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A STUDY IN PHYSIOGRAPHIC ECOLOGY IN NORTHERN FLORIDA

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(WITH TEN FIGURES)

Introduction

Ecological investigations of the coastal plain of southeastern United States, with few exceptions, have not been undertaken from the standpoint of the relation of physiography to the successional history of the plant associations, nor has the classification of this region been satisfactorily established in comparison with other forest formations of the United States. SCHIMPER (11) mapped this portion of the coastal plain (with the exception of southern Florida) as temperate rain forest. SARGENT (10) classified it as the southern maritime pine belt. The first classification is obviously inconsistent, and the second is open to question if by pine forest is meant a climax formation.

Except for HARSHBERGER'S detailed treatment of the coastal plain in his *Phytogeographic survey of North America*, studies of this particular region have been scattered, and usually of exceptional localities. On the Gulf Coast, HILGARD in soil surveys in Mississippi and Louisiana paid special attention to plants as soil indicators, outlining associations on this basis. Studies of island plant life in the Mississippi River sound and delta were made by LLOYD and TRACY (8); while MOHR in his *Plant life of Alabama* grouped

various plant associations belonging to the different geological divisions of the coastal region of that state, comparing the flora in its relationships with adjoining regions and with the West Indies and Mexico. More recently, HARPER has contributed numerous publications containing ecological data, as the result of extensive observations and explorations in various parts of the coastal plain, his most complete works being a phytogeographic study of the Altamaha grit formation of Georgia (5), and publications in the reports of the State Geological Survey of Florida (6, 7).

The area described in this study is included mainly in Leon County, Florida. This county is situated half-way between the east and west boundaries of the northern part of the state, bordering the Georgia line and distant about 20 miles from the Gulf of Mexico. The area is approximately 675 square miles, and as a whole is located immediately west of the 84th meridian and between 30 and 31° north latitude.

The topography is diversified, and a soil survey (14) of this county locates and describes 12 soil types (including meadow and swamp), of which the most extensive are those also common to the coastal plain from Virginia south to Florida and west to Texas.

This section of Florida has had a varied history, dating back to early Indian tribes and the first Spanish explorers. According to narratives of DE SOTO's followers, the fame of this country as the "land of plenty" extended to eastern and central Florida, and made it a desirable place to seek for possession and settlement. During the several hundred years of history chronicling invasions and resettlement, therefore, successive clearings of the forest, from the more fertile soils at least, must have been made. About the time of the establishment of the capital at Tallahassee (1823) near the center of the county, WILLIAMS (15) described "abundant groves of oak, hickory, beech, and magnolia crowning the hills and covering their slopes." Such early pictures are of interest now in considering the upland forests.

Physical features

CLIMATE.—Weather records have been kept at Tallahassee since 1885 (3). The mean summer temperature averages 79°.7, autumn

68°, winter 53°, and spring 67°.6 F., indicating a moderate and equable yearly temperature. There are records of severity, however, the lowest temperature for the state being recorded from Leon County, −2° F. on February 13, 1899. Frost may be expected from November 1 until April 1, the frost record for 18 years giving the date of the first killing frost in autumn as November 4, the last killing frost in spring as April 6, the average date of the first killing frost in autumn as December 5, and the average date of the last killing frost in spring as March 3.

The mean annual precipitation for the Tallahassee station (3) is 57.12 inches, and there are 2 marked periods of rainfall; one (the lesser) in winter culminating in March, and the other (more excessive) culminating in July. This summer rainfall averages 26.8 inches, and the winter rainfall 17.9 inches, the summer rains occurring almost daily as afternoon thunderstorms, while the winter rains are more evenly distributed between day and night. The year is divided thus into wet and dry seasons, more or less marked, April and November being the driest months.

There are no reliable records for relative humidity, although for northern Florida the percentage of relative humidity is highest in September and lowest in April.

These climatic effects combined tend to make spring (April period) the hardest season for plants, so far as the moisture relations are concerned.

PHYSIOGRAPHY.—Limestones of the Oligocene period are considered now to be the oldest rocks of Florida and to form the rock basis for most of the state (9). These limestones also are the surface rock over much of northern Florida, and indicate the earliest and most persistent land surface during subsequent geological history. The presence so near the surface of readily soluble and easily disintegrated rock has doubtless had important influence upon the present topography and drainage, as well as upon the character of some of the soil.

Crossing the country from north to south, the most striking topographical feature is the division of the surface into 2 distinct parts, a highland and a lowland. By this division about two-thirds of the surface is included in the highland, which is a portion of the

narrow upland extending along the northern edge of Florida and into Georgia, and which, on its sea-facing side, often drops abruptly to the more recent coastal strip.

The general elevation of the upland is betweeen 100 and 200 ft. above sea level. The surface is gently rolling with series of broadly rounded or flat topped hills, in general extending east and west, and alternating with open, troughlike valleys. Many of the valley streams are mere swampy or boggy tracts, or they may pursue sluggish courses which end blindly, spreading out on the surface of the ground at the lowest part and soaking gradually into the soil. Others end in ponds which occupy basin-like depressions, or may drain into the larger lakes and sinkholes. In this hill region the sinkhole origin of many large lakes as well as small ponds, and the sinkhole formation along the line of some of the valleys at present, suggest that the depressions of this upland division may be due in large part to subterranean erosion. At any rate, no considerable part of the drainage is now carried off on the surface.

Southward from the edge of the highland there is a gradual slope to the Gulf, the surface being varied only by low swells of sandy soil. The St. Mark's River cuts across these sands in the southeastern corner of the county, part of its present course being due to underground solution. The Wakulla River, having its origin in the flatwoods, flows across the southern part of the county as a typical pre-erosion stream, but is soon lost underground, to emerge at length in Wakulla Spring, one of the finest large springs in the state. Some of the small lakes are quite deep and constant, while the majority are mere pine barren ponds, partially or entirely dried out at times. Other depressions are swampy tracts known variously as "bays," "galls," and "sloughs."

SOILS.—As throughout the coastal plain, the soils are chiefly types of sandy series, the Soil Survey (**14**) stating that only about one-half square mile of soil as heavy as loam or clay would be found in the land surface of the county. The hills are covered by soils described as derived from the Lafayette formation, while the valleys and less elevated portions are covered with Columbia sands deposited during a late period of submergence.

Of the Lafayette derivation, the Orangeburg fine sandy loam and the Norfolk fine sandy loam are the most extensive, and represent 2 types found only within the coastal plain of southeastern United States (1). The former is distributed chiefly in 2 belts across the Gulf Coast states and also west of the Mississippi River, constituting the higher lands. The Norfolk fine sandy loam extends from Virginia to northern Florida and west to Texas. In topography it is similar to the Orangeburg, and together these 2 soils are considered the most important for general agriculture, forming the greater part of the so-called "clay hammock lands" (13), characterized by a telling percentage of clay in their subsoils and esteemed for their fertility. The subsoil of the Orangeburg gives the designation of "red hills" so commonly used in descriptions of southern Georgia and of northern Florida, for the freshly cut or eroded subsoil is a bright red sandy clay. The subsoil of the Norfolk is a yellow sandy clay or clay loam.

Of the sedimentary deposits, the Norfolk sand covers the largest area, being the most widely distributed soil of the coastal plain from New Jersey southward (1). It is characterized by low elevation and generally level surface from the immediate shore line inland.

Corresponding, then, with the 2 general topographic divisions there are 2 general soil divisions, that of the more elevated regions having clayey subsoil, while the rest is nearly pure sand.

Vegetation in relation to physiography

UPLANDS

Clay hammock lands

In the study of the upland on these soils, there are few evidences of primeval forests, but it is easy to follow recent reforestation and thus to gain an idea of the succession under present conditions.

The methods of agriculture as long practiced in these regions soon exhausted the soil and led to clearing of fresh tracts. The use of these for a few years and their abandonment and return to forest afford object lessons of all stages of second growth. Also on

some agriculturally less desirable lands it is possible to see a forest recently undisturbed; likewise on some of the old and extensive estates groves have been preserved and illustrate what the forests may have been before the civil war. Clearing and exhaustive cotton growing soon reduce the humus and bring about soil vitiation, which exposure intensifies, resulting in a more xerophytic state.

