RESEARCH ARTICLE

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Tree Encroachment of A Sawgrass (*Cladium jamaicense*) Marsh within an Increasingly Urbanized Ecosystem

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ABSTRACT: Fire suppression and altered water drainage often change community structure and species composition in human-dominated ecosystems. We describe the decline of sawgrass marshes between 1940 and 2002, and assess the current condition of remnant marshes within the MacKay Tract, an isolated wetland embedded within rapidly developing eastern Orlando, Florida. We tested the correlation between live sawgrass and presence of adult hardwood trees and seedlings (primarily red maple, *Acer rubrum*) and describe vegetation in plots with different levels of tree encroachment. Total area occupied by open sawgrass in the MacKay Tract has declined dramatically the last 60 years; in 2006, open sawgrass comprised only 12% of the area covered in 1940. Tree basal cover was negatively associated with live sawgrass and positively related to red maple seedling density, but not associated with dead sawgrass tussocks. Sawgrass was positively correlated with the second axis of a non-metric multidimensional scaling ordination on understory plant assemblage, while red maple seedlings and several species associated with disturbed areas were significantly negatively correlated with this axis. Another nine plant species were positively correlated with the first axis, while *Osmunda cinnamomea* (cinnamon fern) was negatively associated with it. We suggest that woody species are continuing to colonize what is left of the sawgrass marsh. Without intervention (e.g., restoring hydrologic flow and fire), the sawgrass (*Cladium jamaicense* Crantz) area within the marsh will continue being replaced by woody and exotic species.

Index terms: drainage, fire suppression, Florida, marshes, Orlando, red maple, sawgrass, urban ecosystems, wetlands

INTRODUCTION

Fire and hydrology control the structure and function of most Florida ecosystems (Ewel 1990; Menges and Hawkes 1998; Boughton et al. 2006). Fire suppression and altered water drainage, which occur as human-disturbed ecosystems such as the Everglades, lead to changes in community structure and species composition (Davis 1994) that often diminish ecological value. Altered communities also favor colonization by invasive species, thereby decreasing the abundance and distribution of native species (Hobbs and Huenneke 1992; Daehler 2003; Seabloom et al. 2003; Hendrickson et al. 2005).

Sawgrass (*Cladium jamaicense* Crantz) is a dominant species in some plant assemblages characteristic of the southeastern United States, particularly the Everglades (Ewel 1990). Sawgrass is found throughout Florida (Davis et al. 1994; Burch 2003; King et al. 2004; Duever 2005) and ranges as far north as Virginia and as far west as Texas (Niering 1985). It reproduces sexually and asexually, with broad interdigitation of clones that may extend over 200 m^2 (Ivey and Richards 2001). Sawgrass frequently forms dense stands in nutrient-poor areas, leaving little space for other plant species (Dykyjova and Kvet 1978; Niering 1985). These monotypic stands support diverse invertebrates and provide habitat for many vertebrates (Jordan et al. 1994; Darby et al. 2001; Vaughan and Shephard 2005). Sawgrass is well adapted to low-nutrient environments, but it is at a competitive disadvantage with species such as *Typha domingensis* Pers. in high-nutrient environments (Davis 1991; Newman et al. 1996; Miao and Sklar 1998; Lorenzen et al. 2001).

Altered environmental conditions can modify community structure of sawgrass marshes. In the Everglades, increased water depth and frequent fires contribute to encroachment of sawgrass by cattail (*Typha* spp.) (Davis 1994). Elsewhere fire suppression combined with hydrological changes allowed red maple (*Acer rubrum* L.) and other native and exotic species to extensively colonize Florida sawgrass marshes (Duever 2005). When annual accumulation of dead plant material is not fully recycled or burned, sawgrass marshes tend to fill in and black muck soils increase in depth (Niering 1985). The filling-in process ultimately converts marsh to wet meadow, although this invasion may not occur if water levels remain high. Greater amounts of litter reduce mean light interception levels, which in turn reduce sawgrass recruitment and clonal survival (Imbert and Delbe 2006).

The MacKay Tract in Orlando, Florida, exemplifies a wetland ecosystem that has slowly changed through invasion of hardwood and weedy species, caused in part by fire suppression and altered hydrology. The MacKay Tract was once a marsh dominated by sawgrass with a fringe of hardwood trees. Historically, encroachment of sawgrass by hardwood trees was prevented by recurrent fires and flooding as well as grazing by cattle. Our objective was to analyze the current condition of the sawgrass marsh within the MacKay Tract with reference to potential tree encroachment. We assessed the correlation between live sawgrass and the presence of hardwood adult trees and seedlings, primarily of red maple. We suggest that colonization by woody species of the remaining sawgrass marsh is ongoing, and, without restoration, the sawgrass marsh will continue to be colonized by woody species and exotic species, ultimately resulting in an extremely different ecosystem.

