Presettlement Fire Regimes in Southeastern Marshes, Peatlands, and Swamps

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ABSTRACT

Presettlement fire regimes in wetland vegetation can be deduced or reconstructed by synthesizing knowledge of fire behavior on adjacent uplands with information about soils, salinity, landscape factors, remnant vegetation, and historical records. Presettlement fire-return intervals in different parts of the southeastern wetland landscape ranged from nearly annual, up to 300 years, and vegetation was distributed accordingly along this fire frequency gradient. Prediction of vegetation stature and species composition in relation to fire can be made with some confidence in marshes, in the wettest swamps, and on uplands. In large peatlands, however, stochastic factors created a shifting mosaic before European settlement, in which any one of several competing communities could exist for a time on the same soil series, depending upon environmental conditions at time of burn. Before modern fire suppression, peatland vegetation was controlled primarily by master gradients of fire frequency and organic matter depth. There was a third, minor fertility gradient. Distribution of peatland vegetation types along these gradients is complex but is summarized here using a table of 32 cells defined by 8 fire frequency classes and 4 organic soil depths. While many marshes and swamps in the southeast differ little from their presettlement species composition, few peatlands, even those considered natural areas, have escaped major alteration in species dominants. A large percentage of modern pocosins can be shown to be successional from canebrake and other frequent-fire types in the absence of fire. At the other end of the spectrum, in Virginia and North Carolina, large areas now categorized as pocosin were dominated by white cedar (*Chamaecyparis thyoides*), an infrequent-fire type, as late as 1900. In most cases, major shifts in vegetation type were selected for unwittingly in the process of fire suppression or logging. When designing a fire management regime in peatlands today, the method selected will determine whether the treatment will perpetuate what is there (the usual choice) or a return to one or more of the presettlement community types.

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INTRODUCTION

The landscape that greeted the first settlers in the South was swept and sculpted by fires, with frequencies ranging from as often as every 1 to 3 years, to as infrequent as 300 years. On the Coastal Plain, only a few sites, probably less than 5% of the landscape, were completely protected from fire. Fire shaped vegetation and distributed species into fire-frequency zones and niches. In marshes, fire interacted with two more important gradients, salinity and water depth, to structure vegetation, but in the great peatlands fire shared importance with depth of organic matter as one of the two master influences.

After some years of work it became apparent to me that there could be little understanding of wetland floristics and vegetation structure without considering the pervasive role of fire. The use of tables (see Tables 1, 2 and 3), comparing different fire frequencies with soil factors was an attempt to be rigorous, in order not to miss what might be happening on a particular soil type at a particular fire frequency. A number of unusual communities, such as sweetgum/canebrake (Table 2, Cell 12), were thus detected that otherwise might have been overlooked, or passed off as anthropogenic artifacts. Considering that it required 64 cells in Tables 2 and 3 to relate peatland vegetation to natural fire regimes, it is apparent that complexity of natural wetland vegetation is at least an order of magnitude greater than previously known.

This paper is an interpretation of natural fire regimes in southeastern wetlands, based on some 482 study plots (mostly in North Carolina and Virginia), along with personal observations in all of the nine coastal states from Virginia to Texas. My purpose is to reconstruct presettlement vegetation and presettlement fire regimes in these wetlands, as a guide to managing them and to restoring samples of the most fire-dependent types.

METHODS

The field work and observations presented here are summarized from Frost 1989; Frost et al. 1990; LeGrand et al. 1992, research for a dissertation (Frost 1995a), and studies on presettlement vegetation (Frost 1995b; Frost et al. 1986; Ware et al. 1993). Types of data collected include tenth-hectare vegetation plots and non-plot vegetation data, soil samples, peat depth measurements, salinity, and information on stand disturbance history. Historical vegetation records, where available, were used in interpreting results. Vegetation was examined and recent fire history determined in 482 plots on 76 different wetland soil series, all either histosols or mineral soils with aquic modifiers. Vascular plant nomenclature follows Kartesz (1994), updated from Radford et al. (1968), which was used throughout the study.

Vegetation and Soil Data—0.1-hectare Plots

118 0.1-ha plots were sampled by laying out a 20 × 50 m plot with 25 herb subplots placed down the centerline. All woody stems greater than 1 m tall were tabulated by species in 2.54 cm (1 in) diameter size classes. This data was used to calculate basal area for all woody species in each plot. In addition several trees, usually pines, were cored in each wooded plot to determine stand age. Within each of the 25 herb subplots, percent cover was estimated for all species below 1 m in height. Soil samples were collected and analyzed for soil nutrients, pH, base saturation, cation exchange capacity (CEC) and weight/volume ratio. Soil texture was determined by the hydrometer method, and soil organic matter content was determined by percent of weight lost on ignition. Soil data, herb and woody cover were used in analyses with TWINSPAN and CANOCO computer programs (see Frost 1995a).

Organic Matter Depth

For all organic soils or soils with organic epipedons, depth to mineral soil was measured for correlation with organic matter depth-dependent vegetation types like canebrake. Since organic matter depth appeared to influence fire behavior and wetland vegetation strongly, peat depth was measured in all marshes, peatlands and swamps. For the deeper soils, 1.1 meter fiberglass rods were used as peat depth probes. Additional rods were screwed on as they were pushed down into the peat. Fiberglass rods were found to have the fortuitous property of transmitting vibrations so that the grittiness of a sand bottom can be clearly felt while rotating the rod under slight downward pressure, and clay is felt as perfectly smooth rotation, so the underlying substrate several meters down can be readily differentiated into sand, clay, or loam.

Fire Frequency and Fire History Data

Time since last fire, and sometimes 1 or 2 earlier fires, was determined for all plots. This was done in a number of ways. In marshes, fires were dated by using annual bud scale scars on shrubs to age stems in the marsh or at the upland fringe. In peatlands, even-aged size classes of shrub or saplings could be used to date fires occurring within the previous 20 years. Older fires could sometimes be dated by coring fire scars on surviving trees.

Other Stand History

Older trees often predate 20th century fire suppression. Fire scars and tree cores are often revealing of conditions under the earlier fire regime. If the oldest trees are of different species than the younger, a major shift in fire regime may be indicated. Tree stem size-class distribution data were used in estimating previous vegetation on the site, and to help interpret the nature of succession since last fire, logging or other disturbance. In many stands the number and size of old, cut pine stumps were tabulated as evidence of the amount of pine in the previous forest or in the present stand before selective removal of pine. On selected plots the number of wind-thrown trees or trees with broken major limbs was tabulated as evidence of storm disturbance regime. Notes were taken on site on disturbance history, and a final assessment of data was made in the field as to composition of the previous stand. This was used as a first approximation of likely presettlement vegetation type for each plot.

Non-plot Data

In another, less intensive type of sampling, all species were recorded from each soil series in a study area. Species were listed by the layer in which they occurred and dominants were recorded in 6 layers: canopy, subcanopy, shrub layer, herb layer, vines and epiphytes. Cover was estimated in 5 cover classes. Approximately 364 lists of species were collected and used, along with the 118 1/10 ha plots above, for TWINSPAN classification. This method was not area specific, but length of lists and area covered were very similar to 1/10 ha data. Results of vegetation analysis are reported elsewhere (Frost 1995a).

Historical Data

Around 400 site-specific historical references to original vegetation—mostly trees, but also some shrubs and herbs–were obtained for the region. These and references to community types, such as "canebrake", "pocosin", or "juniper swamp" were used for plotting fire frequency indicator species (Frost 1995a) and communities to assist in mapping presettlement fire frequency. About 150 black and white historical photographs, obtained from various archives and historical publications, were used for interpreting historical fire regimes.

Presettlement Fire Frequency and Vegetation Methods

Specific methods for approximating presettlement fire frequency include use of landscape and environmental factors, historical evidence, and remnant natural vegetation. These methods are covered further in Frost (1995a).

RESULTS AND DISCUSSION

Assumptions About the Natural Fire Environment

On the lower coastal plain terraces, where lightning ignitions were frequent enough to preempt fuel that might otherwise have been ignited by Indians, nearly all presettlement fire should have been growing season burns (Komarek 1964; 1968). The role of Indians in burning the southeastern landscape was probably insignificant on most of the Coastal Plain and the less-dissected parts of the Piedmont, but may have come into play in more topographically diverse parts of the upper Coastal Plain, Piedmont, and mountain environments, where fire compartments[1] were much smaller and a larger proportion of the landscape would escape lightning fires each year. This differs from Indian effects on the Pacific Coastal Plain where the thunderstorm frequency is much lower than in the Southeast and where frequent Indian burning has been documented from early Spanish records (Timbrook et al. 1982).

It is also assumed that fire frequency is related to fire compartment size, since a single ignition in a 1,000 km^2 compartment without a natural firebreak could have burned the whole area, while a 1,000 km^2 area with 20 separate fire compartments might require 20 separate ignitions to burn the same amount of land.

Presettlement Fire Frequency Regions

Use of the term "presettlement" refers to vegetation conditions and natural fire regime as they existed at time of first European contact. This varies, since first exposure of the land to European influences came at different times in various parts of the South. Presettlement in east Florida, for instance, means around 1565, in southeastern Virginia it means 1607, in the southern Appalachians it means around 1800, and in central Alabama it was as late as 1821. Figure 1 is a first-approximation map of fire frequency regions of the South under the natural presettlement lightning fire regime, along with whatever influence there may have been from the use of fire by Indians. The source of ignition, whether lightning or Indians, is irrelevant, since the fire frequency regions are based on historical records of fire-influenced vegetation that actually existed, whatever the cause. See the classic work of Komarek (1964, 1968) for background on the role of lightning.

Figure 1 is a regional fire frequency map, based on a classification of land-surface forms (Hammond 1964; Anon. 1970). Extensive simplification and adjustments for soil and climatic factors were made to the original map. The original was essentially a slope map, coded for the following: 1) percent of the landscape that is flat or only gently sloping, 2) amount of local relief from the stream bottoms to ridge tops, and 3) whether the flat or gently-sloping parts are located on uplands or in bottomlands.

The first characteristic above, the proportion of the landscape that is flat, can be partially correlated with fire compartment size, since in the parts of the landscape that have greater than 80% flat or gently sloping surfaces, the areas without natural firebreaks are quite large. Some, especially in Florida or the Pamlico Terrace of North Carolina, contain more than 2,000 km^2 without a natural firebreak. The third characteristic is also important in interpreting fire behavior because if the flat parts of the landscape are in fluvial bottomlands, the role of fire should be much less important than if they were on upland flats or tablelands.

The basic land-surface form map of Hammond was modified in several ways. Most of the landscape in which more than 80% is flat or only gently sloping was designated as having a fire-return interval of 1 to 3 years. This interpretation is supported by remnant vegetation and numerous historical records (Frost, see publications above). In Virginia, however, where typical southeastern fire vegetation reaches its northern limits, the vegetation described in historical records indicates that fire frequency did not reach the 1 to 3 year class. This may be because of a shorter fire season, and/or lack of fire-facilitating species like wiregrass and longleaf pine. Boundaries between classes were adjusted accordingly. Areas having 50 to 80% of the upland landscape flat or gently sloping were assigned to the 4 to 6 year class, but vegetation in large areas of sands adjacent to more frequent-

[1] A unit of the landscape with no natural firebreaks, such that a lightning ignition in one part would be likely to burn the whole unit unless there were a change in weather or fuel conditions (Frost 1995a).

