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THE LATE QUATERNARY VEGETATION HISTORY OF THE SOUTHEASTERN UNITED STATES[1]

❖4183

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INTRODUCTION

The Quaternary vegetation history of the unglaciated United States east of the Mississippi River has been reviewed in recent years by Whitehead (80, 81, 83) and, in a continental context, by Wright (87, 88). The emphasis in the present review is on Florida, the Coastal Plain from Georgia to Virginia, and the southern Appalachians (Figure 1). This region has the highest density of studied sites and presents a transect from tropical vegetation in southern Florida to temperate mesic forest in the mountains. New studies from Tennessee and Alabama are also considered (25, 26, 28, 29). The sequence of events closer to the Late Wisconsin ice margin in the central Appalachians has recently been described in detail (73) and is not reconsidered here. The review focuses on the time since 30,000 BP (radiocarbon years before present). This is the period for which there is good time control by radiocarbon dating and for which most information is available. Interglacial and older Pleistocene floras in the Southeast are little known.

The history of vegetation in the Southeast continues to be of contemporary interest for three reasons:

1. The great development of ocean-core studies in the 1970s provides evidence by inference or by transfer-function for the reconstruction of past climates (13, 50, 55). Climate can also be inferred from pollen analysis (4, 20) of lake and bog sites. Both sources of climatic inference have practical and theoretical limitations, but it is of great interest to compare the two data

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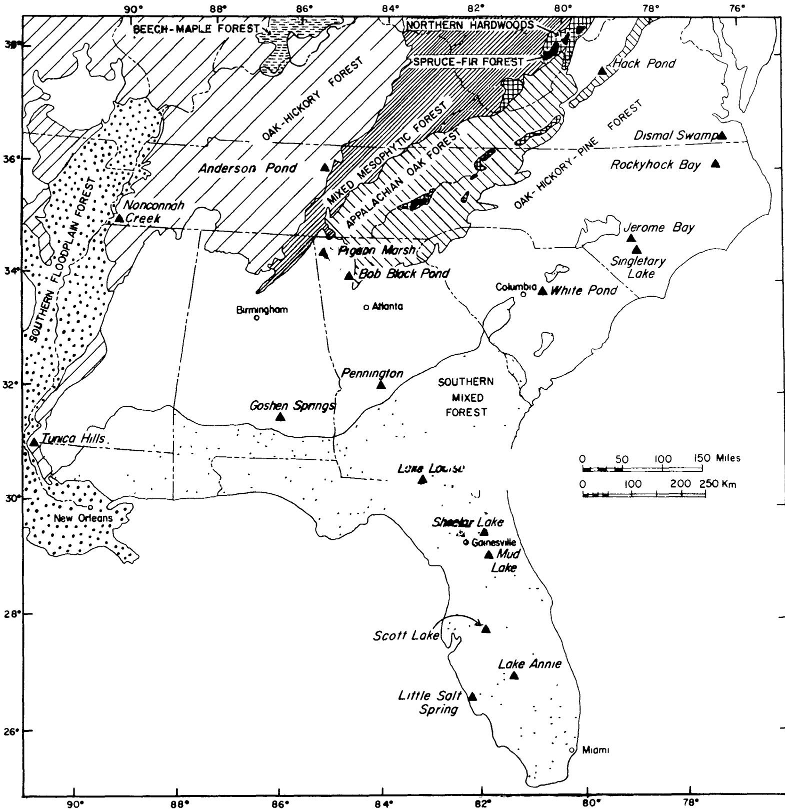

Figure 1 Vegetation map of southeastern United States, after Küchler (41), showing location of the major pollen sites referred to in the text.

sets. Ocean-core records can only be transferred into climatic terms by a modeling process, which depends on assumptions that may be difficult to quantify with confidence. It is important to validate them by the independent data set provided by the terrestrial record of vegetation. This has special significance in low and mid-latitudes where few sites have been investigated by pollen analysis (52). Oxygen-isotope stratigraphy in ocean cores also provides a basis for global stratigraphic correlation (56, 57) in cores spanning long periods of the Quaternary. The alignment of more detailed but more fragmentary stratigraphic records from land with the ocean-core stratigraphies has scarcely begun (55).

2. Understanding of how plant communities respond to climate change is improving (20, 69). Species appear to act independently under the pressure of changing climate by expanding or contracting their population sizes

at any one locality. Unsuccessful species decline in numbers or become extinct locally, while the successful ones invade new localities. Thus plant communities are readily changed by addition or loss of species (20, 69). Present-day behavior of species may not have characterized them in the past, suggesting that transfer functions (77) have limitations in making inferences from fossil plants about past climates (20). Today's plant assemblages of the Southeast may not have existed in the past under different climatic circumstances. Their nature can only be established from the fossil record. The timing and rate of change from one stable assemblage of biotic communities to another as the Quaternary climate changed are of both stratigraphic and ecologic interest (55, 69).

3. There is a continuing interest in where and how the remarkable biota of the Southeast survived during the Quaternary (46, 83). The many cases of plant and animal taxa with very limited ranges (8, 21, 22), the remarkable disjunctions to eastern Asia known since Asa Grey (35), and the survival of evolutionarily archaic forms such as ganoid fish, plethodontid salamanders, alligators, and magnolias are the material of classical biogeography (22). Their occurrence acquires a new interest in the light of our present knowledge (*a*) that the ranges are not of great antiquity, as classical biogeography supposed (8, 9), but the vegetation generally in low and mid-latitudes was profoundly altered by Quaternary climatic change (43, 61, 62, 63), and (*b*) that modern ranges and biotic communities probably took shape during the Holocene.

