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The Xeric Sandhill and Savanna Ecosystems of the
Southeastern Atlantic Coastal Plain, U.S.A.

by

Norman L. CHRISTENSEN

1. Introduction

In a region where annual rainfall exceeds 140 cm and falls year-round, xeric sandridges and savannas seem unlikely. On the southeastern coastal plain one may travel from swamp forest to xeric pine-oak forest in a horizontal distance of less than 100 meters involving topographic change of less than 4 meters. These ecosystems are among the most diverse and floristically unique in the southeastern United States.

The uniqueness of the Coastal Plain is, in part, a consequence of the mantle of poorly weathered Quaternary sediments deposited during several variably extensive marine encroachments. During this period the upland vegetation of the northern Coastal Plain shifted between oak, beech and hickory-dominated forests in mesic localities, perhaps not unlike extant Piedmont forests, and pine-dominated forests in dryer localities (DELCOURT 1978, WATTS 1979), to spruce and hemlock forests (FREY 1953, WHITEHEAD 1967, WATTS 1979). The former forest types being characteristic of interglacial periods and the latter characteristic of full glacial time. The southern coastal plain (northern Florida, southern Georgia) was continuously vegetated by a mixture of deciduous broadleaf trees and evergreen conifers, with relative abundances shifting in response to long-term climatic changes (DAVIS 1946).

Based on the descriptions of early travelers (e.g. CATESBY 1754,

BARTRAM 1791), one judges that most of the upland coastal plain sands were dominated by pines, particularly longleaf pine (*Pinus palustris**), with an open herbaceous understory at the time of European settlement. Because of their relative infertility, these ecosystems were not heavily farmed during the eighteenth and nineteenth centuries. However, these areas were important sources of timber and naval stores during this period. Nearly all these communities have been cut over.

The vegetation varies floristically with changes in soil moisture and nutrients. For ease of discussion, I have divided communities into xeric sandhills and sandridges, and savannas and flatwoods. These represent modal situations and intermediate communities are quite common.

2. Xeric sandhills and sandridges

2.1. Soils

The xeric sands of the coastal plain are a collection of poorly differentiated sediments and residua derived primarily from three sources (MURRAY 1961). The Fall-line Sandhills are a more or less continuous formation of rolling hills extending from southern North Carolina through Georgia on the upper coastal plain along the "fall-line" with the Piedmont. The oldest and most weathered sands, these soils may be residual products of the underlying Tuscaloosa formation (COOK 1956, HERON 1958, DUKE 1961). These hills are often higher in elevation than the Piedmont to the West, perhaps owing to the low amounts of surface runoff and erosion associated with their sandy soils. The second set of sands is associated with the lower and middle coastal plain and appears to be of aeolian origin. These coarse, poorly weathered sands include the very infertile St. Johns and St. Lucie soil series which occur on upland areas (bay rims) surrounding the numerous elliptical depressions (Carolina Bays) scattered throughout the middle Coastal Plain. Third, coastal dune deposits provide sandy soils on lower, more re-

* All taxonomic citations according to RADFORD et al. (1968)

cently exposed marine terraces (COLQUHOUN 1969). WOODWELL (1956) refers to these as "ridge and bay" areas. The distribution of these various sand types is indicated in Figure 1.