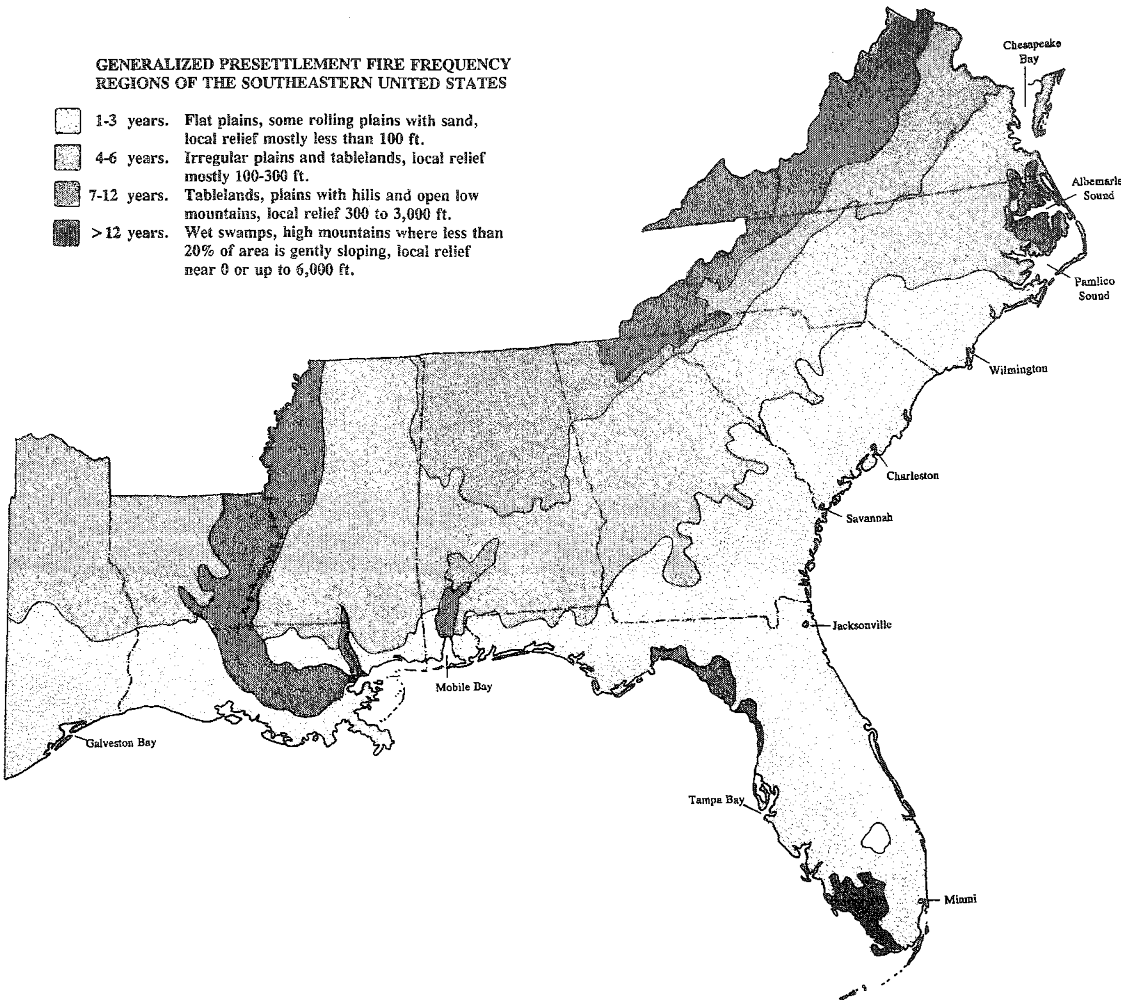

Fig. 1. Presettlement fire regimes of the southeastern United States. Derived from regional fire compartment size, topography, historical records, climate, vegetation remnants and soils. Frequencies are for the most fire-exposed parts of the landscape. Each region contains variously fire-protected areas with lower incidences of fire.

fire areas in Georgia and the Carolinas, was reassigned to the next more frequent fire class. In south Texas these 50 to 80% areas were also upgraded because of the drier climate and the continuity and natural flammability of prairie fuels.

Assignments of fire frequency classes to different parts of the landscape in Figure 1 are based on a method in Frost (1995a) which uses field observations, interpretation of historical photographs, and historical occurrences of fire-indicator species and communities. Canebrake, for instance, is an indicator of a general fire frequency of every 4–6 yrs (Table 2), and there are numerous historical references to canebrake in the 4–6 yr region in Figure 1. The fire frequency classes defined are intended to represent the average regional fire-return interval for the most fire-exposed parts of the landscape, especially flats, uplands, and south slopes. Conversely, varying proportions of the land within each category occur in naturally fire-protected sites. On the Coastal Plain these include islands, peninsulas, wet swamps and some fluvial bottomlands (Harper 1911, 1913, 1914). In the other provinces, fire-safe sites or partially fire-protected sites include north slopes, large fluvial bottomlands, mountain coves and steep-sided stream valleys. In the original landscape, fire-protected sites may have only occupied about 1–5% of the Coastal Plain, up to 15% of the Piedmont, and 25% of the Mountains.

The 1 to 3 year fire frequency class includes mostly flat plains having 80% to 100% of the landscape flat or gently sloping. Some areas of rolling plains are included where 50–80% of the land is gently sloping and more than 50% of the land surface is covered with sand. Local relief is mostly less than 30 m (100 ft) but some areas with up to 90 m (300 ft) are included, particularly where soils are sandy. Succession on poor, sandy soils is slow, facilitating persistence of grass fuels, and sand is conducive to spread of flammable rhizomatous shrubs which increase in density at lower fire frequencies (Frost 1995a).

The 4 to 6 year fire frequency range covers irregular plains and tablelands which have 50–80% of the uplands flat or gently sloping. Local relief is mostly 30–90 m (100–300 ft) (note that elevation can be much higher than local relief). This includes some upper coastal plain terraces and most of the Atlantic and Gulf Piedmont.

The 7 to 12 year fire frequency class includes plains with hills, tablelands of the southern Appalachians, open high hills and open low mountains. Relief is mostly 90 to 150 m (300 to 500 ft), but may range up to 300 m (1,000 ft) in the Appalachian tablelands of northern Alabama, and up to 915 m (3,000 ft) in the flammable pitch pine communities of the southern Blue Ridge.

Fire-return intervals longer than 12 years occurred in a number of situations. The kinds of vegetation present suggest that high elevation sites in the Appalachians had a lower fire frequency than in the lower mountains. There are also some large coastal swamps that were too wet to burn or had vegetation such as white cedar that seemed to resist all but crown fires, so that the average fire return interval was greater than 12 years (Frost 1995a).

I assume here that the larger the natural fire compartment, the higher the fire frequency, because in large fire compartments there might be several lightning ignitions per year, and just one ignition could burn the whole compartment if conditions were right. Moving up from the coastal flats inland, onto older, more dissected coastal plain terraces, the fire compartments decrease in size so that it would take more lightning ignitions to burn the same amount of land. Fire frequency should then decrease. The corresponding decrease in compartment size and fire frequency should be expected to continue on the Piedmont. However, the Piedmont is a dissected plain, and has regions where there are extensive upland flats and gently rolling slopes without significant firebreaks. Topography increases dramatically in the upper Piedmont foothills and lower mountains of the Southern Appalachians, where lightning ignition records indicate that the natural fire frequency was about 7 to 12 years (Frantz and Sutter 1987; Frost 1990; Barden 1977; Barden and Woods 1973). Beyond the Blue Ridge, in the higher mountains extending from Georgia through Virginia, nearly all the land is in slope, and average fire frequency may have been lower. Lightning ignitions in the mountains, however, are still common (Frantz and Sutter 1987; Frost 1990). In summer, 1993, there were three lightning ignitions around 915 m (3000 ft) elevation within a kilometer of one of my study sites on Shortoff Mountain, Burke County, NC, and in my experience, nearly every south slope in the Southern Appalachians shows signs of past fire.

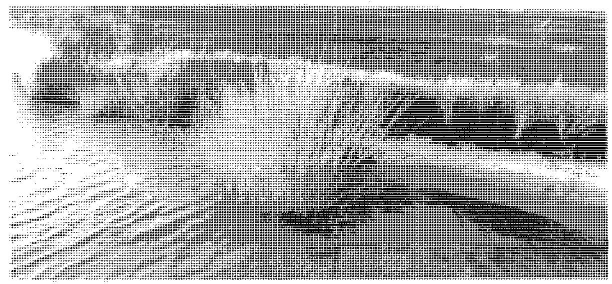

Fig. 2. Brackish marsh dominated by *Juncus-Distichlis*, salinity 1.1%, taken the day after a burn. Marshes are fine-textured fuels; will burn upwind, downwind, and when standing water is on the surface. All above-ground biomass was consumed except for the lower 10 cm of *Juncus* stems and a narrow strip of *Juncus roemerianus* and *Spartina alterniflora* along the shoreline, with *Spartina patens* on the low sand berm. Scattered tall stems are seaside goldenrod (*Solidago sempervirens*).

Presettlement Fire Regimes in Marshes (Table 1)

Evidence of past fires can be discovered in nearly all southeastern marshes. The most readily accessible kinds of evidence are even-aged shrub classes, which can be used to date the last fire, and fire char on old woody snags within and on the borders of marshes. Marsh vegetation creates fine-textured fuel and carries fire very efficiently (Fig. 2). Before European settlement, most marsh fires were probably ignited by fire moving through vegetation on adjacent uplands. Some fires must have originated with lightning strikes in marsh, and there is at least one reported case of spontaneous ignition in Gulf Coast marshes in very hot weather (Viosca 1931).

Table 1 shows general successional trends of marsh vegetation under four levels of salinity. Levels are given in parts per thousand of chloride and other salts, determined by refractometer. Salinity ranges for the four levels are as follows: fresh water, 0 to 0.5 PPT; oligohaline, 0.5 to 5 PPT; brackish, 5 to 30 PPT; and saline, over 30 PPT. Two strong master gradients seem to explain most of the variation in plant species distribution in southeastern coastal marshes. The salinity gradient is most striking. In some systems like that of Currituck Sound in North Carolina and Virginia, changes in marsh vegetation from freshwater to salt may be followed downstream for some 80 km (50 mi) along the long-attenuated salinity gradient before reaching an outlet to the ocean. The second obvious gradient is the complex master gradient of water depth/frequency of flooding/duration of flooding. The fire frequency gradient is much less important than the preceding two in salt and brack-

Table 1. Common dominant species under the spectrum of presettlement fire regimes. Of the two master gradients readily apparent in marshes, the first, the salinity gradient is represented on the Y axis. The second major factor, the water depth/frequency of flooding/duration of flooding complex gradient is partially accounted for within cells of the table. For example, in Cell 1 SPAL is found on wetter sites, and *Juncus-Distichlis* on drier sites. Under presettlement conditions the fire frequency gradient was third in importance.

MARSH VEGETATION OF THE SOUTHEASTERN U.S., DISTRIBUTED ALONG MASTER GRADIENTS OF FIRE FREQUENCY AND DEPTH OF ORGANIC SOIL

FIRE FREQUENCY

SALINITY ⇑	1-3 YEARS	4-6 YRS	7-12 YRS	13-25 YRS	26-50 YRS	51-100 YRS	100-300 YRS	NEVER BURNED
SALINE 3-4% (30-40 PPT) ROW 1	SPAL or JURO-DISP CELL 1	SPAL or JURO-DISP CELL 2	SPAL or JURO-DISP CELL 3	SPAL or JURO CELL 4	SPAL or JURO CELL 5	SPAL or JURO CELL 6	SPAL or JURO CELL 7	SPAL or JURO CELL 8
BRACKISH 5-30 PPT ROW 2	JURO-DISP-SPPA with diverse salt marsh herbs CELL 9	JURO-DISP, SPPA, mixed salt marsh herbs CELL 10	JURO-DISP, or CLJA, PHAU, MYCE, IVFR, BAHA CELL 11	JURO or PHAU, CLJA, MYCE, IVFR, BAHA CELL 12	JURO or PHAU, CLJA, MYCE, IVFR, BAHA, JUVI CELL 13	JURO or PHAU, CLJA, MYCE, IVFR, BAHA, JUVI CELL 14	JURO or JUVI, CLJA, PHAU, MYCE, IVFR, BAHA CELL 15	JURO or JUVI, PHAU, CLJA, MYCE, IVFR, BAHA (hypothetical) CELL 16
OLIGOHA-LINE 0.3-5 PPT ROW 3	Diverse mixed salt marsh, fresh marsh, and swamp species CELL 17	Diverse spp. with patch and zone dominants conspicuous by end of cycle CELL 18	JURO-mixed species with dominants in patches and zones, MYCE CELL 19	JURO, SCAM, TYAN, TYDO TYLA, SPCY PHAU, CLJA in dominant zones, MYCE, PEPA, tree saplings. CELL 20	SPCY, CLJA PHAU or ACRU, PITA, PIEL, PEPA, NYBI, TADI/MYCE CELL 21	SPCY, CLJA, PHAU, or TADI, PITA PIEL, NYBI ACRU, PEPA /MYCE CELL 22	TADI, NYBI ACRU (NYBI is more salt-tolerant than TADI)/swamp forest shrubs and herbs CELL 23	TADI, NYBI, ACRU/swamp forest shrubs and herbs CELL 24
FRESH 0-0.3 PPT ROW 4	Diverse fresh marsh & swamp graminoids & forbs CELL 25	Diverse fresh marsh & swamp graminoids & forbs CELL 26	Diverse species, MYCE, ACRU, CLJA, ferns CELL 27	ACRU, NYBI, TADI, MYCE CLJA, swamp herbs CELL 28	ACRU, NYBI, TADI/ swamp shrubs & herbs CELL 29	TADI, NYBI, ACRU forest, CHTH forest patch mosaic CELL 30	TADI, NYBI forest, CHTH forest patch mosaic CELL 31	TADI/NYAQ, NYBI, ACRU, swamp forest CELL 32

