VEGETATION OF SELECTED UPLAND TEMPORARY PONDS IN NORTH AND NORTH-CENTRAL FLORIDA

Linda V. LaClaire[1]

ABSTRACT

Vegetation was sampled in 13 temporary ponds located in uplands of north and north-central Florida. The ponds were selected for study because they represented potential breeding sites for 2 rare amphibians, the gopher frog, *Rana capito aesopus*, and the striped newt, *Notophthalmus perstriatus*. Vegetation in the non-forested depression ponds was analyzed in order to determine if a set of characteristic species was present in each. These date then could be used to identify breeding sites for the two species and to provide information for use in the development of management plans for the sites. The study ponds generally fill during winter rains and completely dry down during the summer, but, during the period of this research, Florida was experiencing a relatively dry period, and some ponds did not fill on an annual basis.

A total of 112 vascular plant species were identified in the pond basins. *Panicum hemitomon* was the only species present at each pond. Other common species included *Andropogon glomeratus*, *Rhexia mariana* var. *mariana*, *Eupatorium leptophyllum*, *Rhynchospora* spp., *Ilex glabra*, *Cephalanthus occidentalis*, and members of the family Eriocaulaceae. Similarities between ponds generally resulted from similarities in hydrologic cycle, defined as the period of time since each had held water, and the proximity of ponds to each other. The vegetation of each pond reflected a pattern of zonation or banding commonly described for temporary ponds in other regions. Wetland index values calculated for each pond fit wetland designation criteria, including a basin that had not formed a pond for 7 years, Dry Pond. Species richness and diversity were highest in ponds that had recently dried down and lowest in flooded ponds and Dry Pond.

RESUMEN

Se muestreó la vegetación de 13 estanques temporarios en las tierras altas del norte y norte-centro de Florida. Se seleccionaron los estanques que representaban potenciales sitios reproductivos de dos especies raras de anfibios, el sapo excavador de Florida, *Rana capito aesopus*, y la salamandra rayada, *Notophthalmus perstriatus*. Estos estanques, que ocupan bajos en areas no forestadas, se ajustan a un patrón general de llenado durante las lluvias de invierno y de completo vaciamiento durante el verano. Florida

[1] The author is a Wildlife Biologist of Herpetology and Avian Ecology at the U. S. Fish and Wildlife Service, 6578 Dogwood View Parkway, Suite A, Jackson MS 39213, USA.

LACLAIRE, L. V. 1995. Vegetation of selected upland temporary ponds in north and north-central Florida. Bull. Florida Mus. Nat. Hist. 38, Pt. I(3):69-96.

experimentó un período relativamente seco durante este estudio y por lo tanto, algunos estanques no se llenaron anualmente.

Las comunidades vegetacionales se identificaron en base a información de transectos y búsquedas de circuitos en las cuencas de los estanques. Con el objeto de determinar sin un número de especies características pudiera ser utilizado para la identificación de sitios de reproducción de las dos especies de anfibios, se realizaron análisis vegetacionales. Se identificó un total de 112 plantas vasculares provenientes de cuencas en los estanques. *Panicum hemitomon* fue la única especie presente en cada estanque. Otras especies comunes fueron *Andropogon glomeratus*, *Rhexia mariana* var. *mariana*, *Eupatorium leptophyllum*, *Rhynchospora* spp., *Ilex glabra*, *Cephalanthus occidentalis* y miembros de la familia Eriocaulaceae. Las semejanzas vegetativas entre estanques, estuvieron por lo general correlacionadas con similaridades en el ciclo hidrológico (el tiempo transcurrido desde que cada estanque tuvo agua) y la cercanía entre estanques. La vegetación en cada estanque reflejó un patrón de zonación comunmente descrito para estanques temporarios en otras regiones. Los valores de índices de humedales calculados para cada estanque cayeron dentro del rango descrito para humedales, incluyendo una cuenca que no formó estanque durante 7 años. La riqueza y diversidad de especies fueron máximas en estanques secados recientemente (< 1 año desde inundación) y mínimas en estanques inundados y en estanques secos por varios años.

INTRODUCTION

Vegetation data from upland temporary ponds in north and north-central Florida were collected as part of a larger project to determine the ecology and distribution of two rare amphibians, the Florida gopher frog, *Rana capito aesopus*, and the striped newt, *Notophthalmus perstriatus* (LaClaire 1992; Franz and Smith 1993). Temporary ponds are required breeding habitat for these upland-dwelling amphibians (Moler and Franz 1987). In order to ensure the survival of these two species, effective management of their breeding habitat is imperative.

An understanding of the temporary pond plant community is essential to the development of appropriate management plans for these pond basins. The wetland vegetation of temporary ponds is an important source of available nutrients for pond-dwelling plants and animals and of humified organic matter that may be crucial to the ability of a pond to hold water (LaClaire 1992).

It is especially important that management practices do not alter the existing hydrology of a temporary pond basin. Alteration of the hydrologic regime may seriously impact the development of hydric soils, structure of the plant community, and temporal use by amphibians. Both reduction of the water budget and stabilization of water levels have figured prominently in the ecological decline of many undrained Florida wetlands (Lowe 1986). For example, use of temporary ponds as water retention basins stabilizes the water level and may result in successional changes toward a community dominated by emergent genera such as *Pontederia* sp., *Typha* sp., or *Scirpus* sp., rather than the grass/sedge community (Botts and Cowell 1988) required by many species of amphibians for egg attachment. The high variability and instability of the hydrologic component of the temporary pond environment results in a community which is highly susceptible to other disturbance (Gopal 1986).

The objective of this study was to provide information on the vegetative community of upland temporary ponds in north and north-central Florida. Little information is available on the species composition and distribution in these wetlands. Plant community structure was investigated with the goal of formulating some generalizations about the pond habitat which could be used to identify the type temporary pond used for breeding by the gopher frog and/or the striped newt. To fulfill the study objective the following questions were asked:

1) What plant species characterize each pond basin?
2) How similar is the vegetation of each site to each other?
3) Does the vegetation reflect a pattern of structure, association, spatial shift, or zonation?
4) Since considerable attention has been focused on wetland designation criteria, does the vegetation of each pond correspond to a wetland index value indicative of wetland?
5) What is the effect of hydrology on species richness, diversity, and distribution?

ACKNOWLEDGEMENTS

I thank Kenneth S. Clough, Richard (Dick) Franz, C. Kenneth Dodd, Jr., and Lora Smith for field assistance; Cary Norquist and Sidney McDaniel for plant identification; Robert L. Jones for computer assistance; and an anonymous reviewer whose comments significantly improved the manuscript. I am especially grateful to Dick Franz for encouragement and support. This work was undertaken in partial fulfillment of the requirements for the degree of Master of Science at the University of Florida.

TEMPORARY PONDS

Defining a Temporary Pond

Temporary wetlands can be defined as natural bodies of water which experience a recurrent dry phase of varying duration (Williams 1987). The hydrologic emphasis in these wetlands is on the cyclic nature of drying and re-filling as permanent waterbodies are also capable of drying completely in exceptional years. In addition, selection has occurred in temporary wetlands for species adapted to this cyclic drying and filling and results in periodic bursts of productivity that fuel these systems (Patrick and Khalid 1974; Brinson et al. 1981; Reddy and Graetz 1988).

A temporary pond is a small (generally less than 5 hectares), isolated, temporary wetland that is depressional in nature. There is considerable confusion of terms in dealing with these small temporary wetlands, both among regulatory agencies and in the literature. Terms used to describe them include flatwoods marshes/ponds, ephemeral ponds/wetlands, highlands marshes, pineland depressions, depression meadows/marshes, St. John's wort ponds, seasonal marshes/ponds, intermittent ponds, and vernal pools (Holland 1988; Florida Natural Areas Inventory and Florida Department of Natural Resources 1990; Kushlan 1990). Some of these terms allude to the fact that temporary ponds are difficult to identify as wetlands during their dry cycle (Means 1990).

Hydrology

Hydrology is the major factor influencing and maintaining the community of wetland plants in the temporary pond basin (Mitsch and Gosselink 1986). External water inputs transport nutrients into the system and mobilize those bound in vegetation and soil. Water depth, duration, and frequency of flooding all influence the formation of hydric soils and the presence of hydrophytes within the pond (Gosselink and Turner 1978). The hydroperiod of temporary ponds is highly variable, depending upon elevation, basin characteristics, and rainfall patterns (Means 1990). Some ponds may fill and dry on an annual basis while others may contain water only in the wettest years.

