Fire Regimes and Trees in Florida Dry Prairie Landscapes

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ABSTRACT

Historically, pine savannas characterized landscapes across the Gulf Coastal Region, including most of Florida. Treeless habitats (historically called "prairies") also occurred as lowland inclusions in savanna landscapes. What restricted trees from prairies? We develop a conceptual model that is based on prior models of prairie-forest landscapes. We use predicted relationships between trees and graminoids to explore how fire and seasonal flooding might influence the continuum from closed-canopy forests to open-canopied savannas to treeless prairies. The starting model predicts community position along this continuum as a function of fire frequency. We then modify this conceptual model to include evolutionary adaptations of trees that result in survival of frequent, low-intensity fires. Finally, we modify it to incorporate postulated interactive effects of fire and seasonal flooding on trees and graminoids. This model may be useful in predicting characteristics of savanna-prairie mosaics in the southeastern United States. We apply this model to the dry prairie landscape of central Florida. We examine two regions with pine flatwoods and dry prairies: Myakka River State Park (Sarasota and Manatee Counties) close to the Gulf coast and Avon Park Air Force Range (Polk and Highlands Counties) in the interior of the peninsula. For these two regions we compare local climatic conditions predicted to facilitate the occurrence of pine flatwoods and dry prairie. Specifically, we compare the conditions likely to result in lightning fires in the two regions and compare those with the likelihood of post-fire flooding in pine flatwoods and dry prairies in each of the two regions. These climatic patterns indicate a close temporal association of fires and flooding during the summer growing season at both sites. The increase in frequency of lightning strikes in April-June occurs at the same time that the mean rain-free interval reaches a maximum and the mean ground water levels reach a minimum. Thus, large fires in the landscape are expected at this time. Within a few weeks the frequency of thunderstorms increases, resulting in frequent rains. Rapid increases in mean water levels saturate the soil. Consequently, early lightning season fires are followed soon by flooding. Thus, environmental conditions predicted not to favor trees occur seasonally in dry prairie landscapes. We anticipate that subtle differences in the likelihood of surface soil saturation will influence survival of trees, resulting in prairie inclusions in the pine flatwoods landscapes of central Florida.

INTRODUCTION

Historically, pine savannas characterized landscapes across the Gulf Coastal Region of North and Central America (Wahlenberg 1946, Platt 1999, Passmore 2005). Along the northern Gulf of Mexico, this pine savanna biome extended across both west and east Gulf coastal plains. In addition, pine savannas extended inland from the coast into the Appalachian foothills, northward into the southern Atlantic coastal plain, and southward into the subtropical coastal plain in southern Florida (Fig. 1). Further south, this biome was present on lowland limestone outcroppings of a number of Caribbean islands and in lowland coastal areas of Central America. In all these regions pine savannas were the most common ecosystem in upland non-flooded habitats (Platt et al. 1988a, Schwartz 1994, DeCoster et al. 1999, Platt 1999), but also extended downslope into transiently flooded habitats (Bridges and Orzell 1989, Abrahamson and Hartnett 1990, Stout and Marion 1993, Schmitz et al. 2002).

Pine savanna landscapes have often been depicted as monotonous "pine barrens" extending unbroken across vast landscapes. This characterization has been based on a two-layered physiognomy (Gilliam and Platt 1999, 2006). The occurrence of often one, but never more than a few species of trees in the overstory resulted in pine savannas being relegated to initial post-disturbance seres of proposed successional pathways that were hypothesized to culminate in hardwood forests (see discussion in Platt 1999). The groundcover typically is a highly diverse mixture of grasses, forbs, and shrubs (Peet and Allard 1993, Platt 1999, Schmitz et al. 2002, Kirkman et al. 2004, Platt et al. 2006). Plant species composition, especially of the groundcover, changed across the geographic region, from west to east to subtropical Gulf coastal plains, generating high regional biodiversity (Sorrie and Weakley 2001, 2006). As a result, many variations on the basic pine savanna theme occurred within the biome (Bridges and Orzell 1989, Frost 1993, Peet and Allard 1993, Harcombe et al. 1993, Stout and Marion 1993, Platt 1999 and references therein).

Many local inclusions occurred within pine savannas. These were characterized by a non-savanna physiognomy in that either the ground cover or the overstory was missing. Hardwood tree-dominated "hammocks" with low-diversity ground cover and a continuous overstory at

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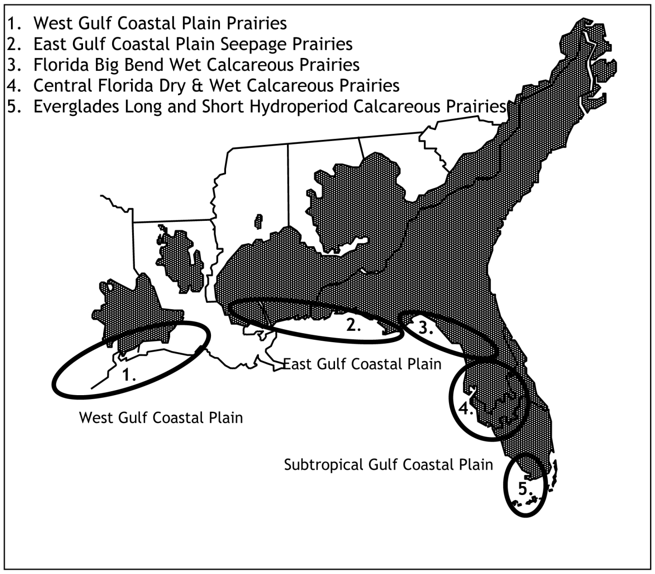