SPECIES ACRONYMS: **ACRU**: Acer rubrum (Red Maple), **BAHA**: Baccharis halimifolia (Silverling), **CHTH**: Chamaecyparis thyoides (Atlantic White Cedar), **CLJA**: Cladium jamaicense (Sawgrass), **DISP**: Distichlis spicata (Saltgrass), **FRCA**: Fraxinus caroliniana (Water Ash), **IVFR**: Iva frutescens (Marsh Elder), **JUVI**: Juniperus virginiana (Red Maple), **JURO**: Juncus roemerianus (Black Needle-rush), **MYCE** Myrica cerifera (Wax Myrtle), **NYAQ**: Nyssa aquatica (Tupelo or Water Gum), **NYBI**: Nyssa biflora (Swamp Black Gum), **PEPA**: Persea palustris (Red Bay), **PHAU**: Phragmites australis (communis)(Common Reed), **PIEL**: Pinus elliottii (Slash Pine), **PITA**: Pinus taeda (Loblolly Pine), **SPAL**: Spartina alterniflora (Salt Marsh Cordgrass), **SPCY**: Spartina cynosuroides (Tall Cordgrass), **SPPA**: Spartina patens (Saltmeadow Cordgrass), **TADI**: Taxodium distichum (Baldcypress). **TYAN**: Typha angustifolia (Narrow-leaved cattail, **TYDO**: Typha domingensis, **TYLA**: Typha latifolia (Cattail).

ish marshes than in interior peatlands, but is important in regulating succession in fresh and oligohaline marshes. Table 1 relates salinity on the vertical axis to fire frequency on the horizontal axis. The water depth gradient is only partly accounted for within cells. For example, in cell 21 the tall marsh species *Spartina cynosuroides, Cladium jamaicense,* and *Phragmites australis* persist in wetter sites while drier, interior sites undergo succession to swamp hardwoods, pine, red cedar, cypress, and wax myrtle. Fire and successional effects at intervals greater than 100 years are somewhat hypothetical since few marshes other than those on islands have escaped fire that long, and even islands may have been burned, first by Indians and later by Europeans. The following classification makes no attempt to take into account regional effects of sea level rise and land subsidence.

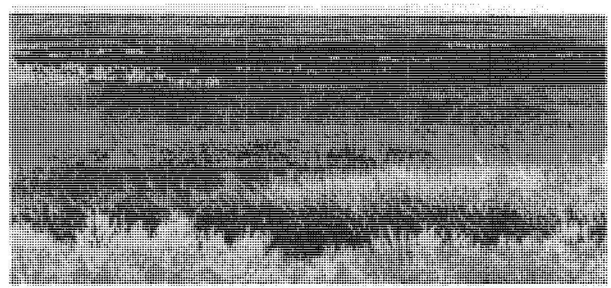

Fig. 3. Frequently burned brackish marsh with 25 species per 1/10 ha—relatively high diversity for brackish marsh (Cedar Island National Wildlife Refuge, North Carolina).

Fig. 4. Fire suppressed marsh, on opposite side of road from that in Figure 3. Heavily dominated by black needlerush with only 8 species per 1/10 ha and 98.8% cover of *Juncus* and *Distichlis*. *Juncus roemerianus* (black needle-rush) builds up a deep thatch of dead stems, penetrable only by its own spears, perhaps the reason for the needle-tips.

True Salt Marsh Vegetation (Table 1, Row 1)

While fire has been shown to have a number of effects on nutrient release and productivity increase in marsh (De la Cruz and Hackney 1980; Hackney 1982), it has little impact on floristics in true salt marshes. Plant species diversity is low in true salt marshes because few species are able to tolerate the combination of high salinity and standing water (Sculthorpe 1967). Of 94 marsh communities examined for this study, there were 305 vascular plant species, but only 16 of these occurred in true salt marshes (salinity > 3%). In a similar study in Mississippi, of some 300 marsh species, only 12 were mentioned in saline habitats (Eleuterius 1973). Common dominants in the present study were *Spartina alterniflora* (saltmarsh cordgrass)in wetter sites and *Juncus roemerianus* (black needle-rush) in slightly drier sites across all fire frequencies. In a 0.1-ha plot for this study on a site that was flooded twice daily by the tides, only one vascular plant, *Spartina alterniflora,* could be found.

Brackish Marsh Vegetation (Table 1, Row 2)

Species diversity increases as salinity decreases, water depth decreases and fire frequency increases. Fire removes the heavy thatch that builds up in 2 to 5 years, opening up habitat for colonization, but in brackish marshes diversity is limited to the relatively small number of species able to tolerate the brackish range. Still, there are enough potential species to give a three-fold increase in species richness when frequent fire maintains habitat open for colonization (Fig. 3). In addition to the common salt marsh dominants above, other frequent species include the shrubs *Baccharis halimifolia* and *Iva frutescens*; and the herbs *Borrichia frutescens, Spartina patens, Aster tenuifolius, Aster subulatus,* and *Limonium carolinianum.* Fire suppression at higher salinities within the brackish range commonly leads to heavy dominance by juncus (Fig. 4), while shrubs may invade the less saline areas. Red cedar (*Juniperus virginiana,* sometimes called var. *silicicola*) may become established at lower fire frequencies (Fig. 5), especially on lenses of sandy soils in marshes and around the periphery (Table 1, cells 12–16).

Oligohaline Marsh Vegetation (Table 1, Row 3)

Frequently-burned oligohaline marshes maintain high species richness by drawing on four pools of species. First are the true salt marsh species, which may still turn up as scattered individuals or patches in marshes that have little measurable salinity. Second are fresh marsh

Fig. 5. Woody succession in fire-suppressed brackish marsh, Salinity 5–10 PPT. Red cedar, loblolly pine, red maple and shrubs like wax myrtle and *Baccharis halimifolia* are replacing tall sawgrass and *Juncus,* which in turn probably replaced more diverse marsh graminoids and forbs under the original fire regime; about every 4–6 years on adjacent uplands. In more exposed coastal locations such succession may be prevented or retarded by storm-driven salt water intrusion (Conner and Askew 1993).

species, some of which have some tolerance for salt. Third are swamp herbs like *Ptilimnium capillaceum, Peltandra virginica* and several polygonums, which also find suitable microhabitats in oligohaline marshes. Fourth are species limited to or reaching their best development in the oligohaline range like *Sagittaria lancifolia, Triglochin striata* and *Cladium mariscoides.* Unusual dominants like *Eryngium aquaticum* or *Eleocharis rostellata* may sometimes be found under the two most frequent fire classes. Zonation of marsh dominants is least evident in the 1-to 3-year fire frequency class, where regular removal of thatch allows constant establishment of shade-intolerant herbs, maintaining diversity. Reduction of fire frequency to intervals longer than four years leads to increasing patch dominance (Frost 1995a). Successive reduction in fire frequency, as has happened throughout the South, leads to dominance of oligohaline marshes by a few tall marsh species and *Juncus roemerianus.* The sites with lower salinity or shallower water undergo succession to red maple, wax myrtle, pine and cypress. Such succession is slower in oligohaline sites, however, than in freshwater sites, and is subject to being reset by fire or saltwater incursion during major storms (Frost 1995a).

True Fresh Water Marsh Vegetation (Table 1, Row 4)

True fresh marshes in the South are most extensive in Florida, but may sometimes be found elsewhere along freshwater rivers at sea level, where sediment deposition creates new substrate that is colonized by marsh vegetation. These marshes may in turn succeed to red maple and swamp forest in the absence of fire.

Presettlement Fire Regimes and Recent Succession in Peatlands

Tables 2 and 3 summarize the variation in southeastern peatlands that can be attributed to the two master gradients of fire frequency and organic matter depth. Each row of cells may also be taken in part as a successional series. For instance the community found in cell 18, on soil that is not too infertile, with organic matter one meter deep, and with a fire frequency of 4 to 6 years, most commonly may be expected to be canebrake. Under presettlement conditions this may have been essentially a stable community, except for drift in fire frequency resulting from fluctuations in climatic conditions over decades or centuries. Any reduction of fire frequency would be expected to result in a shift to the next community to the right. In the case of canebrake, reduction of fires from every 4 to 6 years to 7 to 12 years would allow the establishment of pocosin shrubs which would overtop and suppress the cane before the next fire. Further reduction to 13 to 25 years would lead to high pocosin with a substantial canopy of low trees by the end of each cycle. Total fire exclusion, initiated at any cell in the table, should initiate simple succession leading eventually to the cell farthest to the right.

Canebrake, as used here, refers to any stand with a dominant layer of *Arundinaria gigantea* having at least 50% cover. The term pocosin, as used by the Algonquian Indians, referred to any natural wetland opening in the forested landscape. In ecological terms it has come to be limited to sclerophyllous evergreen shrub bog. Canebrake in large peatlands may be treeless, but both canebrake and pocosin commonly have pond pine (*Pinus serotina*), in any density from scattered single trees to closed-canopy patches. See Weakley and Schafale (1991) for a classification of pocosins in the Carolinas.

Most of the southeastern wetland landscape has undergone a series of fire frequency shifts in the twentieth century, one or more steps to the right in Tables 1, 2 and 3. This shift to less fire-frequent vegetation complicates the interpretation of wetland vegetation. Changes resulting from reduction in fire frequency, however, must be taken into account in any attempt to manage natural vegetation. Using these tables, historical records, soil maps and remnant vegetation, it is possible to get an approximation of where modern sites fit in the multidimensional fire landscape.

Tables 2 and 3 may be thought of as overlays, each having depth of organic matter on the vertical (Y) axis and fire frequency on the horizontal (X) axis. With Table 2, the slightly more fertile sites, on "top", and Table 3, the most oligotrophic sites, on "bottom", the Z axis then represents the fertility gradient. Each of the three axes are master gradients named for what appears to be the most important component gradient. The fire frequency gradient, for instance, subsumes season of burn, a secondary gradient. Actual frequency of fire is easiest to study in the field, since the date of last fire can almost always be determined on site, and frequency alone seems adequate to explain most of the variation in the tables that is attributed to fire. It should be noted, however, that stand-destroying fires in certain types of peatland vegetation probably occurred only during the spring/summer lightning season, perhaps at times when foliar moisture was low (see white cedar mosaics in cells 22, 23, 30 and 31).

The organic matter depth master gradient subsumes hydroperiod, which seems less important in peatlands than in marshes or swamps, since saturation with standing water for much of the year is a prerequisite for peat accumulation. Most southern peatlands would be lakes if the peat were removed and the ditches or underlying drainages were blocked. Peat exposed by drainage oxidizes and disappears over years or decades (Ruffin 1861; Frost 1987). The assumption about subsuming hydroperiod under the organic matter depth gradient, however, holds only for peatlands, not for swamps. For a discussion of hydrologic relations of fluvial swamps see Wharton et al. (1982), and for an illustration of the relationship of fire frequency and hydroperiod in Florida swamps see Ewel (1990).