When a temporary pond drains, productivity is lowered and aerobic decomposers begin rapidly breaking down the accumulated organic matter (Cole and Fisher 1979; Reddy et al. 1986). Temporary ponds are detrital systems, and most of the organic production decomposes before entering the detrital food chain (Mitsch and Gosselink 1986). The vegetation of the pond basin is readily and almost completely decomposed on a cyclic basis (Gopal 1986). The breakdown of organic matter facilitates maintenance of a temporary pond rather than a permanent one.

Life History Strategies of Wetland Plants

Three key life history traits can be used to characterize wetland species (van der Valk 1981). These are life span, propagule longevity, and propagule establishment requirements. Propagules may be seeds or vegetative structures, and a single species may have both modes of reproduction which function under different hydrologic regimes.

Wetland plants include both annuals and perennials. Annuals may be found on exposed soil during drawdowns or may occur as submersed or free-floating aquatics (van der Valk 1981). Due to the ephemeral nature of annuals, perennials may serve as better wetland indicators. The most prevalent life history strategy among temporary pond aquatic species is represented by vegetatively reproducing perennials (van der Valk 1981).

Plant species may be considered drawdown species, standing water species, or generalists relative to propagule establishment (van der Valk 1981). The majority of emergent species germinate primarily on exposed areas free of vegetation. They require exposure to light and/or alternating extremes of temperature. Vegetative propagule formation may occur in response to drawdown and accompanying temperature changes (Gopal 1986). Submersed, free-floating, and floating-leaved species have seeds that require a flooded substrate for germination. There are also species that can be considered generalists which germinate in both exposed and inundated conditions (Gerritsen and Greening 1989). Relative species' abundances fluctuate due to modes of germination and frequency and duration of wet/dry cycles in the pond basins. Spatial gradients in seed bank density and viability may be later expressed in spatial patterns of adult populations and can result in patterns of zonation (Lowe 1986).

Structure of Vegetation in Temporary Ponds

The distribution of water in time and space is the single most important factor influencing the occurrence of temporary pond macrophytes. Soil moisture is an important component. Plants in the temporary pond environment demonstrate a range of adaptations for tolerating inundation. Their distribution may follow hydrologic patterns and result in a zonation of vegetation in the pond basin (Laessle 1942; Lippert and Jameson 1964; van der Valk and Davis 1976; Abrahamson et al. 1984; Bridges and Orzell 1989; Kushlan 1990). Concentric rings of different species and vegetative types can occur in temporary ponds as band-like divisions related to hydrology and slope (Lippert and Jameson 1964; Weller 1979). A typical pattern of zonation in a temporary pond has several discrete components, depending on soil moisture and the extent of flooding in the basin. The center of a flooded pond often contains floating-leaved plants. This inner zone is typically surrounded by vegetation with submerged roots growing in wet edges. Extending out from this zone, in damp ground surrounding the wet areas, is a band of tall and short emergents, such as sedges, rushes, and grasses. Other grasses and composites occur in drier margins of the ponds followed lastly by water-tolerant shrubs or trees in transitional zones (Lippert and Jameson 1964; Weller 1979; Kushlan 1990; LaClaire and Franz 1991). The bands of vegetation move back and forth across the pond basin in a reflection of changing soil moisture conditions (LaClaire and Franz 1991).

The wetland plants occurring in these basins have evolved adaptations to alternating wet/dry periods and often require this cycle of inundation/drawdown for their survival (van der Valk 1981). In other words, periodic water level changes, including periodic drought, are required for maintenance of the temporary pond plant community. The magnitude and frequency of the water level changes can be perceived as gradients of a normal environment along which the different wetland plants are distributed (Gopal 1986).

Basic information on the vegetation of temporary ponds in south and west-central Florida is available from several studies (Huffman 1982; Abrahamson et al. 1984; Botts and Cowell 1988), but a detailed description of the vegetation of temporary ponds in north and north-central Florida previously has been lacking. An overview of freshwater marshes in Florida was written by Kushlan (1990). He described zones of vegetation, determined by hydroperiod, elevation, and water depth, as typical of large highland marshes (central ridge of Florida) and flatwoods marshes (pine flatwoods). The zonation and species composition within these marshes have similarities to temporary ponds. Species in common with temporary ponds are described below. *Nymphaea* sp. Occurred in deep water centers with *Panicum hemitomon* on higher ground, intermixed with *Leersia hexandra*, *Juncus* sp., *Polygonum* sp., and *Lachnanthes caroliniana*. Farther upslope, *Rhynchospora inundata*, *R. tracyi* (flatwoods marsh), and *Eleocharis* sp. occurred. The uppermost zone of the flatwoods marsh, which completely dried-out each year, supported a wet prairie association with a variable species composition dominated by *Hypericum fasciculatum*, *Amphicarpum muhlenbergianum*, *Panicum abscissum*, and *Xyris* spp.. Flatwoods marsh terminated abruptly in a border of woody vegetation containing *Serenoa repens*, *Cephalanthus occidentalis*, *Salix* sp., *Fraxinus* sp., *Ilex glabra*, *Lyonia* sp., and slash pine (*Pinus elliottii*), or dry prairie. *Panicum hemitomon* marshes dominated the higher ground on sandy substrates and typically had a *Sphagnum* mat. *Andropogon* spp. and *Spartina bakeri* were also mentioned as occurring in some marsh associations.

The distribution of vegetation within the temporary pond basin results from a predictable sequence of events summarized below (LaClaire and Franz 1991). There is a growth flush of aquatic and marsh vegetation following the rainy season. As the pond basins begin to dry, the above-ground growth of most species gradually senesces and decomposes, leaving behind only seeds or below-ground vegetative propagules and roots. Upon completion of pond drying, another characteristic plant community appears. Species in this assemblage have short vegetative cycles and generally disappear before ponds refill. As soil moisture continues to drop, most plants disappear, and only those with fibrous stalks remain. In some instances, ruderal species may then move into the basins.

Fire can also be an important element in the distribution of wetland vegetation in temporary ponds. Fire suppression, for example, may result in fire intolerant species invading the pond basin and altering the plant community structure. *Panicum hemitomon* re-sprouts rapidly after fire and, as a result, can develop dense monotypic stands. Other plants, such as *Hypericum fasciculatum*, may be killed by fire, but their seeds are adapted to germinate after the plant has been burned.

MATERIALS AND METHODS

Description of Study Sites

The four sites selected for this study of temporary wetland vegetation were chosen because they contained breeding ponds for the Florida gopher frog and the striped newt. These amphibians occur in xeric conditions found in sandhill and scrub habitats, except during the breeding season, when they move to temporary ponds embedded within this landscape. Temporary ponds selected for study were located in north and north-central Florida and were associated with karst landscapes overlain by acidic, sandy soils. As a result of acids leaching from the pinelands through these well-drained soils, the limestone has slumped to form numerous sinkholes and depressions, some of which have developed into temporary ponds. Thirteen temporary ponds were chosen for study within the Apalachicola National Forest (ANF) in Leon County, the Katharine Ordway Preserve-Carl Swisher Memorial Sanctuary (OSMP) and the Welaka Research and Education Center (WREC) in Putnam County, and the Ocala National Forest (ONF) located in Marion and Putnam counties. Of the 13 ponds, 9 were known breeding sites for either the striped newt or the gopher frog (Table 1). Unfortunately, due to the effects of drought, it could not be determined with certainty whether or not the remaining four ponds represented breeding sites for these species. However, the data obtained may be useful at a later date when amphibian surveys of these sites are completed. Individual pond names, designations, and basin descriptions are given below.

Table 1. Dimensions of all temporary pond basins studied. Amphibian breeding codes are: 0=unknown, 1=*Notophthalmus perstriatus*, 2=*Rana capito*, 3=both species.