PALEOCLIMATIC AND STRATIGRAPHIC CONTEXT

The study of $^{18}O/^{16}O$ ratios in planktonic organisms preserved in ocean cores has provided a global framework for Quaternary stratigraphic correlation (56). During glacial periods isotopically light ice accumulated on the continents, leaving the oceans slightly enriched in ^{18}O. Glacial periods can be defined by maximum divergence of $^{18}O/^{16}O$ ratios from the present, representing the most extensive ice sheets and the lowest sea levels. In interglacial periods oxygen isotope ratios, ice-sheet cover, and sea level approximate present values. Intermediate conditions of inferred ice cover are "interstadial." Several episodes can be recognized in the last 100,000 years from mid-latitude North Atlantic cores [Figure 2; (55, 57)]. Glacial conditions existed briefly from about 84,000 to 73,000 BP, followed by a long undifferentiated interstadial from 73,000 to about 30,000 BP. At 30,000 a climatic deterioration began, culminating in the glacial maximum of 18,000 BP (13). Interglacial conditions were restored by 13,500 BP in the North Atlantic at 54°N (55) and interrupted at that latitude by a brief re-advance of polar water about 10,000 BP (55). Unfortunately, equally

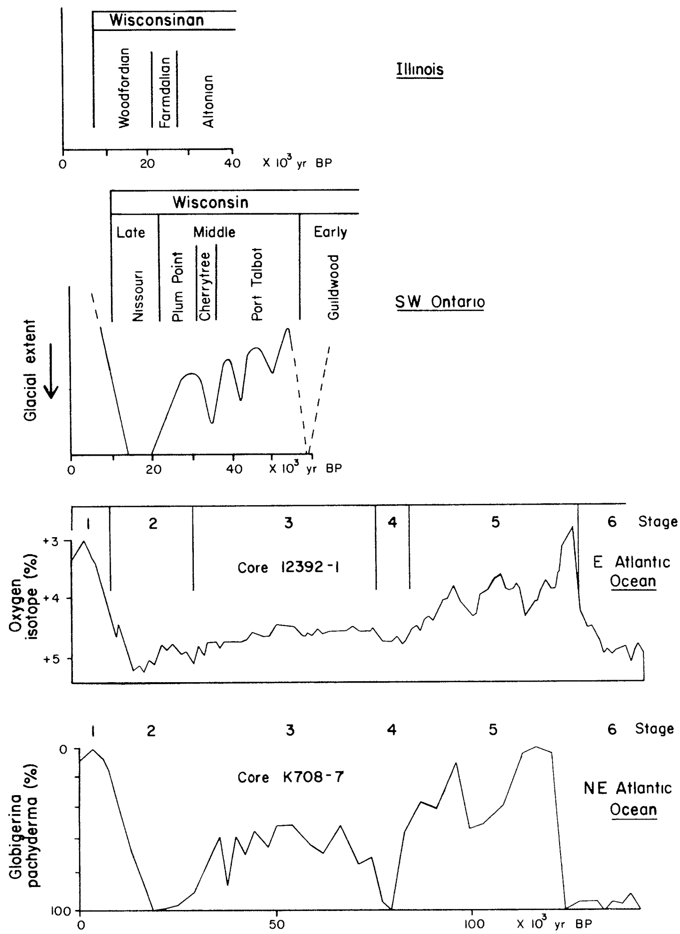

Figure 2 $^{18}O/^{16}O$ and Foraminifera profiles from two cores in the eastern North Atlantic (55, 57) compared with land stratigraphy from eastern North America (3, 86). Stage numbers after Emiliani (31).

detailed studies of the western North Atlantic are not available because of slow sedimentation (2) and because the Bermuda region lacks sediments suitable for study (50).

Temperature maps of surface water in the North Atlantic for 18,000 BP have been reconstructed for the four seasons, making use of transfer-function analysis of foraminiferal assemblages (50). These show that the western Atlantic from the Florida peninsula north to Cape Hatteras had ocean surface temperatures only 3°C lower than those of today, with some penetration of northern plankton species (50). North of Cape Hatteras a rather steep gradient in temperature and plankton composition extended to a polar front located at about 42°N latitude. In this part of the west Atlantic, winter surface temperatures differed little from today, but summer was much colder (15°C). The North Atlantic Drift appears to have been deflected east at the latitude of Cape Hatteras. One might presume that at 18,000 BP the climate in Florida and the southern Coastal Plain was similar to that of today, but that from North Carolina northward to the glacial margin it was much colder. However, a map of the 18,000 BP July climate (34) calculated from the estimated ocean-surface temperature, extent of ice sheets, and the continental albedo suggests that the July 18,000 BP climate of the southeastern United States was much colder (by about 12°C), drier, and windier than today. The validation of these estimates by pollen analysis is of considerable contemporary interest.

In ocean cores slow sedimentation and bioturbation may obscure fine stratigraphic detail. On land more precise dating and better estimates of rates of change from one relatively stable condition to another can be expected. In principle a lake core with a fast sedimentation rate should yield a better stratigraphic record from the Late Wisconsin and Holocene than the oceans, but the climatic interpretation of the record is more complex (20).

No independent Pleistocene stratigraphy exists at present for the Southeast. The well-known Illinois system (80) has been applied (28, 67, 70), as has the stratigraphy of the Lake Erie region of Canada (3, 49, 81, 83). The Illinois system identifies a Late Wisconsin ("Woodfordian") glaciation, beginning at 22,000 BP and ending at 12,500 BP, preceded by a relatively warm "Farmdalian" interstadial from 28,000 to 22,000 BP, in turn preceded by a long nonglacial but cold "Altonian" representing all of the to define the end of the Wisconsinan. However, as change had begun earlier record (3, 49) may not find expression in the southeastern United States. A "Farmdalian" warm phase is not evident in ocean cores (Figure 2).

Definition of the end of the Wisconsin glaciation also poses difficulties (65). In ocean cores the change from glacial to interglacial conditions defined by $^{18}O/^{16}O$ ratios is determined by the rate of ice melting and mixing of ocean waters. The most rapid change was taking place between 14,000 and 13,000 BP, so that an arbitary date of 13,500 BP may be used to define the end of the Wisconsin. However, as change had begun earlier and continued later, the arbitrariness of the date must be emphasized. Similarly, on land the climatic changes inferred from sediments record changes in size of plant populations, but the timing of a detectable response is affected by inherent biological limitations such as generation length and number of years before reproduction, maximum potential migration rates of tree populations, and proximity of the sampling site to a major vegetational ecotone (20, 65). For these reasons the record of the transition from "glacial" to "interglacial" conditions is time-transgressive from lower to higher latitudes, and a single date valid everywhere for the end of the Pleistocene is unattainable (65).

In this review it is assumed that interstadial conditions existed before 22,000 BP, but the existence of a "Farmdalian" warm phase between 28,000 and 22,000 BP remains to be tested. After about 22,000 BP, glacial conditions prevailed, reaching their extreme expression at about 18,000 BP. Melting of ice sheets was taking place rapidly about 13,500 BP, but the definition of the end of the Pleistocene must be considered independently at each site.