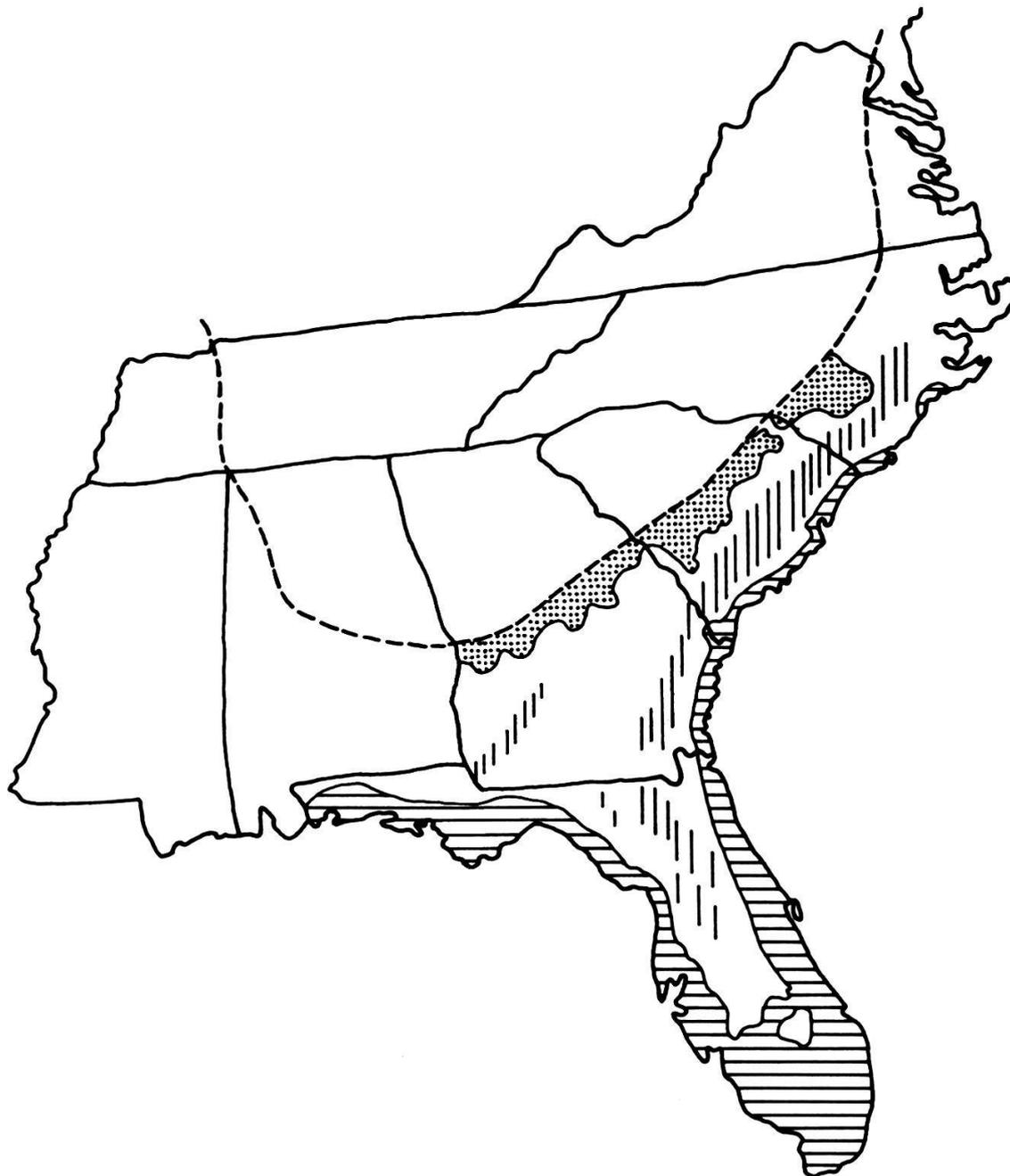


Figure 1. Distribution of coastal plain sand. The dashed line indicates the distribution of the Fall-line Sandhills; the vertical hatching indicates the distribution of aeolian and marine sands; the horizontal hatching represents the distribution of sand associated with coastal features.

All of these xeric sands are generally classified as psammaquents (BUOL 1973) and have little profile development. Organic matter content in the upper few centimeters of soil may approach 0.5-1% however below 5 cm, organic matter accounts for less than 0.5% of total soil weight. In some areas a spodic horizon composed of precipitated organic compounds may occur near the level of the average water table (1-2 m). This is most typical of sand rimes of the middle coastal plain. In areas where sands have been deposited over peats, organic "lenses" may also occur at various depths. In the sandhills clay layers and lenses underlying the sand may result in perched water tables and seepages which dramatically affect the composition of the vegetation above them.

From a silvicultural standpoint, these sands are rather unproductive, being particularly low in nitrogen and phosphorus (RALSTON 1978).

One other feature of these soils which has greatly influenced evolution of the plants which inhabit them is that the surface layer of 1 cm is often highly leached and very white resulting in high surface albedo. WELLS (1932) commented that the sun shines up as well as down in these areas. The result is very high levels of solar radiation.

2.2. *Vegetation*

On floristic and physiognomic grounds, these ecosystems can be divided into two distinct groups, the longleaf pine-turkey oak forests and the sand pine scrub. The understory of the former is characterized by a sparse cover of herbs, particularly grasses whereas that of the latter is dominated by evergreen shrubs.

