

# Impacts of Fire and Hydrological Regimes on Vegetation in Depression Wetlands of Southeastern USA

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## ABSTRACT

Depression wetlands are common in the Coastal Plain of the southeastern United States. Throughout the Southeast, these wetlands occur in depressions known as limesinks (caused by collapse of subsurface limestone), or Carolina bays (elliptical, oriented depressions of unknown origin). The hydrologic regimes of the wetlands are characterized by seasonal or longer term fluctuations in water levels, due primarily to regional precipitation patterns. Although the hydrologic regime is the principal factor determining vegetation and soil types, the interaction of fire with the hydrologic regime is important. Experimental work at the community and species level shows that fire during drought periods is a mechanism that promotes species richness, particularly in depression wetlands dominated by grasses and sedges and associated wetland/upland ecotones. Winter fire followed by inundation can lead to shifts in dominance of emergent vegetation. A conceptual model of wetland vegetation dynamics that incorporates fluctuating hydrologic conditions and episodic disturbances is proposed. Fragmentation, artificial firebreaks, and changes in surrounding land use may prohibit fire occurrence even in areas managed with prescribed burns. Long-term fire suppression may result in establishment of hardwood species that in turn significantly affect the occurrence of fire in the wetland.

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## INTRODUCTION

Wetlands that are isolated and unconnected to surface drainages are found throughout the southeastern United States. These wetlands develop in shallow topographic depressions in an otherwise flat landscape, although their geomorphic features may differ significantly in origin, age and substrate across the region. Although the biota of these non-alluvial wetlands varies widely, many similarities in floristics and vegetation types, range of hydrologic regimes, soil types and natural and human-induced disturbances exist among them (Table 1). Many southeastern depression wetlands are analogous in form or ecological function to other isolated wetlands in North America, such as prairie potholes of the midwestern United States (Kantrud et al. 1989), vernal pools of California (Zedler 1987), and coastal ponds (interdune ponds) of the north Atlantic Coast (Schneider 1992; Phillips and Shedlock 1993).

This paper synthesizes components of previous vegetation studies in southeastern depression wetlands within a framework of fire and hydrologic regimes as primary disturbance agents in these systems. Specifically, elements of existing models of wetland vegetation dynamics are critiqued relative to their applicability to these wetlands and are integrated with new perspectives into

a conceptual model for herb-dominated depression wetlands in the Southeast. Hypotheses about the ecological importance of wetland-terrestrial ecotones in modifying these disturbance regimes are developed with implications for management needed to maintain the biological integrity of depression wetlands.

## DEPRESSION WETLANDS

Carolina bays, a type of depression wetland, are formed in shallow, ovate-shaped depressions of the southeastern Coastal Plain, extending from Maryland to Georgia. These depressions are distinctive in their ovate shape and NW-SE orientation (e.g., Sharitz and Gibbons 1982). Carolina bays may range in length from 50 m to 8 km. The geologic origin and the age of these geomorphically-distinct depressions are unknown, although many theories of their origin have been proposed. Some explanations offered for depression formation include wind and wave action (Odum 1952), meteorites (Prouty 1952), and ground subsidence following dissolution of substrate minerals (Smith 1931; Siple 1967; Kaczowski 1977). These theories are reviewed by Sharitz and Gibbons (1982), Savage (1982), and Richardson and Gibbons (1993).

Table 1. Summary of characteristics of southern depressional wetlands.