Glacial Conditions: The Late Wisconsin, 22,000–13,500 BP

The Laurentide ice sheets extended far to the south between approximately 22,000 and 13,500 BP. There is great regional variation in the timing of advances and retreats of ice lobes (89) in the Great Lakes region at the margin of the main ice mass, but this is not reflected in the behavior of southeastern vegetation. Late Wisconsin vegetation of a rather homogeneous type is known from Rockyhock Bay, North Carolina [Figure 3; (83)], Singletary Lake, Bladen County, North Carolina (32, 33, 81), White Pond, South Carolina [Figure 4; (74)], Quicksand Pond and Bob Black Pond in Bartow County, northwestern Georgia (67), and Anderson Pond at the western margin of the Cumberland Plateau, Tennessee (25, 26). At all of the sites the pollen flora is dominated by pine with some spruce, broad-leaved trees, and diverse herbs of prairies or sandhills. Pine makes up 60–80% of the pollen. It has been identified at a few sites as *Pinus banksiana* (jack-pine) from fossil needles and characteristically small pollen grains (25, 67, 79), and pollen of jack-pine size occurs predominantly or exclusively at all sites. *Pinus resinosa* (red pine) pollen is similar in size to that of jack-pine, but there is no positive evidence from macrofossils that red pine was present. *Picea* (spruce) needles occur at the Bartow County sites and at Anderson Pond, but the three species cannot be distinguished by needle morphology. Cones of *Picea glauca* (white spruce) occur in terrace deposits in Louisiana dated to 12,740 BP (10, 30) and at Pennington, Georgia, dated to 21,300 BP [Figure 1; (74)]. *Picea rubens* has been tentatively identified by pollen morphology at White Pond (74) and Anderson Pond (25, 26). Whitehead (83) showed that *Picea mariana,* which has smaller pollen grains than the other two eastern spruces, was the common species at Rockyhock Bay. Probably all three species were widespread in the Southeast. While identification of spruces by needle morphology does not seem promising, Birks & Peglar (5) have recently shown that the three species can be distinguished by pollen morphology and size characteristics. Pollen of *Abies* (fir) has been noted with low frequency at most sites, but macrofossils have not been found.

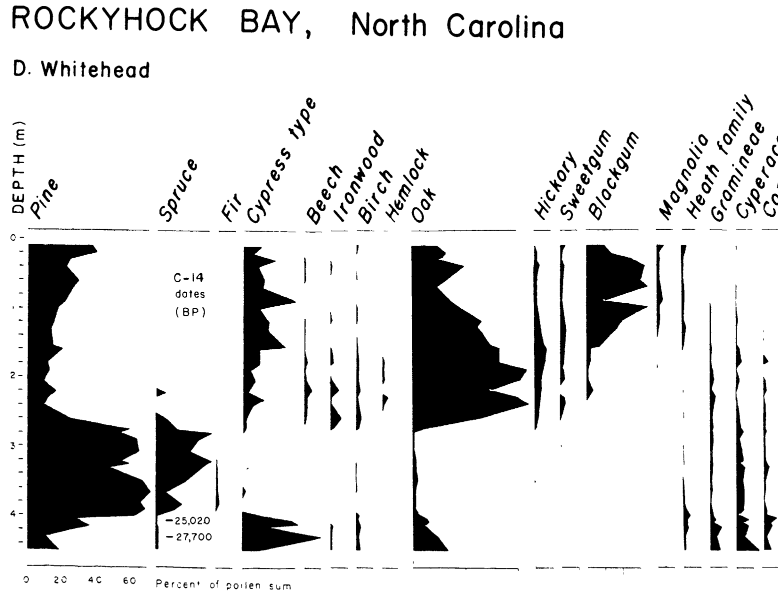

Figure 3 Abbreviated pollen diagram for Rockyhock Bay, North Carolina, on the coastal plain. Redrawn from Whitehead (83).

Among the broad-leaved trees, *Quercus* (oak) provides up to 9% of the pollen in the Bartow County ponds. *Ostrya/Carpinus* (ironwood) and *Carya* (hickory) are constantly present in small quantity, and there are traces of other deciduous trees. At Coastal Plain sites oak and other broad-leaved trees are rare at 18,000 BP.

At all sites the herbs include *Artemisia* (wormwood), *Ambrosia* (ragweed), Tubuliflorae (other composites), grasses, and sedges, an assemblage characteristic of prairies (47). *Polygonella* spp. (jointweeds) and *Selaginella arenicola* (sand clubmoss, at White Pond) occur on coarse sandy soils, including fossil dunes. Herbs rarely exceed 10% of the total pollen.

Although the sites appear to have homogeneous floras, regional differences exist. Whitehead (78, 83) recorded "northern" herbs from Singletary Lake and Rockyhock Bay, including *Lycopodium* spp. (clubmosses), *Sanguisorba canadensis* (burnet), and *Schizaea pusilla* (curlygrass fern). These have not been found in South Carolina or Georgia.

The jack-pine/spruce/herb flora has a definable geographic distribution and altitudinal occurrence. In northern North Carolina (83), the Shenandoah Valley of Virginia (17), and the Dismal Swamp (82) the percentage of spruce in the pollen counts is much higher than farther south. In southern Pennsylvania (73) the forest was spruce-dominated without jack-pine, which did not appear until northward tree migrations began at the end of

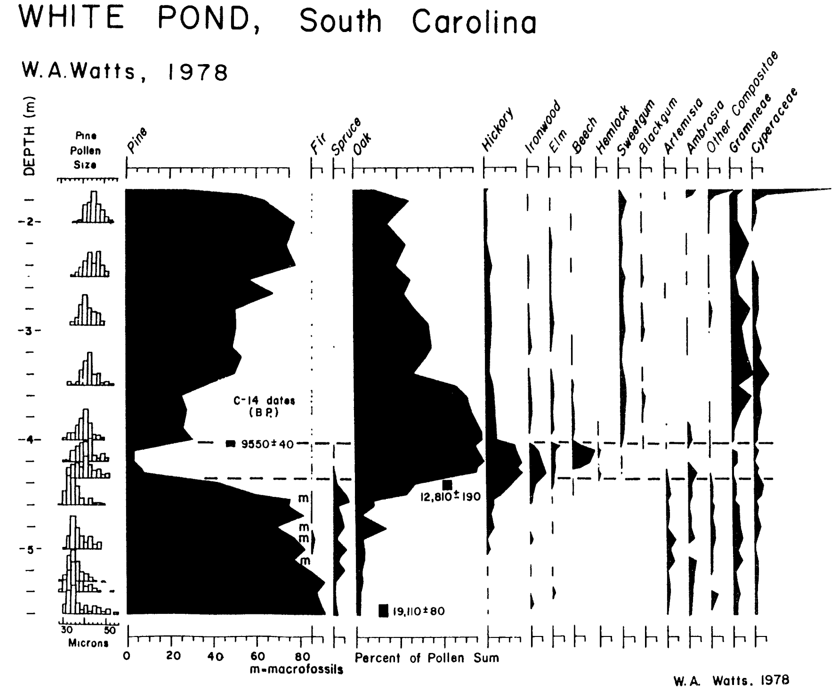

Figure 4 Abbreviated pollen diagram for White Pond, near Columbia, South Carolina. Extracted from Watts (74).