METHODS

Study Site

The MacKay Tract in Orlando, Florida, is within approximately 103.09 ha of undeveloped land in Unincorporated Orange County (Parcel ID 09-22-31-0000-00-031; Figure 1), Florida. The University of Central Florida owns and manages 54.55 ha of this property, which is near its Orlando campus. In 1935, sawgrass marshes covered 75% of the MacKay Tract and its adjacent undeveloped area (Publication of Archival Library and Museum Materials, Florida Department of State). The sawgrass has been increasingly invaded by encroaching trees, mostly red maple. Over the past 30 years, the tract has been steadily surrounded by residential and commercial development, resulting in fire suppression and drainage changes.

Over the past 50 years, elimination of hydrologic linkages and seasonal sheet flows shifted the MacKay Tract's seasonal hydrological cycles. Between 1947 and 1954, parts of the MacKay Tract drainage were altered by culverts, canals, and retention ponds. Seeps fed the marsh in the past but these are no longer present (L. Ehrhart, Emeritus Professor, University of Central Florida, pers. comm.; Figure 1).

Data Collection

Using aerial photographs (Publication of Archival Library and Museum Materials: Aerial Photography Florida, Florida Department of State; 1940, 1947, 1954, 1957, 1966, 1974, 1984, 2002), we described the change in area covered with sawgrass between 1940 and 2002. We imported images into Adobe Photoshop, visually sketched the limits of sawgrass, and calculated its proportional contribution to the total study area. Sawgrass cover was readily identified because of its lighter color and solid texture. We divided the MacKay Tract polygon identified as sawgrass in 1940 into three regions: (1) current (by 2002 aerial photograph) sawgrass, (2) current intermediate tree cover, and (3) current dense tree cover. These strata allowed us to better sample the gradient of current tree canopy cover compared to a completely random site-selection procedure. We used a random point selection procedure (Hawth's Analysis Tools v3.2 2006) for Arc Map (ESRI v9.1) to establish three reference points within each stratified region (total $N = 9$ plots). Each random reference point was located in the field using a GPS (Trimble Pro-XR, Trimble Navigation Limited, Westminster, Colorado, 1 m accuracy) and marked with a 1.5 m polyvinyl chloride (PVC) pole.

Within a 15 m radius around each reference point, we mapped, identified, and measured the stem (or stems) diameter (Forestry Suppliers diameter tape, accuracy 1 cm) of each tree $\leq$ 10 cm dbh. This diameter cutoff clearly distinguished trees from shrubs. We estimated the basal area of each tree assuming circular shapes for every stem transversal area, and summed areas for each tree and plot. In each plot, we located four points 5 m from a reference point in the four cardinal directions, and used them as centers of 2 m diameter circular subplots. We recorded all vascular plants within each subplot and counted the number of *Acer rubrum* seedlings and live and dead sawgrass tussocks. We identified species using Wunderlin and Hansen (2003) and its supporting online database (Wunderlin and Hansen 2004). We estimated species richness and calculated diversity using Shannon-Wiener Index (H') and Simpson's Index (L) and their corresponding transformations (Magurran 1988).

$$H' = -\sum_{i=1}^{s}(p_i \ln p_i),$$

and its transformation,

$$e^{H'} = \exp(H').$$

$$L = \sum_{i=1}^{s} p_i^2,$$

and its transformation,

$$D = \frac{1}{L},$$

Data Analysis

We used linear regression to assess the association between tree basal cover with red maple seedlings, and with live and dead sawgrass tussocks, and the relationship between living and dead sawgrass tussocks with red maple seedlings. We ordinated our plots using Nonmetric Multidimensional Scaling (NMS) (PC-ORD v5.0; Mather 1976; McCune and Grace 2002) with Sorensen as a distance measure. We started with a random configuration and ran 100 iterations with 50 runs for real data and 20 for randomized data. We assessed dimensionality using 0.005 standard deviations in stress as stability criteria. We repeated this procedure three times to evaluate solution stability.