The exposed Orangeburg soil readily washes, and plants can get a hold on the steep bare slopes with difficulty. Soil lichens and mosses, however, soon form a gray-green coating, especially if partially shaded. Species of *Cladonia* and *Baeomyces* are among these earth lichens.

Fields relapsing from tillage soon grow a mixture of ruderals and native plants. *Cenchrus carolinianus* Walt., *C. tribuloides* L., *Erianthus divaricatus* Hitch., *E. brevibarbis* Michx., *Andropogon virginicus* L., *A. Elliottii* Chapm., *A. scoparius* Michx., *Gerardia purpurea* L., *G. fasciculata* Ell., *G. tenuifolia* Vahl., *Aplopappus divaricatus* Gray, and *Eupatorium capillifolium* Small, with prostrate species of *Rubus* (*R. trivialis* Michx. and *R. cuneifolius* Pursh) are common plants soon covering the old fields, which in a short time are dotted with the seedlings of pioneer pines. Of these pines, *P. echinata* Mill. (short-leaved yellow pine) is by far the most abundant, although other species occur, as *P. Taeda* L. (loblolly or old-field pine), *P. caribaea* Morelet (Cuban or slash pine), and occasionally *P. clausa* Sarg. (sand or spruce pine), and *P. palustris* Mill. (long-leaved yellow pine). *Quercus virginiana* Mill. (live oak) is a broad-leaved evergreen pioneer, and *Diospyros virginiana* L. (persimmon) and *Liquidambar Styraciflua* L. (sweet gum) are deciduous trees soon growing with the dominant pines. *Sassafras variifolium* Ktze. and *Prunus angustifolia* Marsh. are thicket formers. *Pteris aquilina* L. is an abundant fern characteristic of these xerophytic pioneer stages of the old fields.

The pines which spring up in such numbers, if not disturbed, grow rapidly, and on the whole uniformly, and comparatively soon form a forest of trees of similar height and diameter. Where burning or pasturing does not interefere, a dense shrubbery quickly develops, including a variety of seedling trees and shrubs. Of these

developing trees, oaks are most numerous, *Q. falcata* Michx. (Spanish or red oak) and *Q. stellata* Wang (post oak) being the principal pioneers. *Q. virginiana* Mill. persists, being a tree of almost every habitat, from hydro-mesophytic to xerophytic. When forming groves of large, wide spreading trees, draped with *Tillandsia usneoides* L. (Spanish moss) and supporting on the trunks and

FIG. 1.—*Quercus virginiana* on hammock soil

branches a growth of *Polypodium polypodioides* Hitch., this live oak is the typical tree of the mesophytic "hammock," a term used in these regions of the south to designate lands supporting a forest growth of deciduous and broad-leaved evergreen species, correlated with a rich and fertile soil (fig. 1). The evergreen *Ilex opaca* Ait. grows well in the shade of the pines; and *Cornus florida* L. develops under taller trees, sometimes forming an under forest, with some of the trunks 12–18 inches in diameter at 2 ft. from the ground, the widely spreading tops meeting overhead, while above them rise the pines. *Pyrus angustifolia* Ait. (wild

crab) is a small tree characteristic of the pine wood borders and more open parts.

Mingled with the oaks are hickories, *Carya alba* K. Koch being the prevalent species, and a characteristic member of the developing oak forest. The mixed assemblage of small trees and taller shrubs accompanying the oaks and hickories include *Ilex vomitoria* Ait. (an evergreen), several species of *Crataegus* (especially *C. consanguinea* Beadl., *C. robur* Beadl., *C. panda* Beadl.), *Rhus copallina* L., *Callicarpa americana* L., and *Vaccinium arboreum* Marsh. Low shrubs are *Ceanothus americanus* L., *Gaylussacia dumosa* T. and G., *Rosa humilis* Marsh., and *Yucca filamentosa* L.; while common woody vines with persistent or evergreen leaves are a number of species of *Smilax* (*S. pseudochina* L., *S. bona-nox* L., *S. glauca* Walt.), *Gelsemium sempervirens* Ait., and *Lonicera sempervirens* L.

The herbaceous growth in the pine forest, when undergrowth is not disturbed, is not abundant, but in woodland burnt over or cleared, grasses and sedges spring up and often make pasturage. Blooming early in the spring, *Oxalis stricta* L., *O. corniculata* L., *Phlox pilosa* L., *Scutellaria integrifolia* L., *Salvia lyrata* L., *Houstonia purpurea* L., *Specularia perfoliata* A.DC., *Antennaria plantaginifolia* Rich., *Pyrrhopappus carolinianus* DC., and *Chrysogonum virginianum* L. are herbs which indicate xeromesophytic conditions. In more mesophytic places *Houstonia rotundifolia* Michx. and *Mitchella repens* L. may be found in bloom at almost any date, the latter with flowers and fruits at the same time.

There is no vernal flora, nor can a definite flowering season be set, but there is overlapping and irregularity in the prolongation of the blooming season, conditions related to the spring drought and to the extended growing season due to the climatic causes. The most showy season, so far as the herbs are concerned, is after the summer rains, during the late summer and the fall, when *Agrimonia Eupatoria* L., *Schrankia uncinata* Willd., *Lespedeza hirta* Ell., *L. striata* H. and A., *L. violacea* Pers., *Polygala sanguinea* L., *P. verticillata* L., *Helianthemum carolinianum* Michx., *Oenothera biennis* L., *O. linearis* Michx., *Sanicula canadensis* L., *Gentiana villosa* L., *Asclepias verticillata* L., *A. variegata* L., *Trichostema dichotomum*

L., *Salvia azurea* Lam., *Penstemon laevigatus* Ait., *Gerardia flava* L., *G. purpurea* L., *Galium circaezans* Michx., *Eupatorium coelestinum* L., *E. aromaticum* L., *E. album* L., *Liatris scariosa squarrulosa* Gray, *Chrysopsis mariana* Nutt., *Gnaphalium purpureum* L., and *Solidago petiolaris* Ait., make a representative list for the short-leaved pine wood.

The succeeding stage in upland reforestation is that of the oak-hickory forest, in which the characteristic xeromesophytic oaks are dominant. Of these two oaks, *Q. falcata* Michx. seems the more xerophytic, at least it appears on more exposed and drier situations and soils, and slightly in advance of *Q. stellata* Wang., the other pioneer oak. But together, these with *Carya alba* K. Koch dominate the forest which rapidly follows the short-leaved pines.

With the increasing mesophytic conditions (shade, humus, moisture, bacterial, and fungal development), other oaks (*Q. nigra* L., *Q. laurifolia* Michx., and *Q. alba* L.) appear. Other large trees are *Liquidamber Styraciflua* L. and *Nyssa sylvatica* Marsh. The undergrowth is composed of many seedlings of these species and others, with the small trees and shrubs common to the pine forest, as well as more mesophytic species, such as *Ostrya virginiana* K. Koch, *Cercis canadensis* L., *Aralia spinosa* L., and *Viburnum rufidulum* Raf.

The appearance of young *Magnolia grandiflora* L. and of *Fagus grandifolia caroliniana* Fernald and Rehder indicates the approach of the climax and of the transition to the magnolia-beech forest, in which the broad-leaved evergreens and a variety of deciduous trees assemble.

An undisturbed hammock forest of such mesophytic composition, and apparently representative of the climax capable of development on the uplands, contains abundant magnolias of stately proportions (60–80 ft.), equally large beeches, and Florida sugar maples (*A. floridanum* Pax or *A. saccharum floridanum* Sarg.), with intermixed live oaks, white oaks, red oaks (*Q. texana* Buckley), basket oaks (*Q. Michauxii* Nutt.), sweet gums, big bud hickories, and dogwood, with a few old and large short-leaved and Cuban pines as relics. The abundance is approximately in the order named, and all may be hung with Spanish moss. The shrubbery of

this forest includes *Asimina parviflora* Dunal, *Hamamelis virginiana* L., *Evonymus americanus* L., *Stewartia Malachodendron* L., *Aralia spinosa* L., *Symplocos tinctoria* L'Her., *Osmanthus americanus* Br., *Viburnum rufidulum* Raf., and *V. nudum* L., an assemblage of northern and southern species all about equally indicative of similarly mesophytic habitats; while perhaps the most significant thing is the occurrence of young beeches and magnolias, emphasizing the climax conditions.