The sand pine scrub is confined to peninsular Florida. In the same area on sandy soils, longleaf pine-turkey oak forests also occur and there has been considerable discussion regarding the environmental factors which separate them (HARPER 1914, MULVANIA 1931, KURZ 1942, LAESSLE 1958). LAESSLE (1958) has demonstrated that the scrub is confined to the very nutrient deficient sands of relict Pleistocene shorelines whereas other forest types are found on more weathered sands. Presumably the low nutrient conditions give evergreen shrubs a competitive edge compared to deciduous species and herbs.

The lack of this evergreen scrub on similarly nutrient poor sands farther north is probably a consequence of climatic factors, such as shorter growing seasons.

The dominant tree species in the scrub ecosystem is the sand pine *Pinus clausa*. In the understory, several live scrub oaks (including *Quercus virginiana* and *Q. chapmani*), turkey oak (*Quercus laevis*), fetter brush (*Lyonia* spp.), and saw palmetto (*Serenoa repens*). Floristically, the scrub is most similar to the palmetto flatwoods which are characteristic of many Gulf Coastal Plain areas.

The longleaf pine-turkey oak forests dominate sandy soils along the Atlantic Coastal Plain into North Carolina. Longleaf pine (*Pinus palustris*) is the major canopy tree and turkey oak (*Quercus laevis*), along with persimmon (*Diospyros virginiana*), black gum (*Nyssa sylvatica*), and sand oak (*Quercus pumila*), are woody understory dominants. In comparatively moist areas, hardwoods such as blackjack oak (*Quercus marilandica*), sandhill post-oak (*Quercus margaretta*) and sweet gum (*Liquidambar styraciflua*) are common. The wiregrass (*Aristida stricta*) is the dominant understory herb (WELLS and SHUNK 1931). DUKE (1961) prepared a list of psammophytic herbs occurring in the Sandhills region and noted that a very large percentage of the flora of these sandy ecosystems is found only on these sandy soils. Included are a variety of narrow endemic species such as *Pyxidantha barbulata* (*Diapensiaceae*). This high degree of endemism also characterizes many of the cryptogams. For example, *Selaginella arenicola* (*Selaginellaceae*) as well as many moss and lichen species are found here.

These ecosystems vary considerably in their structure, diversity, and productivity in relation to their substrate. The fall-line sandhills support the most substantial and productive forest as well as the greatest diversity of hardwood and herb species (DUKE 1961). The more sterile sand-rims and sandridges have a somewhat more austere flora, with cryptogams often dominating the herb layer (Figure 2).



Figure 2. Longleaf pine-turkey oak forest on the Jones Lake Sand Rim, Bladen Co., N.C. The pines shown here are about 15 meters high and 250 years old. Note the turpentine scar on the center of the tree's bole.

2.3. Autecology

Two factors which clearly have selected for many of the unique morphological and physiological features found among these psammophytes are drought and irradiance. Because of the rapid percolation of water, the upper soil horizons dry quickly. As mentioned previously, the white sands have a high albedo, increasing radiation dramatically. Xeromorphic features, such as micophylly, succulence, thick cuticles, and sunken stomates are found among the herbs and shrubs which depend on these upper soil layers for moisture (WELLS and SHUNK 1931). WELLS (1928) suggested that many species are unable to grow in these sandy soils because they simply cannot extend their roots to the abundant subsurface water before succumbing to drought. WEAVER (1969) found that deep rooted trees and shrubs, such as *Pinus palustris* and *Quercus laevis*, have a nearly constant supply of water. This is particularly true of the middle and lower coastal plain where the water is often within two meters of the surface. I have not observed mid-day xylem sap potentials in *Q. laevis* to exceed -15 bars, even after prolonged drought. As WELLS suggested many supposedly xeromorphic features among deep-rooted inhabitants of these sands may actually be adaptations to high irradiance. WELLS and SHUNK (1931) demonstrated that radiation in these areas was sufficiently high to cause tissue damage in *Quercus laevis*. Characteristics such as verticle leaf orientation in *Q. laevis*, glaucous leaves and leaf pigmentation may be adaptations to high radiation values (WELLS and SHUNK 1931, RAFF 1954).

These sandy soils have a very low adsorptive capacity and are readily leached. Consequently, nutrients are often limiting to plant growth. Based on tissue nutrient values, WEAVER (1969) hypothesized that patterning of various oak species in the Sandhills was a consequence of calcium availability. Reduced nutrient availability undoubtedly contributes to the reduced diversity of the sand rims associated with bay lakes.

Nutrient availability varies spatially in relation to localized accumulations of litter, often associated with shrubs or clumps of wiregrass. For example, concentrations of calcium beneath such accumulations may be

2-5 times higher than in bare areas less than one meter away. Many herbs and woody seedlings are clumped around such accumulations (CHRISTENSEN, unpublished data).