RESULTS

Sawgrass marsh decline

Total area occupied by open sawgrass marsh within the MacKay Tract has declined dramatically since 1940 (Figures 1,2). In the last aerial photograph of the series (2002), sawgrass marsh accounted for only 11.8% of the area originally covered in 1940. In 2002, only three isolated patches remained: 1.18, 3.22, and 7.81 ha, respectively. All three patches were even

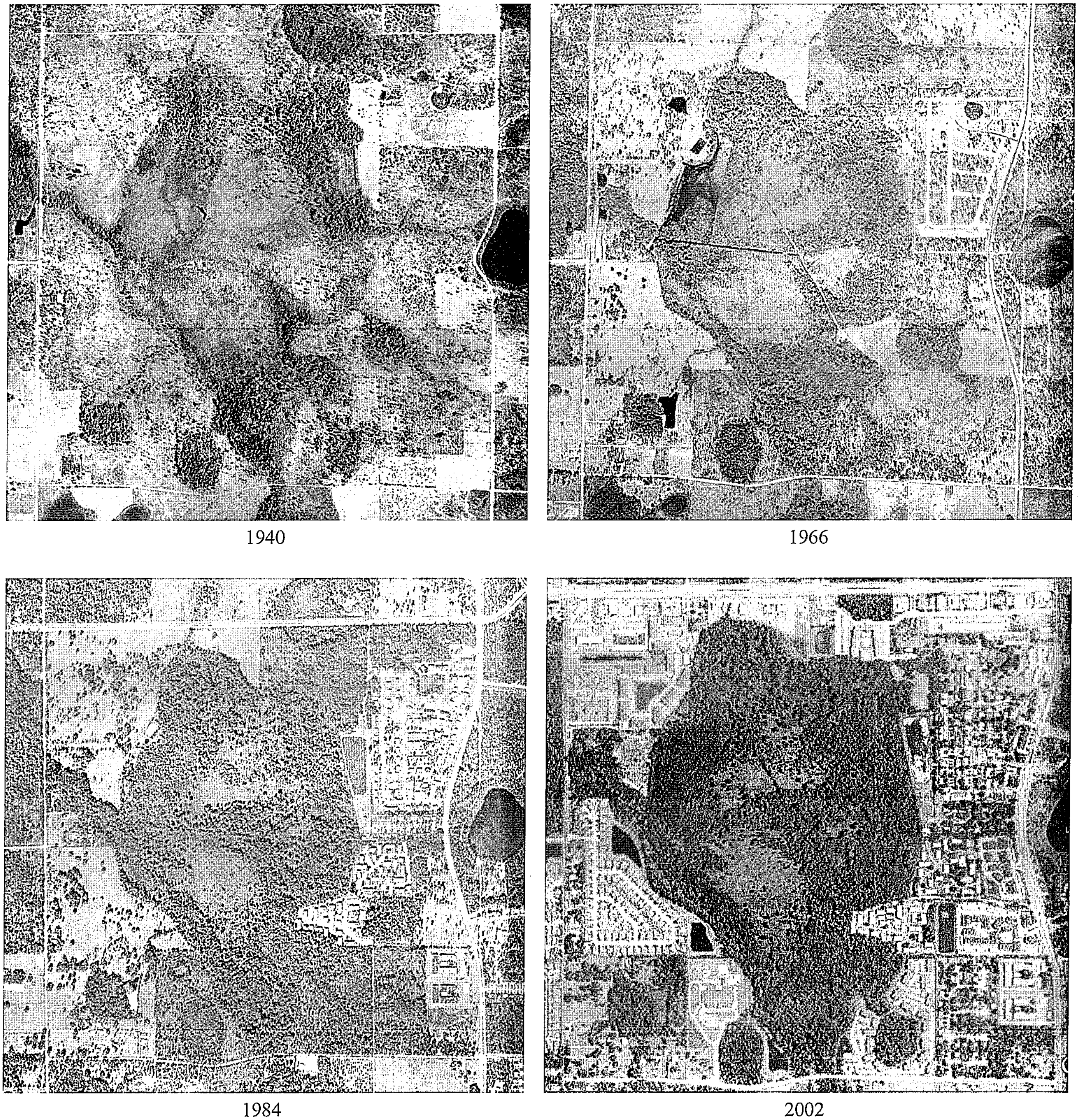

Figure 1. Aerial photographs (by year) of the The MacKay Tract, a wetland in unincorporated Orange County, Orlando, Florida. Notice the increasing tree cover, number of retention ponds and urbanization in detriment of sawgrass. The natural water body east of the MacKay Tract is Lake Lee.

smaller by spring 2008 (J. Fauth, pers. obs.). This decrease in sawgrass cover was associated with a relative increase in area covered by retention ponds (Figures 1, 2), which first appear in the 1954 aerial photograph. Four are apparent in the 1966 photograph, three northwest and one southwest of the MacKay Tract. The circular wetland surrounded by a nascent development in the 1966 image is a natural depressional wetland (Figure 1).