Pond	Breeding Code	Dimensions of Pond Basins N-S	E-W
ANF-1	1	50 m	64 m
ANF-3	3	83 m	80 m
ANF-4	3	35 m	70 m
GP	2	168 m	205 m
BP	3	95 m	95 m
OS	3	87 m	93 m
HP	3	105 m	100 m
DP	0	78 m	69 m
WE-5	0	45 m	93 m
WE-6	0	66 m	63 m
WE-11	0	82 m	96 m
LDP	1	105 m	103 m
RP	3	140 m	144 m

Vegetation of three ponds was sampled in ANF. The ponds were designated as ANF-1, ANF-3, and ANF-4 and were sampled in May 1990. In OSMP, the vegetation of five ponds, Gopher Pond (GP), Breezeway Pond (BP), One Shot Pond (OS), Harry Prairie Pond (HP), and Dry Pond (DP) was sampled in June and July 1990. Breezeway Pond and GP were also sampled in October and November 1989, and the results of that survey are included (LaClaire and Smith unpubl. MS). Vegetation of three ponds in WREC was also sampled in July 1990; pond designations are WE-5, WE-6, and WE-11. Qualitative plant lists were compiled for Lake Delancy Pond (LDP) in ONF and Recess Pond (RP) located on private property adjacent to OSMP. Lake Delancy Pond was sampled January 1990 and June 1991, and RP was sampled every 10 days May through August 1991 as part of another study (LaClaire unpubl. data).

The size of the pond basins, estimated from north-south and east-west axes terminating at the pond/upland boundary, ranged from less than a hectare to approximately 3 hectares (Table 1). These ponds were dominated by grasses, sedges, and herbaceous vegetation, and none were forested wetlands. All of the ponds had historical breeding records for either the Florida gopher frog or the striped newt with the exception of Dry Pond in OSMP and the ponds located in WREC. Dry Pond was selected because it had been dry for at least seven years prior to the study and represented an extreme in length of the dry phase of temporary ponds. The ponds in WREC were thought to represent potential breeding ponds for the Florida gopher frog. The gopher frog is known to occur in gopher tortoise burrows on site near the ponds (R. Franz pers. comm) but has not been studied in its breeding habitat.

The history of pond drying and re-filling at each site was obtained from knowledgeable sources whenever possible. Unfortunately, hydrologic data were only partially available for the study ponds. The ANF ponds had the longest known hydroperiod and the OSMP ponds the shortest. Since the hydroperiod of each pond could not be compared, inferences about hydrology are based on the only variable known for each pond, months since the pond had held water when it was sampled.

Apalachicola National Forest.-- The Apalachicola study area is located in a region called the Lake Munson Hills on the northwestern portion of the Woodville Karst Plain and in the extreme northeastern corner of the ANF (USDA 1984). The study ponds, ANF-1, ANF-3, and ANF-4, have formed on depressions located on well-drained Ortega sands. These ponds are described in an article by Means (1990). The surrounding forest is composed of native longleaf pine (*Pinus palustris*) with some slash (*P. elliotti*) and loblolly pine (*P. taeda*) and is managed for timber production by the USDA Forest Service. A few scattered oaks surround the pond basins.

Katharine Ordway Preserve-Carl Swisher Memorial Sanctuary.-- The OSMP is located on the Interlachen Karst Plain at the southern flank of Trail Ridge in western Putnam County (Franz and Hall 1991). This is an area of extensive sandhills underlain by well to excessively drained Candler-Apopka soils. The vegetation surrounding the five OSMP ponds and the adjacent RP consisted of longleaf pine/turkey oak (*Quercus laevis*) forests and xeric oak hammocks that are typical elements of sandhill communities.

From the Soil Survey of Putnam County (Readle 1990), some discrimination of soil types can be made in the pond basins. Gopher Pond, BP, and HP were mapped as Placid fine sand, depressional. This soil is in depressional areas on the uplands and has a high available water capacity in the surface layer. Gopher Pond and BP are on the outer fringes of lake basins, and under extreme high water, perhaps a hundred year flood, they would be contiguous with them (USGS map, circa 1935). Harry Prairie Pond is at the outer edge of a wet prairie system but separated from it by a low sand ridge. A connection with the prairie would be possible under extreme high water. Dry Pond was mapped as Ona fine sand, a poorly drained soil typical of ponded areas. One Shot Pond was the only pond in which the soil of the pond basin was not specifically described, because it was improperly mapped as a perennial pond by the Putnam County soil survey (Readle 1990).

Welaka Research and Education Center.-- The WREC lies to the east of the St. John's River valley on an isolated ridge of Candler-Apopka soils and sandhill and scrub vegetation (Readle 1990). The study ponds, WE-5, WE-6, and WE-11, differ from those described above in that they are adjacent to or imbedded within flatwoods (Laessle 1942). Pond WE-5 was located in an area of Placid fine sand, depressional, downslope from longleaf pine/turkey oak sandhills. Pond WE-6 was also downslope from longleaf pine/turkey oak sandhills but was bordered on one side by upland hardwoods such as Chapman's oak (*Q. chapmanii*) and myrtle oak (*Q. myrtifolia*) which are associated with sand pine (*P. clausa*) scrub habitat. The soil mapped here was Pomello fine sand, which is a flatwoods soil with an organic pan below the surface. Pond WE-11 was a flatwoods pond mapped with Pomona fine sand, a poorly drained sand over a loamy subsoil (Puckett 1982). It was near a xeric hammock located on deep sands and containing live oak (*Q. virginiana*) and longleaf pine.

Ocala National Forest.-- Lake Delancy Pond, located in a section of the ONF in southern Putnam County, is an area of sand pine scrub managed by the USDA Forest Service for timber production. It is located on moderately well drained Pomello sand (T. Bailey pers. comm), and the natural vegetation of the area is sand pine, slash pine, scrub live oak (*Q. geminata*), myrtle oak, and saw palmetto (*Serenoa repens*). Approximately 2 km to the east is a sand ridge of Astatula soils that supports forests of longleaf pine and turkey oak. Just prior to the initiation of this study, the forest surrounding the pond had been clear-cut, bedded and re-planted with sand pine. A thick layer of muck and algae were present in this pond and it held water through-out the period of this study without drying.

Climatic conditions.-- Average daily temperatures, annual precipitation, and weather patterns are similar between the Putnam County study sites and the ANF in Leon County (USDA, 1984; Readle, 1990). The average daily temperature for both areas in summer is 27° C and in winter ranges from 11° C (ANF) to 12° C (Putnam County). Annual precipitation ranges from approximately 142 cm per year (Putnam County) to 152 cm per year (ANF). Most of the precipitation occurs in the summer as a result of convective thunderstorms. October and November are the driest months. Rain occurring in the winter results from frontal depressions that originate in the northern U.S. and Canada. Water tables in uplands of north and north-central Florida have seasonal highs in the winter and lows in the summer.

Field Methods

Single linear transects were established in each pond by taking a compass heading of 0° N at the center of each pond and walking perpendicular to the topographic gradient to the surrounding upland edge. The 1989 sampling of BP and GP deviated from this compass heading. A random compass direction was selected for these two transects. Sampling points were begun at the center of each pond and located at 5 m intervals until the upland boundary, as indicated by vegetation (pines or oak hammock), was reached (Abrahamson et al. 1988). If the next 5 m sampling point along the transect was completely within upland habitat, the sampling was terminated at the previous location. Transect lengths varied from 25 to 80 m depending on the size of the pond basin. At each of the sampling points, percent ground cover was sampled within quadrats using a rectangular vegetation sampling frame with dimensions 0.5 m x 2.0 m. To facilitate ocular estimation of cover, 0.1 m portions of the sampling frame were shaded. Percent cover was estimated for all plants (< 1 m tall or non-woody) rooted within the quadrat. Plants were identified to the species level where possible. Bare soil (classified as unvegetated), dead vegetation, surface water, and non-vascular plants were also given cover estimates. In one pond (BP, 1989 sampling), a distinction was made between a ground cover layer and a shrub layer. Shrubs, defined as woody plants greater than 1 m in height, were sampled using 5 m x 5 m quadrats located at 5 m intervals along the transect. In all other pond basins, shrubs at the transect sampling locations were sampled within the same 1 m square quadrat as the ground cover layer.

During each sampling in 1989 and 1990, a survey of the flora was made after the transect sampling. Circuits were made around the pond basins from the center to the upland boundary to opportunistically identify additional species missed on the transects. This method of sampling was also used to obtain species presence/absence data for LDP and RP.

Data Analysis

Analyses were chosen to address the research objective and to fit the field methods used. Plant lists were compiled for each site. Plant species identification and nomenclature follow Wunderlin (1982) and Clewell (1985). Only those 11 ponds sampled using transects during 1989 and 1990 were used in calculations. Total species occurrence data in all ponds, including LDP and RP, were used to make comparisons between sites.