Figure 1. Coastal prairies in the southeastern United States. Ellipses denote five regions along the coast of the Gulf of Mexico that contain treeless coastal prairies as inclusions within pine savanna landscapes. Map adapted from Platt (1999) and Frost (1993). Pine savannas occur as the dominant upland landscapes within shaded areas.

multiple levels (except for gaps) occurred as islands within pine savannas, as well as downslope from pine savannas (Platt and Schwartz 1990, Robertson and Platt 1992, 2001, Harcombe et al. 1993, Kellman and Tackaberry 1993, Kellman et al. 1994, Slater et al. 1995, Kellman and Meave 1997, Passmore 2005). Relationships between hardwood forest inclusions and pine savannas may involve local differences in susceptibility to fire (e.g., Platt and Schwartz 1990, Robertson and Platt 1992, 2001, Harcombe et al. 1993, Kellman and Meave 1997, Passmore 2005).

Treeless habitats (historically called "prairies") occurred along the "Third Coast" (Gulf of Mexico) as inclusions in outer coastal plain savanna landscapes. General geographic locations of treeless habitats are indicated in Fig. 1. These habitats of variable size typically occurred toward the lower end of very gradual topographic gradients between upland pine savannas and wetlands (marshes or other permanent bodies of water; e.g., Kirkman et al. 2000). These prairies include the coastal prairies and seepages of western Louisiana and eastern Texas (e.g., MacRoberts and MacRoberts 1993, Grace et al. 2000, Jutila and Grace 2002), the seepage savannas and wet prairies of the north Gulf coast (e.g., Harper 1914, Frost et al. 1986, Peet and Allard 1993), the dry prairies of central Florida (e.g., Davis 1943, Abrahamson and Hartnett 1990, Fitzgerald and Tanner 1992), and the short- and long-hydroperiod prairies in the Everglades drainage system (e.g., Harper 1927, Davis 1943, DeCoster et al. 1999, Slocum et al. 2003). All of these coastal plain prairies are seasonally wet and dry. They tend to be inundated annually for varying periods of time depending on elevation and local drainage patterns (hence, the use of such terms as wet and dry prairie). Hereafter, we collectively designate these habitats "coastal plain prairies."

WHAT CAUSES TREELESS HABITATS?

The causes of treeless landscapes have been a holy grail of plant community ecology beginning a century ago. The development of different hypotheses resulted in debate in the early-mid twentieth century over whether drought or fire maintained Midwestern tallgrass prairies and kept them from being transformed into forests (see Transeau 1935 and Weaver 1954 for reviews). This debate has generated numerous studies relating forest-prairie boundaries to drought and fire frequency (see Lorimer 1985, Anderson and Brown 1986, Patterson 1992, Cutter and Guyette 1994, Changnon et al. 2003).

What restricted trees from coastal plain prairies? Although the centers of large prairies may have been distal from seed sources of trees, trees occurred along the edges, as well as in patches within the larger treeless areas. Thus, dispersal limitation was unlikely to result in trees not invading these prairies. Similarly, it is unlikely that seasonal flooding restricted the colonization of trees, because moisture and prolonged flooding are tolerated by a number of tree species, provided there are dry periods in which establishment can occur (e.g., cypress, pond and slash pines, tupelo, willows, cottonwoods). Lastly, fire has a negative influence on trees, causing top-kill and complete-kill, especially of small trees (e.g., Glitzenstein et al. 1995). Nonetheless, some tree species occur in fire-frequented habitats, provided there are sufficiently long fire-free intervals in which establishment can occur [e.g., longleaf (*Pinus palustris*), shortleaf (*P. echinata*), pond (*P. serotina*) and south-Florida slash pines (*P. elliottii* var. *densa*), cypress (*Taxodium ascendens*), sabal palm (*Sabal palmetto*)]. Thus, no single hypothesis seems sufficient to explain the occurrence of treeless inclusions in an otherwise forested landscape.

Might there be some combination of fires and flooding that restricted trees from coastal plain prairies? Might specific climatic conditions have favored combinations of fire and flooding that restricted trees from certain landscapes? We hypothesize that coastal plain climates generated frequent natural lightning-season fires in the transition from the dry to wet season, at a time of concurrent seasonal shifts between dry and flooded states. Such close association of fires and flooding potentially could have produced prairies within coastal pine savanna landscapes. In this paper, we modify a conceptual model for relationships between trees and graminoids in savannas (Beckage et al. 2006), applying ideas developed over the past several decades regarding the roles of fires in pine savannas (Gilliam and Platt 1999, Platt 1999 and references therein, 2006, Huffman et al. 2004, Platt et al. 2006). We use this conceptual model to predict effects of fires, flooding, and interactions between these disturbances on trees and graminoids in coastal plain savanna landscapes.

CONCEPTUAL MODEL

The basic model. We begin our exploration of relationships between pine savannas and coastal prairies in the Southeast with a conceptual model. The basic elements (fire, trees, and grasses) are borrowed from prior studies of midwestern and western forest-savanna-prairie boundaries (e.g., Archer et al. 1988, Archer 1989, 1995, Scholes and Archer 1997, Brown and Sieg 1999, House et al. 2003, Jurena and Archer 2003, Lepofsky et al. 2003, Swetnam and Baisan 2003). We assume a continuum between open, treeless prairie and closed canopy forest in which savannas are an intermediate state where trees are present, but do not form a continuous canopy.