Tree abundance and sawgrass distribution

Our plots varied in tree cover. Two plots had no trees > 10 cm dbh while the remaining seven plots had 10 tree species

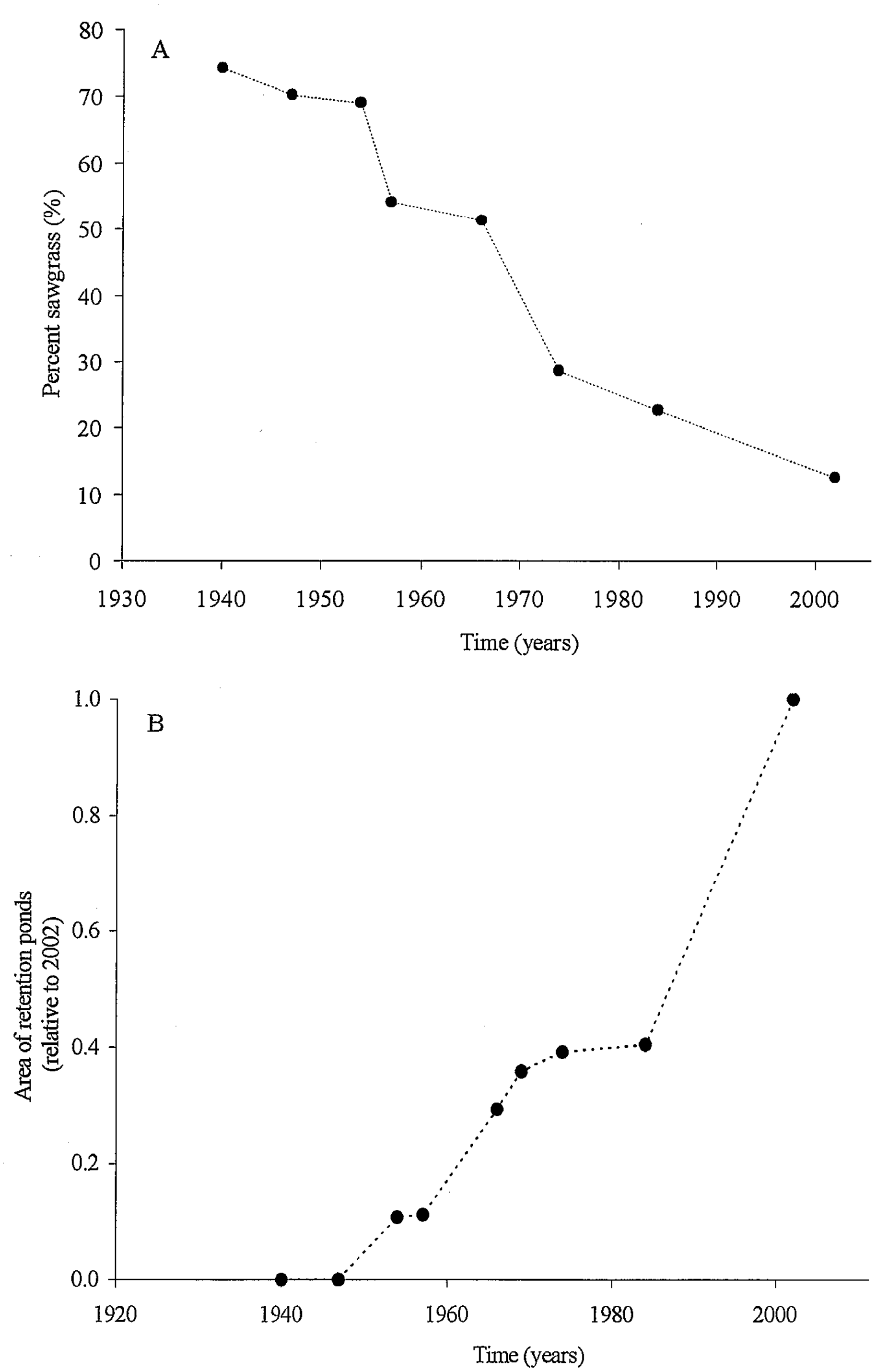

Figure 2. Change in percent area identified as open sawgrass (A) and retention ponds (B; relative to 2002) within the MacKay Tract based on digitized aerial photographs from 1940-2002.

(Table 1). Density of trees > 10 cm dbh varied between 4-20/plot and total basal cover ranged from 0.42-1.85 m^2 /plot (plot area = 706.9 m^2). Red maple was the dominant tree species, comprising > 70% of the individuals and > 80% of basal cover in four plots, and between 19%-49 % of basal cover in three other plots.