	Wetland		
	Carolina bay	Limesink	Basin marshes
Range	SE Atlantic Coastal Plain, NC, SC, GA	Gulf Coastal Plain, GA, AL	North central FL
Other names (herbaceous)	Depression meadow Clay-based bay Flat bottom pond	Grady pond Sinkhole pond	Seasonal pond Highland marsh Prairie marsh
Shape of depression	Elliptical, long axis oriented NW-SE	Irregular to round	Irregular
Origin	Unknown	Dissolution of subsurface limestone	Dissolution of subsurface limestone
Soil type	Mineral or peat	Mineral	Mineral or peat
Vegetation	Grass-sedge, cypress savanna, hardwood swamp, shrub bog (pocosin)	Grass-sedge, cypress savanna, hardwood swamp	Grass-forbs, shrubs
Hydrologic regime	Variable; dependent on rainfall and ET	Variable; drying in most years; mostly dependent on rainfall and ET	Variable; drying in most years; mostly dependent on rainfall and ET
Connection with ground water	Usually none; perched water table	Some perched, some discharge and/or recharge to ground water	Some perched, some discharge and/or recharge to ground water
Rare plants, animals	Yes Yes	Yes Yes	No Yes
Major human threats and disturbances	Agriculture, silviculture and development	Agriculture	Development and agriculture
Former upland landscape	Longleaf pine	Longleaf pine	Longleaf pine

Soils may range from sandy loams to deep peats; however, most Carolina bays have an impervious clay layer below the upper sediments. This clay lens may result in a perched surface water table with ground water connections occurring infrequently, and only at periods when ground water levels are very near the surface (Lide et al. 1995). Several vegetation types occur in Carolina bays. Bays with peaty soils are dominated by evergreen shrubs overtopped by *Pinus serotina* (pond pine). *Taxodium ascendens* (pond cypress) and *Nyssa biflora* (black gum) swamps, and open herbaceous marshes, frequently occur in Carolina bay depressions (Buell 1946; Porcher 1966; Wharton 1978; Sharitz and Gibbons 1982). These intermittently flooded wetlands provide habitat for several rare forbs (Knox and Sharitz 1990; Bennett and Nelson 1991; Kirkman and Sharitz 1994) and are important breeding grounds for many amphibian species (Richardson and Gibbons 1993).

In regions of karst topography, such as southwestern Georgia and southeastern Alabama, limesink wetlands are shallow surface depressions formed from the dissolution of limestone bedrock followed by subsidence of the overlying residuum (Hendricks and Goodwin 1952). The sinks range from small holes with steep sides to shallow, flat expanses of several hectares (Wharton 1978) and depths of a few decimeters to 8 meters (Torak et al. 1991). One theory is that as the depressions age, the bottoms become sealed by an impermeable layer of silt and clay (Hendricks and Goodwin 1952; Hayes et al. 1983). Thus, older depressions may hold water for

extended periods, while younger depressions drain into the underlying residuum (Hayes et al. 1983), possibly directly connecting to ground water systems. The hydrology of other sinks may be driven by springs from deep ground water. Vegetation types are similar to those of Carolina bays and include meadow-like marshes and cypress savannas or cypress/hardwood swamps (Sutter and Kral 1994). Numerous rare species are also associated with limesink depression ponds (Sutter and Kral 1994) and adjacent ecotones (Kirkman and Drew, this volume).

Similar depression wetlands also occur in northern Florida. In particular, depression or basin marshes occur in the central ridge portion of northern Florida and are also probably solution features. Dynamic subsurface conditions cause marshes and lakes in this region to be unstable, perhaps changing from lake to marsh or to dry land within a relatively short time (Kushlan 1990). Flatwoods ponds, or seasonal ponds, occur primarily between the central highlands and the Atlantic and Gulf Coasts. Many of these flatwoods ponds have a perched water table above an impermeable clay layer, although some are also influenced by high water tables (Kushlan 1990). They share some floristic similarities with more southern marshlands such as the Everglades. In Florida, characteristically low topographic relief and high water table often contribute to the development of complex wetland systems of swamps, shrub bogs and marshes. The relationships among these wetlands and among adjacent terrestrial systems are poorly understood (Ewel 1990).

## IMPORTANT ENVIRONMENTAL VARIABLES AND VEGETATION

Four major environmental variables are presumed to contribute to the overall structural and functional diversity of wetlands (Kantrud et al. 1989; Ewel 1990; Kushlan 1990; Mitsch and Gosselink 1993). In most wetland systems the hydrologic regime (depth and duration of flooded conditions) is the major driving force in the establishment and maintenance of specific types of wetlands and wetland processes (Mitsch and Gosselink 1993; Brinson et al., in press. Also, differences in fire frequency, organic matter accumulation, and water source (e.g., water chemistry) are also often key factors in plant community development (Brinson et al., in press). The integration of these factors leads to a complex array of habitat conditions.