We base predictions for changes along this continuum on recurrent natural fire. Characteristics of lightning-ignited fires are based on prior studies and field observations (see review in Platt 1999, Beckage and Platt 2003, Beckage et al. 2003). These fires are assumed to be surface fires ignited by lightning and carried by the groundcover. Further, these fires are assumed to spread across large landscapes in the earliest part of the growing season, during the transition from dry springs to wet summers (Beckage et al. 2003, Slocum et al. 2003). These "transition" season fires are assumed to be the ones most likely to affect savanna-prairie landscapes; the vegetation in transitions between different ecosystems is likely to be dry and thus flammable at this time.

We assume that natural fires influence the relationships between two life form groups—early successional graminoids, and late successional woody plants. These life forms were described in general terms as "early" and "late" species, respectively, in Platt and Connell (2003). The early species are principally sedges (e.g., *Cladium jamaicense*) or warm-season grasses (*Andropogon* sp., *Aristida* sp., *Panicum* sp., *Schizachyrium* sp.). The late species are trees or shrubs, which are assumed to be able to invade when graminoids are present. These late species also are assumed to grow to larger stature, generate shade, and thus block graminoid regeneration (also see House et al. 2003, Beckage et al. 2006).

Disturbances remove late (e.g., trees), but not early (graminoids) species in one of the six general cases involving replacement of an early species by a late species (Platt and Connell 2003). In this case disturbances are predicted not to reinitiate replacement of species because the late species reinvades and replacement is resumed. Succession can be slowed or blocked, however, if there are refuges for early species; thus the early species persists longer or is not replaced. In the case of prairie inclusions within savannas, temporary refuges of graminoids appear not to occur. Large treeless areas of prairies appear persistent over time, as indicated by historical records (e.g., see Harper 1914, 1927, Bridges & Orzell 1989, Frost 1993, Bridges 2006). Permanent refuges also appear unlikely in that few physical differences exist between prairies and surrounding areas with trees, unlike some similar habitats elsewhere (e.g., San Jose and Farinas 1983). Thus, the sole mechanism whereby early species might persist indefinitely is the inhibition of invasion by late species.

Might early species that facilitate fires block replacement by late species (Platt and Connell 2003)? Trees and warm-season grasses differ in their responses to fires. Woody plants may be top-killed by recurrent growing-season fires (Glitzenstein et al. 1995, Drewa et al. 2002, Passmore 2005), especially when high fine fuel loads are present, as when grasses are abundant (Platt et al. 1991, Thaxton and Platt 2006). Woody plants, especially when small, also are more likely to be completely killed by recurrent fires (Olson and Platt 1995, DeCoster et al. 1999, Thaxton and Platt 2006). In contrast, graminoids, especially warm-season grasses, are positively affected by fires. Fires remove litter and above-ground vegetation, stimulating regrowth of culms and clonal growth of genets (Platt 1999). Fires also stimulate flowering and seed production (Platt et al. 1988a, Streng et al. 1993, Brewer and Platt 1994). Thus, fires facilitate increases in fine fuels, both in amounts and continuity across the landscape as a result of their effects on graminoids. This in turn is predicted to reduce densities of trees.

Relationships between trees and graminoids based on studies of prairies are depicted in Fig. 2. In this initial version of the model, trees are assumed to affect warm-season grasses negatively (Fig. 2a). As the density of trees increases, shade increases. As a consequence, the density and above-ground biomass of grasses (and thus a large component of the flammable fine fuels) should decrease. When a closed canopy of trees is present, the grasses should decrease to the point that grass fuels become discontinuous, reducing fire intensity and also potentially disrupting spread of fires. On the other hand, grasses are assumed to affect small trees negatively, but not to affect large trees. As the biomass of grasses increases, mortality of small trees should increase as a result of increased fire intensity (Fig. 2b). The tree component is predicted to decrease progressively with increasing fire frequency as a result of suppressed regeneration of trees. This fire and light-mediated model suggests mechanisms whereby each life form could exclude the other from a landscape. Trees that cast sufficient shade should suppress graminoids. Graminoids that generate sufficient fuel should kill small trees.

Landscape transitions between prairie and forest are predicted to depend on the effects and frequency of disturbance (Fig. 3). Assume that the density-dependent relationships between trees and grasses (as illustrated in Fig. 2) remain the same regardless of the position of the landscape along the continuum from prairie to forest. As the frequency of disturbance increases, mortality of trees increases, favoring grasses, which in turn further increase the mortality rate of small trees. Thus, large trees are removed and replacement of trees is blocked, shifting the landscape toward prairie. If the frequency of disturbance decreases, the landscape shifts back toward forest, as trees are recruited and grow to maturity, suppressing grasses in the process. Thus, given recurrent fires, there is no stable equilibrium,

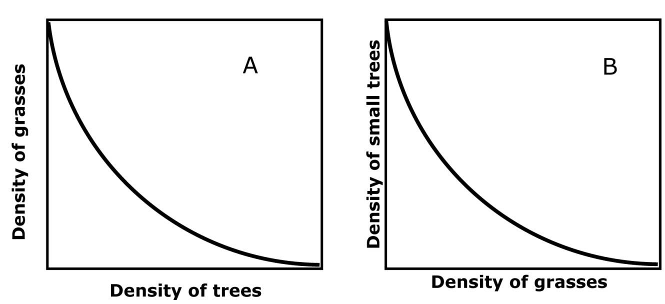

Figure 2. The beginning model, showing possible density-dependent relationships between trees and grasses. A: effects of density of trees on density of grasses. B: effects of density of grasses on density of small trees.