the Late Wisconsin. The record from Anderson Pond shows that forest like that of northwestern Georgia extended to west of the Cumberland Plateau. At Goshen Springs, Alabama (28, 29) the Late Wisconsin section of the core cannot be identified with certainty between the dates 26,000 and 5,620 BP in a slow-sedimenting core and may even be absent because of a possible hiatus (28). There is some evidence from Lookout Mountain in northwestern Georgia (71) that even relatively low mountain crests in the southern Appalachians were not forested. In northern Florida at Sheelar Lake northeast of Gainesville, spruce was absent except for single pollen grains between 23,880 and 14,650 BP (Figure 5). It must have reached its southern limit in the Coastal Plain of Georgia and the Tunica Hills, Louisiana (30). The vegetation at Sheelar Lake was dominated by a two-needle pine that has not been identified to species. Broad-leaved trees with prairie and sandhill herbs made up the remaining 30% of the flora [see Watts & Stuiver (75a)].

The reconstruction of the Lake Wisconsin environment of the Southeast is difficult because of apparent inconsistency between the modern distribu-

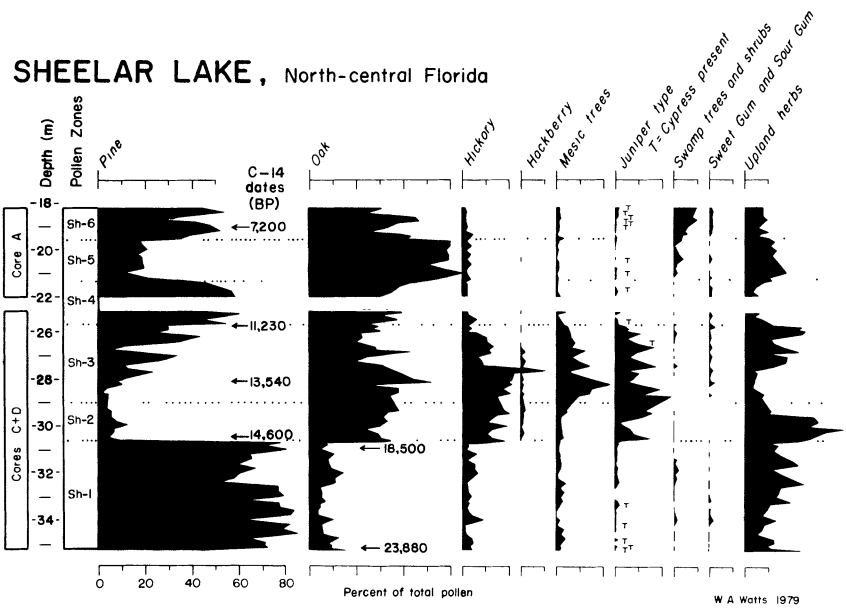

Figure 5 Abbreviated pollen diagram for Sheelar Lake, near Gainesville, north-central Florida. From (75a).

tion and ecology of jack-pine and its glacial-age occurrence. At present jack-pine in New England is limited to the higher mountains. Its main occurrence on the Atlantic Coast near the fossil sites is found in central Maine. If it is legitimate to transfer the Maine climate to the Southeast (74), then the Late Wisconsin climate was as follows (comparative figures for Columbia, South Carolina, in parentheses): January average temperature -10.1°C (7.7°C), July average 19.9°C (27.2°C), number of frost-free days 114 (248), precipitation 1,050 mm (1,060 mm). In the mid-continent the main range of jack-pine lies in a still colder and much drier climate. Sand-plains are a favored habitat for jack-pine in the Great Lakes region, and it is clear that the coarse sandy soils of the Coastal Plain in a colder climate must have provided a similar environment. The occurrence of jack-pine on poorly drained silt loams in Georgia (67), however, emphasizes that the jack-pine/spruce forest was not limited to one soil type. The success of the pine in occupying sites that would seem unsuitable from modern understanding of its habitat preference may perhaps be explained by lack of competition. What is surprising is not so much that spectacular success of the jack-pine but the failure of possible competitors.

This conclusion leads to a search for further environmental/climatic factors that might have made the Late Wisconsin climate exceptionally severe in the Southeast. It was clearly a windy climate, for dune formation caused by southwesterly winds was taking place on the Coastal Plain (59, 60). Ocean-core studies (13, 50) suggest that the July surface temperature of the ocean off the Florida coast was depressed by as little as 2°C, with little change from the present in the Gulf of Mexico. It is not clear that this would be sufficient to explain a major lowering of land temperatures, and the figures may not record a sufficiently large depression of ocean-surface temperature. However, Gates (34), making use of CLIMAP data (13) and further assumptions about land ice-cover and albedo, modeled a reduction of more than 10°C in July temperatures for the Southeast. This is consistent with the climatic interpretation proposed here. However, the only strictly climatic evidence is the temperature lowering inferred from the vegetation, especially jack-pine and boreal spruces (66, 83), and the evidence of windiness and wind direction from Thom's studies of Carolina Bays (59, 60).

Interstadial Conditions: The Mid-Wisconsin Before 22,000 BP

Few sites have a vegetation record older than the pine-spruce zone. At Singletary Lake the pine-spruce zone has silty sediments, underlain by an organic unit older than 35,800 BP (81), designated zone N by Frey (33). This contains important amounts of pollen of oak, *Betula* (birch), hickory, Cupressaceae (white and red cedar, bald cypress), and *Alnus* (alder), as well as traces of *Fagus* (beech). Alder, *Ilex* (holly), Ericaceae (heaths), grasses, and sedges suggest the presence of bayhead vegetation (11), for which there is no evidence in the pine-spruce zone above. Jack-pine is frequent, as determined by pollen size measurement (81), and spruce also occurs. This flora points to a more temperate climate than in the succeeding pine-spruce zone, but jack-pine and spruce indicate substantially lower average annual temperature than in the Holocene. The same type of vegetation can be recognized from before 25,000 BP back until before 30,000 BP at Rockyhock Bay [Figure 3; (83)]. Frey (33) recognized other older phases in the Bladen County lakes that have not been dated, but his P zone is dominated by pines with large pollen grains, perhaps a "southern" species. The age and significance of the older phases are hardly understood. All are "warmer" and more like the Holocene than the pine-spruce zone but are floristically intermediate. Two peat beds from Long Beach, North Carolina (84), have radiocarbon dates centering on 36,000 years and believed to be finite, but with large standard errors. Their pollen content resembles the N zone at Singletary Lake.