2.4. *Successional relations and fire*

KURZ (1942) suggested that the sand pine scrub develops successionally from longleaf pine-turkey oak communities deprived of fire. This now seems quite unlikely. As early as 1914, HARPER emphasized the potential of fire in the origin and maintenance of these ecosystems. Fire return time is 30-60 years and most above-ground fuel is consumed and stems are killed to the ground (WEBBER 1935, HARPER 1940, LAESSLE 1965). Sand pine seedlings establish successfully only after fire or other disturbance and most populations are even-aged. These pines have moderately serotinous cones and, like most of the shrub species found here, they sprout vigorously following fire.

WELLS (1928) argued that the longleaf pine-turkey oak communities were fire disclimaxes and, without fire, these ecosystems would be succeeded by the oak-hickory climatic climax (sensu CLEMENTS 1916). While there is no doubt that the hardwood component of these ecosystems becomes more dominant without fire, this seems hardly to represent a trend towards an oak-hickory climax. Most of the dominant oaks are scrubby, rarely exceeding a height of five meters. Today, many of the most sterile sites are dominated by hardwoods, especially turkey oak. Earlier observations (BARTRAM 1791, WELLS and SHUNK 1931) indicate that these areas were once dominated by pines with relatively sparse understory growth. According to ASHE and PINCHOT (1897), many of the pines were harvested or killed during a long period of turpentine operations. It is not unusual to find an occasional 200+ year-old longleaf pine on even the most xeric sand rim which still bears the scars of turpentine extraction (Figure 2).

The frequency and intensity of fires is variable among these ecosystems. In the Sandhills region and other comparatively productive areas, low intensity surface fires are purposefully set every 2-4 years to reduce hazard of wildfires and to control the growth of understory hardwoods and wiregrass which compete with the pines (WAHLENBERG 1946). Such fires also

create a favorable seedbed for germination and early growth of pine seeds as well as eliminating brown spot fungus in seedlings, an important cause of mortality. On less productive sites, fuel loads may be insufficient to perpetuate a fire and prescribed fires are not used at all. The natural fire frequency (i.e. that which would occur without human intervention) is more difficult to ascertain. WAHLENBERG (1946) estimated that a fire cycle of 4-10 years would result in optimal reproduction of longleaf pine. Ultimately, the fire frequency in these stands depends on the frequency of ignition sources (e.g. lightning) and the accumulation of surface fuels, particularly pine needles in areas of low wiregrass density. The removal of the pines from many of these sandy habitats has undoubtedly reduced fire frequency. This tends to favor hardwood growth and to retard invasion and establishment of longleaf pine. Thus, reestablishment of pine forests on many of these sites may be a very slow process.

3. Flatwoods and savannas

With increased moisture availability, either due to changes in soil or topography, the xeric sandhill vegetation grades into pine-dominated flatwoods and savannas. This vegetational gradient may be quite continuous and many of the sandhill dominants are also common in these moister, floristically more diverse ecosystems. The distinction between flatwoods and savannas is, to a certain extent, artificial. Savannas in the coastal plain are typified by scattered trees (often less than 100 ha⁻¹) with a graminoid understory, whereas the overstory is more dense in flatwoods and a greater diversity of woody shrubs and trees occur in the understory. Intermediate situations are common. Typical flatwood and savanna situations are illustrated in Figure 3.

3.1. Soils

The soils of these pine woods are variable ranging from sands to heavy clark and silts. The sandy soils are often groundwater podsoils



Figure 3a. Longleaf pine-wiregrass savanna in the Green Swamp, Brunswick Co., N.C. This particular area was burned about four months prior to this photograph.



Figure 3b. Longleaf pine-palmetto flatwood near the Okefenokee Swamp, Charlton Co., GA. This area was burned three years prior to this photograph.

(spodosols) with a distinct spodic horizon at depths corresponding to the mean water table (0.5-1.0 m). The clay soils may be gleyed as a consequence of poor drainage, particularly in lowland areas. Other soils are more typically ultisols.

Moisture is less frequently limiting in these soils compared to the sands, however they are generally considered to be poor in nutrients, particularly nitrogen and phosphorus (CHRISTENSEN 1977a, PARROTT 1967, RALSTON 1978, WELLS and SHUNK 1931). These nutrient limitations are a consequence of slow rates of decomposition, low soil absorptive capacity, and water logging.