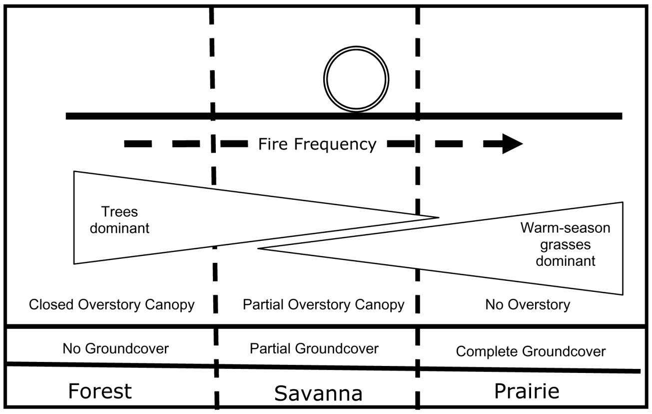

Figure 3. Hypothesized responses of trees and grasses to fire frequency (dashed arrow) in an ecosystem (circle) in a landscape continuum. The continuum extends from forest (left) through savanna (middle) to prairie (right); along this continuum, dominance shifts between forest trees and warm-season grasses (triangles). The consequence of shifts along the continuum includes changes in the extent of overstory and groundcover. The location of the ecosystem along the continuum is projected to depend on the frequency of fires and, hence, length of fire-free intervals. The neutral aspect of the model is depicted by a horizontal line below the circle, indicating that a unit change in fire frequency moves the ecosystem equally in respective directions. Short fire-free intervals are projected to shift ecosystems toward prairies, and long fire-free intervals are projected to shift ecosystems toward forests. Conceptual model adapted from Gilliam and Platt (2006) and Beckage et al. (2006).

but a continually shifting state that depends on the frequency of disturbance (also see Beckage et al. 2006).

This general model can be applied to southeastern coastal savannas (but not, as we shall see, to the prairies). Based on this model, frequent fires should cause mortality of trees, which would favor grasses, shifting landscapes toward prairies. With longer intervals between fires, trees become established and grow to maturity, which would disfavor grasses, shifting the landscape toward forest. Predictions based on this initial model are that, historically, continua from forest to prairie likely existed throughout the Gulf coastal plain, and the frequency of states along these continua depended on fire frequency.

First modification of the model: Evolutionary responses to frequent fire. Evolutionary responses to non-catastrophic disturbances can be viewed as a three-stage sequential process (Platt 1999). Repeated disturbances should favor any individuals that survive the disturbance and can respond in the post-disturbance environment. Moreover, those individuals best adapted for post-disturbance conditions should have greatest fitness, favoring those genotypes. Further, individuals that modify recurrent disturbances in ways that result in increased fitness also should be favored. Such a sequential process of resistance-adaptation-modification should generate an evolutionary feedback loop in which relationships between disturbances and dominant species change as those species become increasingly adapted and dependent on the disturbances.

Frequent fires constitute non-catastrophic disturbances that could generate a sequential evolutionary process of resistance-adaptation-modification for trees in southeastern Gulf coastal plain habitats (Platt 1999). Trees and graminoids that can survive the repeated fires should be favored. Among those species that survive fires, adaptations that enable regeneration in fire-frequented habitats should be favored as well. Subsequently, any modifications of fuels in ways that increase survival and regeneration in fire-frequented habitats should increase fitness. These species therefore become ecosystem engineers, with the ecosystem states being dependent on contributions from a number of species.

Longleaf pine (*Pinus palustris*) and south Florida slash pine (*Pinus elliottii* var. *densa*) are exemplary savanna tree species that have become adapted for fire-frequented habitats (Landers 1991, Platt 1999 and references therein). Mature trees of these species produce large, periodic mast crops and have thick, layered bark, enabling them to survive all but the most intense fires. There also are traits important in the intervals between fires. Seeds germinate in the fall. Seedlings grow rapidly, and produce secondary needles within four-six months, becoming capable of surviving fires by the second year (Grace and Platt 1995). Early stages of longleaf pine survive fires via flame-resistant needles and scale-protected meristems, and when fire does return they respond with indeterminate flushing of needles.

When offspring survive disturbances and are adapted for post-disturbance environments, individuals that promote the disturbances should be favored (Platt 1999). Savanna pines modify fire regimes via needles that when shed, generate fine fuels that burn at high intensity and low ignition temperatures. This generates a positive feedback loop, producing conditions for which longleaf pine is adapted. Other species of pines (e.g., *P. serotina*, *P. echinata*), palms (e.g., *Sabal palmetto*, *Serenoa repens*), and some hardwoods, especially oaks (e.g., *Quercus laevis*, *Q. incana*, *Q. stellata*, *Q. margarettae*, *Q. marylandica*) have also become adapted for frequent fires, but none has the capability for engineering ecosystems as do the savanna pines.

Evolutionary responses to frequent fires change relationships between trees and grasses. Longleaf pine can recruit under conditions of high densities of grasses. Seedlings rapidly develop to a stage where some juvenile pines survive intense fires. This changes the relationship between the density of grasses and the density of small pines. This change is depicted in Fig. 4. Small pines are predicted to recruit regardless of the density of grasses.