To determine the similarities between the plant community at each pond, a number of different methods was used. The most common plant species were determined by finding those present in greater than 60% (7/11) of the ponds. Sixty percent was an arbitrary limit set as indicative of presence in a high percentage of samples, and plants found with this frequency were considered "constant" species (Mueller-Dombois and Ellenberg 1974). The most common plant species were identified from the 1990 transect data alone, then the 1989 transect data and data from the circuit searches were added, and the most common plant species were determined from the combined samples.

Percent cover values were used to calculate the dominant species in each pond basin and for all ponds combined using the 1989 and 1990 transect data. The top three species were chosen as co-dominants from a list of total percent cover ranked from highest to lowest.

The floristic similarity between sites was determined using Sorensen's index of similarity (SI)(Mueller-Dombois and Ellenberg 1974). This index was calculated from species presence/absence and transect data from 1989 and 1990. It is computed as follows:

$$SI = \frac{2C}{A+B} \times 100$$

A = # species, site 1
B = # species, site 2
C = # species, common to both sites

The results from the calculation of similarity indices were used to compare species composition in patterns of zonation previously reported in the literature and determine if similar patterns were present in the study ponds.

To determine if the vegetation of each pond corresponded to an index value indicative of wetland, species identified within quadrats were categorized by their wetland indicator status and given an associated ecological index value (EI) (Table 2) (Reed 1988; Wentworth et al. 1988). Ecological index values range from 1, for obligate wetland species, to 5, for obligate upland species. Plus (+) and minus (-) designations specify, respectively, the higher (more frequently found in wetlands) or lower (less frequently found in wetlands) part of the frequency range for a particular species. When assigning the EI, species with a plus received 0.5 less than the EI for that category and species with a minus received 0.5 more than the EI for that category. Plants identified only to genus were assigned the maximum indicator status category and the maximum EI if there were differences within the genus. A plant community consists of hydrophytic vegetation if visually estimated percent cover of obligate wetland species (OBL) and facultative wetland species (FACW) exceeds coverage of facultative upland species (FACU) and obligate upland species (UPL) or if the EI < 3 (USEPA 1989; USEPA 1991).

Wetland index values (WIV) were calculated for each quadrat for each transect across all ponds and all years using weighted averages of the percent cover data (Wentworth et al. 1988). To calculate this index, relative abundance (R) of each species in each quadrat was determined as percent cover of each individual species divided by the total percent cover of all species in that quadrat. Calculation of the WIV involved taking the sum of products of the relative abundances and ecological index values of all species in each quadrat, divided by the sum of all the relative abundances, as follows:

$$WIV = \frac{\Sigma (R \times EI)}{\Sigma R}$$

R = Relative abundance
EI = Ecological index value

Table 2. Wetland Indicator Status and Ecological Index Values (EI) (Reed 1988; Wentworth et al. 1988).

Category	Symbol	Definition	EI
Obligate Wetland	OBL	Plants that occur almost always in wetlands under natural conditions (estimated probability > 99%).	1
Facultative Wetland	FACW	Plants that usually occur in wetlands (estimated probability > 67% to 99%) but also occur in non-wetlands (estimated probability 1% to 33%).	2
Facultative	FAC	Plants with a similar likelihood of occurring in both wetlands and nonwetlands(estimated probability 33% to 67%).	3
Facultative Upland	FACU	Plants that sometimes occur in wetlands(estimated probability 1% to 33%), occur more often in non-wetlands (estimated probability > 67% to 99%).	4
Obligate Upland	UPL	Plants that occur rarely in wetlands (estimated probability < 1%) but occur almost always in non-wetlands under natural conditions(estimated probability > 99%).	5

Percent cover data from each pond transect were used in conjunction with the wetland indicator status of each species to determine the total percent cover in each pond basin of OBL, FACW, FAC, FACU, and UPL species. These data were compared by hydrologic status of each pond as expressed by months since each pond had held water.

Species richness, Shannon's Index, and evenness were calculated for each set of pond transect data. These data were also compared by hydrologic status at each pond as expressed by months since each pond had held water. Species richness is the total number of species found along each pond transect. Shannon's Index, H', is a measure of the average degree of "uncertainty" in predicting the species of an individual chosen at random from a collection of S species and N individuals in a population (Shannon and Weaver 1949). As diversity increases, Shannon's Index will also increase. The equation describing Shannon's Index is as follows:

$$H' = -\Sigma (p_i \ln p_i)$$

p_i = proportional abundance of each species; estimated from the proportion of the number of individuals of a species to the total number of individuals in the sample.

Evenness, E, was calculated as the ratio of H' to the natural log of species richness. Evenness would be maximum when all species were equally abundant and would decrease toward zero as the community diverged from evenness.

RESULTS

A total of 112 vascular plant species were identified in the 13 ponds across all 3 sampling years. An additional 12 plants were only identifiable to genus. Of the 112 species, 30% were identified in only one of the 11 ponds for which there were transect data; 64 (57%) were identified from the transect data alone; and the balance of the species were identified from circuit searches made through the pond basins. Of the species, 15% were present only in RP and 4% only in LDP. Of the 12 plants identified only to genera, 8 were the same genera as an identified species and may have been one of those species. In addition to the vascular plants, three groups of nonvascular plants were identified. Algae, *Cladonia* sp., and *Sphagnum* sp. were present as ground cover in pond basins.

Only two species, *Panicum hemitomon* and *Andropogon glomeratus*, were present in 60% of the ponds for which there were transect data (Table 3). However, if the data for all ponds are combined, an additional six taxa are present in at least 60% (8) of the 13 ponds. These include *Rhexia mariana* var. *mariana*, *Eupatorium leptophyllum*, *Rhynchospora* spp., *Ilex glabra*, *Cephalanthus occidentalis*, and members of the family Eriocaulaceae. *Rhynchospora* spp. and members of the family Eriocaulaceae were lumped together because of the similar habitat requirements of individual species and their similar zonation within pond basins.

Co-dominant species in the 11 pond basins (Tables 4, 5) were represented by 21 vascular and 2 nonvascular plants. *Panicum hemitomon* had the highest total percent cover in seven of the ponds. It was also a co-dominant in two additional ponds, resulting in co-dominance in 82% of the ponds with transect data. Of the co-dominant species, 78% were present in only one pond, 3 species were co-dominant in two pond basins, and *Eupatorium leptophyllum* was co-dominant in three ponds. Two non-vascular plants, *Sphagnum* sp. and *Cladonia* sp., were each co-dominant in one pond. Of the vascular plants determined to be co-dominants, 52% were OBL, 33% were FACW, 10% were FAC, and 5% were FACU species. No UPL species (Reed 1988) were co-dominants, but *Cladonia* sp. is an upland associated species.

Similarity indices indicated that the similarity between ponds was generally low. There were less than 50% shared species between most pond basins (Table 6). Of the transects sampled in 1990, only five pairwise comparisons of pond vegetation (9%) had greater than 50% of their species in common. When the data collected in 1989 from the two transects in BP and GP were compared to each of the sets of data from the 1990 ponds, only the samples of vegetation from BP and GP shared greater than 50% of their species. The WREC ponds were the least similar to other ponds. The lowest SI was calculated when WE-5 and WE-11 were compared with OS. Similarity indices were highest when the ANF ponds were compared to each other.

Table 3. Plant species present on greater than 60% of 1990 transects (1990) OR in greater than 60 % of all pond basins (ALL), data combined.

Plant Species	1990	All
Panicum hemitomon	11/11	13/13
Andropogon glomeratus	8/11	13/13
Rhexia mariana var. *mariana*	—	11/13
Eupatorium leptophyllum	—	10/13
Eriocaulaceae	—	9/13
Rhynchospora sp.	—	8/13
Ilex glabra	—	8/13
Cephalanthus occidentalis	—	8/13

Table 4. Percentage of total vegetated cover for each co-dominant species from transects in Apalachicola National Forest (ANF) and Welaka Research and Education Center (WE), 1990. WIS=Wetland indicator status (Reed 1988).

		Pond					
Species	WIS	ANF-1	ANF-3	ANF-4	WE-5	WE-6	WE-11
Sphagnum sp.	N/A					6	
Dichanthelium erectifolium	OBL		32	18			
Panicum hemitomon	OBL			8	34	65	54
Rhynchospora corniculata	OBL						15
Rhynchospora glomerata	OBL				20		
Eriocaulon sp.	OBL	13					
Nymphaea odorata	OBL						23
Lachnanthes caroliniana	OBL				16		
Ranunculus sceleratus	OBL	18		48			
Andropogon glomeratus	FACW		11				
Fimbristylis schoenoides	FACW					18	
Eupatorium leptophyllum	FAC+		26				
Dichanthelium acuminatum	FAC	24					
Total % Cover 3 sp. combined	—	55	69	74	70	89	92

Table 5. Percentage of the total vegetated cover for each co-dominant species from transects in Ordway/Swisher Memorial Sanctuary, 1989 and 1990. WIS=Wetland indicator status (Reed 1988).