The undergrowth and herbage are apparently related to the prevalence of the magnolias and other heavily foliaged trees. If these are dominant, the ground is freer of growth and covered with the heavy and slowly decaying leaves. *Mitchella repens* L. is a common floor covering. Root parasites are *Conopholis americana* Wallr. and *Epifagus virginiana* Bart.; while *Monotropa uniflora* L. and *M. Hypopitys* L. occur in abundance in the damp, shaded soil.

To summarize, the forest succession on clay soil of the upland, as shown in phases of reforestation on limited areas but in all stages, we see (1) pines, (2) oak-hickory forest, (3) deciduous broad-leaved evergreen forest. In the pine forest, *P. echinata* Mill. is the dominant species; in the oak-hickory forest, *Q. falcata* Michx. and *Q. stellata* Wang. with *C. alba* K. Koch; in the climax forest, *Magnolia grandiflora* L., *Fagus grandifolia caroliniana* Fernald and Rehder, and a variety of associates.

Sandy soils

In comparison with the uplands of the northern part of the county, those of the south seem like lowlands. Since their geological history has not been the same and the resultant topography is not so distinct, the vegetational aspect also is different. The two regions seem to exemplify two stages in the coastal plain development, the older and the younger. The southern or younger part typifies the marginal portion of the coast, of comparatively recent emergence, and belonging quite entirely to pre-erosion topography, being level, of low elevation, and covered with loose sandy deposits. Almost the whole surface, therefore, may be considered as upland.

The base leveling of this region, supposing no future oscillatory changes of importance, may require a prolonged period, the ero-

sive forces being capable of slight application, but it will not require extensive work as compared with the more elevated regions to the north. The vegetation seems naturally divided, according to small differences in elevation, into the so-called "scrub," the more or less rolling pinelands, and the flatwoods. In a general way these differences also correspond with the soil types, the scrub being associated with Sandhill soil, the pinelands with Norfolk sands, and the flatwoods with Leon sands. For convenience, these 3 general divisions of the pre-erosion uplands will be discussed separately.

SCRUB OAK FOREST.—The oak association seems to mark the sandhill areas, which, owing to the porous sandy subsoil and the lack of organic matter in the soil, would seem to be a decidedly xerophytic habitat. Three small deciduous oaks and a scattering of pines (*P. palustris* Mill. chiefly) make up the tree growth. Of these oaks, *Q. Catesbaei* Michx. seems to be the most xerophytic, as it is sometimes almost alone on the summits of the knolls or ridges. *Q. margaretta* Ashe (suggested as a possible hybrid between *Q. stellata* Wang. and *Q. alba* L. and sometimes, as noted on the more fertile soils, apparently intergrading into well grown *Q. stellata* Wang.) appears in the intermediate positions; while *Q. cinerea* Michx. grows near the bases of slopes. They intermingle in varying proportions over most of the area, growing to about the same height (15–20 ft.), with many scrubby branches, making when thickly planted a scrubby thicket. *Q. geminata* Small, a scrubby live oak, is another species occurring on sandy soil, usually in situations near water or damp places. *Q. virginiana* Mill. and *Diospyros virginiana* L. also grow on the sandhills.

Shrubs are mostly low and with evergreen or persistent foliage, as *Ceratiola ericoides* Michx., *Leiophyllum buxifolium* Ell., *Vaccinium Myrsinites* Lam., *V. stamineum* L., *V. neglectum* Fernald. *Asimina pygmaea* Dunal (with deciduous though coriaceous leaves), *Ceanothus microphyllus* Michx., and *Vaccinium tenellum* Ait. are other low shrubs of the dry sands.

The herbaceous growth, although sparsely distributed, includes a great variety of coastal plain species. Tufts of scattered wire or poverty grass occur on the spaces of bare sand, the most common

being species of *Andropogon* and of *Aristida*. *Pteris aquilina* L. is abundant also. In the spring, *Cassia Chamaecrista* L., *C. nictitans*, L., *Lupinus perennis* L., *L. villosus* Willd., *Tephrosia virginiana* Pers., *T. spicata* T. and G., *Baptisia simplicifolia* Croom, *B. lanceolata* Ell., *Euphorbia corollata* L., *E. Ipecacuanhae* L., *Croton argyranthemus* Michx., *Jatropha stimulosa* Michx., *Amsonia ciliata* Walt., *Scutellaria integrifolia* L., and *Chrysogonum virginianum* L. are early bloomers, the Leguminosae being most abundantly represented. Through the summer and fall a characteristic and representative list includes *Eriogonum tomentosum* Michx., *Eriogonum longifolium* Nutt., *Polygonella gracilis* Meisn., *Petalostemum corymbosum* Michx., *Desmodium rigidum* DC., *Rhynchosia simplicifolia* Wood, *Hypericum Drummondii* Grev. and Hook., *Angelica dentata* Coult. and Rose, *Asclepias tuberosa* L., *Verbena angustifolia* Michx., *V. caroliniana* Michx., *Gerardia fasciculata* Ell., *Elephantopus tomentosus* L., *Eupatorium aromaticum* L., *Trilisa odoratissima* Cass., *T. paniculata* Cass., *Kuhnia eupatorioides* L., *Liatris tenuifolia* Nutt., *L. elegans* Willd., *Chrysopsis graminifolia* Nutt., *C. gossypina* Nutt., *C. mariana* Nutt., *Berlandiera texana* DC., *Solidago odora* Ait., *Aster lateriflorus* Britt., *A. concolor* L., *Silphium Asteriscus* L., *Helianthus radula* T. and G., *H. mollis* Lam., and *Palafoxia integrifolia* T. and G. Many of these are perennials with prostrate or rosette-forming habit, or with pubescent to flocculent coating on leaves and stems, or, as in the case of the species of *Croton*, a scaly coating or with thick and narrow leaves.

PINELANDS.—Passing to the somewhat lower Norfolk sand, which generally surrounds the islands of Sandhill, the transition is marked by the increase in long-leaved pines. The 3 scrub oaks continue as more or less abundant members of the pine forest (fig. 2). *P. palustris* Mill. and *P. caribaea* Morelet are the pines, both of them valuable species for their turpentine and for their timber. *Quercus virginiana* Mill. and the xerophytic oak *Q. marilandica* Moench. occur occasionally, also *Q. pumila* Walt., a low, shrublike species. *Crataegus panda* Beadl., the common hawthorn of the sands in this vicinity and noticeable for its dark, deeply checked bark and irregular crooked-branched habit, and *Bumelia lanuginosa* Pers. are small trees. *Castanea pumila* Mill. is com-

mon in some places, making groves of trees or a low, shrubby growth, spreading by stolons and rapidly covering a considerable area. *Diospyros virginiana* L. is also a tree of these sands, but more frequent as second growth with the short-leaved pines, live oaks, post oaks, Spanish oaks, and sweet gums, as on cleared land which has been cultivated for a time and allowed to revert to forest.

In this reforesting the early stages thus resemble those on the hills, but to these clearings the long-leaved pines with the scrub

FIG. 2.—Long-leaved pine forest on Norfolk sand

oaks may also return. It is on such more fertile spots or where there has been improvement of the soil that the xerophytic scrub oaks, especially *Q. margaretta* Ashe, appear to grow to better size and may mingle for a time with the xeromesophytic oaks, but cannot long compete with the large trees.

The exact relation of these scrub oaks to this type of pine forest is of interest, as they sometimes appear to replace the pines without apparent difference in topography, soil, or drainage. From the fact that these oaks may appear as xerophytic pioneers, and also that they appear in the more xerophytic situations, as on the summits of the ridges of the sandy soil, it may be that they succeed

better than pines on dry, sterile sand, so that when the pines are removed from such lands, the scrub oaks more quickly take possession, while the pines return more slowly and scatteringly. On the other hand, with improved or more mesophytic conditions, the scrub oaks are soon replaced by pines, xeromesophytic oaks, and the succeeding mixed forest.