Gradient analyses of plant community data within individual Carolina bays and similar wetlands in the north Atlantic Coastal Plain support the hypothesis that topographic relief and amplitude of hydrologic regime are the major environmental determinants of patterns of species composition (Lowe 1986; McCarthy 1987; Hodges, in Schalles and Shure 1989; and Keough et al. 1990). However, few studies document species changes through a period spanning the extremes of hydrologic fluctuation in these wetlands.

Many hypotheses pertaining to relationships of southeastern wetland vegetation types and environmental factors are based on anecdotal conjecture rather than rigorous research (Ewel 1990). One such contention suggests that differences in vegetation among limesink depression ponds reflect different stages of successional development; i.e., ponds dominated by grasses and other herbs represent an earlier stage than those forested by pond cypress or black gum (Hendricks and Goodwin 1952). Penfound (1952) and others (Hamilton 1984; Christensen 1988) present a scenario for peaty swamps, hypothesizing that grass-dominated marshes in the Southeast were the outcome of severe or frequent fire in bay forests or cypress swamps. Sutter and Kral (1994) distinguish pond cypress savannas and karst ponds (having zones of forest, grasses, and open water) floristically and maintain that these two wetland types characteristically have different sources of water, although they present no data in this description. Lowe (1986) explains the development of the mosaic of sawgrass and prairie communities in an east-central Florida marsh as due to fire, drawing upon similarities with vegetation patterns associated with fires in the Everglades (Loveless 1959). None of these hypotheses has been tested.

Zonal patterns of vegetation have been described in Carolina bays (Kelley and Batson 1955, Hodges (in Schalles and Shure 1989; Tyndall et al. 1990). Kelley

and Batson (1955) consider these concentric zonation patterns to be a successional series, reflecting a classical pattern of hydrarch succession. Kirkman (1992), however, presents evidence that vegetation changes are probably cyclical, corresponding to cyclic climatic patterns. Drastic vegetation responses may occur rapidly, even over one or two years (Kirkman 1992; Kirkman and Sharitz 1993; Richardson and Gibbons 1993). These studies are discussed in more detail below.

## HYDROLOGY AND FIRE IN HERB-DOMINATED DEPRESSION WETLANDS

In wetlands with perched water tables, hydrologic regimes depend on local precipitation, evapotranspiration, basin size and contour, depth to impermeable layer, and antecedent conditions (Hendricks and Goodwin 1952; Schalles and Shure 1989; Lide et al. 1995). Alternation between persistently wet or dry years have occurred in approximate 30-year intervals in the southeastern United States throughout the last 1500 years (Stahle et al. 1988). Consequently, vegetation in depression wetlands is subjected to irregular changes in degree of inundation on a recurring basis (Lide et al. 1995; Richardson and Gibbons 1993), ranging from seldomly flooded, seasonally flooded, to semi-permanently flooded conditions, except during drought.

In other similar wetlands, the alternation of inundation and drydown causes extirpation of some species and permits periodic recruitment from the seed bank of some species that can germinate and establish only at specific water levels (usually drawdown) (van der Valk and Davis 1978; Keddy and Reznicek 1982). Species that reach reproductive maturity prior to subsequent flooding or other disturbance replenish the seed bank. As a result, floristic richness in many wetlands may be linked with the disturbance regime and seed bank composition (Grubb 1977; van der Valk 1981; Pickett and White 1985; Grubb 1988; Gerritson and Greening 1989; Parker et al. 1989).