3.2. *Vegetation*

In the upper coastal plain flatwoods are frequently successional from cropland abandonment. The dominant pine is loblolly (*Pinus taeda*) and the understory is quite similar to that of successional pine stands on the Piedmont (OOSTING 1942). Understory trees include *Liquidambar styraciflua*, *Acer rubrum*, *Quercus* spp., *Nyssa sylvatica*, *Fraxinus* spp., and *Carya* spp. If left undisturbed, these forests will probably succeed to forests dominated by a mixture of deciduous hardwoods.

On the lower coastal plain, flatwoods again occur primarily on fine-texture soils. However, the understory composition is more unique to the coastal plain. Although saplings of *L. styraciflua* and *A. rubrum* are common, coastal plain elements such as *Ilex coriacea*, *Ilex glabra*, and *Myrica cerifera* comprise a large fraction of understory biomass. The cane, *Arundinaria gigantea* may occur in dense, localized patches. Whereas the above composition would typify the Carolinas (RALSTON and CHRISTENSEN, in preparation), flatwoods of the southern coastal plain of Georgia, North Florida, and the Gulf States, may include several species of scrub oak as well as saw palmetto, *Serenoa repens*. These palmetto flatwoods often have a continuous shrub cover with very few transgressive trees (HILMON 1968).

The species of dominant pine in these flatwoods varies between loblolly, longleaf, and slash (*Pinus elliottii*). Where fire has been excluded for long periods (i.e. 30-50 years), *P. palustris* is less successful. On comparatively dry sites *P. taeda* becomes more dominant and in some areas has

nearly replaced *P. palustris* (RALSTON and CHRISTENSEN, in preparation). Similarly, fire protection has increased the dominance of slash pine in the southern coastal plain where it was formerly confined only to moist sites (LITTLE and DORMAN 1954). Indeed, increased fire frequency may convert many flatwood-type ecosystems to savannas or greatly improve regeneration of *Pinus palustris* relative to other species (CHRISTENSEN 1979, KOMAREK 1974).

Savannas are here defined as ecosystems dominated by scattered trees and a continuous graminoid understory. Vegetational variation among various savanna types has been considered in several studies (WELLS and SHUNK 1928, WOODWELL 1956, VOGL 1973, KOLOGISKI 1977, WILSON 1977), however, there is no agreement on convention for classifying this variation. This lack of agreement is a consequence of the geographically confined areas considered in most of these studies and the fact that the vegetation varies continuously as a function of several factors. Three of the most significant of these factors are moisture, soil type, and disturbance history.

The driest, sandiest savannas are dominated by *Pinus palustris* with an understory of *Aristida stricta*. *Cladonia* species are often abundant on the soil surface between *Aristida* clumps (CHRISTENSEN 1977a). In the southern Coastal Plain, these areas may also support scattered saw palmettos. With moisture conditions (e.g. high water table) on these sands, herb diversity increases markedly. A variety of sedges, particularly *Rhynchospora* spp., *Fimbristylis autumnalis*, and *Carex* spp., codominate with *Aristida*. VOGL (1973) pointed out that many savanna graminoids have their closest floristic affinities with the prairies of the Midwest. In addition, these zones are rich in members of the *Orchidaceae*, *Liliaceae*, as well as a variety of insectivorous plants (WELLS and SHUNK 1931, KOLOGISKI 1977). Insectivorous genera include *Drosera*, *Dionaea*, *Pinguicula*, *Sarracenia*, and *Utricularia*.

In moist sand savannas, *Pinus serotina* may replace *P. palustris*, particularly near the savanna margins. As the mean water table approaches the soil surface, these savannas may abruptly give way to shrub-bog ecosystems.

On fine-textured gleys, *Aristida* shares dominance with *Muhlenbergia expansa*, *Panicum* spp., and sedges. Most of the herbs which occur in the moister zones of sand savannas are also common on these clay substrates

(WOODWELL 1956, KOLOGISKI 1977).

Both WOODWELL (1956) and KOLOGISKI (1977) describe savanna communities where scattered shrubs, particularly *Ilex glabra*, *Gaylussacia* spp., and *Myrica cerifera*, may occur. These situations appear to be a consequence of fire suppression in savannas on marginally moist sites.