		Pond						
Species	WIS	GP (1989)	GP	BP	BP (1989)	OS	HP	DP
Axonopus furcatus	OBL			19				
Leersia hexandra	OBL	22	16					
Panicum hemitomon	OBL	39	12	52	29	22	44	59
Eleocharis rostellata	OBL					14		
Lachnocaulon anceps	OBL			9				
Rhexia mariana	FACW+						10	
Panicum verrucosum	FACW		30		35			
Cyperus odoratus	FACW					22		
Ilex glabra	FACW	7						
Eupatorium leptophyllum	FAC+			20			14	
Pinus palustris	FACU+							13
Cladonia sp.	N/A							15
% Total Cover 3 sp. combined	----	68	58	81	83	58	68	87

Table 6. Sorensen Similarity Indices (SI) calculated from species present along vegetation transects in ponds sampled October-November 1989 (BP-89 and GP-89) and May-July 1990.

	ANF 3	ANF 4	GP	BP	OS	HP	DP	WE 5	WE 6	WE 11	GP 89	BP 89
ANF-1	52	53	31	32	24	52	25	23	15	17	33	26
ANF-3		53	30	31	29	43	24	15	15	8	39	44
ANF-4			19	32	18	37	25	15	15	8	27	32
GP				37	44	48	31	14	21	8	50	50
BP					28	36	42	29	10	11	48	54
OS						32	36	7	20	7	24	34
HP							38	17	26	10	37	36
DP								10	10	11	17	22
WE									46	50	23	22
WE										30	8	15
WE											8	16
GP -89												58

Table 7. Wetland Index Values calculated from transect vegetation data and Wetland Indicator Values. All ponds sampled in 1990 except GP and BP as indicated. M=meters from pond center.

M	ANF 1	ANF 3	ANF 4	GP 90	GP 89	BP 90	BP 89	OS	HP	DP	WE 5	WE 6	WE 11
0	1.03	1.00	1.00	1.20	1.04	1.90	1.90	2.02	1.33	1.04	1.00	1.35	1.00
5	1.25	1.00	1.11	1.09	1.31	1.71	2.08	1.68	1.09	1.59	1.00	1.06	1.00
10	1.22	1.52	1.14	1.09	1.39	2.45	1.36	2.75	2.61	1.05	1.00	1.42	1.00
15	1.72	1.71	1.00	1.17	1.22	1.43	1.76	1.49	1.12	1.33	1.20	1.36	1.00
20	2.74	1.46	1.00	1.00	1.56	1.00	1.18	1.00	1.21	2.72	1.00	1.02	1.00
25	1.50	1.70	1.30	1.00	1.85	1.04	1.04	1.31	1.93	3.03	3.75	3.33	1.00
30	—	1.97	1.41	1.00	1.55	1.08	1.00	1.70	1.79	3.71	—	—	1.00
35	—	1.63	—	1.00	1.70	1.02	1.00	1.81	1.26	3.41	—	—	1.05
40	—	2.14	—	1.00	1.44	1.47	1.00	3.00	1.59	3.66	—	—	1.05
45	—	—	—	1.00	2.00	—	1.00	3.53	1.88	—	—	—	2.15
50	—	—	—	1.15	—	—	—	—	—	—	—	—	—
55	—	—	—	1.00	—	—	—	—	—	—	—	—	—
60	—	—	—	1.15	—	—	—	—	—	—	—	—	—
65	—	—	—	1.80	—	—	—	—	—	—	—	—	—
70	—	—	—	1.77	—	—	—	—	—	—	—	—	—
75	—	—	—	2.04	—	—	—	—	—	—	—	—	—
80	—	—	—	2.57	—	—	—	—	—	—	—	—	—
MEAN	1.58	1.57	1.14	1.30	1.51	1.46	1.33	2.03	1.58	2.39	1.49	1.59	1.13

Table 8. Percent Cover by Wetland Indicator Status, 1990 transects. 0 months since water indicates a pond was flooded when sampled.

Pond	Months Since Water	Total Percent Cover				
		OBL	FACW	FAC	FACU	UPL
ANF-1	1	51	22	26	< 1	0
ANF-3	0	48	23	29	0	< 1
ANF-4	0	90	5	5	1	0
GP	12	72	23	2	2	1
BP	19	62	18	20	0	0
OS	4	41	45	9	3	2
HP	16	46	34	14	6	0
DP	84	69	3	1	27	< 1
WE-5	0	81	4	3	13	0
WE-6	0	72	26	0	2	0
WE-11	0	96	3	0	1	0

Table 9. Species richness (S), Shannon's Diversity Index (H'), and Evenness (E) calculated from the 1989 and 1990 transect data. 0 months since water indicates that ponds were flooded when sampled.

Pond	Months Since Water	S	H'	E
ANF-1	1	15	2.07	0.76
ANF-3	0	16	1.91	0.69
ANF-4	0	15	1.71	0.63
GP (90)	12	17	1.92	0.68
GP (89)	4	15	2.14	0.79
BP (90)	19	10	1.42	0.61
BP (89)	11	13	1.66	0.65
OS	4	19	2.28	0.77
HP	16	12	1.81	0.73
DP	84	9	1.30	0.59
WE-5	0	11	1.76	0.74
WE-6	0	11	1.17	0.49
WE-11	0	9	1.29	0.59

Wetland index values were calculated for each quadrat for each vegetation transect in 1989 and 1990, and a mean was calculated for each pond (Table 7). The lowest mean value was 1.13 in WE-11, and the highest mean value was 2.39 in DP. These results are to be expected since, at the time of sampling, all Welaka ponds were flooded, and DP had been dry longer than any other study pond. Calculation of the total percent cover along the transects in each pond basin for each category of wetland indicator class revealed that all ponds except OS had OBL species as the largest component of total percent cover (Table 8). In OS, there was only a slightly higher percent cover of FACW when compared to OBL (4%). Even DP, which had been dry for at least 84 months, maintained a total percent cover of OBL of 69%.

Species richness (Table 9) ranged from a low of nine species in DP and WE-11 to a high of 19 species in OS. The ponds in ANF had the highest average species richness, and the WREC ponds had the lowest. Species richness in ONF ponds was similar to that in the ANF ponds. Among the ANF ponds and among the WREC ponds, species richness was similar, but OSMP ponds varied from the lowest to the highest number of species. Species richness was very high in RP, but, this result was expected since the number of vegetation samples obtained from this site were much higher than any other pond basin.

Calculation of Shannon's Index (H') resulted in a range of values from 1.17 in WE-6 to 2.28 in OS (Table 6). Evenness (E) ranged from 0.49 in WE-6 to 0.79 in

GP(1989) (Table 9). The amount of time since each pond had held water when sampled is also presented in Table 9.

DISCUSSION

Pond Similarities and Differences

The similarities found in plant community composition between ponds was based primarily on the presence of the eight most commonly found taxa and the study site within which each pond was located. Both similarities and differences between ponds were related to differences in each pond's hydrologic cycle, as measured by the time since each pond had held water. This related directly to soil moisture conditions (LaClaire 1992). Flooded ponds lacked some of the dry meadow species but had floating-leaved species that were absent from the dry ponds. Dry meadow species and plants responding to declines in soil moisture conditions were more abundant in dry pond basins. This is demonstrated by the low similarity when WE-5 and WE-11 are compared to OS. The flooded WREC ponds had greater than 80% total cover of OBL but very low total percent cover of FACW (4% and 3% respectively). One Shot Pond, which had been dry for 4 months when sampled, had 41% total cover of OBL and 45% FACW. The FACW species were responding to drawdown and specific moisture conditions for which they are adapted.

Only four of the study ponds were sampled when drawdown had been recent, and ruderal or annual/short-lived perennial type species, except for *Eupatorium leptophyllum*, were not common in the pond basins. The transects in BP and GP from 1989 and OS were sampled when drawdown had occurred less than 1 year previous. One pond, ANF-1, had been dry only for a month when sampled, but this was too soon for emergent vegetation to respond to the change in the environment. All the other ponds were either flooded or had been dry a year or longer. As a result, most of the co-dominant species identified in the ponds were perennials, as were most of the total species identified across all ponds and all years. Of course, additional species may have been present as vegetative propagules or as seeds in the seed bank of ponds. Since annuals have a short life cycle, frequent sampling would be required for a complete species list.