Coupled with the hydrologic regime are additional factors such as fire and other drought-related disturbances that contribute to the overall vegetation dynamics (Kirkman 1992). Fire apparently has been a recurring phenomenon in these wetland habitats, although little attention has been given to its role in maintaining vegetation. Early historical records by colonial naturalists indicate a high fire frequency in the southeastern United States, much of which was attributed to Native American activities and lightning-caused ignition (Christensen 1981). The depression wetlands in the Southeast are positioned within landscapes that were once, if not presently, dominated by *Pinus palustris*, *P. elliotii*, or *P.*

*taeda* forests. These forest communities are fire-maintained (i.e. require fire for regeneration). The natural frequency of fire due to summer lightning ignition is estimated at about 2–3 year intervals in *P. palustris* forests and about 5–10 year intervals in *P. elliottii* forests (Wright and Bailey 1982). Historically, during drought, the probability of naturally occurring fire spreading into depression wetlands from surrounding uplands would have been high.

Fire has been described for several southeastern United States wetland plant communities including savannas, grass-sedge bogs, shrub bogs and swamp forests (Christensen 1981). Charcoal fragments have been found throughout pollen and peat profiles in several Carolina bays (Buell 1946; Wells and Boyce 1953). Brooks et al. (1993) date charcoal fragments in a Carolina bay in South Carolina to approximately 4500 years B.P.

## APPLICABILITY OF PREVIOUS WETLAND VEGETATION MODELS

Conceptual models of vegetation change in the Okefenokee Swamp, Georgia (Hamilton 1984) and southern Florida wetlands (Duever 1984; Duever et al. 1986; Gunderson and Loftus 1993), which incorporate both hydrologic and fire factors, generalize successional relationships between major wetland types. The direction of change from one wetland vegetation type to another is driven by deviation from an average frequency/depth of inundation or average frequency/severity of fire. These models do not address cyclic changes within a single wetland type based on natural fluctuations in the hydrologic regime. Other wetland vegetation models which illustrate cyclic vegetation patterns, e.g., prairie marshes (van der Valk and Davis 1978) and vernal pools (Zedler 1987) do not incorporate fire regimes. van der Valk's (1981) generalized model of wetland vegetation dynamics, which is based on life-span, propagule longevity and establishment requirements of species, predicts presence of species but not necessarily dominant vegetation. Competition and presence of existing vegetation before draw down are not considered.

## INTERACTION OF FIRE AND HYDROLOGIC REGIME IN HERB-DOMINATED CAROLINA BAYS: A CONCEPTUAL MODEL AND SUPPORTING EVIDENCE

A conceptual model of vegetation dynamics in herb-dominated Carolina bays that incorporates fluctuating hydrologic conditions and episodic disturbances (Figure 1) was developed from multi-faceted experimental and descriptive studies (Kirkman 1992). The model outlines

the hydrologic conditions within Carolina bays and the dominance by emergent grasses in the intermediate stages of inundation. This model is probably applicable to other depression wetlands in the region besides Carolina bays because of morphological and species composition similarities.

Kirkman and Sharitz (1993) identify several mechanisms that appear to contribute to the community changes associated with such wide ranges of hydrologic fluctuations (Table 2). In particular, relative growth responses of indicator species (perennial grasses) to flooding conditions, relative drought tolerances of the dominant grasses, species responses to fire and to fire followed by inundation, and persistence in the seed bank are examined (Kirkman 1992; Kirkman and Sharitz 1993; Kirkman and Sharitz 1994).

Vegetation which was mapped from color infrared and natural color photography, in grass-dominated Carolina bay wetlands before and after a record 10-year drought, demonstrates that vegetation patterns shift spatially during decade-long dry periods (Kirkman 1992). The bays examined were deeply inundated during the late 1970s and early 1980s (Sharitz and Gibbons 1982; Schalles 1979; Lide et al. 1995).

Due to the gradual slopes of bay depressions, the water depth gradient or soil moisture gradient shifts with the fluctuating hydrologic regime. As expected, upland species encroach along the margins as they become dry and, as the soil surface is exposed, aquatic species decline. With permanent drainage, a terrestrial community develops (Figure 1). Changes in abundances and relocation of stands of *Panicum hemitomon* Schultes, *Manisuris rugosa* Nuttall (Kuntze) and *Leersia hexandra* Swartz. appear to be indicators of intermediate hydrologic change in these wetlands (Kirkman 1992). These grasses are dominants in many Carolina bays and other depression wetlands, and they usually occur in nearly monospecific stands. Following subsequent reinundation, the woody species that invade during dry periods are eliminated (Kirkman, pers. obs.), thus resetting the cyclical phase.