Tree cover affected live sawgrass and red maple seedling density but was independent of dead sawgrass tussocks. We found a significant "U" shaped quadratic association between basal tree cover and number of live sawgrass tussocks (Figure 3; P = 0.02). Basal tree cover was significantly and positively associated with density of red maple seedlings (Figure 4; P = 0.05). Plot 1 contributed to explain, but did not completely determine, the "U" shape of the association between basal tree cover and number of live sawgrass, and had disproportionate influence (Mahalonobis = 2.0; Quinn and Keough 2002) in the regression between basal area and red maple seedlings. Its elimination did not change the rank of the quadratic model between basal tree cover and live sawgrass, but improved the fit of the model for basal tree cover and maple seedlings ($r^2 = 0.91$ without the outlier). This plot had 10 maple trees (> 10 cm dbh) surrounded by open areas dominated by sawgrass. These trees contributed to the large basal area, and characterized a very different assemblage (see ordination below) transitional between open sawgrass marsh and the more closed-canopy assemblages. Numbers of red maple seedlings (data log +1 transformed) were negatively related to live sawgrass tussocks (Figure 5; P < 0.001). Dead sawgrass tussocks were not significantly associated with live sawgrass, tree basal cover, or density of red maple seedlings.

Understory species diversity

We found a total of 54 vascular plant species in our 2 m diameter circular subplots (Appendix). Understory species richness was highest in Plot 1 (25 understory species; D = 19.69 and $e^{H'} = 21.80$), which had the highest red maple basal cover, and in Plot 9, which had the most tree species (24 understory species; D = 18.85 and $e^{H'} = 20.94$). Understory species richness was lowest in sawgrass-dominated plots (2-8 species; D = 2.00-6.23 and $e^{H'}$ = 2.00-6.94). There was a nearly significant quadratic relationship (Figure 6; P = 0.067) between tree basal density and understory species richness.

Two-dimensional NMS reached a final solution after 60 iterations (Figure 7; P = 0.004 that a similar final stress could have been obtained by chance). The first axis explained 27% and the second axis explained 34% of the variance based on

Table 1. Number of trees (> 10 dbh) and basal area (m^{-2}; in italics) per 706.8 m^2 plot in the MacKay Tract, Orlando, Florida. Current forest canopy assessed from 2002 aerial photographs. Numbers in the heading identify the plots.

	Tree canopy category by 2002								
	Intermediate			Low			High		
Tree species	1	2	3	4	5	6	7	8	9
Acer rubrum L.	10 *1.85*	17 *1.20*	5 *1.25*	4 *0.18*			2 *0.04*	5 *0.64*	1 *0.08*
Gordonia lasianthus (L.) Ellis			1 *0.02*						
Ilex cassine L. var. *cassine* Dahoon			1 *0.30*					4 *0.10*	
Magnolia virginiana L.							3 *0.04*		13 *0.20*
Persea borbonia (L.) Spreng.								2 *0.23*	1 *0.01*
Pinus elliottii Engelm.								2 *0.58*	
Quercus laurifolia Michx.									1 *0.01*
Quercus nigra L.									2 *0.10*
Quercus virginiana P. Mill.									1 *0.02*
Unknown		1 *0.01*							
Total	10 *1.85*	18 *1.21*	7 *1.57*	4 *0.18*	0 0	0 0	5 *0.08*	13 *1.55*	19 *0.42*

the r^2 between distances in ordination and original space. Tree basal cover was positively correlated with the first axis ($r^2 = 0.65$). Sawgrass was positively correlated with the second axis ($r^2 = 0.89$), while red maple seedlings were negatively correlated with this axis ($r^2 = 0.45$). Several other species associated with disturbed areas (e.g. *Erechtites hieraciifolius* (L.) Raf. ex DC. [fireweed], *Eupatorium capillifolium* (Lam.) Small [dogfennel], *Morella cerifera* (L.) Small [wax myrtle], and *Rubus* spp. [blackberries]) were significantly negatively correlated with this second axis (Appendix). Nine other plant species were positively correlated with the first axis while *Osmunda cinnamomea* L. (cinnamon fern) was negatively associated with it (Appendix). *Callicarpa americana* L. (American beautyberry) was positively associated with the first and negatively associated with the second axes.