3.3. Autecology

Nutrient limitations seem to influence the development of savanna and flatwood vegetation significantly. This is perhaps most clearly demonstrated by the abundant insectivorous flora. Insectivory appears to have evolved as a means of securing nutrients from non-soil sources. PLUMMER and KETHLEY (1964) showed that nutrients were indeed transported from the decaying insect mass in the pitchers of *Sarracenia flava*, a common savanna inhabitant. CHRISTENSEN (1977b) found that insectivory could ameliorate nitrogen and phosphorus deficiencies in this same species.

Fire has had an obvious role in the evolution of life histories in many savanna species. For example, flowering in *Aristida stricta* occurs primarily after fire (WELLS and SHUNK 1931). PARROTT (1967) found that the removal of leaves, either by clipping or fire, would stimulate flowering, however, nutrient enhancement associated with burning results in more flowering stalks and greater seed production (CHRISTENSEN 1977a). Many other savanna species show this same general flowering pattern. One can conclude from this pattern that probabilities of successful establishment in inter-fire periods are poor, thus selection has been for reproduction immediately after fire. Low nutrient levels, reduced light at the soil surface, and allelopathic interference have all been implicated as factors reducing survival probabilities of seedlings in unburned areas (CHRISTENSEN 1977a, ROBERTS and OOSTING 1956, WELLS and SHUNK 1931).

Perhaps the best-known fire-adapted life history pattern in savannas is that of the longleaf pine (*Pinus palustris*). Longleaf pine seedlings establish most successfully on bare mineral soil following fire (WAHLENBERG 1946). In the first 3-5 years of growth most of the resources of the seedling are invested into an extensive root system including a massive tap root, with

little or no apical growth. The apical bud is protected during this period by a grass-like whorl of leaves and nonflammable scales. After attaining sufficient size, the seedlings initiates apical growth. This initiation often coincides with the next fire, through fire per se is not the stimulus (ALLEN 1964). During the successive 3-5 years, rapid apical growth carries the apical bud above the zone of most surface fires.

3.4. Successional relations and fire

Successional relations, particularly with respect to fire, vary among savannas. In dryer, sandy areas, long-term fire suppression results in the accumulation of large quantities of dry *Aristida* foliage and a diminution of herb species diversity (CHRISTENSEN 1977a, PARROTT 1967). Lower herb productivity in these areas may be a consequence of reduced nutrient availability and perhaps the allelopathic affect of decaying *Aristida* litter (CHRISTENSEN 1977a). Hardwood species typical of the xeric sands, such as *Quercus laevis* and *Diospyros virginiana* may invade. However, the accumulation of very flammable fuel greatly increases the probability of fire, which, in turn, result in more diverse and productive postfire communities. The typical fire frequency fore these areas is 4-10 years (CHRISTENSEN 1979).

With somewhat moister conditions, the pattern of succession is similar only, as mentioned before, woody shrubs tend to become more common. As a consequence, the ecotone between such savannas and adjacent shrub-bogs becomes much less abrupt. Again, fuel accumulation in these communities tends to increase the probability of fire with time, though greater water availability may decrease flammability. It seems likely that fire is the factor responsible for the frequently sharp transitions from savannas to shrub bogs.

On heavier soils, succession from herb-dominated to tree and shrub-dominated conditions may be more rapid. In the absence of fire, these areas may lose their savanna character in a matter of a few years. This appears to be particularly true of savannas of the southern and Gulf Coastal Plain (KOMAREK 1974).

Summary

The xeric ecosystems of the Coastal Plain support a very unique flora. The driest Pleistocene sands of peninsular Florida are dominated by sand-pine-scrub vegetation, whereas other sandy habitats are dominated by longleaf pine-turkey oak forests. With increasing moisture these ecosystems grade into pine flatwoods and savannas. Plant growth is limited by water and nutrients in most of these ecosystems with fire playing a significant role in vegetational dynamics.

Zusammenfassung

Das xerische Oekosystem der Küstenebene (Coastal Plain) der südöstlichen U.S.A. umfasst eine einzigartige Flora. Die trockensten Pleistozän-Sande der Halbinsel Florida werden durch *Pinus clausa*-Buschvegetation geprägt, während auf den übrigen sandigen Standorten ein *Pinus palustris-Quercus laevis*-Mischwald dominiert. Mit zunehmender Feuchtigkeit gehen diese Oekosysteme in Flachland-Föhrenwald und Föhrensavanne über. Das Wachstum der Pflanzen ist in den meisten dieser Oekosysteme begrenzt durch die geringe Wasser- und Nährstoffversorgung, wobei das Feuer in der Vegetationsdynamik eine wichtige Rolle spielt.

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