Stem elongation under inundated conditions occurs for *L. hexandra*, *M. rugosa*, and *P. hemitomon* (Kirkman and Sharitz 1993), an adaptation for survival in flooded conditions exhibited by numerous wetland plants (Cookson and Osborne 1978; Jackson 1985; Jackson 1990). In both experimentally controlled studies and field observations, a positive relationship between the degree of stem elongation and increased water depth occurs in *P. hemitomon* and *L. hexandra*. *Manisuris rugosa* stems elongate in response to flooding but not depth of flooding (Kirkman and Sharitz 1993). Maximum elongation (i.e., greatest depth tolerance) occurs

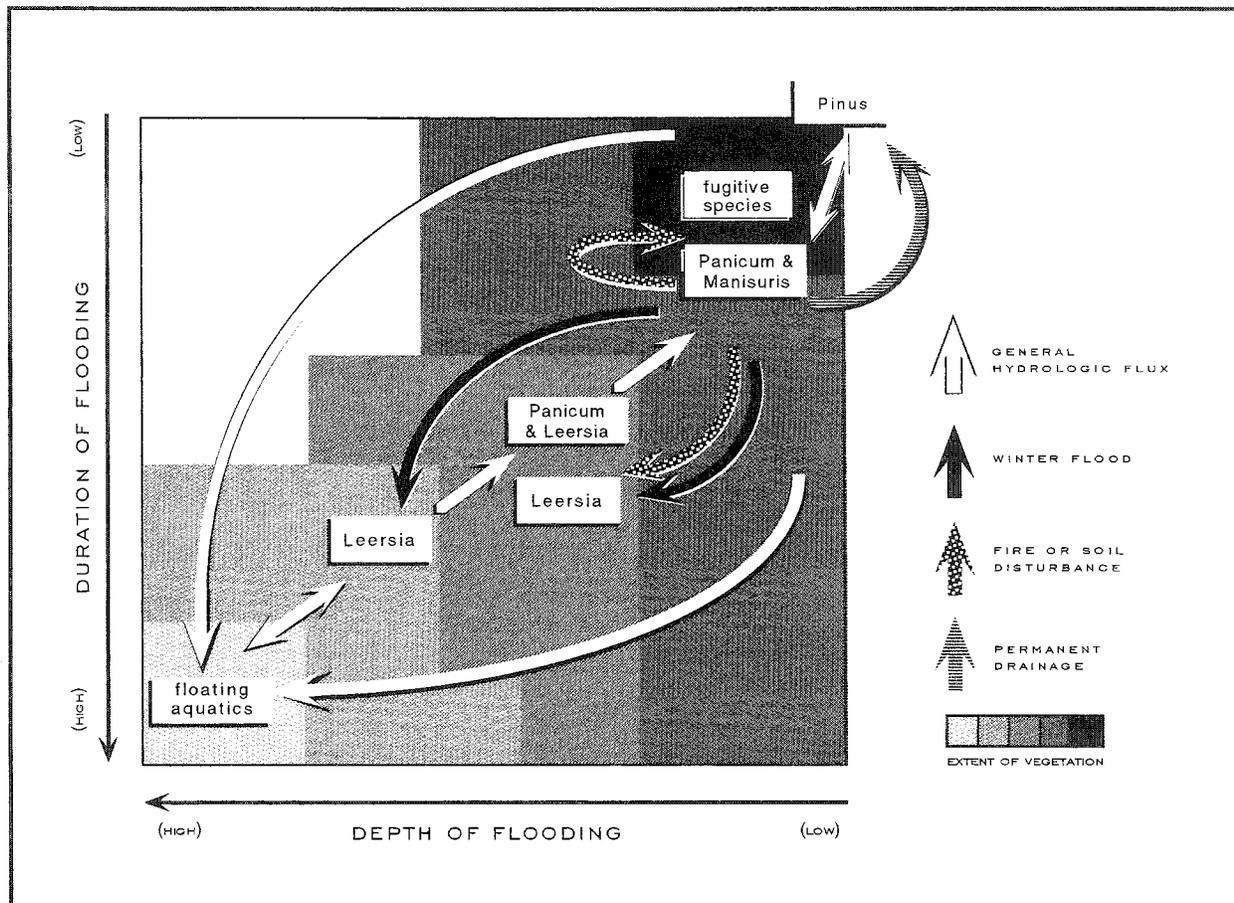


Fig. 1. Conceptual model of vegetation dynamics in Carolina bay wetlands.