DISCUSSION

Human alteration of fire and hydrological regimes and cessation of cattle grazing likely caused the major decline of sawgrass cover and the increased tree basal area within the MacKay Tract. We do not know what other parameters changed, but it is conceivable that they include sedimentation rate, nutrient enrichment, or a number of other factors influenced by concomitant land-cover changes. Our study is consistent with previous evidence that boundaries among wetlands and adjacent vegetation are dynamic and influenced by water level and disturbances (Peroni and Abrahamson 1986; Landman and Menges 1999; Warren, II et al. 2007; Matlaga et al., unpubl. data). Marshes with an interrupted fire regime have a greater amount of woody species and lianas, while regularly burned marshes develop a larger and more diverse herbaceous assemblage (Imbert and Delbe 2006). Cattle grazing can help to maintain wetland community diversity and affects

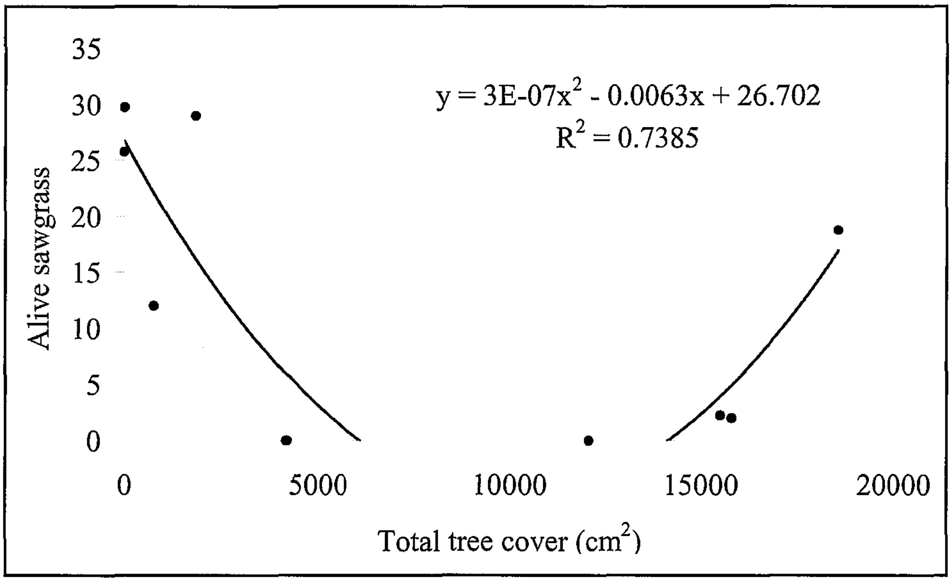

Figure 3. Regression between live sawgrass and total tree basal cover (cm^2 per 706.86 m^2 circular plot) on nine plots within the MacKay Tract, Orlando, FL.

hydrological conditions. In the Central Valley of California, plant and aquatic faunal diversity were higher and cover of exotic annual grasses lower in continuously grazed than ungrazed vernal-pools. Higher evapotranspiration due to the abundant vegetation in the ungrazed treatment reduced pool inundation (Marty 2005). However, excessive grazing by livestock decreases plant cover and diversity and increases water turbidity, deteriorating habitat conditions (Jansen and Healey 2003).

The complex interaction of fire and hydrology likely determine sawgrass marsh persistence (Pendergrass et al. 1998). Without reintroducing fire and restoring seasonal flooding, impoverished hammocks dominated by red maple will continue to replace sawgrass within the MacKay Tract. Tree encroachment of sawgrass is self-reinforcing because the presence of mature trees increases seedling recruitment by red maple and other woody species. There is evidence of burning: fire scars in *Acer rubrum* cored in some parts of the MacKay Tract (C. Knickerbocker, pers. obs.). However, these scars are difficult to date because *A. rubrum* does not yield clear seasonal rings. Historically, sawgrass communities burned every 3-25 years, usually near the low end of this estimate (Wade et al. 1980). Prescribed burns are routinely used to maintain pastures in Florida, and the presence of burn scars, cattle trails (too narrow to be discerned on Figure 1), and a pasture road with a corral on its southeast terminus are evidence of active cattle grazing until at least 1966.