The ability of savanna pines to recruit under conditions of frequent fire also changes the effects of frequent fires on landscapes (Fig. 5). If juvenile pines are likely to survive recurrent low-intensity fires (especially those engineered by pines), the frequency of disturbances needed to maintain prairie increases markedly. Savanna pines are unlikely to be eliminated from the landscape, even under conditions of annual or biennial fires. Thus, it is unlikely that prairies can be generated in Gulf coastal landscapes through fires alone. Moreover, increasing intervals between fires is predicted to shift the landscape rapidly toward forest. In this version of the model, southeastern coastal prairies are not predicted to be stable landscapes: fire-adapted trees inevitably should invade and engineer ecosystems in ways that facilitate their persistence.

Returning to the model of Platt and Connell (2003), inhibition appears insufficient for early species to ex-

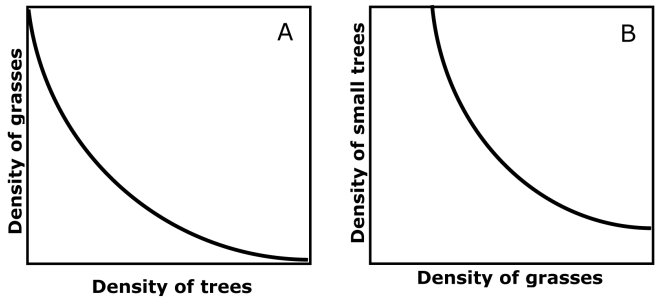

Figure 4. Postulated density-dependent relationships between fire-adapted trees and grasses. A: effects of density of trees on density of grasses. B: effects of density of grasses on density of small trees. Note that small trees are likely to be present at all densities of grasses.

clude late species, even if disturbances such as fire occur frequently. The late species is subject to selection for characteristics that enhance survival of frequent non-catastrophic disturbances, reducing the likelihood that inhibition will occur. Thus, the absence of late species in ecosystems is not explained by relationships involving single disturbances or postulated relationships between early and late species.

Second modification of the model: Evolutionary responses to multiple disturbances. Environmental conditions other than fire generate stressful conditions that potentially act as environmental sieves (Harper 1977, Van der Valk 1981) or filters (*sensu* Keddy 1992), blocking or slowing invasions by trees (D'Antonio and Thomsen 2004). Prolonged flooding, especially in southern bottomland forests, has been shown to affect trees. Many tree species can withstand brief flooding. Nonetheless, prolonged flooding waterlogs soil, which results in low oxygen levels in roots. Trees in flooded habitats with long hydroperiods thus are chronically stressed (Whitlow and Harris 1979, Hook 1984, Kozlowski et al. 1991). Similar

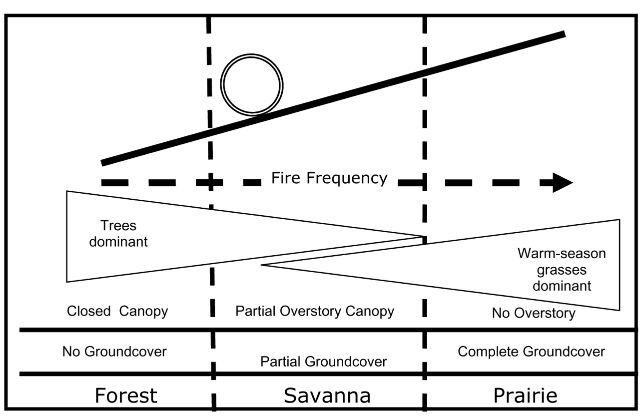

Figure 5. Predicted effects of a fire-adapted tree on the effects of fires on the transition along the prairie-forest continuum. Figure modified from Fig. 3 to depict effects of adaptations of trees to fires. The model is no longer neutral with respect to the occurrence or absence of a fire moving the ecosystem equally in respective directions; instead, increased fire frequency is needed to shift the ecosystem towards savanna and prairie states. For those tree species with life cycle stages that survive fires and grow into the overstory even with frequent fires (e.g., *Pinus palustris*, *P. elliottii* var. *densa*), even very high fire frequencies may not shift the ecosystem toward a treeless prairie state.

stresses are less pronounced for graminoids in flooded habitats because their roots contain more airspace (Kercher and Zedler 2004) or aeration of roots can occur as long as parts of live or dead culms remain above water level (as for example, *Cladium jamaicense;* Conway 1936, Loveless 1959, Steward and Ornes 1975, Herndon et al. 1991, Urban et al. 1993, Newman et al. 1996, Sorrell et al. 2000). Thus, graminoids have broader tolerance (*sensu* Zedler and Kercher 2004) of flooding than woody species.

Relationships between trees and grasses should change when frequent fires are likely to be followed by prolonged seasonal flooding. Flood tolerant graminoids, especially C4 grasses that recover rapidly from growing-season fires, typically can become tall enough within a few weeks of fire to survive subsequent prolonged flooding in shallow waters (Herndon et al. 1991). Woody species, which are damaged and stressed by growing-season fires (Olson and Platt 1995, Drewa et al. 2002, 2006, Thaxton and Platt 2006), may become severely stressed when the fire is followed by flooding (also see Waring 1991). Grasses thus receive more light and can reach high densities under conditions where small trees are severely stressed by the combination of fire and prolonged flooding.