for *L. hexandra*. Greatest growth and reproduction for all three species occurs in inundated rather than non-inundated conditions (Kirkman and Sharitz 1993). These grasses are robust perennials that reproduce primarily by vegetative means. *Leersia hexandra* and *P. hemitomon* rarely occur, or are absent, in the persistent seed banks of Carolina bays and temporary ponds, even in areas in which they dominate the vegetation. Thus, once established, these species can persist for extended periods, until removed or reduced by episodic disturbances, i.e. deep inundation, fire or soil disturbance.

Because of periodic dry downs, species in Carolina bays must be relatively drought-tolerant as well as flood-tolerant. Biomass allocation studies among these three species suggest that *L. hexandra* has no compensatory allocation of carbon to roots in drier conditions that could serve for increased water absorption, in contrast to the other two grasses (Kirkman and Sharitz 1993). In addition, relative drought tolerances, measured by stomatal conductance and predawn xylem pressure potential, show least stomatal control by *L. hexandra*, followed by *P. hemitomon* and *M. rugosa* (Kirkman and Sharitz 1993).

Table 2. Drought-tolerant and flood-tolerant characteristics examined in Carolina bay wetland plants.

Drought-tolerance	Flood-tolerance
Stomatal control	Persistence in seed bank
Carbon allocation to below ground biomass	Reproduction by rhizomes
Survival after fire	Morphological plasticity (stem elongation)
Late season growth (associated with C <sub>4</sub> plant)	O <sub>2</sub> transport during winter inundation
	Flower production initiated by inundation
	Perenniality with first-year maturation

Fire tolerance has been frequently reported for *P. hemitomon*, which usually resprouts vigorously and rapidly attains pre-burn vigor (Loveless 1959; Wade et al. 1980; Lowe 1986). Findings by Kirkman and Sharitz (1993; 1994) agree with these earlier reports of fire tolerance. However, winter fire followed by inundation significantly decreases emergence of *P. hemitomon*. Kirkman and Sharitz (1993) suggest that standing dead stems may be necessary for oxygen transport during winter inundation, similar to the case of *Typha angustifolia* L. (Jordon and Whigham 1988). Comparable stem removal data for the other two species are not available, although

Table 3. Size and richness of North American freshwater wetland seed banks.<sup>1</sup>

Wetland	Density (mean m <sup>-2</sup> )	Species number	Location	Reference
Carolina bays	72,600	107	SC	Kirkman and Sharitz (1994)
Bogs	165	1	CAN	Moore and Wein (1977)
Bogs	171,800	12	WVA	McGraw (1987)
Lakeshore	10,000	41	CAN	Keddy and Reznicek (1982)
Nontidal marsh	3,200	29	IA	van der Valk and Davis (1976)
Nontidal marsh	29,800	45	IA	van der Valk and Davis (1978)
Nontidal marsh	110,000	50	IA	van der Valk and Davis (1979)
Riverine	2,600	59	SC	Schneider and Sharitz (1986)
Swamp	600	6	GA	Gunther et al. (1984)
Temporary pond	17,900	21	NJ	McCarthy (1987)
Tidal marsh	9,300	52	NJ	Leck and Graveline (1979)
Tidal marsh	27,000	53	NJ	Leck and Simpson (1987)

<sup>1</sup> Adapted from Leck (1989).

this phenomenon is being investigated for *L. hexandra* by Kirkman (unpublished data). A close relative to *L. hexandra*, cultivated rice, is able to produce shoots in anoxic conditions. If *L. hexandra* has similar adaptations for survival in anoxic conditions (as proposed in the conceptual model), it could more effectively survive deep winter inundation or fire followed by moderate winter inundation than could *P. hemitomon* or *M. rugosa*.