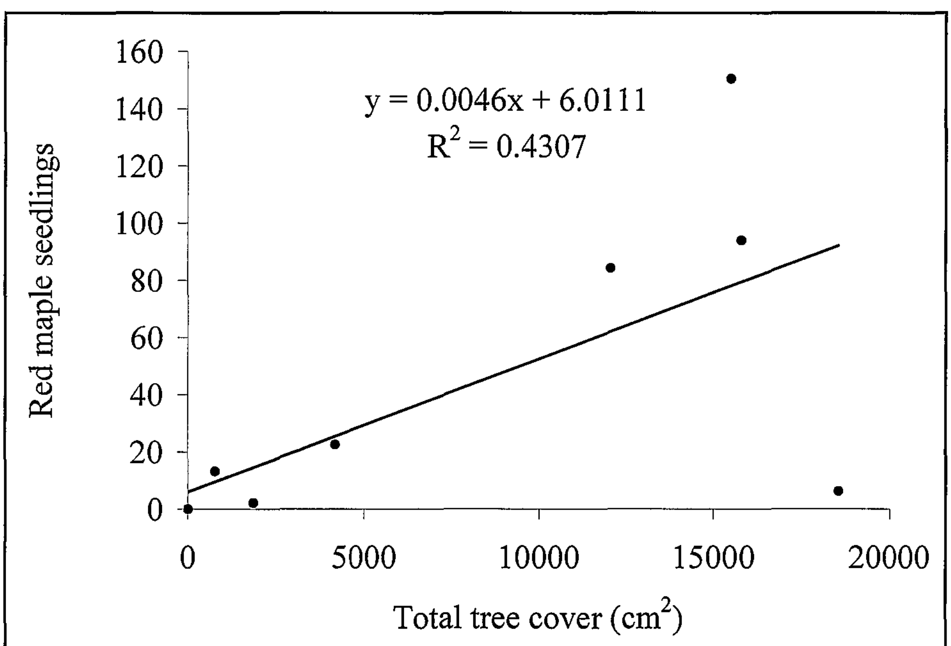

Figure 4. Regression of total tree basal cover (cm^2 per 706.86 m^2 circular plot) as a function of red maple seedlings on nine plots within the MacKay Tract, Orlando, FL.

Although sawgrass is fire tolerant (Forthman 1973; Steward and Ornes 1975; Lee et al. 2005) and intense fires may be partially responsible for maintaining sawgrass habitats (Craighead 1971; Gunderson and Snyder 1994), sawgrass may not survive some fires, particularly those closely followed by flooding. For example, it is difficult for sawgrass to survive post-fire floods if all leaves are completely inundated (Herndon et al. 1991). Historically, waters entered the MacKay Tract's sawgrass marsh from Lake Lee to the east, numerous isolated seeps to its north and east, a small stream in its northwest corner, and wetlands to its south. Waters flowed west out of the marsh, into the Econlockhatchee River floodplain. During the time span we evaluated, the MacKay Tract was drained using canal systems, and subsequent urbanization and road improvements were accompanied by retention ponds that retained stormwater, withholding additional water from the marsh and reducing seasonal flooding.

However, sawgrass is generally well-adapted for intermittent drier periods. In Yucatán, Mḗxico, it is most frequent in nutrient-poor wetlands with occasional droughts (Rejmankova et al. 1996). In the Everglades, sawgrass is dominant in areas that are most susceptible to both drying and burning (King et al. 2004). In areas with relatively uniform hydrological conditions (marsh flats), fire helps to define the border between communities dominated

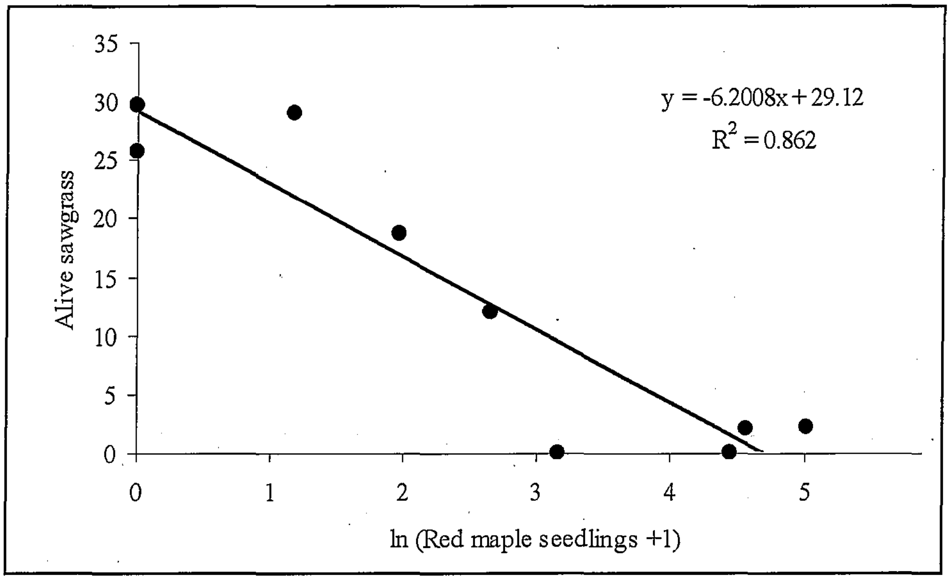

Figure 5. Linear relationship between red maple seedlings (ln transformed) and live sawgrass on nine plots within the MacKay Tract, Orlando, FL.

by sawgrass and maidencane (*Panicum hemitomon* J.A. Schultes) (Lowe 1986). Management directed to restore sawgrass on the MacKay Tract will need to identify burn seasons and hydrological regimes maximizing plant recovery.