The correlation of the North Carolina sites with sub-stages of the Wisconsin farther north is uncertain. At Rockyhock Bay it is established by bracketing radiocarbon dates that the pine-spruce zone correlates with the Late Wisconsin ice advance. The Mid-Wisconsin in this region may have had a rather stable vegetation for a long period in which many elements of the modern vegetation occurred together with northern elements. This is more comparable with the long undifferentiated interstadial of the ocean record (Figure 2) than with the land record near the glacial front.

At Green Pond in Bartow County, northwest Georgia, sediments dated from before 29,630 BP to after 23,600 BP show a tripartite sequence (70). (*a*) Before 29,630, pollen of pine and oak dominated, together with herbs such as *Ambrosia* and other composites. Little can be said about this rather nondescript flora, except that it is temperate in character and suggests a dry climate. (*b*) From 29,630 to about 25,000 BP, oak, hickory, and some *Liquidambar* (sweet gum) are the main components of the pollen assemblage, with little pine. This is interpreted as dry oak-hickory forest. (*c*) From 25,000 until after 23,600 BP, pine became more frequent, spruce was present in small quantity, and the forest was diversified by the local presence of *Taxodium* (bald cypress) and a variety of bayhead shrubs and trees, suggesting increased moisture. *Taxodium* was north of its modern range, which in Georgia and Alabama is virtually confined to the Coastal Plain. This flora is essentially modern, spruce being the only northern element. At Bob Black Pond nearby (67), a flora with diverse pines, spruce, oak, and some pollen of Cupressaceae type (perhaps *Taxodium*) gave way after 22,900 to a flora of jack-pine, spruce, and oak, indicating a sharp climatic change about 23,000 in the direction of coldness and dryness. The appropriate date for the beginning of glacial conditions in Southern Appalachia thus is 23,000 rather than 22,000

The Green Pond sequence resembles an interglacial cycle in its development from "dry" temperate forest to "wetter" forest with bayhead development (38, 63). It is in part "Farmdalian" in age. However, the pre-30,000 vegetation is unknown and may also have been "warm," so that the beginning of an interstadial cannot be delimited at this site.

At Goshen Springs, Alabama (28, 29), the Mid-Wisconsin before 26,000 BP is pine-dominated with oak and traces of other deciduous trees. The pollen diagram continues downward into a period beyond the range of radiocarbon dating with abundant *Castanea* (chestnut), oak, hickory, *Nyssa* (black gum), pine, and frequent beech. This interesting flora is of unknown age. It may be correlated with the N or P zones at Singletary Lake, in which case it is of Early Wisconsin or early Mid-Wisconsin age. The possibility of a Sangamon (Last Interglacial) age cannot be excluded.

Transitional Conditions: The "Late-Glacial," 13,500–10,000 BP

The Late-Glacial period is well defined in northwest Europe and Scandinavia, especially in the classic area of Denmark (37, 45). It dates from approximately 13,500–10,000 BP and corresponds in time with the retreat of glacial ice from northwest Europe at the end of the last glaciation. It is commonly divided into three phases, a phase of pioneer vegetation on recently deglaciated terrain, a phase of interstadial warmth (the Allerød oscillation), and a subsequent time of severe climatic cooling (the Younger *Dryas* period) during which polar water reinvaded the eastern North Atlantic (55). Many authors further describe a tripartite division of the first phase, recognizing a Bølling warm oscillation (37) within it. The regional expression of late-glacial climates in northwest Europe may be a local phenomenon without exact equivalents elsewhere (75).

In North America (87, 88) tundra was locally present in the northern part of Minnesota, bordered to the south by large areas of spruce and *Larix* (tamarack) forest. There is good evidence that some deciduous trees, especially oak and *Fraxinus nigra* (black ash), were present in the spruce forest. The "late-glacial" vegetation seems to have been stable, and there is no evidence for European-style climatic oscillations. The spruce forest deteriorated rapidly about 10,500 years ago, time-transgressively from south to north, and gave way quickly to mixed forest of conifers and hardwoods with little spruce (87, 88). In the northeastern United States (73) tundra bordered by spruce forest lay south of the Late Wisconsin ice. As the ice retreated a complex series of migrations took place in which spruce forest was invaded and replaced in sequence by jack-pine, fir, *Betula papyrifera* (paper-birch), *Pinus strobus* (white pine), and other tree species. Once the migrations began they seem to have continued unchecked until at least 9,000 BP, when the forest achieved a new stability. The sequence of invasions and the localities from which invasions were initiated are of great interest, because they give insight into the location of refuges during glacial periods.

White Pond (74) contains one of the most clear-cut cases of a distinctive transitional flora from Wisconsin to Holocene (Figure 4). Around 12,810 BP jack-pine and spruce forest disappeared abruptly and were replaced by forest with abundant oak, hickory, beech, ironwood, and elm. This clearly mesic deciduous forest collapsed about 9,550 BP and gave way to mixed oak and pine forest with little pollen of mesic trees. The climate is impossible to determine because there are no good modern analogs. Values of 15% for hickory are not known today, and the ironwood percentages are also high. In comparison with the Late Wisconsin, the climate must have had higher annual temperatures, a longer growing season, and abundant available moisture during growth. Whitehead (82) makes a similar assessment of the transitional flora at Dismal Swamp. After 9,550 BP the climate may have become both too warm and dry for mesic forest, with too high a frequency of lightning-caused fires. At Rockyhock Bay (Figure 3) and Singletary Lake the transitional phase is oak-dominated, but *Tsuga* (hemlock), birch, and ironwood make up about 10% of the pollen. Hemlock and birch do not occur in significant quantity farther south, suggesting that their glacial refuges must have been in the northern Coastal Plain or the nearby Central Appalachians. Whitehead gives a date of 11,000 BP for the transitional beech maximum at Singletary Lake (83) and a date as young as 10,000 BP for the birch maximum and hemlock arrival at Rockyhock Bay (83). At Sheelar Lake (Figure 5; W.A. Watts, unpublished) mesic trees were present as early as 14,610 BP, with a beech maximum at 13,540 BP.