There seem, therefore, to be two possible phases of succession on the sandy soils. On the more sterile sands, the scrub oaks may be the pioneers before the long-leaved pines; or, if the pines be removed, these oaks may follow, to give place, with improvement of soil and moisture, to xeromesophytic pines and oaks, and then to the oak-hickory forest, leading toward the climax forest sooner or later. But on soil neither excessively drained nor poorly drained, the scrub oaks will accompany the long-leaved pines, yielding, where more mesophytic growth is favored, to the short-leaved pines and their following as outlined. Groves of short-leaved pines are not uncommon within the long-leaved pine association, especially where there may be some admixture of clay, as when the Norfolk sand is in close association with such types of soils as the Orangeburg and Norfolk fine sandy loams.

The growth of shrubs in these long-leaved pine woods is noticeably scanty and the species relatively few. The frequent burning over of these woods and their utilization for turpentine no doubt prevent a natural growth from starting. However, the contrast with the short-leaved pine forest on the hills is very great in this respect, and the xerophytic conditions are correspondingly greater; hence succession or the renewal of the forest is delayed. The shrubs noted commonly in the pinewoods on sandy soils are *Rhus copallina* L., *Ceanothus americanus* L., *Ilex vomitoria* Ait., *Vaccinium arboreum* Marsh., *V. virgatum* Ait., *V. stamineum* L., *V. Myrsinites* Lam., *V. neglectum* Fernald, *Leiophyllum buxifolium* Ell., *Kalmia hirsuta* Walt., and *Gaylussacia dumosa* T. and G., the Ericaceae being the most numerous. The variety of herbs in these pine forests is striking, many of them being those of the "scrub," the families prominently represented being Compositae, Leguminosae, Euphorbiaceae, Scrophulariaceae, Polygalaceae, and Labiatae, chiefly xerophytic species.

FLATWOODS.—From the dry pinewoods to the flatwoods areas the change is indicated, not by the prevailing tree growth, but by the shrubs and herbs. These mark a most decided difference (fig. 3). The long-leaved pines continue to form the forest, apparently succeeding best on these poorly drained sands. This is

FIG. 3.—In foreground saw palmettos and wire grasses and herbs characteristic of flatwoods, giving way in background to long-leaved pine-scrub oak association.

perhaps the explanation of the specific name of *Pinus palustris* Mill., although this particular pine is by no means a typical swamp tree, as for example is *P. serotina* Michx., nor is it as tolerant of inundation even for a time as is its associate *P. caribaea* Morelet.

The shrubby growth of these flatwoods is made up of dwarf species, seldom rising above 3 ft., and chiefly evergreens. Fires

may be one of the chief causes preventing development of undergrowth, but the presence of these low shrubs adjoining bays and ponds, where fires have been able to do small damage to the natural growth, seems to prove the character of the shrubbery. Dwarf oaks are common (*Q. myrtifolia* Willd., *Q. minima* Small, and *Q. nana* Willd.), with persistent, leathery leaves and mostly bearing abundant fruits. *Myrica cerifera pumila* Michx., *M. carolinensis* Mill., *Ilex glabra* Gray, *Hypericum myrtifolium* Lam., *H. galioides* Lam., *H. aspalathoides* Willd., *H. opacum* T. and G., and *Kalmia hirsuta* Walt. are other shrubs with persistent foliage. *Pyrus arbutifolia* L. f., *Rhododendron nudiflorum* Torr., *R. viscosum* Torr., *Lyonia nitida* Fernald, *Andromeda ferruginea* Walt., *Vaccinium stamineum* L., and *V. Myrsinites* Lam. are also shrubs of the damp to wet sands.

The most conspicuous index, however, of subsoil more or less saturated is *Serenoa serrulata* Hook. f. (saw palmetto). As soon as this palmetto appears with the turpentine pines, poor drainage is to be inferred. The herbs also are strikingly characteristic of undrained soil with its lack of aeration and consequently of assimilable nitrogenous substances. The Leguminosae, so abundantly represented on the Sandhill soil and in the long-leaved pinewoods on the dry sands, do not appear. Besides the grasses and Compositae, the families most in evidence here are Eriocaulaceae, Juncaceae, Liliaceae, Orchidaceae, Sarraceniaceae, Droseraceae, Polygalaceae, Melastomaceae, Onagraceae, Gentianaceae, Scrophulariaceae, and Lentibulariaceae. Representatives of these familes are *Eriocaulon decangulare* L., *E. compressum* Lam., *Juncus Elliottii* Chapm., *J. debilis* Gray, *Xerophyllum asphodeloides* Nutt., *Spiranthes praecox* Wats., *Calopogon pulchellus* R. Br., *Sarracenia flava* L., *S. psittacina* Michx., *S. Drummondii* Croom, *S. minor* Walt., *Drosera brevifolia* Pursh, *Polygala lutea* L., *Rhexia mariana* L., *R. glabella* Michx., *R. virginica* L., *R. ciliosa* Michx., *Ludvigia pilosa* Walt., *L. alternifolia* L., *Viola lanceolata* L., *Eryngium virgatum* Lam., *Sabatia Elliottii* Steud., *S. paniculata* Pursh, *Gentiana Porphyrio* G. Gmel., *Gerardia filifolia* Nutt., *Seymeria tenuifolia* Pursh, *Pinguicula lutea* Walt., *P. pumila* Michx., *Utricularia subulata* L., and *U. cornuta* Michx. The species of *Sarracenia*

are often associated with a luxuriant growth of *Lycopodium alopecuroides* L. or *L. carolinianum* L. and with beds of sphagnum and other mosses. *Osmunda cinnamomea* L., *O. regalis* L., *Onoclea sensibilis* L., *Woodwardia areolata* Moore, and *W. virginica* Sm. are typical bog hydromesophytes and abundant ferns of this habitat. A complete analysis of the flora of these low woods probably would include a longer list than for any other habitat in the county, and would be evidence of the edaphic character of this association.

Summarizing the vegetation as described for the uplands on sandy soils, the long-leaved pines are dominant and constitute the most extensive type of forest. Of these two species, *P. palustris* Mill. and *P. caribaea* Morelet, the latter ranges more widely in habitat, occurring from mesophytic to hydrophytic habitats, even enduring inundation. The former is not a typical swamp tree nor does it succeed well in soil subject to inundation for any length of time. On this account, probably, *P. caribaea* Morelet, a dominant species for the southern Florida pinewoods, is reported to be gradually replacing *P. palustris* farther north. On mesophytic soils these pines are displaced by the more mesophytic species, while on the drier soils or excessively drained sands the scrub oaks succeed better and take possession. *P. palustris* belongs typically, therefore, to sandy soils with subsoil well drained to saturated or forming hardpan, soils in which few other trees would flourish. Since such habitats predominate, owing to the present physiographic conditions on the coastal plain, the present long-leaved pine forest may be looked upon as edaphic, the species of pines, within their respective climatic ranges, being pioneers in these comparatively primitive habitats.

PRE-EROSION DEPRESSIONS

Throughout the coastal plain, depressions not resulting from recent erosive processes present a variety of edaphic studies. Many of these low places are filled for all or part of the time with surface water, or they may be sufficiently depressed below the water table to contain a permanent amount of water. Others may be mere swampy or boggy tracts, or during dry seasons prairie-like. The relation of these surface features to the formation of peat,

especially in Florida, has been investigated and reported by HARPER (**6**), whose descriptive classification of habitats and extensive lists of peat-forming plants present a summary of the plant associations of the various sorts of swamps, marshes, bogs, ponds, lakes, and streams.

The water of these pre-erosion depressions, with their (usually) sandy basins, is characteristically dark-colored, appearing blackish when in quantity, being rich in organic matter, and having a more or less acid reaction.

Lakes, ponds, and streams

The vegetation of the ponds and of the slowly moving waters of the sluggish little streams is not decidedly different, differences depending rather on the depth of water and on the amount of movement. In shallow, permanent water the aquatics are arranged in the usual zonation, from those submerged or floating to those rooted in the muck or sand of the bottoms and to the amphibious plants of the margins.