During very wet or very dry conditions, recruitment from the seed bank becomes a more significant factor influencing vegetation change. Species richness and density of seed banks of the Carolina bays are among the highest reported for wetland habitats (Table 3). These seed banks do not necessarily reflect the corresponding standing vegetation. Perennials with first-year reproductive maturity are abundant in the seed bank. In a habitat with irregularly recurring disturbances, this life-history trait increases the probability of survival. Several regionally rare taxa persist in the seed bank during unfavorable environmental conditions. Fire and soil disturbance during dry down can result in the recruitment of fugitive species (e. g., *Iva microcephala*, *Croton elliotii*, *Panicum verrucosum*, *Panicum wrightianum*) two of which are considered rare in their range (Kirkman and Sharitz 1994). The axis of vegetation change along a decreasing flood depth and duration gradient also corresponds to a species richness gradient that becomes maximal before dominance by terrestrial vegetation (Figure 1).

## POTENTIAL ECOTONE INFLUENCES ON FIRE REGIMES

In the southeastern U.S., the functional relationship between terrestrial and aquatic ecosystems has been recognized primarily in riparian systems (Lowrance et al. 1983; Gregory et al. 1991). In riparian zones, terrestrial inputs (both surface and subsurface inputs of nutrients and sediments) are rapidly modified, with nutrient re-

moval occurring within the first 3 meters. A similar role may occur in depression wetlands or in the ecotone around the wetland. Ecotones may also have a significant role as a fire corridor between fire-managed uplands and depression wetlands.

Processes and properties of ecotones associated with depression wetlands are likely to be both spatially and temporally dynamic, reflecting changing hydrologic conditions.

Ecotones are often assumed to have greater species richness than adjacent systems and may be more sensitive to change in environmental conditions. Consequently, these intermediate areas could potentially serve as indicators of change outside natural environmental amplitudes (Naiman et al. 1989). Wetland ecotones may also be the preferred habitat of some rare species, such as *Schwalbea americana* L., a federally endangered plant species that appears to require fire for flower production (Kirkman and Drew, this volume). Often, overlying the hydrodynamics is a fire regime in which season, intensity, or return interval of burning may affect the vegetative composition of the ecotone. A change in vegetation in the ecotone could influence nutrient transformations, the fire regime within the wetland, or even possibly the hydrologic regime itself (Figure 2).

The ecotonal areas between depression wetlands and uplands have been vulnerable to both direct and indirect structural modifications because of long-term land use practices. For example, undisturbed ecotonal areas associated with limesinks in southwest Georgia are often composed of vegetation gradients extending from long-leaf pine/wiregrass with increasing abundance of slash pine to dominance by wetland herbaceous species (Kirkman, pers. obs.) In these communities, fire will likely travel into the wetland when dry conditions prevail because of pyrogenicity of the pine needles and wiregrass. Agricultural fields or firebreaks adjacent to wetlands appear to have an indirect effect on ecotones by serving as