The "late-glacial" transitional flora displays marked variation in its expression and timing from site to site. The development of mesic forest began in northern Florida and extended time-transgressively to South Carolina. Throughout the southern part of the Coastal Plain and the northern part of the Florida peninsula there were extensive forests with oak, beech, hickory, ironwood, and other broad-leaved trees. In North Carolina the mesic forest was much more weakly developed, with more oak and fewer mesic trees, including hemlock and birch, which did not occur in the southern localities. Southern Peninsular Florida seems to have remained dry, without any development of mesic forest (72).

In the Appalachians at Quicksand Pond (67) spruce and ironwood both expanded as the jack-pine forest declined after 13,560 BP and oak began its increase. The same persistence of spruce and expansion of ironwood are strikingly evident between 13,000 and 10,000 BP at Anderson Pond (25, 26) before the Holocene oak-dominated forest was established. Except for ironwood, the development of mesic forest is relatively weakly expressed at Quicksand and Anderson Ponds. In contrast, at Pigeon Marsh (71) beech made up 15% of the pollen at 10,820 BP, in association with spruce, ironwood, and significant quantities of *Juglans cinerea* (butternut).

Conditions at the Temperate/Tropical Vegetation Transition: Lake Annie, South-Central Florida

Lake Annie (elevation 36 m) lies at the southern tip of the Florida Highlands, a low ridge bounded to the east by a well-marked escarpment (51). The ridge is covered by fossil sand dunes and contains many sinkhole lakes, of which Lake Annie is one. Off the ridge is flat land, the area of mass occurrence of tropical plants (44), extending to the Everglades. Lake Annie lies in an ecotone between tropical and temperate vegetation and is geographically well-placed to preserve a record of interaction between the two formations. However, the presence of fossil dunes with distinctive local vegetation of *Pinus clausa* (sand-pine) scrub with endemic species means that the site is likely to be strongly influenced by local factors.

The oldest sediments at Lake Annie (Figure 6) contain a flora in which pollen of *Ceratiola ericoides* (rosemary), *Polygonella* (both *P. ciliata* and

P. fimbriata types), *Ambrosia,* other composites and grasses, and microspores of *Selaginella arenicola* are frequent, with a diversity of other herbs (71). Herbs contribute about 50% of the pollen. Tree pollen, mainly oak but with significant amounts of pine at some levels, makes up the remainder. Radiocarbon dates show that this flora was present from before 44,300 BP to after 33,300 BP. The *Ceratiola/Polygonella* flora has a good modern analog in the distinctive rosemary scrub of the crests of exceptionally dry steep-sided dunes in the Lake Annie area, where oak scrub is confined to inter-dune hollows. The interpretation is that from before 44,300 BP to after 33,300 BP the dry-dune *Ceratiola/Polygonella* association predominated. There may have been unstable dunes with blowing sand in the driest areas. If present at all, pine or oak woodland may have been confined to low areas with adequate soil moisture. *Ambrosia* provided 10–15% of the total pollen at all levels in the lower part of the Lake Annie core. It does not occur in natural associations inland in southern Florida today. Fossil *Ambrosia* fruits similar to those of *A. artemisifolia* occur in the lower part of the Lake Annie core.

Between 33,300 and 13,010 BP only 70 cm of sediment accumulated, an extraordinarily slow sedimentation rate. There is no evidence of a hiatus. The only significant change in the pollen diagram is a decrease in *Ceratiola* and an increase in pine, so that the environment does not seem to have changed much. This has been confirmed by close-interval sampling (W.A. Watts, unpublished). At 13,010 BP a high pine peak marks the opening of the Holocene. It is uncertain whether this represents a climatic event that favored extensive development of pine forest or a purely local expansion of pine caused by reduction in fire frequency. The species involved may have been sand-pine, of which a fossil needle has been found.

In the early Holocene oak reached its highest frequency (50%) in the pollen diagram at 10,410 BP. The sand-dune plants *Ceratiola, Polygonella,* and *Selaginella* are much reduced or absent in the oak zone, but composites and grasses remain abundant, and *Ambrosia* is as common as before 13,000 BP. It is supposed that dunes were stabilized by closed oak scrub, perhaps with local sclerophyllous oak forest in the early Holocene; but substantial areas of open prairie-like vegetation must also have existed. The post-13,000 changes in flora can be accounted for primarily by increased precipitation, though other climatic factors, such as temperature and wind force and direction, may also have played a role.

Shortly before 4,715 BP *Ambrosia* became infrequent. From this date to the present, pine supplied 50% or more of the pollen rain, and pollen of *Myrica* (wax myrtle), *Gordonia* (loblolly bay), *Ilex, Serenoa* (saw palmetto), *Magnolia virginiana* (sweet bay), and various Ericaceae became frequent. This seems to represent the establishment of the modern flora with

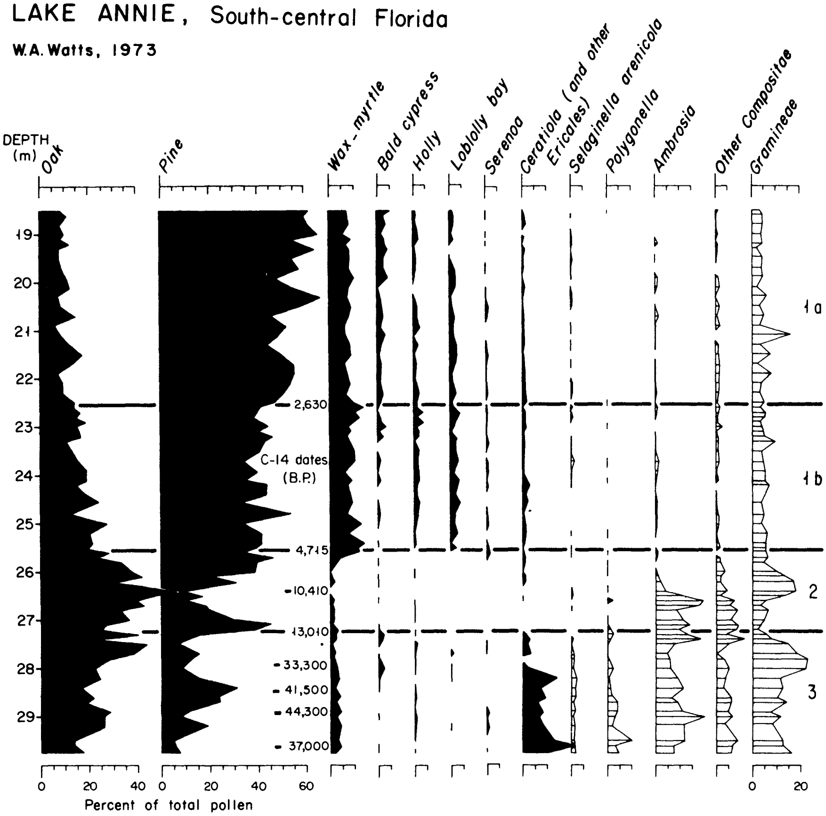

Figure 6 Pollen diagram for Lake Annie, south-central Florida. From Watts (72).