Lists of aquatics for the ponds and lakes include among the submerged and floating forms *Potamogeton* spp., *Ceratophyllum demersum* L., *Myriophyllum heterophyllum* Michx., *Lemna valdiviana* Philippi, *Castalia odorata* Woodv. and Wood (and the variety *C. odorata gigantea* Fernald), *Nymphaea advena* Ait., *Brasenia Schreiberi* Gmel., *Nelumbo lutea* Pers., *Nymphoides aquaticum* Fernald, *Utricularia inflata* Walt., *U. biflora* Lam., and *U. purpurea* Walt.

In marginal zones, *Panicum hemitomum* Schult., *P. condensum* Nash, *Dulichium arundinaceum* Britt., *Eriocaulon decangulare* L., *E. compressum* Lam., *Mayaca Aubleti* Michx., and *Bacopa caroliniana* Robinson usually grow in shallow water; while the common strand plants are *Fuirena squarrosa* Michx., *Hemicarpha micrantha* Britt., *Rhynchospora corniculata* Gray, *Syngonanthus flavidulus* Ruhland, *Drosera brevifolia* Pursh, *Hypericum virginicum* L., *H. gentianoides* BSP., *Hydrocotyle umbellata* L., *Bartonia* spp., *Diodia virginiana* L., *D. tetragona* Walt., *Spermacoce parviflora* Gray, *Houstonia angustifolia* Michx., *Lobelia glandulosa* Walt., and *Pluchea foetida* DC. The cypresses (*Taxodium distichum* Rich. or

T. distichum imbricarium Sarg.) when present are the chief tree pioneers in the ponds, advancing farthest into the deeper water, reaching from the zone of high water, perhaps, to the extreme limit of the occasional low water, into the zone of water lilies and submerged aquatics (fig. 4). *Cephalanthus occidentalis* L. is a close companion of the cypresses and advances into the standing water

FIG. 4.—Cypresses advancing into deeper water

as a shrub pioneer. The hydrophytic species of *Nyssa* (*N. aquatica* L., *N. sylvatica biflora* Sarg., and the less frequent or local *N. Ogechee* Marsh.), germinating and growing in shallow water, may accompany the cypresses or may spread over the shallow ponds to form the so-called "gum swamps" (fig. 5).

Approaching the shores or in the shallow water of the margins, these trees are joined or surrounded by a zone of marginal shrubs and small trees. Among those which commonly grow in this zone are *Salix longipes* Anders., *Magnolia virginiana* L., *Persea pubescens*

Sarg., *Crataegus viridis* L., *C. aestivalis* T. and G., *Cyrilla racemiflora* L., *Cliftonia monophylla* Britt., *Ilex Cassine myrtifolia* Sarg., *Acer rubrum* L., *A. rubrum tridens* Wood, *Hypericum fasciculatum*

FIG. 5.—Gums (*Nyssa* spp.) forming a gum swamp; trees show swollen bases, and a seedling in center of picture has germinated and is growing in the dark water.

Lam., *H. myrtifolium* Lam., *H. microsepalum* Gray, *Lyonia nitida* Fernald, and *Leucothoe racemosa* Gray.

On the edge of moist but not inundated soil, species of *Myrica* may grow, while *Serenoa serrulata* Hook. and *Ilex glabra* Gray mark

the line of high water. Here live oaks, water oaks, sweet gums, and the swamp and pond pines appear, beginning a meadow or swamp, or quickly giving way to the immediate upland climax (fig. 6). *Smilax Walteri* Pursh is the liana significant of inundated soil, while *S. laurifolia* L. and *S. lanceolata* L. are marginal lianas on moist soil.

FIG. 6.—Lake margin, showing cypresses in water, shrub zone within range of high water, and live oaks on rising ground.

Ponds which dry out during the season are often encircled by hawthorns, *C. viridis* L. being a common marginal species, and *C. aestivalis* T. and G. may fill a shallow or transient pond and convert it into a "mayhaw pond." On areas of clayey soils, willows, maples, sweet gums, and button bushes are the commoner marginal trees and shrubs; while the chief variations in ponds on sandy soils are due to the presence of cypresses or of gums as the tree pioneers,

the composition of the shrubbery about the margin, and in succeeding climax.

Pre-erosion streams, being slow and shallow, do not differ much from the ponds as described. The aquatics in moving water are not so numerous, but the shore growth is more varied, and may grade, with the drainage, into bordering strips of meadow on lowland hammock by which the streamways are conspicuously marked from the adjoining pine forests.

Waters flowing from limestone springs and which are clear and more calcareous have a somewhat different vegetation from that of the acid, brown waters of the other streams. *Liquidambar Styraciflua* L. is a tree of the sometimes inundated margins, and *Ulmus americana* L., *Fraxinus caroliniana* Mill., *F. profunda* Bush, *Quercus nigra* L., *Salix longipes* Britton, *Acer rubrum* L., *Ilex Cassine* L., *Cornus stricta* Lam., and *Cephalanthus occidentalis* L. are common. Canes (*Arundinaria tecta* Muhl.), reeds (*Phragmites communis* Trin.), and saw grass (*Cladium jamaicense* Crantz), with bulrushes (*Scirpus* spp.) are marginal marsh plants.

Swamps and meadows

FLOWING WATERS.—Swampy borders of varying width or overflow strips of meadow are the almost invariable accompaniment of pre-erosion branches, creeks, and rivers, the width of the overflow area depending upon the topography and upon the consequent drainage basin, and upon the volume of the stream. By the accumulation of humus and as improved drainage is secured, these meadow areas in many cases tend to extend outward or upward and often come to occupy wider spaces than would be explained solely by the fluctuations of the stream. From the adjoining vegetation they are marked off by species ranging from hydrophytic to extremely mesophytic. The swampy character extends as far as the soil continues saturated, and in this zone there occur trees of the pond margins, such as cypresses, gums, willows, birches, ashes, water hickory, and water elm (*Planera aquatica* J. F. Gmel.).

On slightly rising ground, but still within range of the high water, there occur pines (*P. caribaea* Morelet, *P. serotina* Michx., *P. palustris* Mill., and *P. glabra* Walt.), with a variety of oaks, such

as *Q. nigra* L., *Q. laurifolia* Michx., *Q. Michauxii* Nutt., also *Carpinus caroliniana* Walt. and *Liquidambar Styraciflua* L. (fig. 7).

Many shrubs and small trees belong to these swampy margins, making a dense growth to the water's edge, with intermingling

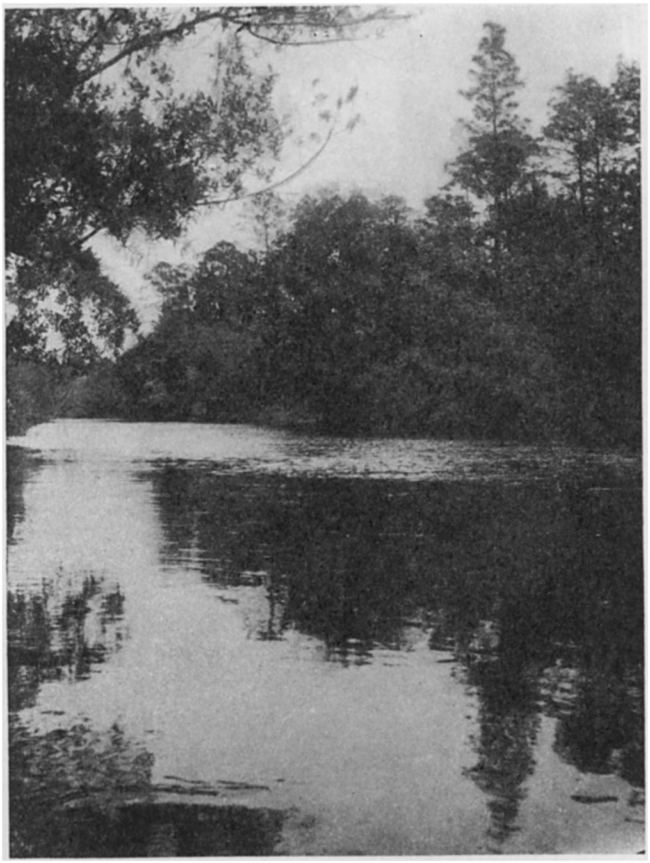

FIG. 7.—Exterior view of Ocklocknee River meadow, showing dense deciduous growth at swampy edges; pines coming in on higher ground.

myricas, bays, and mixed shrubbery, among which are *Itea virginica* L., *Rhus Vernix* L., *Cyrilla racemiflora* L., *C. parvifolia* Raf., *Sebastiana ligustrina* Mill., *Ilex Cassine* L., *I. decidua* Walt., *Cornus stricta* Lam., *Clethra alnifolia* L., *Rhododendron* spp., *Andromeda ferruginea* Walt., *Cephalanthus occidentalis* L., *Pinckneya pubens*

Michx.; with also a variety of lianas such as *Smilax Walteri* Pursh, *S. laurifolia* L., *Berchemia scandens* Trel., *Trachelospermum difforme* Gray, and *Aster carolinianus* Walt.