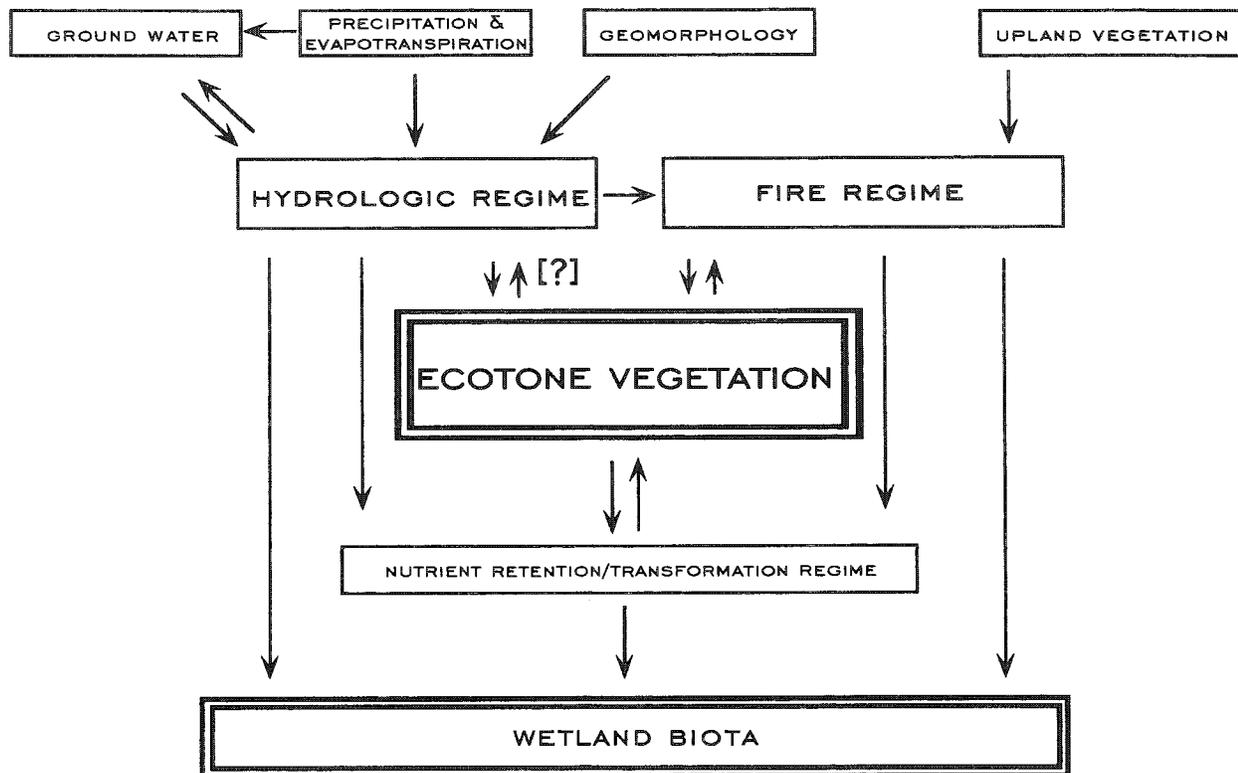


Fig. 2. Conceptual model of abiotic and biotic influences on wetland biota.

a barrier to fire. Fire suppression promotes the encroachment of hardwoods (in this region, particularly establishment of *Quercus virginiana*).

An alternate argument may be, however, that the hydrologic regime associated with the wetland permits only infrequent fire in the ecotone, and thus hardwoods could become established during prolonged dry periods. Once established the hardwoods could persist in wetter conditions. In either case, the presence of a hardwood border (rather than a longleaf pine/slash pine gradient) probably alters the fire frequency in the wetland. Even with prescribed burning of the uplands, increases in moisture retention of the hardwood litter and differences in pyrogenic properties from that of pine-dominated ecotones would likely deter the movement of fire. These hypotheses need to be rigorously tested among different depression wetland types.

## CONCLUSIONS

Although hydrologic regimes primarily drive vegetation changes of herb-dominated depression wetlands, disturbances enhance species coexistence, allow recruitment of fugitive species, and thus maintain species richness. Maximum species richness in these wetlands is probably balanced by disturbance and local successional dynamics. Conservation management goals should focus

on mechanisms for enhancing endemic species richness and the maintenance of fugitive and sometimes rare species (Kirkman and Sharitz 1994). In the absence of naturally occurring fires, such strategies should consider episodic fire associated with prolonged drought periods, as a desirable component in the preservation of herb-dominated depression wetlands.

Many of the unanswered questions and comparative information about southeastern depression wetlands reflect a major management concern: a functional definition of width of the border surrounding these wetlands required to protect wetland biota and processes. Concerted research efforts integrating studies of the biota, hydrology, fire corridors and other ecotonal functions with comparisons across the region are essential to provide the information needed to develop ecologically sound management strategies and regulatory policies for these wetlands.

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