While recent fire history and depth of organic matter were determined for all sites studied, the fertility gradient is less readily apparent and far less accessible for study, as has been observed by others (Christensen 1977; Walbridge 1986). The "fertility" master gradient used here subsumes several putative gradients. Soils with higher pH, slightly greater nutrient availability, and shallower organics, are classified here as more fertile. Also, organic soils overlying sandy aquifers seem to be more fertile, perhaps because of subsurface transport of nutrients from uplands. While soil samples were collected and analyzed for texture, pH, CEC, and several nutrients at many sites, the assessment of fertility was largely based on landscape position, vegetation stature, and apparent access to or isolation from nutrient sources. For example, many large peatlands show radial drainage, with rainfall the only source of nutrient input. Vegetation on such sites often takes on a bowl-like structure, with dwarfed shrubby vegetation in the center (see Cells 58 to 60 in Appendix) and increasingly taller vegetation radiating outward in all directions to the contact with mineral soil. In the case of one large peat dome, potassium has been shown to be the limiting nutrient in the center of the vegetation bowl (Walbridge 1986).

Fertility was also assessed, in part, on the behavior of individual species in different habitat and landscape situations. Cane (*Arundinaria gigantea*), for instance, is absent from the most oligotrophic peat domes, but it may form extensive, pure stands on shallow histosols where pH of the underlying substrate is moderate, and in small stream bottomlands. Also subsumed under fertility, are any considerations about the chemical and physical composition of peat or muck, the plant species from which peat was originally formed, the amount of mineral matter incorporated, and the texture of underlying substrate.

In addition to providing a description of presettlement vegetation, Tables 2 and 3 also may be used to map natural vegetation, and determine original natural vegetation and fire regime for restoration of a specific site. If, for example, you have a historical record of canebrake but it no longer occurs on the site, find canebrake in cells 10, 11, 18 and 19 to get the most likely fire regimes of 4 to 6 and 7 to 12 years for this community type. Then, since these communities occur most commonly on soils with organic matter 10 cm to 1 m in depth, use current soil maps to locate soils in the site with the appropriate range of characteristics. The portions of these soils that are not naturally fire-protected by streams, steep slopes or swamps are the most likely sites to restore canebrake on the management unit.

Where there are no historical records, the table may be used with a soil map and topographic map to determine the most likely type or range of wetland vegetation under the presettlement fire regime. Use Figure 1 to find the regional fire frequency. Then look at topography and landscape factors. If there are no steep slopes, lakes or streams large enough to act as natural firebreaks, accept the regional frequency. Then for each soil type find the appropriate vegetation cell or cells. If substantial firebreaks are present, adjust vegetation one or more cells to the right.

Presettlement Natural Vegetation Types on Moderately Fertile Sites

Table 2 (Cells 1–32) illustrates these vegetation types(see Appendix A for details on vegetation of each cell). Species lists and plot data are available elsewhere for many cells (Frost 1995a).

Despite the designation "fertile" as used here, and with exception of sites like calcareous marl prairies in Florida (Fig. 6) or wetlands receiving runoff from uplands with fine-textured soils, vegetation in Table 2 is found on soils that are typically acid and relatively infertile. The difference between this and Table 3 is that soils in Table 2 are less disastrously acid and infertile, in agricultural terms, than those in Table 3, which include the most nutrient-limited soils in the southeastern landscape. The gradient of fertility, while less striking

Table 2. Cells show common dominants for each combination of fire frequency and organic matter depth. Local dominants vary with the geographic range of each species and for Row 1 with differences in soil texture. See text for further cell descriptions.

PRESETTLEMENT DISTRIBUTION OF PEATLAND VEGETATION OF THE SOUTHEASTERN U.S. ALONG MASTER GRADIENTS OF FIRE FREQUENCY AND DEPTH OF ORGANIC SOIL

CELLS 1-32: MODERATELY FERTILE SITES

FIRE FREQUENCY

ORGANIC MATTER DEPTH ⇓

	1-3 YEARS	4-6 YRS	7-12 YRS	13-25 YRS	26-50 YRS	51-100 YRS	100-300 YRS	NEVER BURNED
Seasonally wet mineral soils ROW 1	Species-rich wet prairie with graminoids and grass-leaved forbs CELL 1	Species-rich wet prairie, with dwarf shrubs CELL 2	ANGL, ARGI, CLJA, ILGL, CYRA, CLMO, tree saplings CELL 3	Small ACRU, NYBI, LIST, PISE, PITA, PIEL, TAAS CELL 4	Dense ACRU, NYBI, TAAS, LIST, PISE, PITA, PIEL/ ARGI, Shrubs CELL 5	PITA, PIEL, TAAS, QUMI, PISE, ACRU, LIST/ sparse ARGI, ferns CELL 6	TADI, FRPE, LIST, ACRU, NYBI, QUMI other bottomland oaks/mesophytic herbs CELL 7	TADI, NYBI, FRPE, LIST, ACRU, bottom-land oaks CELL 8
Soils with thin organic layers, 10-30 cm thick ROW 2	Wet prairie and bog graminoids and forbs, patches of ARGI, ANGL CELL 9	Dense canebrake CELL 10	Alternating canebrake and pocosin CELL 11	PISE, ACRU, PITA, PIEL, TAAS, LIST/ ARGI CELL 12	PISE, PITA, PIEL, TAAS, LIST, NYBI/ PEPA, MAVI CELL 13	PISE forest, PITA, PIEL, TAAS, bottomland hardwoods, bay forest CELL 14	TADI, NYBI, FRPE, LIST, PITA/ ACRU, FRCA/ Carex, swamp herbs CELL 15	TADI, NYAQ, NYBI/ ACRU, FRCA, ULAM/ swamp shrubs, herbs CELL 16
Shallow histosols, 30-100 cm thick ROW 3	Open bog with dwarf shrubs, graminoids, pitcher plants, short cane, mosses CELL 17	Dense canebrake CELL 18	Alternating canebrake and pocosin CELL 19	PISE/ canebrake, alternating with PISE-ACRU tall pocosin CELL 20	Patch mosaic: PISE forest, ACRU forest, CHTH forest, bay forest with PEPA, MAVI CELL 21	Patch mosaic: CHTH forest, TADI/ACRU forest, PISE forest, NYBI forest, bay for. CELL 22	Extensive CHTH forest and patch mosaic as in Cell 22 CELL 23	TADI in wet swamps, cycling ACRU forest in peatlands (hypothetical) CELL 24
Deep histosols, peat deeper than 1 m ROW 4	Open bog with low shrubs, pitcher plants, grasses and sedges CELL 25	Canebrake or Low pocosin with ANGL, and bog herbs CELL 26	Alternating canebrake and pocosin, or medium to tall pocosin CELL 27	Tall pocosin with PISE, GOLA, ACRU; PISE forest, bay forest, CHTH patch mosaic CELL 28	Patch mosaic of types seen in Cell 22 CELL 29	Extensive CHTH forests and patch mosaic of types seen in cell 22 CELL 30	Extensive old growth CHTH forests and patch mosaic of types in cell 22 CELL 31	TADI in wet swamps, cycling ACRU forest in peatlands (hypothetical) CELL 32

SPECIES ACRONYMS: **ACRU**: Acer rubrum (Red Maple), **ANGL**: Andropogon glomeratus, **ARGI**: Arundinaria gigantea (Cane), **CHTH**: Chamaecyparis thyoides (Atlantic White Cedar), **CLJA**: Cladium jamaicense (Sawgrass), **CLMO** Cliftonia monophylla (Black Titi), **CYRA**: Cyrilla racemiflora (Titi), **FRCA**: Fraxinus caroliniana (Water Ash), **FRPE**: Fraxinus pennsylvanica Red Ash), **GOLA**: Gordonia lasianthus (Loblolly Bay), **ILGL**: Ilex glabra (Gallberry), **LIST**: Liquidambar styraciflua (Sweet Gum), **MAVI**: Magnolia virginiana (Sweet Bay), **MYCE**: Myrica cerifera (Wax Myrtle), **NYAQ**: Nyssa aquatica (Tupelo or Water Gum), **NYBI**: Nyssa biflora (Swamp Black Gum), **PEPA**: Persea palustris (Red Bay), **PIEL**: Pinus elliottii (Slash Pine), **PITA**: Pinus taeda (Loblolly Pine), **TAAS**: Taxodium ascendens (Pond Cypress), **TADI**: Taxodium distichum (Baldcypress).

than fire frequency or organic matter depth, is necessary to explain adequately the diversity of southeastern peatland vegetation.

Seasonally Wet Mineral Soils
(Table 2, Row 1, Cells 1–6)

Row 1 shows the nature of vegetation in transition from peatlands to wet mineral soils and upland vegetation. Soils are mostly Aquults, Aquepts, Aquods, Aquents and Aqualfs. Each cell of this row condenses much more complexity than those below because these transitional communities are distributed along the clay, loam, sand complex gradient of soil texture which, along with fire frequency, becomes one of the two master gradients required to explain original natural vegetation of uplands. Row 1 does not attempt to explain all the variation on wet mineral soils but is included to show some of the principal types on peatland margins. Soils are those just downslope from soils dry enough to support wet longleaf pine savanna.

Soils with Thin Organic Layers
(Table 2, Row 2, Cells 9–16)

Vegetation occurs on soils with thin organic epipedons 10–30 cm thick. These soils occur sometimes only in narrow bands, sometimes in broad zones, where deep organics feather out onto wet mineral soils, or contact upland slopes. The great canebrakes of the South, recorded in numerous historical accounts, were centered in Cells 10 and 18, with fire frequency around every 5 yrs. In addition, large portions of the peatlands with a slightly lower fire frequency, experienced a cycle of alternating canebrake and pocosin (Cells 11 and 19). In this situation, cane dominates for 3 or 4 years after fire and pocosin dominates after 7–8 years. This phenomenon, apparently widespread in original peatlands, has never been described. The site has the appearance of pure canebrake in the years immediately following fire (Fig. 7). Within its range, pond pine is usually the only tree to survive canebrake fire. Pocosin shrubs resprout after fire but are suppressed by the dense cane, which may reach 2 m in the first full growing season. The shrubs are very slow to regain their pre-burn stature. Eventually, however, toward the end of the fire cycle, shrubs overtop and suppress the cane, and the community aspect becomes that of pond pine pocosin, although cane stems are common upon closer inspection (Fig. 8). The next fire resets the process. In one pair of 0.1-ha plots on either side of a fire line in this type, the plot burned in the preceding year had 567,200 cane stems per ha, while the side which had grown for 8 years since last fire had 67,200 stems per ha, or about 0.1 as many. The immediate dominance of cane seen after a burn suggests that only 10% of the potential stems have the ability to maintain the entire rhizome mat until the next burn. With further reduction in fire frequency, succession proceeds to various kinds of forest communities and cane is almost entirely eliminated by 26–50 years. One unusual variant, where peat soils feather out onto low mineral flats (Cells 12 and 5), is sweetgum/canebrake (see Appendix for dynamics of this and other communities).

Fig. 6. Wet prairie zone between slightly drier pine rockland on the left and slightly wetter cypress head in Florida (Table 2, Cells 1 & 2). Similar treeless zones are found rangewide where frequently-burned longleaf pine savannas contact pocosin wetlands (Table 3, Cells 33 & 34).

Shallow Histosols (Table 2, Row 3, Cells 17–24)

These communities occur on soils with intermediate organic matter depth, mostly shallow histosols (Terric Medisaprists). With frequent fire these soils are typical of the great peatland canebrakes. With less frequent fire, Cells, 22 and 23, along with Cells 29, 30 and 31 of the next row, appear to provide the optimum organic soil depths and fire regimes for maintenance of white cedar in pure stands. Patch dynamics become complicated, however, and the same site has the potential to support pure white cedar, pure *Taxodium* or various mixtures with *Nyssa biflora,* red maple, red bay and sweet bay. The patch mosaic may shift on a scale ranging from decades to centuries (Fig. 9). The species that assume dominance on a particular site after stand-replacing fire appears to depend upon stochastic processes and conditions at time of fire (Frost 1987). These include depth to water table, foliar moisture (Blackmarr and Flanner 1968), wind velocity, and time since last fire. If the stand is killed but peat is too moist to burn, white cedar is likely to seize the site quickly with a dense blanket of new seedlings from the seed bank (Akerman 1923; Korstian 1924). On the other hand, if evapotrans-

Fig. 7. Alternating canebrake and pocosin, canebrake phase, taken 3 months after wildfire. Community is composed of two clear dominants, pond pine and cane (Table 2, Cell 19). Unburned pocosin on the other side of a fire plow line can be seen in the background.

piration has drawn down the water table a half meter or more, the surface peat can burn and the seed bank will be destroyed. If the peat burn is deep, a stand of *Taxodium ascendens* may seed in and the site may be pooled when the water table returns to its seasonal high level. After a century or two, peat rebuilds to the general land surface and the next fire has the potential to return the site to white cedar. Most of these processes were documented in the virgin pyromosaic communities of Figure 9.