Beyond reach of frequent inundations, in soil enriched by accumulation of humus, the most mesophytic stage is reached, and the meadow grades into the lowland or river hammock, where a mixed forest of many species develops. *Fagus grandifolia caroliniana* Fernald and Rehder and *Magnolia grandiflora* L. may appear here, with *Celtis mississippiensis* Bosc., *Liriodendron Tulipifera* L., *Halesia carolina* L., *H. diptera* Ell., *Chionanthus virginica* L., and others, forming rich forests of varying composition along the streams. In these forests is an assemblage of mesophytic shrubs, such as *Alnus rugosa* Spreng., *Hamamelis virginiana* L., *Aesculus Pavia* L., *Styrax* spp., and *Viburnum* spp., with lianas and climbing shrubs, such as *Decumaria barbara* L., *Wistaria frutescens* Poir., *Sageretia Michauxii* Brong., *Rhus Toxicodendron* L., *Psedera quinquefolia* Greene, *Cissus Ampelopsis* Pers., *Cissus arborea* Des Moulins, *Vitis rotundifolia* Michx., *V. aestivalis* Michx., *Bignonia capreolata* L., *Tecoma radicans* Juss., and the mesophytic species of *Smilax*. Ferns of the swampy or wetter soils are *Osmunda* spp., *Onoclea sensibilis* L., and *Woodwardia* spp. Of more mesophytic habit are *Aspidium Thelypteris* Sw., *A. patens* Sw., and *Asplenium Filix-femina* Bernh. On the water oaks, black gums, and various other trees *Phoradendron flavescens* Nutt. is abundant, and also *Tillandsia usneoides* L., the ever common epiphyte.

It is to be noted that the character of a well developed stream or river hammock of the region is quite the same wherever occurring and within the boundaries of whatever soils. The telescoping of swamp and hammock complicates the successional phases and is usually extreme, since even slight differences in elevation or drainage are sufficient to modify the vegetation extensively.

QUIET WATERS.—The so-called "bays" are examples of shallow undrained swamps supporting a more or less dense growth of shrubs or small trees. *Magnolia virginiana* L., *Persea pubescens* Sarg., and *P. Borbonia* Spreng. are the real "bays," but the list of plants for these boggy ponds includes a variety of other species, as cyrillas,

grapes, hollies, hypericums, hawthorns, and ericads, and such trees as cypresses, gums, and slash and swamp pines.

There is little suggestion of any definite succession in the composition of the bay or similar swamp. However, *Magnolia virginiana* L., *Persea pubescens* Sarg., and *Ilex Cassine myrtifolia* Sarg. seem to advance into the more hydrophytic portions and appear near the center of the swamp surrounded or followed by the grapes, ericads, and myricas; while *Ilex glabra* Gray, *I. lucida* T. and G., and *Serenoa serrulata* Hook., with *Hypericum* spp. grow beyond the standing water. Frequently *Ilex Cassine myrtifolia* Sarg. is so abundant as to make a fairly impenetrable thicket.

FIG. 8.—Cypresses advancing into waters of an undrained pond, gradually forming a cypress swamp.

An undrained pond may develop into a cypress swamp, the cypresses growing as closely as their swollen bases and groups of projecting knees permit (fig. 8). Around the margin of such a swamp there may be a mingling of oaks, gums, and pines, but more frequently there is a sharp transition to the forest of the upland adjacent, and the edge of the swamp is abruptly marked by the ranks of flat-topped cypresses. When the gums mingle with the cypresses or are the most abundant or only trees, a gum swamp develops, these trees also having swollen or bulging bases. *Tillandsia usneoides* L. gives a characteristic touch to their appearance, especially in winter when the trees are leafless.

The herbs of such swamps are mainly those of pond margins and of the flatwoods, as *Panicum hemitomum* Schutts, *P. condensum* Nash, *Aristida spiciformis* Ell., *Eleocharis* spp., *Fuirena squarrosa* Michx., *Rhynchospora* spp., *Eriocaulon* spp., *Mayaca Aubleti* Michx., *Burmannia biflora* L., *Polygala cymosa* Walt., *P. ramosa* Ell., *Hypericum petiolatum* Walt., *H. virginicum* L., *Ludvigia alternifolia* L., *L. glandulosa* Walt., *Gerardia linifolia* Nutt., *Lobelia amoena* Michx., and *L. glandulosa* Walt.

In certain low places, as at the bases of slopes, water may ooze through the sandy soil to collect on the surface in little pools or pockets, with intervening hammocks of dark muck, or may slowly drain away, sometimes forming the source of a small stream. In this way small branches or considerable tributaries may originate, and by their union form creeks or small rivers. In other cases sloughs and ponds may be formed, such boggy spots often being designated "galls." In vegetation they resemble the bays, often surrounded by or advancing to a hammock stage by the accumulation of humus and the gradual building up of the soil.

Bayheads scarcely differ from these, also being the sources of small branches. In these, typical trees are *Magnolia virginiana* L. and *Persea pubescens* Sarg., with a bordering shrubbery of more or less mesophytic character.

Sloughs are low, flat passageways between swamps or bodies of water. In these passageways the water may be still or but slowly moving, while during the dry season they may be entirely dried out. Cypresses, sour gums, swamp pines, and swamp maples are common slough trees, with live oaks, water oaks, holly, and sweet gums on the edges. Swamp shrubs, including a variety of the ericads, cyrillas, gallberries, hypericums, with the saw palmetto, out of reach of the standing water, are numerous.

Prairies

Prairies are comparable to swamps in being depressions below the general surface and lacking surface drainage. They may be flooded during the rainy seasons and dry at other times, and their vegetation consists typically of herbaceous associations, especially the grasses. No extensive natural prairies exist in connection with the pre-erosion topography under description here, although many of the small ponds and lakes may temporarily become prairie-like, their beds during the dry seasons being overgrown with grasses and other herbage, in which introduced plants, as weeds, make a miscellaneous assemblage.

EROSION TOPOGRAPHY

The northern part of Leon County, having been exposed probably as long as any other section of Florida or of the immediate Gulf

Coast, and being in parts above the general level, should afford illustrations of erosion topography. The conditions are unusual, however, since the presence of limestone so near to the surface has brought about the development of extensive subterranean as well as surface erosion, and the topographic features are thus modified in such ways as to complicate ecological analysis. In considering the region as a whole, it appears that the surface features may be largely due to the underground erosion. The lakes, sinkholes, and enclosed valleys seem evidence of this.

Surface erosion

BRANCHES AND CREEKS.—The trough of almost every valley has a waterway marked by an aggregation of trees and shrubs. The stream is usually an insignificant affair so far as the amount of movement of the water is concerned, and consequently the erosive work accomplished by such a stream is slight. Its course may be found to lead, by a slight rise, to a bayhead where the water is seeping from the base of a slope; or it may issue from a spring whence the water may flow across the ground, spreading out into a miry tract; or, as in the clayey soil of the hills, a definite channel will be cut or gullied down the slope; or the spring will eat back into the hill as a narrow ravine and a small clay canyon thus be cut along the steeper part of the grade. The erosion work lessens as the level is reached, the washing and gullying of the steep banks grade and widen them, and in this way the little streams are gradually bringing the soils of the hills to the valleys.