We depict this hypothesized relationship between densities of small trees and grasses in Fig. 6. We propose that treeless habitats within larger regions containing trees result from interactive effects of natural disturbances (fires) and abiotic conditions (flooding). High natural frequency of fires, coupled with facilitation of frequent fires by graminoids, is predicted to exclude trees from seasonally flooded wetlands. When natural disturbances produce ecological conditions that prevent regeneration by late species, permanent refuges are generated for early species capable of surviving such conditions (Platt and Connell 2003). The close juxtaposition of fire and flooding in coastal prairies may result in slow-responding woody species not being able to adapt to the conditions generated in these environments.

We modify our model to include these interacting disturbances and their unfavorable combined effects on trees. In Fig. 7, the effects of frequent fires are predicted to interact with effects of frequent post-fire flooding to reduce survival of juvenile trees, generating treeless land-

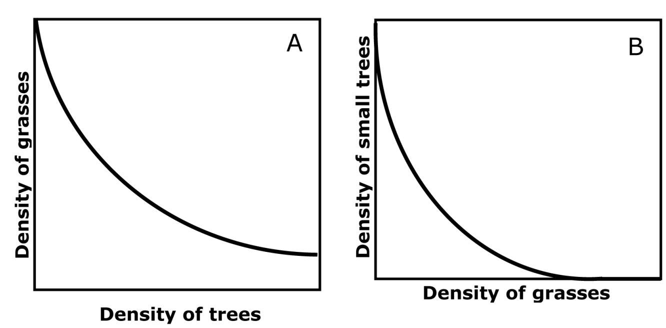

Figure 6. Postulated density-dependent relationships between fire-adapted trees and grasses under conditions of annual flooding. A: effects of density of trees on density of grasses. B: effects of density of grasses on density of small trees. Note that grasses are present at all densities of trees, but small trees are not present at all densities of grasses.

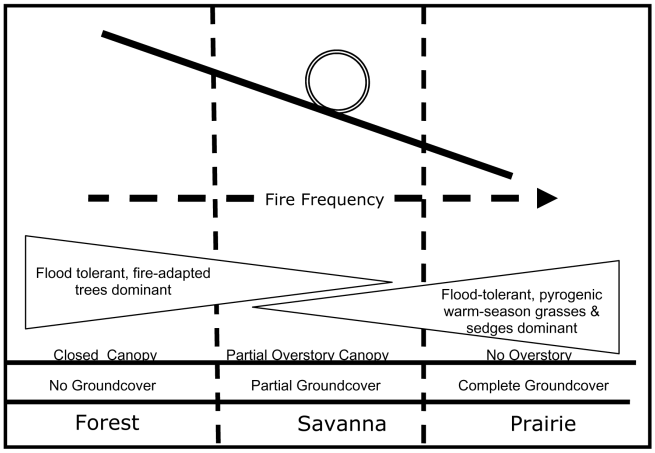

Figure 7. Predicted effects of frequent flooding on the effects of different fire frequencies along the prairie-forest continuum. Figure modified from Fig. 3. Increases in fire frequency shift the ecosystem toward a prairie state because frequent flooding stresses even fire-adapted trees, making them vulnerable to fire; long fire-free intervals are needed to shift the ecosystem toward savanna and forest states when flooding occurs annually. In seasonal habitats, where there is prolonged annual drought followed by annual flooding, fire-flooding interactions may tend to shift the ecosystem strongly toward prairie states. The few trees present are ones that are adapted to withstand frequent prolonged flooding and that also are fire resistant (e.g., *Taxodium ascendens*).

scapes. Only when fire-free intervals are long are trees likely to occur. Moreover, increasing fire frequency is predicted to shift the landscape rapidly toward prairie.

APPLICATION OF THE CONCEPTUAL MODEL TO CENTRAL FLORIDA

Landscape and climatic conditions in central Florida. We predict that prairies should occur in southeastern coastal plain landscapes when lightning-initiated fires are followed by shallow floods during the growing season after those fires. Such combinations of conditions are most likely toward the low ends of elevation gradients and may be especially likely where very subtle topographic gradients are likely to impede drainage during the growing season. We apply the modified model to central Florida. We examine two regions with pine flatwoods and dry prairies: Myakka River State Park (Sarasota and Manatee Counties) close to the Gulf coast, and Avon Park Air Force Range (Polk and Highlands Counties) in the interior of the peninsula. For these two regions, we compare local climatic conditions predicted to facilitate the occurrence of dry prairie, the conditions likely to result in lightning fires in the two regions, and the likelihood of post-fire flooding in pine flatwoods and dry prairies in each of the two regions.

We used three characteristics of seasonal synoptic weather conditions to predict interactions between fire and hydrology in central Florida: length of time since rain, ground-water levels, and lightning frequency. First, following Olson and Platt (1995), we calculated mean rain-free intervals (mean number of days until next occurrence of >5 mm rain/day for each day of the year). We used number of days with <5 mm rainfall as the rain-free interval, assuming that precipitation less than this would likely evaporate and not enter the ground water. Records were obtained from the National Weather Service. Second, ground water levels at Myakka River State Park were obtained from wells sampled by the Florida Department of Environmental Protection (pine flatwoods: Bee Island which contains longleaf pine flatwoods; dry prairie: the wilderness area in the southern part of the park). Ground water levels in the eastern section of the Avon Park Air Force Range (in the region of the range containing flatwoods and dry prairie) were obtained from South Florida Water Management District wells. Data for each site were records of 10-20 years; these data were converted to depth of ground water above/below ground level at the well. Third, numbers of lightning strikes per km^2 per year were obtained from the 1986-1995 Florida lightning climatology data (Hodanish et al. 1997).