species-rich oak scrub (42) and bayheads. The increase in pine pollen may represent the establishment of large stands of *Pinus elliottii* (slash pine), the common pine of most habitats in southern Florida today.

Pollen of *Taxodium* does not occur frequently until about 2630 BP. This suggests that the tree may have been invading southward to form swamps in southern Florida. Thus the well-known stands of "dwarf" *Taxodium* in the Everglades (18) are of recent geologic origin.

There is no evidence that northern forest species found a refuge near Lake Annie at the time of the Wisconsin glaciation, and the climate seems to have been unsuitable for mesic temperate forest trees and for tropical vegetation at all times in the last 44,000 years. The Late Wisconsin climate at Lake Annie is not differentiated into identifiable interstadial and glacial episodes. In this it resembles other mid-latitude pollen records from the eastern Mediterranean (63) and western Iran (64) and also the ocean-core record

(Figure 2). Highly differentiated Mid and Late Wisconsin climatic sequences may be a function of proximity to the fluctuating margin of the Laurentide ice sheet, rather than a response to world climatic change. The dry Wisconsin climate also seems to have been characteristic of mid and low latitudes (63, 64).

Interglacial Conditions: The Holocene, 10,000 BP to the Present

At Lake Louise (68) the Holocene record begins at 8,510 BP, with high percentages of oak pollen (70%) and hickory (7%), associated with grasses, chenopods, *Ambrosia, Iva, Artemisia,* and other composites (Figure 7). Pines and mesic trees are infrequent. The interpretation is that the predominant plant cover was dry oak forest or sclerophyllous oak scrub with hickory and that bluestem prairie was present (41), like the patches of prairie recorded in the Black Belt of Alabama before settlement (39). Some authors (54) doubt that any natural prairie existed there and attribute open spaces to clearance by man or to natural catastrophes. The universal abundance of pine in the Southeast today makes it impossible to find a modern analog for the early Holocene vegetation. The vegetation suggests a dry

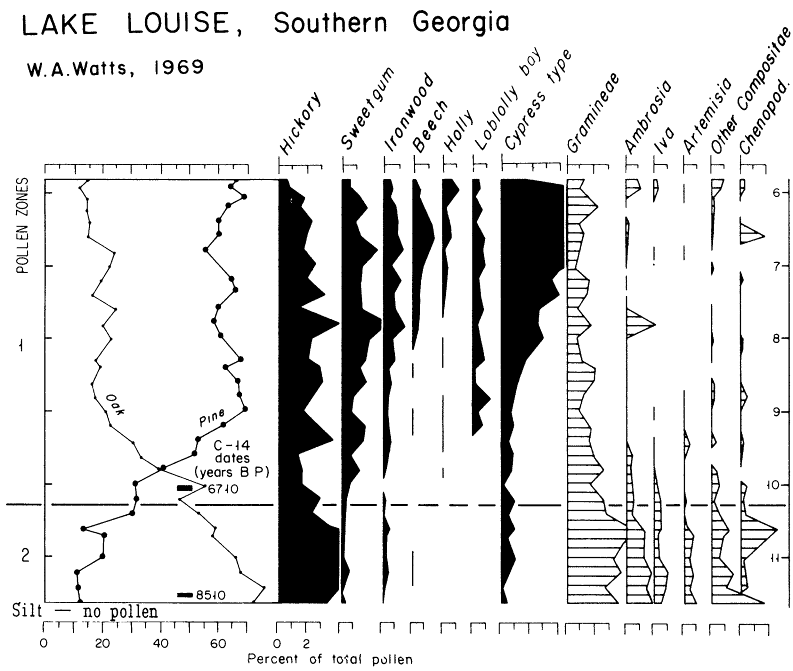

Figure 7 Abbreviated pollen diagram for Lake Louise, southern Georgia. Extracted from Watts (68).

climate, possibly warmer than today, in which available moisture was a limiting factor for forest growth and diversity of tree species. Mud Lake (66) and Scott Lake (68) have closely similar records. The early Holocene period of oak dominance is the "hypsithermal" of the Southeast.

At both Lake Louise and Mud Lake the early-Holocene deposits overlie silt or sand, and organic deposits beyond the range of radiocarbon dating lie below. The lakes appear to have been dry from the early Holocene far back into the time of the Wisconsin glaciation, providing an argument that the climate may have been even drier in the earliest Holocene than later (68). However, at Sheelar Lake (Figure 5) broad-leaved mesic forest with beech was the predominant cover during the late-glacial transition from 14,000 to 11,000 BP. Absence of sediment at Lake Louise and Mud Lake seems to be explained by a low water table in the Florida aquifer (53) caused by reduced precipitation during the Wisconsin glaciation. This was contemporary with maximum glacial sea-level depression at about 15,000 BP (6). Sea level rose rapidly between 12,000 and 8,000 BP, after which a further rise of 5.8 m is recorded in the Everglades (6). However, sites such as Lake Louise and Sheelar Lake are relatively elevated and remote from the sea, and their dry condition may not reflect only the lower sea level. It seems more probable that the Florida aquifer was depleted by much reduced rainfall during the Wisconsin and that it was not recharged until the early Holocene.

Experience at Lake Annie and Sheelar Lake has shown that in the region underlain by the Florida aquifer only lakes that now have about 20 m water depth held water and deposited sediments in the period from the Late Wisconsin to 8,000 BP. At Little Salt Spring (12) the water level was 26 m below the present spring surface 12,000 years ago. The mesic forest after 14,000 BP must have depended on abundant precipitation and probably lower temperatures than now. The free-draining coarse sandy soils of much of Florida and the Coastal Plain must have provided a testing environment for mesic forest at times of drought during the period of lowered water table. Strong differentiation of vegetation between more and less water-retentive soils might be expected.