Differences between the ponds are obvious from the fact that 78% of the co-dominant species identified in each pond were present in only one pond. However, many of these co-dominant species, as well as other component species of the ponds, shared life histories that were in some way adapted for the cyclic changes in the temporary pond basin. The most obvious similarity was the dominance of perennial species in the ponds. Other similarities involved adaptations developed in response to changes in hydrologic cycle. Several species (*Dichanthelium sabulorum*, *Juncus repens*, and *Sagittaria graminea*) showed a wide range of shoot and leaf growth forms or growth phases depending on soil moisture conditions. Others (for example, *Hypericum fasciculatum*) had a needle-like leaf form typical of many stress tolerant species (Grime 1979). Other species responded in the same way to a particular stage in the hydrologic cycle. This can be seen in ponds where drawdown had been recent. Some plants represented species that colonize the bare mud which becomes available after drawdown. Rapid plant growth was supported by the nutrient-rich, moist soil present in a temporary pond at this time. The period available for growth may be relatively short, and, thus, these species were annuals with a high potential growth-rate or short-lived perennials that were adapted to exploit this intermittently favorable environment (Grime 1979). *Panicum verrucosum* (an annual) is an example of this type of strategy. It had the highest percent cover on the 1989 transects in BP and GP and had set seed at the time of sampling. In 1990, the species was not found in either BP or GP. It is likely that its disappearance reflects the declining level of soil moisture between sampling events (LaClaire 1992) and that continued drought conditions did not favor seed germination. Another example of a drawdown species is the annual or short-lived perennial, *Cyperus odoratus*. It shared the highest percent cover with *P. hemitomon* on transects in OS. It occurred at the lowest elevation in the pond center and disappeared shortly after it set seed (LaClaire unpubl. data). This result fits a pattern where the deep area of a pond or marsh changes community composition seasonally depending on drying conditions (Botts and Cowell 1988). A perennial species, *Eupatorium leptophyllum*, was co-dominant in BP (1990), HP, and ANF-3. This ruderal species is also adapted to exploit the bare soil exposed after the pond dries. However, it requires less soil moisture, as indicated by its FAC+ status, and so moves into the pond basin later in the pond drying cycle than *P. verrucosum* or *C. odoratus*. It occurred throughout the pond basins when soil was exposed and moisture conditions were appropriate.

Some differences between ponds can be explained by differences in the surrounding habitat. Low similarity between the WREC ponds and other study ponds can be explained partly by the association of flatwoods vegetation with the WREC ponds and not the other study sites. Another explanation may relate to the selection of these ponds for study. None of the ponds at WREC has been verified as breeding ponds for the Florida gopher frog or the striped newt. If they are not, in fact, breeding sites, this may relate to differences in the pond plant communities. The higher similarities that resulted when ponds were compared within study sites suggests other unknown habitat variables.

Panicum hemitomon was the only species present in every pond sampled. The distribution of this species was a good indicator of the extent of previous flooding in the pond basin, and its highest elevation in each pond roughly corresponded to the average high water mark (Abrahamson et al. 1984; Lowe 1986; LaClaire unpubl. data). *Panicum hemitomon* cannot tolerate long-term flooding, and, thus, its absence in flooded pond centers demonstrated a persistent flooding event. The above-ground growth of *P. hemitomon* tends to be fibrous and resistant to decomposition. Its stalks may remain standing even if a pond has not filled for several years, and it is able to survive many years of dry pond conditions, as exemplified by the results from DP. Due to its tendency to grow in thick, monotypic stands, it probably acts to maintain the wetland environment by inhibiting the growth of upland species and reducing the oxidation of the soil organic matter that is crucial for nutrient cycling in the pond basin. In this way, *P. hemitomon* protects the wetland environment; the hydric soil and seedbank remain intact until another flooding event.

Pond Zonation

The results of this study and previous work in upland temporary pond basins in north and north-central Florida (Franz and Hall 1991; LaClaire and Franz 1991; LaClaire 1992) have revealed a pattern of zonation with similarities to other descriptions of temporary ponds (Fig. 1). Water-filled ponds often contain floating-leaved plants and submergents in the deepest areas (Water Lily Zone) and tall and short emergents at the pond edge (Sedge Prairie Zone). When the ponds dry, emergent grasses fill these zones in the previously flooded portions of the basin. Further upslope, a band of *Hypericum fasciculatum* (Sandweed Zone) commonly occurs, typically followed by a band of *Andropogon* spp. (Bluestem Grass Zone). Continuing upslope, additional bands of vegetation are found in dry meadows (Dry Meadow Zone) that occur as transitional zones adjacent to the longleaf pine dominated uplands. In some ponds, a fire shadow is present upslope of the Dry Meadow Zone which contains fire intolerant evergreen shrubs (Evergreen Shrub Zone) and oaks (Xeric Hammock Zone).

The two most common plant species found in the study ponds, *Panicum hemitomon* and *Andropogon glomeratus*, created the most obvious zonation in the pond basins overall. Both of these species are perennials with tall, persistent stems that are resistant to decomposition. *Panicum hemitomon* was the dominant species in the Sedge Prairie Zone and often defined its boundaries. *Andropogon glomeratus* defined the Bluestem Grass Zone. In temporary ponds, *P. hemitomon* reproduces most commonly vegetatively, but *A. glomeratus* sets seed that are wind-dispersed. The result of these differences in reproduction can partially explain overlapping zones in some of the ponds. *Panicum hemitomon* occurred generally as a uniform zone. *Andropogon glomeratus* was generally present along the outer edges of the pond, but it was also present in dry pond centers probably as a result of conditions appropriate to its seed germination.

The six additional species considered most common in the combined data sets represented typical plants of temporary pond zones with the exception of *Eupatorium leptophyllum*. Species dominance and the extent of zonation within

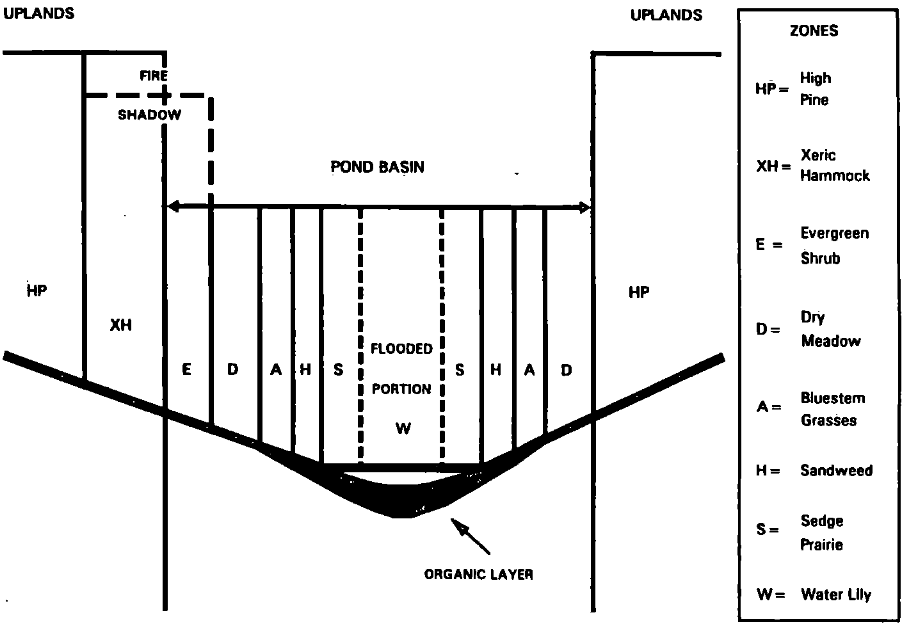

Figure 1. Plant community structure in temporary pond basins.

each study pond varied depending on water depth or, if ponds were dry, on how recently ponds had held water. *Rhynchospora* spp. and members of the family Eriocaulaceae were the most common plants in the Sedge Prairie Zone after *Panicum hemitomon*. These species were co-dominant in flooded ponds and those recently dried (ANF and WREC ponds, OS) and less common in ponds that had been dry longer. *Rhexia mariana* var. *mariana* occurred as part of the Dry Meadow Zone. Two shrubs, *Ilex glabra* and *Cephalanthus occidentalis*, were also "constant" species in the study ponds. They are typical members of the Evergreen Shrub Zone and are indicative of a lack of fire in at least part of the basin.