Application to central Florida preserves with flatwoods and dry prairie. Relationships between the climatic variables are depicted in Fig. 8 (coastal dry prairie at Myakka River State Park) and Fig. 9 (interior dry prairie at Avon Park Air Force Range). Both sites are similar in general climatic patterns.

These sites follow pronounced seasonal patterns of rainfall and surface-water levels. They are typically flooded during much of the summer growing season. Rains are frequent between July and September, and ground-water levels are at or above the surface. Rains are less frequent, and ground-water levels start to decrease in October. The interval between rains increases to about two weeks or more until December. During January and February rains are again more frequent, and ground-water levels increase slightly. Beginning in April and continuing into May, rains decrease and ground-water levels decline, reaching minimum levels in May at both sites. Rain frequency increases markedly during late May and June with the onset of summer thunderstorms, and ground-water levels rise rapidly.

Cloud-ground lightning strikes also show pronounced seasonal patterns. During the dry season, from November to March, there is almost no lightning at either site. Beginning in April, the frequency of lightning strikes increases, reaching a mid-summer peak in June, July, and August. During September and October, lightning strikes decrease in frequency to low dry-season levels at both sites.

These climatic patterns indicate a close association between fires and flooding during the summer growing season at both sites. The seasonal increase in frequency of lightning strikes during April-June occurs at the same time that the mean rain-free interval reaches a maximum and the mean ground-water levels reach a minimum. Thus, numerous and potentially large fires in the landscape should be likely within this time interval, especially when the preceding dry season has below-average rainfall. Within a few weeks however, the frequency of thunderstorms increases, resulting in frequent rains. Rapid increases in mean water levels saturate the soil. Consequently, early lightning season fires are followed within a short period of time by flooding. This combination, illustrated in Fig. 7, is exactly that juxtaposition of climatic conditions we predict should result in the absence of trees in seasonally wet coastal plain prairies.

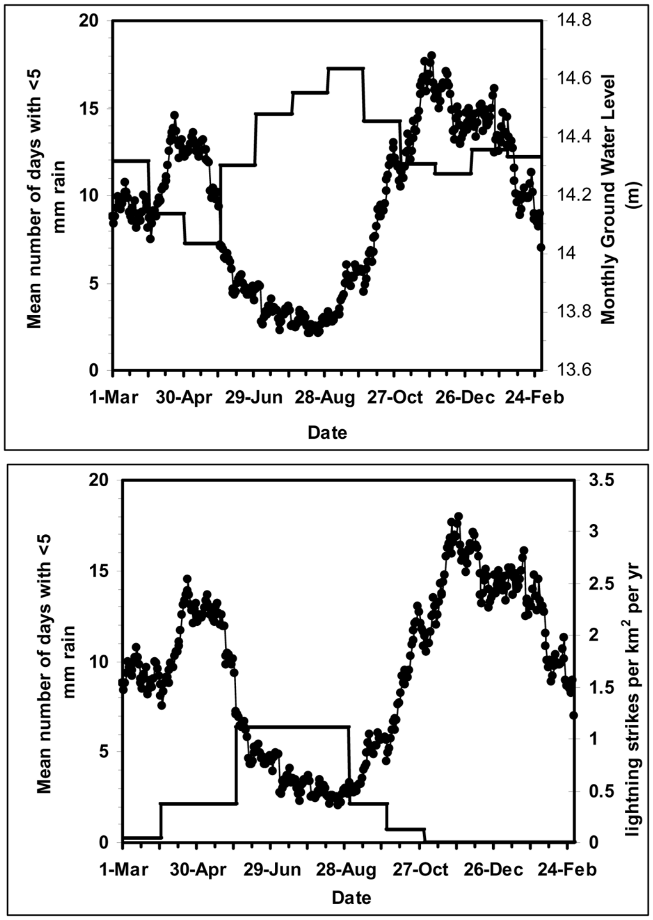

Figure 8. Climatic conditions in Myakka River State Park, Sarasota County, Florida. The mean number of successive days with <5 mm rainfall for a given date of the year (black dots) is plotted against the successive dates in a year. Data are for Sarasota, Florida for the period from 1944-1997. The light black line connects the mean rain free intervals for successive dates. Upper: The histogram is the mean ground water level in the Wilderness Preserve, located in the pine flatwoods/dry prairie matrix of the southern section of the park (1990-2001). Lower: The histogram is the mean number of cloud-ground lightning strikes per km^2.

