed boreal-continental character inferred from the presence of jack pine and spruce. This is compatible with high water levels in lakes, because the reduced length of the frost-free season and the generally lower temperatures would limit evaporation. The interpretation of lowered temperature, decreased precipitation, and prevalent windiness, however, is not consistent with model simulations of the 18.000 yr B.P. climate, which show no variation or an actual increase in precipitation (Peterson et al., 1979), but the existing model attempts to simulate summer temperatures only, so it would be premature to identify a discrepancy until other seasons have also been simulated. By 15,000 yr B.P. the expansion of oak and hickory at White Pond is an important indication that the climate had begun to warm.

White Pond shows clearly and with good dating control the expansion of deciduous forest that characterized the beginning of the Holocene in the Coastal Plain. Forest of

oak, beech, hickory, and ironwood lasted from about 13,000 to about 9500 yr B.P. The generalized pollen diagram from Singletary Lake and other Bladen County Lakes (Frey, 1953) shows relative abundance of the same species, together with birch. At Rockyhock Bay (Whitehead 1973, 1980) Carya plays no significant role, and the important mesic trees are Tsuga, Betula, Fagus, and Ostrya/Carpinus. These four genera never exceed 10% of the pollen rain, Ostrya-Carpinus, the commonest, reaching a maximum of 5%. In contrast, the sum of Fagus, Ostrya-Carpinus, and Carya at White Pond exceeds 30%, and there was clearly a more diverse broadleaved forest in South Carolina than farther north. At White Pond Betula and Tsuga are in very small quantity. Tsuga was never significant at White Pond, and its populations in the earliest Holocene, and perhaps also its Pleistocene refuge area, must have been north of South Carolina. It was frequent in North Carolina and at Hack Pond in the Shenandoah Valley of Virginia (Craig, 1969). Beech had its major populations and perhaps its Pleistocene refuge farther south. Its abundance at White Pond is matched by early Holocene abundance at Pigeon Marsh in northwestern Georgia (Watts, 1975b), where it was accompanied by Carya, Ostrya-Carpinus, and Juglans cinerea (butternut), but with only traces of Tsuga.

The Fagus-Carya assemblage has important climatic implications. The forest seems to have been "mesic," though the term must be used with caution (Davis et al., 1973), and most of the tree species occur today in favorable localities within pine and oak forest. The mass expansion of Fagus, Ostrya-Carpinus, and Carya probably required a cooler and moister climate than today. The percentage values for Carya are higher than any recorded in the later Holocene or in surface samples. High Fagus percentages are known from northern hardwoods forest in New York State and farther north, and perhaps that area

provides an approximate climate analog for the beech-hickory assemblage at White Pond.

The Allegheny Plateau in western New York has northern hardwoods forest in which Fagus grandifolia, Acer saccharum, and Betula alleghaniensis (yellow birch) make up 50% or more of the trees, either singly or in combination. Fagus provides from 10 to 30% of the Holocene pollen rain in the region (Miller, 1973), and Ostrya-Carpinus as much as 10%. The climate record from Franklinville on the Allegheny Plateau shows a January average of -5.7° , July average of 19.6°C, 125 frost-free days, and precipitation of 980 mm. If this is a valid analog for the Fagus/Carya assemblage at White Pond, it means that January temperatures were higher and the growing season slightly longer than in the jack pine/spruce period. The abundance of Tsuga, Betula, and Acer saccharum in the pollen counts from western New York (Miller, 1973), and the relatively low component of Carya in the pollen rain and in the forest, suggest that this area is more satisfactory as an analog for Singletary Lake or Rockyhock Bay and that a still more exact analog should be sought farther south. Beech, hickory, and abundant oak occur together at sites in both the mixed mesophyte forest and the northern oak-chestnut region (Braun, 1950), but often with chestnut (Castanea dentata), hemlock, or black gum. A transect of surface samples from western Tennessee to eastern North Carolina and passing through the major vegetation types of the region (H. Delcourt, 1978) shows highest value of 4% for Fagus and 8% for Carya. Beech may well be the most demanding tree of the assemblage. Fowells (1965) notes that it is a mesophytic species with high water requirements during the growing season. A close modern analog of the Fagus/Carya assemblage is probably not available, because Carya species are generally not abundant as far north as western New York, but the forest probably occurred in a

climate with somewhat higher winter temperatures, longer growing season, and greater availability of water in the growing season than on the Allegheny Plateau today.

The late Holocene at White Pond shows that, in a Coastal Plain site where the pollen rain is derived from the upland, pine and oak taken together provide as much as 90% of the pollen, with little pollen of other trees. *Liquidambar* and *Nyssa* are exclusive to this zone. They are the commonest hardwoods in the South Carolina Coastal Plain today.

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