RAVINES.—In the shady and moist ravines there grow numerous liverworts and mosses, with soil lichens in the upper zone and with ferns along the edges and in the niches. Of the ferns, *Polypodium polypdioides* Hitch. grows on the moist clay banks, also *Asplenium platyneuron* Oakes, *A. resiliens* Kunze., *Polystichum acrostichoides* Schott., *Aspidium Thelypteris* Sw., and *A. patens* Sw. As the stream broadens and shallows and the banks are lowered, reeds, canes, and marsh grasses border the edges, while trees and shrubs develop to form a meadow hammock.

RIVERS.—The Ocklocknee River is an example of an extended stream, rising in Georgia and cutting its way across the latest

deposits of the coast. For most of its course along the western border of Leon County its banks are edged by bluffs of varying elevation (50–100 ft. above sea-level). These are apparently the ancient banks, eroded during a previous period. At places these bluffs approach close to the present low banks, so that the valley varies in width. The erosion work of the river is of small importance, and in its bordering meadow and overflow land it resembles a pre-erosion stream. The low bluffs are generally well wooded and the undergrwoth is often denser and of a more mesophytic type than is that of the upland forest.

Examples of small erosion creeks are to be seen in the southwestern edge of the county, where a series of drainage streams flow from the bays on the Leon sand across the strip of Norfolk sand to empty into the Ocklocknee River, and have cut ravine-like valleys in the sands, in which the most mesophytic trees, including *Magnolia grandiflora* L., *Fagus grandifolia caroliniana* Fernald and Rehder, *Liriodendron Tulipifera* L., *Carya alba* K. Koch, *Acer* spp., *Carpinus caroliniana* Walt., and *Prunus caroliniana* Mill., grow with a rich undergrowth. Entering one of these eroded valleys from the upland of monotonous pine forests, one witnesses the extremes which the region can support.

LAKES.—The surface erosion along the shores of the larger lakes is of small importance, as the shores are usually sloping and the wave action is slight. The trees of the uplands may extend to the water's edge or there may be tracts of fine hammock forest. Other lakes resemble slow fluctuating streams, with cypresses in the shallow water.

Subterranean erosion

The underground solution and the resultant caving in or settling of the ground surface continue to play a part in modifying the topography.

SINKHOLES.—The formation of sinkholes may take place suddenly and expose the limestone, forming depressions, usually circular, varying in size and depth. In case there is no opening through which the water may reach an underground channel, the rainfall and the surface waters may accumulate to form a pond.

In such sinks the water rises and falls with the amount of precipitation and surface drainage. Other sinks are dry, having one or more openings in connection with the underground drainage system.

The cliffs and ledges of limestone, if exposed, soon wear off, soil collects, and gradually the sides become overgrown. The soil collecting in the bottom supports growth of trees and shrubs usually more mesophytic than those of the immediate upland, the shade and the moisture favoring the growth of such seedlings. Liverworts and mosses may be found on the damp soil at the base of a sink and often in the crevices of the sides. *Adiantum capillus-veneris* L. belongs to such situations, as also *Polypodium polypodioides* Hitchc., *Asplenium platyneuron* Oakes, and *Polystichum acrostichoides* Schott. *Panicum dichotomum* L. and *Opelismenus setarius* L. are grasses in the shady ravine-like situations, as pioneers on the sides.

If the sink contains water, pond plants will enter and cypresses or gums may grow. If the base is covered or finally filled with soil, water oaks, live oaks, sweet gums, dogwood, and holly are common sinkhole plants. White oaks, red maples, black gums, and sweet gums are other trees occurring about the sinkhole margins.

SPRINGS.—Many springs are the results of channels in the limestones, occurring where the streams emerge from underground. In the clear, cool, calcareous water of such springs there is not much plant growth, although around the margins are grasses, sedges, sagittarias, and reeds.

LAKES AND PONDS.—The relation of the large lakes to sinkhole formation has been mentioned, sinks or openings occurring in their basins through which the more or less complete drainage of the waters of the lake may take place suddenly or gradually. When these sinks become closed by obstructions or stoppage, the water will again fill the basins (**12**). By the drainage of such lakes, sometimes large areas of the basins may become prairies, which unless again flooded or otherwise used, may gradually approach the forest stage.

STREAMS.—Underground channels sometimes become surface streams by the caving in of the roof of the cavern. Frequently a section may be left to form a natural bridge. Such is the case

with the St. Mark's River, which emerges from a subterranean course as a series of sinklike ponds, and finally as a surface stream flowing across the sands to the Gulf. At the natural bridge the banks are definite and rise directly from the water level. A rich hammock borders the banks, the trees and shrubs growing close to the water's edge.

Summary

This local study of the Gulf section of the coastal plain may serve to suggest several points in the successional history of the plant associations of the region. Extremes of xerophytic, hydrophytic, and mesophytic societies are to be found. The most xerophytic association is represented by the long-leaved pine-scrub oak forest of sterile, sandy soil. The most mesophytic association is that of the hammocks, occurring on the upland as the climax and also as a temporary climax in the river valleys, being composed of a large variety of species, deciduous and evergreen, of which *Fagus grandifolia caroliniana* Fernald and Rehder is perhaps the most significant deciduous tree, and *Magnolia grandiflora* L. the principal tree among the broad-leaved evergreens. Between these two extremes are the gradations from pioneer pines through the pine-oak and oak-hickory stages. Telescoping and rapid growth in the later stages are characteristic and confusing.

The long-leaved pine-saw palmetto association on the flat, poorly drained sands presents a large edaphic problem. With improvement in drainage, aeration of the soil, and consequent promotion of soil organisms and their work, the change to a mixed forest can take place, as is seen along the streams as well as in local hammocks which have evidently been built up gradually. Drainage of the subsoil brings scrub oaks in place of the saw palmetto into association with the long-leaved pines, and the succession outlined from dry pine woods to the climax forest will naturally follow. With slight depression of the surface a change to a moorlike swamp results.

The various types of swamps, characterized by the prevailing species, as the cypress swamps, gum bogs, pine swamps, and bays, and their transitions to the surrounding forest, furnish opportunities for intensive studies.

Comparative observations

In considering the upland forests in their successional stages, data concerning the evaporation, soil moisture, and certain climatic factors, and their relation to the associations discussed, have been collected. Evaporation records were secured by the use of Livingston atmometers, following the investigations of FULLER (4) and others. Rain-correcting valves were used, the cups were kept standardized to the same unit, and computations made accordingly.

Stations were established in a mesophytic forest of the climax type, in a Spanish oak-post oak-hickory forest, in a short-leaved pine forest, in a beech opening in the short-leaved pine forest, in the dry pine woods (long-leaved pines), in the scrub oaks association, and in the flatwoods. Meadow stations were also placed, but their records are not complete. The stations were located in as nearly typical situations as possible, the atmometers in each case being placed at the surface of the ground. All records demonstrate a constantly high evaporation as one of the climatic results, and all show a general relation between the evaporation and precipitation periods, there being two marked maxima for all the stations, the major one being between the winter and the summer rainfall, corresponding to the April and early May dry season, the other evident in late September and early October, after the summer rains have ceased. All records show a sudden rise in spring from the lowest point in December or January to the April or May maximum (June for the long-leaved pine forest). This corresponds generally to the period of the vernation of the deciduous species and to the renewal of foliage by many of the evergreens. Winter records for the highland stations were uninterrupted by frost through two consecutive winters, but each lowland station suffered once or twice each winter.