Fig. 8. Alternating canebrake and pocosin, tall pocosin phase 8 years after fire (Table 2, Cell 19). Site is immediately adjacent to the canebrake seen in Figure 7, separated only by the fire plow line that stopped the fire. Cane stems are still common, although only 10% of the number in the adjacent canebrake, and are inconspicuous among the tall pocosin foliage. Quick return to dominance after a fire indicates that a relatively small number of cane stems are able to maintain the rhizome mat until fire returns.

Soils with Deep Peat (Table 2, Row 4, Cells 25–32)

Organic matter in this class most commonly ranges from 1 to 2.5 meters. Peat thicker than 2.5 meters is only occasionally found, since the great peatlands mostly are formed on poorly-drained upland flats or very slight bowl-shaped depressions. Deeper organics occur where V-shaped drainages lead out of peatlands, and in estuarine swamps bordering rivers and sounds where organic accumulation keeps pace with rising sea level. Some deep peat deposits have standing water at least part of the year in peat burnouts near their centers. This may be due in part to the poor drainage, which leads to slight peat doming, with higher peat accumulation in the center than around the periphery. Elevated peat is subject to water table drawdown by evapotranspiration during summer drought. Summer drawdown of more than a meter has been reported (Ingram and Otte 1982), and a fire during such a time may burn into the peat. The vegetation sequence under different fire regimes is very similar to that for Row 3. Canebrake is less common because deep peats tend to be more acid and infertile. Examples of canebrake, however, on peat more than 2 m deep were seen where the underlying substrate was nonacid.

One feature of this row, best developed in Cells 25 and 26 is pyrophytic low pocosin, not previously described. Some classifications (Schafale and Weakly 1990) only designate a community low pocosin when woody stature is limited by severe nutrient deficiency. In the original landscape, however, some pocosins that were part of large fire compartments would have been ignited frequently by fires in adjacent longleaf pine savannas. Some areas would have been maintained in low pocosin just because of the fire frequency. Thus two low pocosin community types probably occurred in presettlement vegetation, trophic low pocosin and pyrophytic low pocosin. The second type required fires on such a large landscape scale that it can no longer be found in the fire-suppressed landscape. The significance of both types of low pocosin, in terms of species richness, is that they both permit coexistence of a variety of graminoids, orchids, pitcher plants, and other bog species that are excluded from pocosin in larger stature classes. The orchids and graminoids that often appear after a pocosin burn are probably remnants, indicating a higher fire frequency in the past.

Presettlement Natural Vegetation Types on Severely Nutrient-Limited Sites (Table 3, Cells 33–64)

Some of the stands in this table may represent the most infertile extremes in the southeastern wetland landscape (Walbridge 1986). Such sites are less common than those in Table 2 but this may not have always been the case. Much of the existing wild landscape has been fertilized by nitrogen fixed by automobile engines; by input of phosphorus and potassium from wind deflation of agricultural fields in the spring after plowing and fertilization; and by sulfur from industries. Nutrient data are available to support the assertion of infertility in some cases (see cells 57 to 61), but, as mentioned earlier, most interpretation of fertility is based on observations of species behavior and robustness in different habitats.

Seasonally Wet Mineral Soils (Table 3, Row 1, Cells 33–40)

As in Table 2, Row 1 shows the nature of vegetation transitional from peatlands to wet mineral soils and considers only part of the variation on these soils which are just barely too wet to support moist longleaf pine savanna. One difference over more fertile sites seen in Table 2, is the persistence of open communities like wet savanna and prairie without frequent fire. Most of the best remaining examples of this type are in Florida in sites like the oval moist prairies in Apalachicola National Forest. The best examples outside Florida are the wet prairies interspersed with longleaf pine savannas at Grand Bay Savanna on the Alabama-Mississippi state line and on the Sandhill Crane National Wildlife Refuge in Mississippi. These include sites with the highest species density known in the South, with up to 40 species per square meter or 100 species per 100 square meters (Norquist 1984; Peet and Allard 1995). Dominants include a variety of graminoids such as wiregrass (*Aristida stricta*) and toothache grass (*Ctenium aromaticum*); rare endemics including *Sporobolus teretifolius* of the mid-Atlantic coast or cutthroat grass (*Panicum abcissum*) in south central Florida (Myers and Ewel 1990); and grass-leaved members of the lily family such as *Pleea tenuifolia* and *Tofieldia racemosa.* Examples were originally found as far north as the former Burgaw Savanna in North Carolina (Wells 1932), now destroyed. On fine-textured wet soils frequent fire was probably of only secondary importance in maintaining the community. The combination of long hydroperiod and clayey soils seems to be deadly to most woody species. Even so, an occasional fire is still needed, since even these sites are slowly colonized by shrubs and saplings of wetland trees. Extreme fire frequency was a coincidence of the landscape setting rather than a requirement for sustaining the prairie community. On the other hand, wet loamy or sandy soils, readily permeable to roots and rhizomes, are subject to more rapid woody invasion, and open remnants are rare. The only large areas with circumannual fire today are found on several military bases in the South. Intermediate succession across Row 1 leads to more pocosin-like forests than those of Table 2.

Fig. 9. White cedar patch mosaic (Table 2, Cells 21, 22, 23, 29, 30, 31). This remarkable infrared image shows a virgin pyrophytic patch mosaic with trees up to 300 years old, perhaps the best remaining example in the South. The light colored 2-lobed "mitten" in center is an area invaded by a wind-driven crown fire from the south (right side of photo) 2 or 3 decades ago. This is superimposed on a white cedar stand (black patches), dating from a crown fire also driven from the south about 90 years ago. Immediately adjacent areas have *Taxodium*/red maple stands (white dots are tree crowns) dating to fires 200 and 300 years ago which apparently burned deep enough into the peat to pool water, creating habitat for pure cypress stands. Other patch elements are *Nyssa biflora* forest, and tall pocosin (in the more frequently burned interior, beyond top edge of photo). Black area at bottom left is the Alligator River (Alligator River National Wildlife Refuge, North Carolina).

Soils with Thin Organic Layers (Table 3, Row 2, Cells 41–48)

At high fire frequency, Cell 41 and Cell 33 of the Row above provide a characteristic soil and fire regime combination for some of the rarest and most fire-dependent plants, including unusual species like Venus's flytrap (*Dionaea muscipula*), *Sarracenia psitticina,* and rare and endangered species such as *Lysimachia asperulaefolia, Asclepias pedicellata,* and *Parnassia caroliniana.* Reduction of fire frequency leads to dominance by pocosin shrubs and then dense wetland forest, with almost complete disappearance of the herb species.

Shallow Histosols (Table 3, Row 3, Cells 49–56)

Cells in this group differ from the corresponding row in Table 2 by the absence of cane. Most communities

Table 3. Cells show common dominants for each combination of fire frequency and organic matter depth. Local dominants vary with the geographic range of each species and for Row 1 with differences in soil texture. See text for further cell descriptions.

PRESETTLEMENT DISTRIBUTION OF PEATLAND VEGETATION OF THE SOUTHEASTERN UNITED STATES ALONG MASTER GRADIENTS OF FIRE FREQUENCY AND DEPTH OF ORGANIC SOIL

CELLS 33-64: SEVERELY NUTRIENT-LIMITED SITES

FIRE FREQUENCY

⇓ ORGANIC MATTER DEPTH

	1-3 YEARS	4-6 YRS	7-12 YRS	13-25 YRS	26-50 YRS	51-100 YRS	100-300 YRS	NEVER BURNED
Seasonally wet mineral soils ROW 1	Species-rich wet prairie sim. cell 1. ARST, PLTE, SPTE, CTAR, TORA CELL 33	Species-rich wet prairie, dwarf shrubs CELL 34	Wet prairie, MYCE, ILGL CELL 35	Thicket of dense, small PISE, PIEL, NYBI, bay forest/shrubs CELL 36	Dense ACRU,NYBI, LIST, PISE, PIEL/MAVI, PEPA/Shrubs CELL 37	PISE forest, PIEL, ACRU, LIST/MAVI, PEPA/ ferns CELL 38	TADI, ACRU, NYBI, swamp herbs CELL 39	TADI, NYBI, ACRU CELL 40
Soils with thin organic layers, 10-30 cm thick ROW 2	Diverse wet prairie and bog gramin-oids, forbs, and insectivorous plants CELL 41	Wet prairie with insectivorous plants and dwarf shrubs CELL 42	Low or medium pocosin CELL 43	Medium pocosin CELL 44	Tall pocosin, PISE forest, bay forest CELL 45	PISE forest, NYBI & ACRU forest, bay forest CELL 46	TADI, NYBI/ swamp herbs CELL 47	TADI, NYBI/ swamp herbs CELL 48
Shallow histosols, 30-100 cm thick ROW 3	Open bog with pitcher plants, dwarf shrubs, graminoids CELL 49	Low pocosin with pitcher plants, other bog species. CELL 50	Low or medium pocosin CELL 51	Scrubby PISE/ medium pocosin CELL 52	PISE-GOLA forest, bay forest with PEPA, MAVI, ACRU CELL 53	Patch mosaic: PISE-GOLA forest, CHTH forest, TADI/ ACRU, NYBI forest, bay for. CELL 54	Patch mosaic: CHTH forest, TADI/ACRU forest, NYBI forest, bay forest CELL 55	TADI in wet swamps, cycling ACRU forest in peatlands (hypothetical) CELL 56
Deep histosols, peat deeper than 1 m ROW 4	Open bog with pitcher plants, grasses and sedges, dwarf shrubs CELL 57	Low pocosin, with pitcher plants, other bog species CELL 58	Low pocosin CELL 59	Low pocosin CELL 60	Low or medium pocosin CELL 61	Medium pocosin (hypothetical) CELL 62	Tall pocosin, PISE-GOLA forest, bay forest (hypothetical) CELL 63	TADI in wet swamps, cycling red maple forest in peatlands (hypothetical) CELL 64

SPECIES ACRONYMS: ACRU: Acer rubrum (Red Maple), ANGL: Andropogon glomeratus, ARGI: Arundinaria gigantea (Cane), ARST: Aristida stricta (Wiregrass), CHTH: Chamaecyparis thyoides (Atlantic White Cedar), CLJA: Cladium jamaicense (Sawgrass), CLMO Cliftonia monophylla (Black Titi), CTAR: Ctenium aromaticum (Toothache Grass), CYRA: Cyrilla racemiflora (Titi), FRCA: Fraxinus caroliniana (Water Ash), FRPE: Fraxinus pennsylvanica (Red Ash), GOLA Gordonia lasianthus (Loblolly Bay), ILGL: Ilex glabra (Gallberry), LIST: Liquidambar styraciflua (Sweet Gum), MAVI: Magnolia virginiana (Sweet Bay), MYCE: Myrica cerifera (Wax Myrtle), NYAQ: Nyssa aquatica (Tupelo or Water Gum), NYBI: Nyssa biflora (Swamp Black Gum), PEPA: (Persea palustris (Red Bay), PIEL: Pinus elliottii (Slash Pine), PITA: Pinus taeda (Loblolly Pine), PLTE: Pleea tenuifolia, SPTE: Sporobolus teretifolius, TAAS: Taxodium ascendens (Pond Cypress), TADI: Taxodium distichum (Baldcypress) TORA: Tofieldia racemosa (False Asphodel).

have the classic appearance of low or medium pocosin. Only with the longer fire-return intervals do forests develop. While white cedar may be found occasionally, more typical components of the patch mosaic are pond pine-*Gordonia* forest or bay forests dominated by sweet bay, red bay and red maple.