The most common species, and their representative patterns of zonation, have been described from other ponds with fluctuating water levels in similar habitats on the lower coastal plain (Huffman 1982; Abrahamson et al. 1984; Lynch et al. 1986; Botts and Cowell 1988; Bridges and Orzell 1989). The most common overlap between the study ponds and the literature were the grasses, sedges and herbs of the Water Lily and Sedge Prairie Zones such as species of *Panicum*, *Rhynchospora*, *Xyris*, and the Eriocaulaceae. Other dominant species frequently mentioned in the literature were *Hypericum fasciculatum* and *H. myrtifolium*

(Sandweed Zone), *Andropogon glomeratus* (Bluestem Grass Zone), and *Rhexia mariana* var. *mariana* (Dry Meadow Zone).

The importance of seed banks in maintaining the temporary pond community was not addressed directly in this study. However, the seed bank is likely to be very important to the maintenance of the wetland community and a contributing factor to pond zonation. Many wetland plant species disperse floating seeds and/or require specific intervals of inundation or desiccation for seed germination (van der Valk 1981). The position of these species may be dependent on the extent of flooding in the basin before drawdown, as well as the duration of drawdown (Lowe 1986; Hull et al. 1989). An overlapping distribution of plant species perhaps indicates similar hydrologic tolerances, but it may also indicate similar suitability of the substrate for seed settling, seed germination, and plant growth after the seeds have dispersed to that position (Hull et al. 1989).

Wetland Index Values (WIV)

All of the temporary pond basins studied had WIV less than 3, and, as a result, their plant communities can be considered wetland vegetation according to the Federal Manual for Identifying and Delineating Jurisdictional Wetlands (USEPA 1989). Wetland index values generally increased along the transects as the upland boundary was reached. However, there was not a simple relationship between the index values and a gradient of soil moisture, described by meters from the pond center, because of confounding elevation and substrate effects (LaClaire unpubl. data). The lowest mean WIV was calculated for WE-11. This was the result of the almost complete dominance (96%) of this pond basin by OBL. The highest mean WIV was calculated for DP and was a result of the co-dominant UPL species found in it. However, DP maintained OBL as the highest total percent cover and, as a result, maintained its status as wetland.

Species Richness, Diversity, and Hydrology

The relationship between status of each pond in its hydrologic cycle, as represented by time since it was flooded, and species richness and diversity is complex. The lowest species richness was found in DP, which had been dry longer than any other pond basin, but also in WE-11, which was flooded at the time of sampling. Both ponds had low values for evenness as a result of dominance by *Panicum hemitomon*, 59% of total cover for DP and 54% of total cover for WE-11. Welaka pond #11 was almost entirely flooded (35/45 m along the transect) and this

Table 10. Typical species of pond zones and their occurrence within study areas of ANF (1), WREC (2), OSMP (3), and ONF (4). LF=Life form: A=annual, P=perennial, A/P=annual or short-lived perennial, S=shrub, T=tree. Pond Zone: W=water lily, S=Sedge Prairie, H=Sandweed, A/DM=Andropogon/Dry Meadow, E=Evergreen Shrub, XH=Xeric Hammock, HP=High Pine.

		Pond Zone						
LF	Species	W	S	H	A/DM	E	XH	HP
P	*Sagittaria graminea*	1,3						
P	*Pontederia cordata*	2						
P	*Nuphar luteum*	3,4						
P	*Nymphaea odorata*	2,4						
P	*Polygonum* spp.	1,2,3						
A/P	*Ranunculus scleratus*	1						
P	*Dichanthelium erectifolium*		1,2,3					
P	*Panicum hemitomon*		1,2,3,4					
A	*Panicum verrucosum*		3					
A/P	*Cyperus* spp.		3					
A/P	*Eleocharis* spp.		2,3					
P	*Fimbristylis* spp.		2,3					
A	*Psilocarya scirpoides*		3					
P	*Rhynchospora* spp.		1,2,3,4					
P	*Juncus repens*		1,3					
P	*Eriocaulon* sp.		1,2,3					
P	*Lachnocaulon anceps*		3,4					
P	*Lachnanthes caroliniana*		2,4					
A/P	*Xyris* spp.		2,3,4					
S	*Hypericum fasiculatum*			1,3				
P	*Amphicarpum muhlenbergianum*				1,2,3			
P	*Andropogon glomeratus*				1,3,4			
P	*Rhexia mariana* var. *mariana*				1,2,3			
S	*Ilex glabra*					1,2,3,4		
S	*Ceratiola ericoides*					3		
S	*Lyonia lucida*					2,3		
S	*Lyonia mariana*					1,4		
S	*Vaccinium* spp.					1,3		
S	*Serenoa repens*						2,4	
T	*Quercus geminata*						1,3,4	
T	*Pinus elliottii*							1,2,3,4
T	*Pinus palustris*							1,2,3,4

contributed to its low species richness and diversity due to domination of the pond by a few obligate wetland species. In contrast, the ANF ponds were flooded only along short lengths of the vegetation transects. The higher species richness and diversity in ANF ponds was a reflection of the more variable moisture regime and, thus, greater habitat complexity. The highest species richness and diversity, and second highest level of evenness, were found in OS, which had been dry for 4 months when the vegetation was sampled.

Clarification of this pattern is possible when co-dominant species and their corresponding wetland indicator status are considered. In DP, the second and third ranked most abundant vegetative cover along the transect represented species that were either facultative upland or upland associated. In WE-11, however, all three of the co-dominant species were obligate wetland plants. The co-dominant species in OS were a mix of obligate and facultative wetland species. The high species richness and diversity in OS resulted from germination and growth of species adapted to the drawdown cycle of temporary ponds. Mud exposed after the pond dried was colonized rapidly, and at the time of sampling many of these plants had set seed. When OS was visited 6 months later, the pond center was devoid of live above-ground vegetation (LaClaire unpubl. data). The plants had senesced and already were undergoing rapid decomposition.

A comparison of species richness in BP and GP between the first and second vegetation sampling adds further insight. The number of species in the first sampling compared to the second sampling was 13 to 10 in BP and 15 to 17 in GP. There was a drop in diversity, as indicated by H', for both ponds even though species richness for GP increased. The apparent discrepancy in H' for GP can be explained by comparing the average percent of live vegetation versus dead vegetation occurring in quadrats in the two different years. In 1989, live vegetation averaged 124% cover and dead vegetation averaged 31%. Greater than 100% cover in GP (1989) indicated the presence of layering in the quadrats, another important aspect of species diversity. In 1990, live vegetation decreased to 63% of the total cover and dead vegetation increased to 53%. Even though species richness increased, the total cover represented by these species decreased by almost 50%.

CONCLUSIONS

Composition and Structure of Temporary Pond Basin Vegetation

A total of 112 vascular plant species were identified in the study ponds. Of these, only *Panicum hemitomon* was found in every pond sampled. Though species composition of individual ponds tended to be dissimilar, the species represented components of a pattern of zonation that was consistent between ponds. Hydrology determined the extent of zonation through direct and indirect effects on the composition of the wetland plant community. Each pond's position in its hydrologic cycle was reflected in its co-dominant species, species richness, and diversity. Species richness and diversity were highest in ponds which had dried-down less than one year previous to sampling and lowest in flooded ponds and ponds which had been dry for several years.

The high percentage of OBL in pond basins and the low WIV, in most cases, resulted from the presence of *Panicum hemitomon*. This species appears to have an important role in maintaining temporary pond basins, as exemplified by its presence in DP, which had been dry for over 7 years when sampled. Long-term persistence of *P. hemitomon* may reduce the rate of oxidation of organic matter, reduce soil moisture loss, and inhibit growth and establishment of upland adapted plant species.

Conservation Implications

Because temporary pond vegetation is adapted to cycles of wet/dry, any one sampling of a pond will give only a small picture of the total community composition. This has important implications for the current dispute over wetland delineation. If wetland hydrology indicators were narrowed to exclude hydric soils and wetland vegetation as hydrology indicators, temporary ponds would not consistently meet the wetland criteria (USEPA 1991). However, wetland indicator values from this study, conducted during a period of drought, clearly identified the plant communities of all ponds studied as hydrophytic (Reed 1988; USEPA 1989).

Although most wetland plant species in temporary ponds senesce and die back, some of the most common plants are those most resistant to decomposition and may be useful in determining wetland boundaries (i.e. *Panicum hemitomon*, *Hypericum fasiculatum*, *Rhexia mariana*, and *Andropogon glomeratus*).