After 11,000 BP at Sheelar Lake and 9,500 BP at White Pond, the climate became unfavorable for mesic broad-leaved forest, probably because of a combination of higher average annual temperatures and longer growing season. Water stress during the growing season may have reduced the competitiveness of the mesic trees. Lightning-caused forest fires (11) in a new climatic regime may also have been important in eliminating the mesic forest.

At White Pond (73), oak forest with 20% pine replaced mesic oak-beech-hickory forest after 9,550 BP (Figure 5). Oak with little pine dominated in the early Holocene at Singletary Lake (81), Rockyhock Bay (83), and

Dismal Swamp (82), where an oak-hickory assemblage is dated from 8,200 to 3,500 BP. Oak also predominated in the early Holocene at Hack Pond (17), Quicksand Pond (67), Anderson Pond (25, 26), and Goshen Springs (28, 29). At Pigeon Marsh (71) the early-Holocene flora is rich in oak, sweet gum, hickory, chestnut, and black gum.

The increase of pine at the expense of oak is general in the later Holocene in the southern Appalachians, Coastal Plain, and Florida. It is visible though weakly expressed west of the Appalachians at Anderson Pond (25, 26). At Lake Louise pine was spreading at the expense of oak from before 6,710 BP until about 5,000 BP, when a stable proportion of about 65% pine to 15% oak pollen was established (Figure 7). The protracted growth of the pine population suggests a slowly changing climate. As pine expanded, prairie plants were eliminated, and black gum, sweet gum, ironwood, *Vitis* (vine), and other trees and climbers became established. By 5,000 BP most of the elements of the species-rich modern forest around Lake Louise had been assembled. From 5,000 BP onward, bayhead plants such as *Gordonia, Itea* (Virginia willow), *Ilex,* and Ericaceae became prominent. *Taxodium* expanded at the same time, and still more over the last 2,000 years. The development of waterlogged peaty soils and of deep peat deposits with their characteristic bayhead vegetation with cypress swamps in shallow water dates from the middle Holocene (68, 72, 82).

Lake Louise is close to the western margin of Okefenokee Swamp. The increase in *Taxodium* pollen in the last 2,000 years may reflect local events at Lake Louise or the more general establishment of large cypress stands in the Southeast. Whitehead (82) dates the expansion of *Taxodium* in Dismal Swamp to 3,500 BP. Radiocarbon dates from bottom sediments of Okefenokee "prairies"—open areas of treeless swamp—show that sedimentation began in topographically low areas between 6,585 and 6,235 BP (14). At the eastern margin of the swamp, dates of 5,140 and 5,260 BP are recorded for basal sediments (7). Swamping began about 6,500 BP and was extensive by 5,000 BP. "Prairies" in Okefenokee have not changed greatly since peat formation began. Their continuity is attributed by Cohen (15, 16) to a continuous, uniform rise in water table, the common occurrence of fires, and peat depths greater than elsewhere in the swamp. Okefenokee peats show abundant evidence of past fires, with many charcoal-rich horizons. Rockyhock Bay (81) has a similar history of expansion of bayhead and swamp trees and shrubs after 6,800 BP.

Simultaneously with the development of swamps and peaty habitats pines expanded everywhere, but different species must have been involved at different sites, if only on the basis of modern distributions. Lake Louise lies in the region of large presettlement stands of *Pinus palustris* (long-leaf pine) (36), but the common pine of South Florida at Lake Annie is *P. elliottii* (slash pine). *P. clausa* (sand pine) is locally abundant on fossil dunes in Florida. At Hack Pond fossil needle fragments of *P. rigida* (pitch pine) occur in the late-Holocene sediments (17). The change from oak to pine is correlated with a high stable water-table and expansion of swamps and bogs. The spread of acid communities may suggest that soil leaching was occurring on the upland under the influence of increased rainfall between about 7,000 and 5,000 BP. An alternative hypothesis is that the vegetation development was the inevitable outcome of long-term soil-forming processes taking place from the beginning of the Holocene in a climate that showed little variation.

NEW TECHNIQUES AND PROBLEMS

Interest in the paleoecological interpretation of pollen diagrams has resulted in the development of new techniques and approaches in the northern United States that are now beginning to be used in the Southeast. At the same time certain problems specific to the Southeast require attention.

Pollen Influx Counts

Estimates of pollen influx (19) have been made at Singletary Lake (81), Rockyhock Bay (83), White Pond (74), Anderson Pond (25, 26), and Lake Louise (68). The data have not been as valuable as might have been hoped, probably because the pollen profiles record landscapes that were always forested. Dramatic differences in influx values between forested and unforested landscapes such as are known from the Late Wisconsin of New England (19) do not exist. Also, slow and variable sedimentation rates make it difficult to make realistic calculations of influx values. In Appalachia the only available sites are small ponds, with slow sedimentation rates, changes of sediment type, and loss of matrix by oxidation.

Pollen Surface Samples and Modern Analogs

Surface pollen counts are available from North Carolina (85), Tennessee (25, 26) and Mud Lake, Florida (66). The method is valuable in identification of modern analogs for fossil floras. It could be used more extensively in the Southeast, especially if pollen counts of immediately presettlement age can be related to forest reconstructions made from General Land Survey Office records (23, 24, 27). The Southeast may prove more intractable for pollen-surface-sample studies than the Midwest (47, 48, 76), because the great abundance of pines in the modern flora makes it almost impossible to find analogs for vegetation dominated in the past by oak, mesic trees, or prairie plants. The attempt to make paleoclimatic reconstructions by use of transfer functions (77) cannot as yet be undertaken in the Southeast because of an insufficient data base. The same is true of any attempt to map changing patterns in Pleistocene and Holocene pollen records by isopollen lines (1).

Fire Ecology

The role of fire in southeastern ecosystems has been documented by Komarek (40) and Christensen (11). However, no evidence exists to show whether fires were more or less frequent, for example, in the oak zone than in the pine zone at Lake Louise (68), an obvious question in any effort to reconstruct the environments and paleoclimates of the two zones. The methodology of fine charcoal stratigraphy to illustrate past fire history as developed by Swain (58) has not been applied to any Coastal Plain site. The role of fire in increasing the nutrient influxes to lakes (90) in the Southeast is also still uninvestigated, as are most aspects of paleolimnology.

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