Deep Histosols (Table 3, Row 4, Cells 57–64)

Cells in this row constitute the true ombrotrophic low pocosins, which are able to maintain their low stature without fire. Nevertheless, some large areas of in this category did burn at a nearly annual rate. Those that did seem to have been more like open bogs rather than low pocosin. One annually-burned peatland of some 325 km^2 (125 mi^2), was described in 1852 as being covered with "coarse grasses" (Emmons 1860). A second visitor to the same site in 1856 said it was dominated by *Andropogon glomeratus* and low shrubs with *Sarracenia flava* and *S. purpurea* (Ruffin 1861). No frequently burned sites are presently available for study since no large peatlands still burn at this frequency. It would be very valuable if a site could be found where this fire regime could be experimentally reestablished.

True ombrotrophic pocosins may persist for decades without fire. Sheep Ridge Low Pocosin in the Croatan National Forest, NC is the longest-persisting low pocosin known, with vegetation still only around waist high after more than 30 years of fire exclusion (Fig. 10). Here, on deep, oligotrophic peat, phosphorus has been demonstrated to be the limiting nutrient, with nearly all of the supply tied up in vegetation and microorganisms (Walbridge 1986). Titi (*Cyrilla racemiflora*), *Zenobia pulverulenta,* red bay and *Lyonia lucida* are dominant, along with nine other pocosin shrubs. Herbs are limited to *Scleria,* a few clumps of *Andropogon glomeratus,* scattered pitcher plants (*Sarracenia flava* and *S. purpurea*) and a few other species of pocosins and wet savannas, which are able to persist in the interstices between the low shrubs. Particularly interesting species are *Cassandra calyculata* and *Lilium catesbaei.* The persistence of low pocosin for more than three decades suggests that this is one of the most infertile sites in the Southeast.

Cells 62 through 64 show hypothetical vegetation under continued fire exclusion. It is unlikely that natural vegetation occurred under these conditions without fire. Longer fire-return intervals are possible on more fertile peatlands because white cedar and other forests appear to have considerable resistance to all but wind-driven crown fires. On severely nutrient-limited sites, however, the low sclerophyll shrub layer is simply too susceptible to fire. The probability of very infertile sites, which retain the flammable low pocosin physiognomy, escaping fire for more than 13–25 years seems remote under the re-

Fig. 10. Possibly the most nutrient-limited site in the Southeast, Sheep Ridge Low Pocosin is still only waist high after more than 30 years of fire exclusion. Trees are pond pine (Table 3, Cell 61). Walbridge (1986) has shown phosphorus to be the limiting nutrient (Croatan National Forest, North Carolina).

gional natural fire regimes (Fig. 1). The hypothetical future vegetation under long-term fire exclusion should be medium pocosin, high pocosin with scrubby pond pine, *Gordonia* and red maple forest, as vegetation slowly accumulates additional phosphorus from atmospheric input. In large peatlands, ultimate succession in the absence of fire is hypothetical, but some stands excluded from fire for 75 years seem to be approaching a cycling red maple climax.

CONCLUSION

Peatlands of the southeastern U.S. once experienced landscape-scale fires that burned for weeks or months (Fig. 11). Fire frequency and peat depth were the two master gradients governing presettlement peatland vegetation. Lightning ignition, which once sustained the master fire gradient, is clearly no longer a significant factor in the landscape. Except in the most remote areas, fires are extinguished before they can burn as much as a hectare (Jennings 1989). As a consequence, the Southeast's original vegetation, structurally complex and diverse, is undergoing massive simplification, as dominant vegetation shifts to the right in the three fire frequency tables.

On uplands, longleaf pine communities have been reduced to less than 3% of their original extent (Frost 1995b). In peatlands, both canebrake and white cedar have been eliminated from all but 1% of their original habitat (Frost 1987).

Fresh and oligohaline marshes show decline in species richness, and loss of certain rare, fire-dependent types like *Eryngium aquaticum* and *Eleocharis rostellata* marsh, while brackish and salt marsh have been

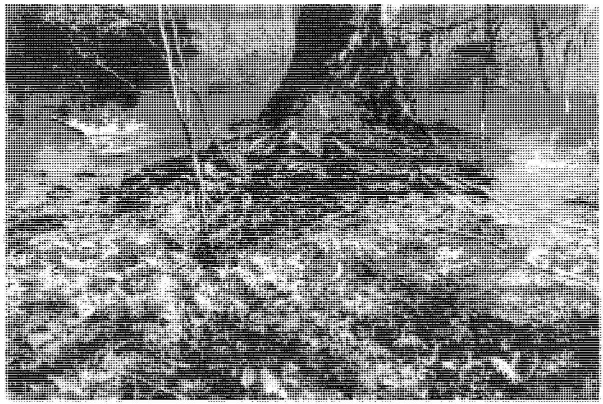

Fig. 11. Litter fire in dry *Nyssa biflora* swamp, still creeping 2 weeks after a hot, wind-driven wildfire that burned more than 90,000 acres of canebrake and pocosin. In presettlement times, fires in wetlands may have burned all summer, creeping through swamps, smoldering in peat, and flaring up when more flammable vegetation was reached or conditions of humidity and wind reached critical thresholds. Ferns being consumed are *Woodwardia areolata*. (Allen Road fire of April 1985, Hyde, Tyrrell and Dare Counties, NC).

little affected. The great peatland and fluvial canebrakes of the South have been almost entirely replaced by pocosin, bay forest and the various scrub and forest communities described in Table 2, cells 12, 13, 20, 21 and 28. In turn, much, perhaps 50% or more, of our existing "pocosin" communities were something else (open bogs, canebrakes and white cedar) under the original fire regimes. Only the true ombrotrophic pocosins seem to have remained unchanged.

Many rare plants are now limited to pocosin/savanna ecotones. Some of these species were probably originally also native to pyrophytic low pocosin—pocosin kept low by frequent fire—which may have been more widespread than trophic low pocosin—those sites kept low by extreme nutrient limitation. Other rare species sites in peatland interiors benefitted by fires that traversed wetlands to reach sand lenses and other islands of habitats now isolated from fire. It is critical to understand the pervasive role of fire in shaping natural vegetation of southeastern wetlands, in order to manage and restore natural areas, and preserve rare species dependent upon fire. Understanding the regional fire regime permits reconstruction of fire history on a site-by-site basis. The possibilities that open up include the ability to accurately delineate presettlement vegetation; learning how to conduct landscape-scale fires in wetlands; and the restoration of marshes, bogs, canebrakes and white cedar forests. The renewed interest in fire ecology, and the pioneering efforts in burning large or difficult-to-manage wetlands offer hope for protection and restoration of the original spectrum of species and community diversity in southeastern wetlands.

APPENDIX

Descriptions of peatland vegetation to accompany Tables 2 and 3, vegetation cells 1–64.

CELLS 1–32. MODERATELY FERTILE SITES:

Cell 1. Wet prairie with a nearly annual (1 to 3 yrs) fire frequency. Most communities in this class are addressed in cell 33 in the table for more infertile sites. The few wet prairie sites with higher nutrient status may include the marl prairies of south Florida, which are dominated by species like *Muhlenbergia filipes*, sawgrass (*Cladium jamaicense*), *Rhynchospora* and *Xyris*, and the numerous other species found in treeless areas between pine rocklands and cypress heads (Figure 6). In the Carolinas, this cell is represented by rare wet savannas which have marl near the surface in an otherwise acid landscape, and have site-limited rare species like *Oxypolis canbyi* (e.g. Lanier Quarry Savanna). As discussed in cell 33, fire frequency as high as 1 to 3 years was probably not a requirement for maintenance of these wet sites, but a consequence of the regional fire regime.

Cell 2. Wet prairie with 4 to 6 yr fire frequency. This group occurred in portions of the landscape with smaller fire compartment sizes, slightly more topography, or adjacent to vegetation slightly less conducive to fire spread. Small examples can be found in a number of areas managed with controlled fire, including Florida's Apalachicola National Forest and several southern military bases. Dominants on clayey soils are similar to those in cell 1. On loams and sands low forms of pocosin shrubs such as *Myrica*, gallberry (*Ilex glabra*), *Clethra* and *Cyrilla* may be conspicuous toward the end of each fire cycle. Regional variation in dominants, and with different degrees of wetness, may include *Andropogon glomeratus, Pleea tenuifolia, Ctenium aromaticum, Sporobolus* spp., and sparse or patchy cane (*Arundinaria*), along with a great variety of other species of wet savannas and bogs. In Virginia, one of the northernmost such sites, now vanished, was dominated by *Tofieldia racemosa* (Fernald 1940).

Cell 3. Wet mineral soils with 7–12 yr fire frequency. On all but the wettest sites, reduction of fire frequency to this level allows firm establishment of regionally prevalent wetland shrubs such as *Myrica*, titi (*Cyrilla racemiflora*), black titi (*Cliftonia monophylla*), *Ilex, Vaccinium,* and any of the other pocosin species. Larger grasses like *Andropogon glomeratus, Panicum virgatum,* cane, or sawgrass may increase in importance, and the site may have the appearance of a prairie-shrub patch mosaic.

Cell 4. Wet mineral soils with 13 to 25 yr fire frequency. Small trees of red maple (*Acer rubrum),* swamp black gum (*Nyssa biflora*), sweet gum (*Liquidambar styraciflua,* pond pine (*Pinus serotina),* loblolly (*Pinus taeda*) or slash pine (*P. elliottii*) form a scrubby wetland forest toward the end of the cycle. Most stems are killed by fire and the resulting sprout community is similar in appearance to high pocosin but red maple sprouts quickly dominate. Where soil is loamy or sandy, cane may be important. Herbs may be almost nonexistent in the dense canopy shade for most of the cycle.

Cell 5. Wet mineral soils with 26 to 50 yr fire frequency. Woody stems on such sites are dense, with dominant subcanopy and shrub layers. Canopy trees regionally include red maple, loblolly pine, slash pine or even white oak and other hardwoods, often with cane, gallberry or other shrubs as dominants. Fire at around 26 years may kill most stems to the ground while many pines and hardwoods may survive at the longer end of the cycle. Much stochastic variation in survival and dominant canopy species is possible depending upon wind, density of understory and other conditions at time of burn. An interesting phenomenon of this phase is that cane may become abundant or even dominant in the understory following accumulation of 5 to 15 cm of organic matter, but it may then be eliminated by a growing season burn that removes the organic surface layer.

Cell 6. Wet mineral soils with 51 to 100 yr fire frequency. With this fire-return interval, wetland trees like slash pine, loblolly pine, red maple and bottomland oaks have time to become large enough to resist fire, thus shading out much of the potentially flammable understory. So, when fire does occur, fewer trees are killed and the principal effect is elimination of the smaller size classes of understory stems. In contrast with the thickets in Cell 4, these stands are often quite open beneath the canopy. Scattered cane stems and patches are found in some stands. Accumulated deep pine needle litter smothers the herb layer except for a few tall species like cinnamon fern (*Osmunda cinnamomea*) and royal fern (*O. regalis*).

Cell 7. Wet mineral soils with 100 to 300 yr fire frequency. As pines are replaced by shade-tolerant wetland hardwoods like red maple, *Nyssa biflora,* and swamp chestnut oak (*Quercus michauxii*), the pine needle duff layer is replaced by herbs, typically swamp species of *Carex* and broadleaved herbs. Fires have little effect other than damaging exposed roots and leaving basal scars on some of the trees.

Cell 8. Wet mineral soils completely protected from fire. Natural examples can be found on small islands in wet swamps surrounded by permanently saturated soil or standing water, and with no understory vegetation capable of carrying fire to the site. Such sites may be dominated by baldcypress (*Taxodium distichum*) and *Nyssa biflora,* and slightly higher areas may support nearly pure stands of beech or beech-magnolia.