Data from this study could be used as a model to predict the temporary pond wetland type, occurring in uplands of north and north-central Florida, used for breeding by the Florida gopher frog and striped newt. The data also provide a foundation for the development of temporary pond management strategies. However, there are probably many other plant species present in these wetlands which were not identified by this study. Additional data collected during wet years, and tracked seasonally, would give a more complete picture of the plant community.

LITERATURE CITED

Abrahamson, W. G., A. F. Johnson, J. N. Layne, and P. A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. Florida Sci. 47:209-250.

Botts, P. S., and B. C. Cowell. 1988. The distribution and abundance of herbaceous angiosperms in west-central Florida marshes. Aquatic Bot. 32:225-238.

Bridges, E. L., and S. L. Orzell. 1989. Longleaf pine communities of the West Gulf Coastal Plain. Nat. Areas J. 9:246-261.

Brinson, M. M., A. E. Lugo, and S. Brown. 1981. Primary productivity, decomposition, and consumer activity in freshwater wetlands. Ann. Rev. Ecol. Syst. 12:123-161.

Clewell, A. F. 1985. Guide to the vascular plants of the Florida panhandle. Florida State Univ. Press, Tallahassee, USA.

Cole, J. J., and S. G. Fisher. 1979. Nutrient budgets of a temporary pond ecosystem. Hydrobiologia 63:213-222.

Florida Natural Areas Inventory and Florida Department of Natural Resources. 1990. Guide to the natural communities of Florida. Florida Dept. Nat. Res., Tallahassee, USA.

Franz, R., and D. W. Hall. 1991. Vegetative communities and annotated plant lists for the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam County, Florida. Ordway Preserve Research Ser., Rept. No. 3, Florida Mus. Nat. Hist., Gainesville, USA.

Franz, R., and L. L. Smith. 1993. Distribution and status of the striped newt and Florida gopher frog in peninsular Florida. Final report submitted to Florida Game and Fresh Water Fish Comm., Nongame Wildl. Prog., Tallahassee, USA.

Gerritsen, J., and H. S. Greening. 1989. Marsh seed banks of the Okefenokee Swamp: Effects of hydrologic regime and nutrients. Ecology 70:750-763.

Gopal, B. 1986. Vegetation dynamics in temporary and shallow freshwater habitats. Aquatic Bot. 23:391-396.

Gosselink, J. G., and R. E. Turner. 1978. The role of hydrology in freshwater wetland ecosystems. Pp. 63-78 *in* R. E. Good, D. F. Whigham and R. L. Simpson (eds.). Freshwater wetlands: Ecological processes and management potential. Academic Press, New York, USA.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York, USA.

Holland, R. 1988. What about this vernal pool business? Pp. 351-355 *in* J. A. Kusler, S. Daly, and G. Brooks, eds. Urban Wetlands: Proceedings of the National Wetland Symposium. Omnipress, Madison, Wisconsin, USA.

Huffman, J. M. 1982. Pine flatwoods and seasonal ponds of southwest Florida: An illustrated guide. Senior Thesis, New College, Sarasota, Florida, USA.

Hull, H. C., Jr., J. M. Post, Jr., M. Lopez, and R. G. Perry. 1989. Analysis of water level indicators in wetlands: Implications for the design of surface water management systems. Amer. Water Res. Assoc., Tech. Publ. Ser. TPS-89-3, Minneapolis, Minnesota, USA.

Kushlan, J. A. 1990. Freshwater marshes. Pp. 324-363 *in* R. L. Myers and J. J. Ewel, eds. Ecosystems of Florida. Univ. Central Florida Press, Orlando, USA.

LaClaire, L. V. 1992. The ecology of temporary ponds in north-central Florida. M. S. Thesis, Univ. Florida, Gainesville, USA.

LaClaire, L. V., and R. Franz. 1991. Importance of isolated wetlands in upland landscapes. Pp. 9-15 *in* M. Kelly, ed. Proc. 2nd Ann. Mtg., Florida Lake Mgmt. Soc., Winter Haven, Florida, USA.

Laessle, A. M. 1942. The plant communities of the Welaka Area. Univ. Florida Publ., Biol. Sci. Ser. 4:1-143.

Lippert, E. E., and D. L. Jameson. 1964. Plant succession in temporary ponds at Willamette Valley, Oregon. Amer. Midl. Nat. 71:181-197.

Lowe, E. F. 1986. The relationship between hydrology and vegetational pattern within the floodplain marsh of a subtropical, Florida lake. Florida Sci. 49:213-233.

Lynch, J. M., A. K. Gholson, Jr., and W. W. Baker. 1986. Natural Features Inventory of Ichauway Plantation, Georgia. Volume 2. Report prepared for Ichauway Plantation, Newton, Georgia and the Nature Conservancy, Southeast Regional office, Chapel Hill, North Carolina.

Means, D. B. 1990. Temporary ponds. Florida Wildl. 44:12-16.

Mitsch, W. J., and J. G. Gosselink. 1986. Wetlands. Van Nostrand Reinhold, New York, USA.

Moler, P. E., and R. Franz. 1987. Wildlife values of small, isolated wetlands in the southeastern coastal plain. Pp. 234-241 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, eds. Proc. 3rd Southeastern Nongame and Endangered Wildl. Symp.. Georgia Dept. Nat. Res., Atlanta, USA.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, USA.

Patrick, W. H., Jr., and R. A. Khalid. 1974. Phosphate release and sorption by soils and sediments: Effect of aerobic and anaerobic conditions. Science 186:53-55.

Puckett, C. 1982. Natural resources facilities and user policy and procedures at the Welaka Research and Education Center. Inst. Food Agric. Sci., Univ. Florida, Gainesville, USA.

Readle, E. L. 1990. Soil survey of Putnam County Area, Florida. Natl. Coop. Soil Surv., U. S. Dept. Agric., Washington, D. C., USA.

Reddy, K. R., T.C. Feijtel, and W. H. Patrick, Jr. 1986. Effect of soil redox conditions on microbial oxidation of organic matter. Pp. 117-148 *in* Y. Chen and Y. Avnomelech, eds. The role of organic matter in modern agriculture. Martinus Nijhoff Publishers, Boston, Massachusetts, USA.

Reddy, K. R., and D. A. Graetz. 1988. Carbon and nitrogen dynamics in wetland soils. Pp. 307-318 *in* D. D. Hook, W. H. McKee, Jr., H. K. Smith, J. Gregory, V. G. Burrell, Jr., M. R. DeVoe, R. E. Jojka, S. Gilbert, R. Banks, L. H. Stolzy, C. Brooks, T. D. Matthews, and T. H.Shear, eds. The ecology and management of wetlands, volume 1: Ecology of wetlands. Timber Press, Portland, Oregon, USA.

Reed, P. B., Jr. 1988. National list of plant species that occur in wetlands: national summary. U.S. Fish Wildl. Serv., Biol. Rept. 88(24).

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. Univ. Illinois Press, Urbana, USA.

USDA (United States Department of Agriculture). 1984. Soils and vegetation of the Apalachicola National Forest. Forest Service, Southern Region, U. S. Dept. Agric., Washington, D.C., USA.

USEPA (United States Environmental Protection Agency). 1989. Federal manual for identifying and delineating jurisdictional wetlands. Washington, D.C., USA.

______. 1991. Proposed revisions to the federal manual for delineating wetlands. U. S. Envir. Protec. Agcy., Washington, D.C., USA.

van der Valk, A. G. 1981. Succession in wetlands: A Gleasonian approach. Ecology 62:688-696.

van der Valk, A. G., and C. B. Davis. 1976. Changes in the composition, structure and production of plant communities along a perturbed wetland coenocline. Vegetatio 32:87-96.

Weller, M. W. 1979. Wetland habitats. Pp. 210-234 *in* P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: The state of our understanding. Amer. Water Res. Assoc., Minneapolis, Minnesota, USA.

Wentworth, T. R., G. P. Johnson, and R. L. Kologiski. 1988. Designation of wetlands by weighted averages of vegetation data: a preliminary evaluation. Water Res. Bull., Amer. Water Res. Assoc. 24(2):389-396.

Williams, D. D. 1987. The ecology of temporary waters. Timber Press, Portland, Oregon, USA.

Wunderlin, R. R. 1982. Guide to the vascular plants of central Florida. Univ. Presses Florida, Tampa, USA.