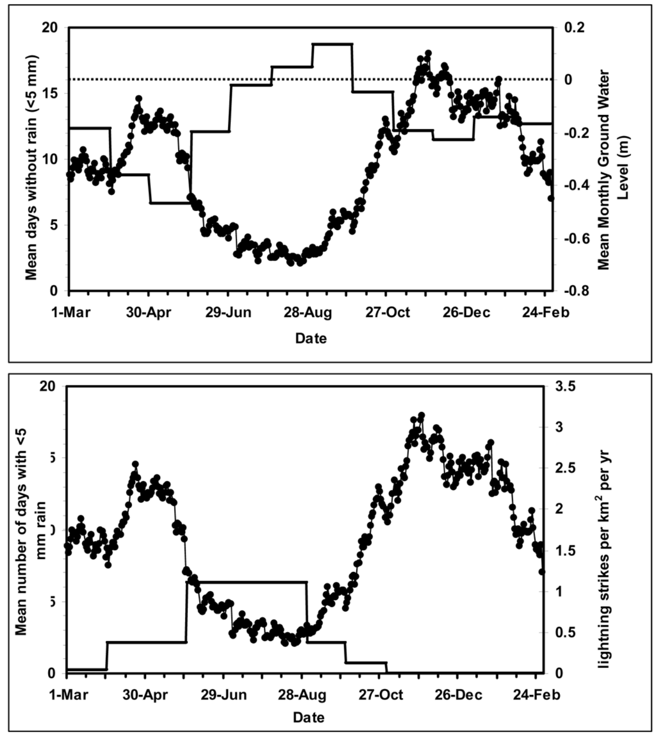

Figure 9. Climatic conditions in the Avon Park Air Force Range, Florida. Data are for Avon Park, FL for the period from 1944-1997. Upper: The histogram is the mean monthly ground water level at Tick Island (1974-2004), located in the pine flatwoods/dry prairie matrix of the eastern section of the Avon Park Air Force Range (Polk County, FL). Lower: The histogram is the mean number of cloud-ground lightning strikes per km^2.

CONCLUSIONS

Savannas, historically dominant upland ecosystems in the southeastern coastal plain, are maintained by fires. Based on predictions made using a conceptual model, we predict that fire-adapted trees such as pines, cypress, and palms are unlikely to be removed from savanna landscapes by fires. Thus, differences in fire regimes *per se* do not account for the existence of treeless prairies as inclusions within coastal plain savanna landscapes.

Prediction of treeless prairies within savanna landscapes results when seasonal hydrology is incorporated into the model based on climate and fire. Fires followed by flooding can produce conditions unfavorable for pines and palms, but increase populations of flood-tolerant, herbaceous groundcover species. Differences in local interactive effects of fires and seasonal flooding based on small changes in elevation should generate mosaics of savannas and prairies. Climate data further suggest a close association of fires and flooding in central Florida. Large landscape-level fires should be concentrated in the transition from dry spring to wet summer after lightning strikes begin, and water levels should normally saturate soils in dry prairies within weeks.

This climate-based model for prairie inclusions within savanna landscapes needs to be validated through study of variation in substrate elevation in local landscapes, coupled with studies of seasonal changes in hydrology within those landscapes. If the fire/hydrology model is validated, successful restoration of landscapes containing prairies is likely to require management of both fire and hydrological regimes. The acceptable magnitude of deviations from natural fire and hydrological regimes is still unknown. Evolutionary models similar to the fire resistance-adaptation-modification model (Platt 1999) for responses to different hydrological conditions, as well as for responses to co-varying fires and hydrology, are needed to develop evolutionary hydrological management models for coastal prairies.

In the meantime we propose that "redneck management" of fires (*sensu* Putz 2003) be used to manage landscapes containing prairies. Management practices, developed over generations by people who lived in the rural coastal south, were based on practical results. Rural settlers in the Gulf coastal region used high fire frequencies during the early part of the spring transition period, primarily during March and early April, to produce spring forage for cattle and game before spring droughts occurred. We propose shifting of prescribed fire to earlier in the spring to obviate consequences of "burn bans," which result in an inability to conduct prescribed fires later in the dry spring period when fires would naturally have occurred. Such fires could be planned to achieve landscape-level consequences of large fires with reduced risk of burning under hazardous conditions. Shifting prescribed fires to earlier in the spring thus should reduce the necessity for conducting prescribed fires later in the growing season after burn bans are lifted or during the subsequent dormant season.

Such a shift in seasonal timing of fire should favor some species over others. For example, early fires should favor groundcover species able to respond during the dry spring and transition period (Platt et al. 1988b, Streng et al. 1993). For example, data from pine flatwoods-wet prairie regions of northern Florida suggest that different species of grasses might be favored by such shifts in seasonal timing of fire. Toothache grass (*Ctenium aromaticum*) flowers more profusely under conditions of early fires, but bluestems (species of *Andropogon*) flower more abundantly when fires occur later in the transition period (Streng et al. 1993). There should be reduced effects on shrubs and trees, but effects should be greater than burning late in the growing season or not burning at all (e.g., Glitzenstein et al. 1995, Slocum et al. 2003). In addition, effects of flooding shortly after fires may be reduced because of the longer interval between fires and floods; as a result local landscape heterogeneity might be changed, resulting in decreased sizes of prairies.[1]

A final consideration involves management within the context of ongoing global climate change. Climate change effects will affect restoration and management for savanna/prairie landscapes over coming decades. Based on our fire-hydrology model, we predict that fires and hydrology should be affected by global changes in climate (e.g., ENSO conditions) that influence local climate patterns such as rainfall and frequency of lightning strikes (e.g., Beckage and Platt 2003, Beckage et al. 2003, 2005). Increases in the frequency of El Niño conditions predicted to occur over the next several decades should result in increased winter rainfall in the southeastern United States. Such increases could result in reduced fire frequency and fire spread across savanna-prairie landscapes, especially at lower elevations such as those where prairies occur. This climatic change could produce a mixed effect on fire management. Such changes could facilitate ecological fire management because dry periods in the spring will be less severe. Nonetheless, efforts will have to be made to ensure that areas that are low in elevation, and thus flood easily (e.g., prairies) are burned frequently.

[1]*Editor's note*: This could create problems for some animal species of the Florida dry prairie, especially the Florida Grasshopper Sparrow, which is sensitive to edge effects and therefore may require large prairie patches for persistence.

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