Cell 9. Thin organic soils with 1 to 3 yr fire frequency. These are open, wet prairie and bog sites, sometimes with very dwarfed shrubs in the herb layer. They may be dominated by very diverse wet prairie and bog graminoids and forbs, with species richness similar to or slightly lower than that for cell 1. Shrubs may out-compete some herbs at the 3 year frequency. Examples of stream bottom canebrakes in this category may be seen on Fort Bragg in North Carolina, where fires have passed through bottomlands about every 2 years in recent times. Such communities, common in historical accounts, are now quite rare.

Cell 10. Thin organic soils with 4 to 6 yr fire frequency. Good conditions for canebrake, especially at the 30 cm depth. See cell 18 for further discussion of canebrake at this frequency.

Cell 11. Thin organic soils with 7 to 12 yr fire frequency. These are alternating canebrake and pocosin sites, especially at the 30 cm depth (see Figures 7 and 8).

Cell 12. Thin organic soils with 13 to 25 yr fire frequency. At this frequency an open canopy of pond pine and red maple reduces density of understory shrubs and intensity of fires. Loblolly pine, slash pine or sweet gum can then become established. Variations include stands dominated by sweet gum with a cane understory of light to medium density. In these sites, coexistence of cane—ordinarily conducive to high-intensity tree-killing fires—and the tree canopy, is maintained in a precarious dynamic balance in which the shading canopy is just thick enough to keep cane density just thin enough so that the trees are not killed by fire. Conversely, cane density is still sufficient to carry fire and maintain an understory largely clear of other species.

Cell 13. Thin organic soils with 26 to 50 yr fire frequency. With continued suppression of the understory, forest stands may form closed canopies of sweet gum, pond pine, slash pine, or red maple in large peatlands, or loblolly or slash pine and hardwoods at peatland/upland contacts and in fluvial bottomlands. There may be occasional canopy or subcanopy stems of red bay (*Persea palustris*) and sweet bay (*Magnolia virginiana*). The understory may be very sparse, consisting of scattered shrubs and patches of cane. Sites in small stream swamps may have narrow zones of white cedar downslope from more frequently burned pine savannas, especially where slopes are steep.

Cell 14. Thin organic soils with 51 to 100 yr fire frequency. This interval permits formation of mature pond pine forest in large peatlands, or various mixtures of loblolly pine, slash pine, sweetgum and bottomland hardwoods elsewhere. Subcanopy is often well-developed, with only scattered stems of cane or shrubs such as gallberry, *Myrica, Ilex coriacea,* and *Lyonia lucida.* The herb layer may be almost nonexistent except for tall ferns like *Osmunda cinnamomea* and *O. regalis.*

Cell 15. Thin organic soils with 100 to 300 yr fire frequency. This uncommon type is most often encountered as a narrow band bordering riverine swamps or in the interiors of large swamps where shade and channels quell most fires moving in from outside. Tall canopy dominants may include baldcypress, pine, *Nyssa biflora, Fraxinus pensylvannica,* and sweet gum with occasional white cedar. Red maple and *Fraxinus caroliniana* may be common in the subcanopy. Shrubs are typically sparse but there may be a well-developed herb layer of *Carex,* grasses, *Woodwardia,* and other swamp herbs.

Cell 16. Thin organic soils completely protected from fire. This type can occur in portions of swamps cut off from the mainland or from large wetland fire compartments by oxbows and stream channels. It occurs as a multi-storied community dominated by bald cypress as old as 1,000 years in virgin stands, most often with a high subcanopy of *Nyssa* (*N. biflora* on slightly drier microsites and *N. aquatica* in the wetter areas). It is characterized by an open, low subcanopy of wetland saplings like red maple, water ash or elm (*Ulmus americana*), an open shrub layer, and a layer of swamp forest herbs.

Cell 17. Organic matter 30 cm to 1 m deep with 1 to 3 yr fire frequency. These are open bogs, with pitcher plants and other insectivorous species, dwarf shrubs, low graminoids, and sometimes cane. One such site was described in the 1930s as covered by vast carpets of fire-following mosses like *Funaria hygrometrica* after each fire (L. E. Anderson, Duke University, pers. comm.), along with *Andropogon glomeratus,* dwarf shrubs, and sphagnum.

Cell 18. Organic matter 30 cm to 1 m deep with 4 to 6 yr fire frequency. These are the classic canebrake soils. Cane rebounds to a height of 1.5 to 2 meters or more within a few months after a fire. Because of the high fire frequency, shrubs have inadequate time between fires to become established in the shade of the tall cane, and cane may be practically the only species present. One such site examined for this study in North Carolina had only 10 species per 1/10 ha: there was 100% cane cover and a density of 450,800 stems per ha. Besides the cane there were ten stems/ha of pond pine, and a few scattered stems of poison sumac (*Toxicodendron vernix*), *Rhus copallina, Aralia spinosa, Prunus serotina, Rubus hispidus, Phytolacca americana, Ilex glabra, Toxicodendron radicans,* and *Smilax glauca.* Combined cover of all species other than pine and cane was less than 1%.

Cell 19. Organic matter 30 cm to 1 m deep with 7 to 12 yr fire frequency. The dynamics of alternating canebrake and pocosin are discussed in the text. This alternating community pair is best developed on soils of this depth, and was probably extensive in peatlands under the presettlement fire regime.

Cell 20. Organic matter 30 cm to 1 m deep with 13 to 25 yr fire frequency. At this frequency, pond pine may form a nearly closed canopy. Shrubs may dominate the understory for much of the cycle. Red maple may dominate in sites or patches where pond pine is lacking. Immediately after fire, cane may recapture the understory and nearly all biomass in the resulting bilayered community consists of pond pine in the canopy and cane below. Shrubs resprout in the shade of these two dominants but are unable to regain more than about 50% of the understory cover until near the end of the cycle. Pine shade may reduce intensity of fires by reducing density of understory shrubs.

Cell 21. Organic matter 30 cm to 1 m deep with 26 to 50 yr fire frequency. Reduction of fire frequency to this level can produce tall, straight pond pine forest. Under the closed canopy are scattered evergreen bay species, including *Persea* and *Magnolia*. Scattered stems of cane persist, and shrubs like *Myrica*, gallberry, and fetterbush (*Lyonia lucida*) are common but do not usually form a closed layer. Because of the shade and deep pine needle accumulation, sometimes as much as 30 cm on the forest floor, herb cover is almost nonexistent. Good examples are rare now, since the tall, straight, dense pond pine stands have all been logged, and few are being regenerated with fire. Logged stands have been replaced by red maple or bay forest. On a landscape level, such stands sometimes occur in a patch mosaic with white cedar. Pure *Gordonia* stands can sometimes be found.

Cell 22. Organic matter 30 cm to 1 m deep with 51 to 100 yr fire frequency. See text and Figure 9 for discussion of the white cedar patch mosaic of which this cell is a part.

Cell 23. Organic matter 30 cm to 1 m deep with 100 to 300 yr fire frequency. Such sites have similar species and operate with dynamics like those in Cell 22. Three hundred years approaches the documented upper limit for age of white cedar, but only a few remnant *Chamaecyparis* may be adequate to maintain the seed bank until the next fire.

Cell 24. Organic matter 30 cm to 1 m deep completely protected from fire. As in cell 16, this situation is not known to occur in the great peatlands. However, completely fire-protected sites can be found in fluvial swamps, with baldcypress dominant. In Virginia and North Carolina, long settled and farmed, there are sites where fire has been completely excluded for 75 years. Among three such sites, one had a few pond pine, and another had a remnant patch of white cedar on the fringe; but all three were heavily dominated by red maple. The maple stands had red maple in the canopy, subcanopy, shrub and herb layers. There was a pocosin-like shrub layer, but no other woody stem was present that could be a candidate for the canopy. On such sites, it appears that the ultimate forest under existing climate with continued fire exclusion will be cycling red maple.

Cell 25. Deep peat soils, greater than 1 m in depth with 1 to 3 yr fire frequency. Plant cover is similar to cell 17, but this type was probably much less extensive, since deep peat zones are often surrounded by pocosin vegetation on shallow peat and pocosin is less likely to carry every fire that passes through upland savannas, into the deep peat communities.

Cell 26. Deep peat soils, greater than 1 meter in depth with 4 to 6 yr fire frequency. Bog herbs and low pocosin shrubs are predominant. Canebrake may occasionally be found in peatlands with organic matter 2 or more m deep where the underlying mineral soil is nonacid. One such site, Light Ground Pocosin in Pamlico County, NC, once had extensive canebrakes on its east side near the contact with an unusual zone of Alfisols, circumneutral soils being very uncommon in the region. Only small patches remain of extensive canebrakes visible on old aerial photos. In some areas the ground is littered with old canes where no living stem persists today. The canopy after 40 years of fire exclusion is a patch mosaic with stands of pure red maple, and mixed stands of pond pine, loblolly pine and *Gordonia.*

Cell 27. Deep peat soils, greater than 1 meter in depth with 7 to 12 yr fire frequency. Such sites have medium to tall pocosin, or in sites with circumneutral basement substrate, alternating canebrake and pocosin. Depending upon site nutrient status, pocosin typically bounces back quickly to a certain height within a year or two after a burn and then increases very slowly. This fire frequency allows pocosin vegetation that is not severely nutrient-limited to reach heights of 3 to 5 m. Herbs are rare except for *Woodwardia virginica* which may be a codominant in the year or two after a burn. *W. virginica,* along with *Lyonia lucida,* often forms an understory beneath the dominant shrub canopy.

Cell 28. Deep peat soils, greater than 1 meter in depth with 13 to 25 yr fire frequency. Tall pocosin is common, with emergent pond pine, red maple and *Gordonia lasianthus,* or pure pond pine forests of shorter, more twisted stature than those of cells 13 and 14. Perhaps because they have more time for building root systems, the tree species produce emergent saplings within a few years rather than remaining for an extensive time in the pocosin shrub layer. These communities form impenetrable thickets tied together with cat-brier (*Smilax laurifolia*), but toward the end of the cycle the tree canopy may be 10 m in height. Red bay and sweet bay add an evergreen component to the understory that can emerge as bay forest with further reduction in fire frequency. Areas in this cell adjacent to white cedar stands may be colonized by white cedar after a fire, forming pure or mixed stands.

Cell 29. Deep peat soils, greater than 1 m in depth with 26 to 50 yr fire frequency. As in cells 21,22,23,30, and 31, this fire-return interval is conducive to patch mosaic formation, better illustrated in the next cell. Patch elements are pond pine-red maple forests, white cedar forest, bay forest, and the others discussed below.

Cell 30. Deep peat soils, greater than 1 m in depth with 51 to 100 yr fire frequency. Within its geographic range, this interval is optimal for Atlantic white cedar, occurring during the most vigorous part of its life cycle and allowing time for massive seed bank accumulation in the wet peat. As with cell 22, pure cypress stands (both *T. distichum* and *T. ascendens*) can become established in pools created by peat burnouts. Other elements of the mosaic include pond pine-red maple forest, *Nyssa biflora* forest, red maple forest, and bay forest. While any of these can occur naturally, most existing examples of *Nyssa,* red maple and bay forest are the incidental result of removal of white cedar. Until the past decade, nearly all logging of white cedar left the logging slash on the ground, inhibiting or completely preventing cedar seedling regeneration. The local understory species took over and formed a new canopy. Some variation of this has occurred nearly everywhere that white cedar formerly was found, and the species now occupies only about 1% of its original range (Frost 1987). White cedar is conspicuously absent from some of the largest peat domes, which include some of the most sterile of peat habitats (see cells 57–64). Most sites with white cedar appear to have a supplemental nutrient source. Sea-level stands adjacent to fresh or brackish water receive occasional storm inundation and more regular aerosol deposition. Stands in small stream systems downslope from uplands can receive nutrients in runoff and ground water, and may also be occasionally flooded. The Dismal Swamp white cedar, historically the largest known stand in the range of the species, at an estimated 112,000 acres (45,000 ha)(Akerman 1923), lies at the toe of the 8 m (25 ft) high Suffolk Scarp and is underlain with a sandy aquifer which could supply subsurface nutrients from the upland plateau to the west (Oaks and DuBar 1974).