Of the upland stations, the average daily evaporation is lowest for the mesophytic climax (magnolia-beech) forest, being 8.5 cc. daily, estimated for a period during which an unbroken record was obtained from December 24 to May 1; this is the most critical period, including from the January minimum to the April maximum. For the same period of time the Spanish oak-post oak forest gave

a record of 9.9 cc.; the beechwood 11.21 cc.; the short-leaved pines 11.67 cc.; the long-leaved pines on Norfolk sand 12.28 cc.; and the scrub oaks 15.3 cc. daily, the reverse of this order being essentially that in which the successional changes as observed occur, from the xerophytic pines and oaks through the xeromesophytic pines and oaks to the climax forest (fig. 9). The beech wood, it must be noted, was subject to pasturing and gave evidence of

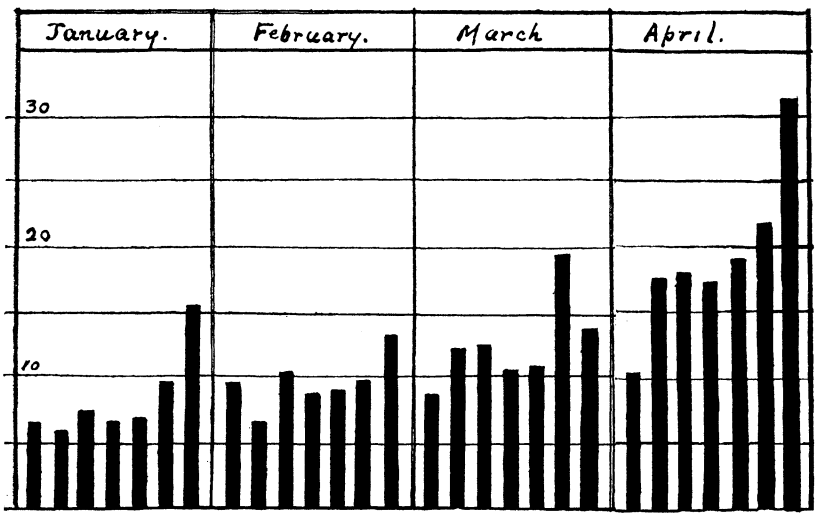

FIG. 9.—Diagram showing comparison in evaporation rate from January to May in (1) mesophytic climax forest; (2) flatwoods; (3) Spanish oak-post oak-hickory forest; (4) short-leaved pine forest; (5) pastured beech forest; (6) scrub oak forest; (7) long-leaved pine forest.

recent burning (probably to promote pasturage), being quite free of undergrowth. Cattle and hogs grazed through this forest and *Erechtites hieracifolia* Raf. appeared among the herbs.

On the basis, however, of the average rate of evaporation estimated for the year, the order is changed. The Spanish oak-post oak association has an evaporation rate very close to that of the short-leaved pines, being 14.00 cc. daily for the former and 14.22 cc. for the latter. Both of these stations were observed without a break from September 1912 to May 17, 1914, and their averages taken accordingly. The two stations are alike in that each has

a dense undergrowth, that of the pine woods being if anything denser than that of the oak forest; indeed, the pine forest is well on its way toward the oak stage. However, there is a difference when the winter and the summer averages are considered. Estimated for the period from June to November, the season during which full foliage of deciduous trees is a large factor, the daily rate for the oaks is 12.49 cc. and for the pines 13.8 cc. In winter (November to June), from the time when the oaks are leafless until they attain full summer foliage, the rates are 15.69 cc. daily for the oaks and 13.70 cc. for the pines. In the beech woods during these seasons, the rates are 13.4 cc. daily for the summer and 17.8 cc. daily for winter, thus showing an approximation to the pines in summer and greater evaporation than either pines or oaks in winter.

The scrub oaks and long-leaved pines behave differently. These oaks average 13.95 cc. for summer (comparable to the short-leaved pines and the open beech woods) and 14.1 cc. for winter; while the long-leaved pines on dry sand show the highest rates, 18.25 cc. for summer and 19.2 cc. daily for winter. The scrub oaks and the long-leaved pines have respectively 15.52 cc. and 17.9 cc. daily average for a period of 18 consecutive months. The scrub oak forest shows less actual variation than any other except the flatwoods, this probably being related to the stunted character of the oaks, their close thicket-like growth, and their habit of retaining the dead leaves most of the winter or until fresh growth starts. In striking contrast, the long-leaved pine forest shows the most extreme variations in range of evaporation of any other station.

The contrast between the two long-leaved pine associations is the greatest of any, as the flatwoods station shows a uniformly lower rate throughout the year than any other and averages 12.99 cc. daily for the 18 months, thus taking the place next in order to the mesophytic climax forest. The summer evaporation for the flatwoods averages 13.24 cc. daily, comparable to that of the scrub oaks and the pastured beech wood. The average winter rate is 11.17 cc. daily, being the lowest, and this is the case although this forest is even more open than any of the others, the shrubs being low and the forest subject to turpentining, burning, and pasturing.

Some experiments to determine the soil moisture relations (by use of the wilting coefficient) were obtained and determined according to the method of BRIGGS and SHANTZ (2). Although incomplete, these tend to confirm the statement that the flatwoods have

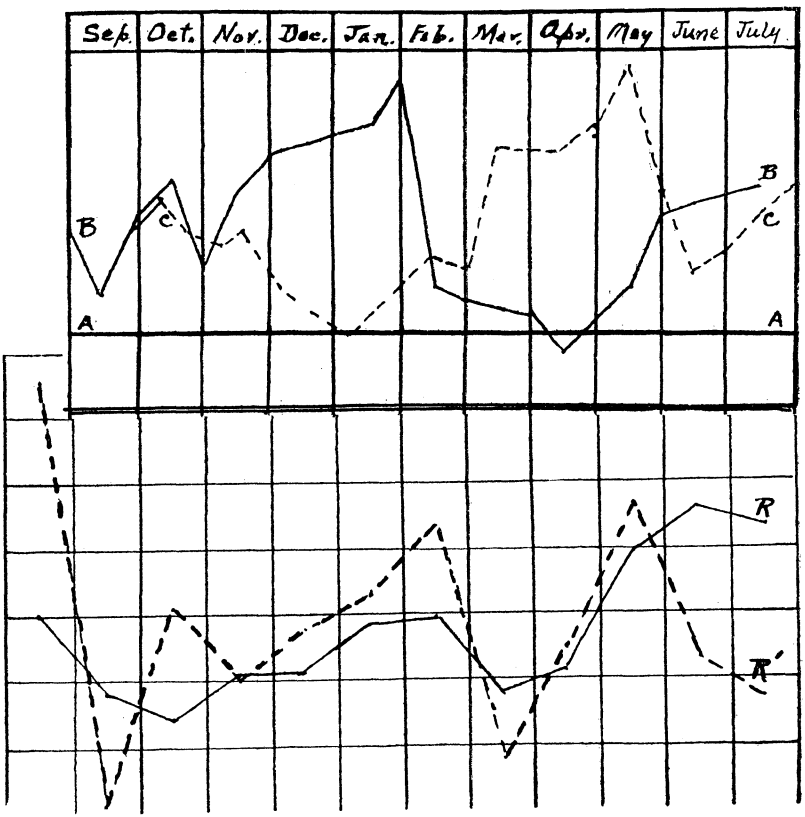

FIG. 10.—Chart showing relation of wilting coefficient and soil moisture of Leon sand, and comparison with precipitation: *AA*, wilting coefficient; *BB*, range of soil moisture from September to June; *CC*, graph of daily evaporation at flatwoods station during same period; *R*, curve of average monthly rainfall (in inches); R^1, curve of rainfall during the period.

the wettest soil, not actual swamp, in the region. The wilting coefficient of soil taken from the first 3 inches of the surface is approximately 5.9, while the average percentage of the soil moisture present during the year is 12.74 (fig. 10). Only once (in April),

at the end of the spring drought, does the percentage of moisture in the first 3 inches of soil fall lower than the wilting coefficient, and then but slightly. The maximum amount is reached in late January and early February, while a summer maximum is reached in July, coinciding with the two periods of rainfall. The curve of the range of the soil moisture agrees quite closely with that of the average daily evaporation, which in this association therefore has a direct relation to the soil moisture and the consequent humidity of the atmosphere at the surface of the soil where evaporation is actively occurring.

Considering the edaphic character of the flatwoods in explanation of its position as determined by the evaporation averages, the order of succession for upland forests as observed seems to have a definite relation to the obtained rate of evaporation. This tends to confirm the observation that in the coastal region studied the present pines are pioneers making a temporary forest, which, owing to present geological, topographical, and soil conditions, may make but slow progress toward the ultimate climax, at least over large areas. When once started, however, the climate favors a rapid mesophytic advance.

To the lectures and teaching of Dr. H. C. COWLES I am indebted for my interest in this subject and for my point of view; to Dr. G. D. FULLER for instructions concerning field work with evaporimeters; and to Dr. J. M. GREENMAN for aid in identification of various plants. Also I acknowledge the assistance of Professor JEROME MCNEILL of Tallahassee, Florida, in the field work and in securing the evaporation and soil moisture readings over an extended time.

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