Cell 31. Deep peat soils, greater than 1 m in depth with 100 to 300 yr fire frequency. White cedar stands up to 300 years of age are known to have dominated the most fire-inaccessible central interior of the Dismal Swamp (Frost 1987, 1989). Even-aged stands of baldcypress 200 years old can still be found in large peatlands (Figure 9). In the latter, red maple may be nearly the only understory tree. In peatlands the life span of red maple seems to be only about 100 years. On part of the site studied in Figure 9, the 200 year-old cypress canopy overtops a well-developed secondary canopy of red maple, the only other substantial layer present. The oldest maple stems present are about 100 years old. Also present are dead trunks, and all size classes of maple replacement stems. The picture clearly presented is a pure cypress canopy, probably originating in a peat burnout during a dry summer 200 years ago. The cypress has persisted for centuries, with the red maple below, completing its life span and replacing itself on a 100 year cycle.

Cell 32. Deep peat soils, greater than 1 m in depth in completely fire-protected sites. Such sites probably do not exist in the big peatlands. There are riverine islands of deep peat which support old-growth baldcypress.

CELLS 33–64. SEVERELY NUTRIENT-LIMITED SITES

Cell 33. Wet prairie with a 1 to 3 yr fire frequency. Flora is similar to cell 1.

Cell 34. Wet prairie with 4 to 6 yr fire frequency. This group is similar to cell 2 except that in more infertile sites, species richness may be higher because of less rapid exclusion by bunch grasses. Shrubs are fewer and of smaller stature than those in cell 2 between burns.

Cell 35. Wet mineral soils with 7 to 12 yr fire frequency. On sterile sites with fine-textured soils, moist prairie vegetation persists, but single stems and patches of low shrubs like gallberry, *Myrica,* and along the Gulf Coast, shrubby *Hypericum* may occur. Cane and other species that require higher fertility are lacking. Various fire-suppressed successional examples are common in the Mississippi coastal meadows.

Cell 36. Wet mineral soils with 13 to 25 yr fire frequency. On sites with clayey soils, moist prairie with shrubs may persist. On sandy soils, readily penetrated by roots and rhizomes, dense thickets may form. Canopy species may be pond pine, *Nyssa biflora* or red maple, with pocosin and bay species in the understory. Typically there is little differentiation into vegetation strata, the whole being one continuous vertical thatch of stems. The appearance after fire is that of medium pocosin, but with numerous emergent dead stems and trunks.

Cell 37. Wet mineral soils with 26 to 50 yr fire frequency. Pure pine forest or forests with various mixtures of pond pine, slash pine, *Nyssa biflora,* and red maple may occur. The understory remains thick, and consists of red bay, sweet bay, and the more shade-tolerant pocosin shrubs like *Ilex glabra, I. coriacea, Myrica cerifera* and *M. heterophylla.* Herbs are nearly absent. Many hardwood stems are killed by fire. Canopy pond pine often survives, tending to maintain its dominance. Resprouting stems of other trees are relegated to canopy gaps.

Cell 38. Wet mineral soils with 51 to 100 yr fire frequency. These communities consist of pine forest, *Nyssa biflora* forest sometimes with *Taxodium,* and red maple forest. Many of these commonly have sclerophyllous evergreen understory with red bay and sweet bay. Herbs, other than a few ferns, are typically lacking.

Cell 39. Wet mineral soils with 100 to 300 yr fire frequency. Very sterile sites in this category are hard to find. Fire is in part responsible for enforcing infertility by driving off nitrogen, while poor sites that go this long without fire are likely to accumulate nutrients just from atmospheric deposition. Also, sites so sheltered from fire are usually in swamps or bottomlands where nutrient transport from uplands or by water comes into play. Some stands of *Taxodium* along acid blackwater streams may fit this category.

Cell 40. Wet mineral soils completely protected from fire. The same comments as for cell 39 apply here. Old-growth *Taxodium* along small, sandy blackwater streams isolated from fire by oxbows and channels are the only candidates. Larger rivers and streams carry nutrients that would shift this cell to table 2.

Cell 41. Thin organics with 1–3 yr fire frequency. These are open wet prairie and bog sites similar to those in cell 9, except that cane is absent and shrub growth is somewhat lower in nutrient-stressed sites. Herb species diversity remains very high. This and Cell 33 provide a characteristic soil and fire regime combination for some of the rarest and most fire-dependent plants, including unusual species like Venus's flytrap (*Dionaea muscipula*), *Sarracenia psitticina,* and rare and endangered species such as *Lysimachia asperulaefolia, Asclepias pedicellata,* and *Parnassia caroliniana.* Dominants, which vary greatly on a local and regional basis, include *Pleea tenuifolia, Sporobolus, Ctenium,* and *Tofieldia racemosa.* Most of the locally available pocosin shrubs can be found, but usually in dwarfed form.

Cell 42. Thin organics with 4 to 6 yr fire frequency. Vegetation and species richness for cells 42, 43, 50 and 51 are drastically different from the corresponding block of cells from Table 2. These soils, apparently too sterile for cane, may have a rich herb flora interspersed with dwarf shrubs. They also include most of the rare species discussed in cell 41 above.

Cell 43. Thin organics with 7 to 12 yr fire frequency. On sterile sites the alternating canebrake and pocosin phenomenon of cell 11 is replaced simply with low or medium pocosin. Species diversity is typically low, limited to 10 or 12 pocosin shrub species as well as *Smilax laurifolia* and *Woodwardia virginica.* Other herbs are sparse, and include a few pitcher plants, orchids, *Xyris, Rhynchospora* or *Carex.*

Cell 44. Thin organics with 13 to 25 yr fire frequency. On sterile sites, medium or high pocosin with pond pine develops over the fire-return interval. Toward the longer cycle, some sites with intermediate fertility also produce emergent *Gordonia,* sweet bay, *Nyssa biflora* and red maple, which are reduced to resprouting stems after fire. Stems of scrubby pond pine may survive into the next cycle.

Cell 45. Thin organics with 26 to 50 yr fire frequency. This interval is long enough for formation of pond pine forest, but the trees are of the characteristically picturesque crooked form, lacking the straight tall trunks of pond pine forest seen in the corresponding cell 21. Because establishment of pine is irregular in this and the preceding cells, pine forest is often interspersed in a matrix of tall pocosin or bay forest in which the canopy dominant is often *Gordonia lasianthus,* with red bay and sweet bay forming most of the subcanopy. *Smilax* and pocosin shrubs make the understory impassable.

Cell 46. Thin organics with 51 to 100 yr fire frequency. These forests resemble those of cell 45, but *Nyssa biflora* and red maple may become components of the canopy and subcanopy. Both species are tolerant of shade and very poor soils, but have spindly, twisted trunks when found on such sites. The dominants in this class sometimes form a patch mosaic with white cedar.

Cell 47. Thin organics with 100 to 300 yr fire frequency. As with other cells in this fire frequency class, it is most often encountered as a narrow band bordering riverine swamps, in this case those bordering acid blackwater rivers. The community may have old baldcypress of reduced stature or *Nyssa biflora* and bay forest species. *Gordonia* is not known to live long enough to survive into this age class and does not reproduce in shade. White cedar is occasionally found.

Cell 48. Thin organics completely protected from fire. This type is limited to small, acid blackwater stream systems. A baldcypress stand along the Black River, a tributary of the Cape Fear River in North Carolina, has been identified as the oldest in the eastern U.S., with trees up to 1,200 years old. These occur on wet, sterile, acid soils. There is nothing in the understory to carry fire, despite the fact that nearby uplands were subject to the highest fire frequency regime.

Cell 49. Organic matter 30 cm to 1 m deep with 1 to 3 yr fire frequency. These are open bogs with pitcher plants, dwarf shrubs, graminoids, especially *Andropogon glomeratus* as described for cell 17, but without cane.

Cell 50. Organic matter 30 cm to 1 m deep with 4 to 6 yr fire frequency. These sites support only low pocosin, maintained by a combination of infertility and frequent fire. Shrub stature is kept low enough to permit a diversity of pitcher plants and other bog species in the interstices.

Cell 51. Organic matter 30 cm to 1 m deep with 7 to 12 yr fire frequency. This is low to medium pocosin with sparse, crooked pond pine emergent over shrubs. *Woodwardia virginica* may be virtually the only herb.

Cell 52. Organic matter 30 cm to 1 m deep with 13 to 25 yr fire frequency. Scrubby pond pines are emergent over medium pocosin with very low species diversity, largely limited to 9 or 10 pocosin shrub species plus *Smilax laurifolia* and *Woodwardia virginica.*

Cell 53. Organic matter 30 cm to 1 m deep with 26 to 50 yr fire frequency. Tall pocosin or scrubby pond pine-*Gordonia* forest with red bay, sweet bay and tall pocosin shrubs, thick and relatively undifferentiated into layers.

Cell 54. Organic matter 30 cm to 1 m deep with 51 to 100 yr fire frequency. As in many of the other cells in the 50–100 year fire frequency class, this fire regime is conducive to formation of a patch mosaic, with different communities depending upon fire behavior and environmental conditions at time of burn. Components of the mosaic include pond pine-*Gordonia* forest. The pines are gnarled and crooked. White cedar forest may occur on less infertile sites. *Nyssa biflora* forest or pond cypress (*Taxodium ascendens*) forest, the trees often straight but small, may also be found.

Cell 55. Organic matter 30 cm to 1 m deep with 100 to 300 yr fire frequency. Similar forest types can be found as in cell 23. *Taxodium ascendens,* in particular, has a great range of tolerance for site fertility. One site examined during this study had a pure cypress canopy about 200 years old, probably dating to a peat burnout. The trees were only 16 to 18 inches in diameter, with very regularly spaced growth rings, most only about 1 mm wide. While cypress is typically slow growing, in fertile river bottomlands it can have growth rings several mm wide in the early years, and two to three times the diameter of those in large oligotrophic peatlands.

Cell 56. Organic matter 30 cm to 1 m deep completely protected from fire. Sites in large peatlands probably do not occur. Very old *Taxodium distichum* may be found on organic soils in acid blackwater stream systems, as described in cells 31 and 47. The hypothetical community in peatlands, should fire continue to be successfully excluded until pines or cypress die off, would be cycling red maple.

Cell 57. Deep peat soils, greater than 1 m in depth with 1 to 3 yr fire frequency. Open bogs with pitcher plants, sundews, *Andropogon glomeratus* and sedges like *Scleria ciliata,* and *Carex.* While there are historical descriptions of such communities (see text), no examples remain.

Cell 58. Deep peat soils, greater than 1 meter in depth with 4 to 6 yr fire frequency. These are herb bogs, similar to Cell 57, but with low pocosin shrubs. Few, if any, large peatlands still burn at this rate.

Cell 59. Deep peat soils, greater than 1 m in depth with 7 to 12 yr fire frequency. These are true ombrotrophic low pocosins with sparse, bonsai pond pine. There are still a few large peatlands which experience wildfire at this rate.

Cell 60. Deep peat soils, greater than 1 m in depth with 13 to 25 yr fire frequency. This cell contains low pocosin with shrub cover dense enough to exclude bog herbs, except for those in small openings between woody plants.

Cell 61. Deep peat soils, greater than 1 m in depth with 26 to 50 yr fire frequency. These very infertile sites may remain in low pocosin for many years without fire (Figure 10).

Cell 62. Deep peat soils, greater than 1 meter in depth with 51 to 100 yr fire frequency. This is the hypothetical extension of existing communities of cell 61, and consists of open pond pine with low or medium pocosin. While large white cedar wetlands may withstand fire for up to 300 years (cells 23, 31), no large, severely nutrient-limited peatlands are known with fire-return intervals as long as that in Cells 61–64.

Cell 63. Deep peat soils, greater than 1 m in depth with 100–300 yr. fire frequency. This type is unknown in nature on extremely sterile sites. Hypothetical vegetation is discussed in the text.

Cell 64. Deep peat soils, greater than 1 m in depth in completely fire-protected sites. As with cell 63, no sites are known. Without fire it seems likely that trees would continue to accumulate enough nutrients to increase stature of vegetation. Based on observations discussed above, hypothetical vegetation, after death of pine and *Gordonia,* would be cycling red maple.

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