The synergistic effect of fire suppression and altered water flow at the MacKay Tract was associated with changes in community structure. Our community ordination indicated two main environmental gradients. The first one increased with tree basal area (mostly red maple) and with the relative importance of weedy shrubs and herbs. Stands in the higher end of the second gradient were located in more central areas of the MacKay Tract and were characterized by sawgrass, no or few trees, and very low plant diversity.

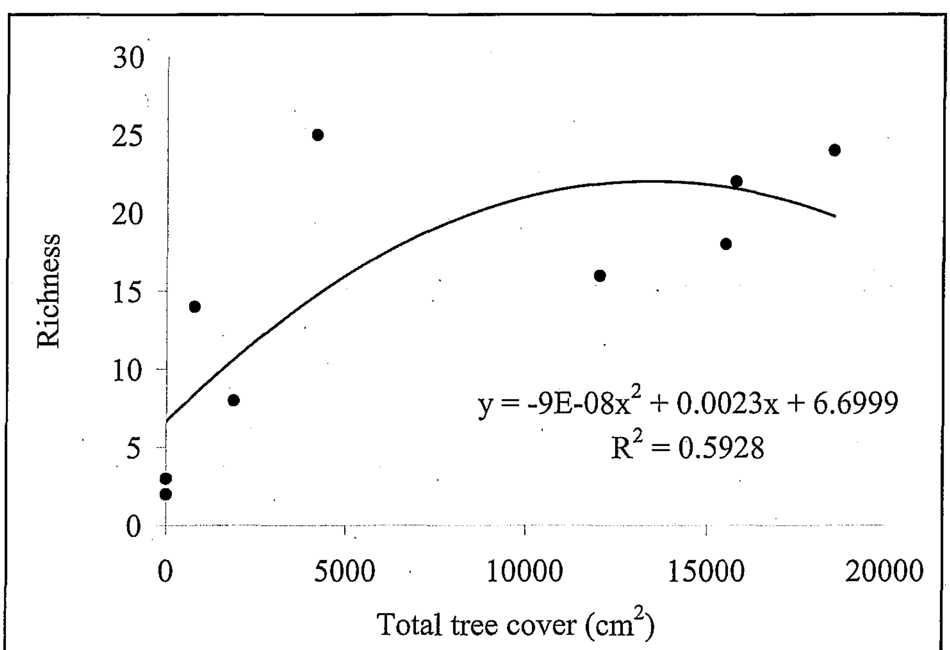

Figure 6. Quadratic relationship between tree basal cover and understory species richness on nine plots within the MacKay Tract, Orlando, FL.

These stands are remnants of the more extensive sawgrass community that once dominated the property, as seen on aerial photographs. Stands with higher values on the first gradient occupied transitional areas, had more trees and larger tree basal cover, and plant assemblages dominated by weedy shrubs and herbs. Within the past 40 years, these stands have replaced sawgrass. Stands with intermediate values on the second gradient also had low values on the first gradient, which differentiated hydric hammocks dominated by *Magnolia virginiana* L. in the canopy and *Osmunda cinnamomea* in the understory from transitional stands dominated by red maple and a diverse herbaceous assemblage.

Our data indicate ruderal species are gaining importance in the remnant sawgrass marshes within the MacKay Tract. There was a positive relationship between understory species richness and basal tree density. Loss of sawgrass due to fire suppression and reduced water levels may release space and nutrients for other herbaceous species (Niering 1985). However, many of the new species (particularly in transitional stands where red maple was dominant) were weedy shrubs and herbs. Damage caused by Hurricane Charlie in 2004 also reduced the tree canopy, opening light gaps and allowing greater intrusion by ruderal and invasive species.

Reintroducing appropriate hydrologic and fire regimes is essential to maintaining the sawgrass marshes in the MacKay Tract. Our data suggest that further encroachment may be controlled with prescribed fire and restoration of historic hydrologic regimes. Because of decades of fire suppression and tree encroachment, large trees and shrubs may need to be removed manually and several burns performed before sawgrass marshes are completely reestablished (e.g., Clark and Wilson 2001). While initial fire re-introduction enhanced wet prairie physiognomy of the Willamette Valley in Oregon, fall-season, low-intensity burns were not enough to eliminate shrub and tree cover (Pendergrass et al. 1998). Similarly, dormant-season fires reduced cover and basal area of *Salix caroliniana* Michx. in a floodplain marsh in east-central Florida, but repeated fires had greater effects than a

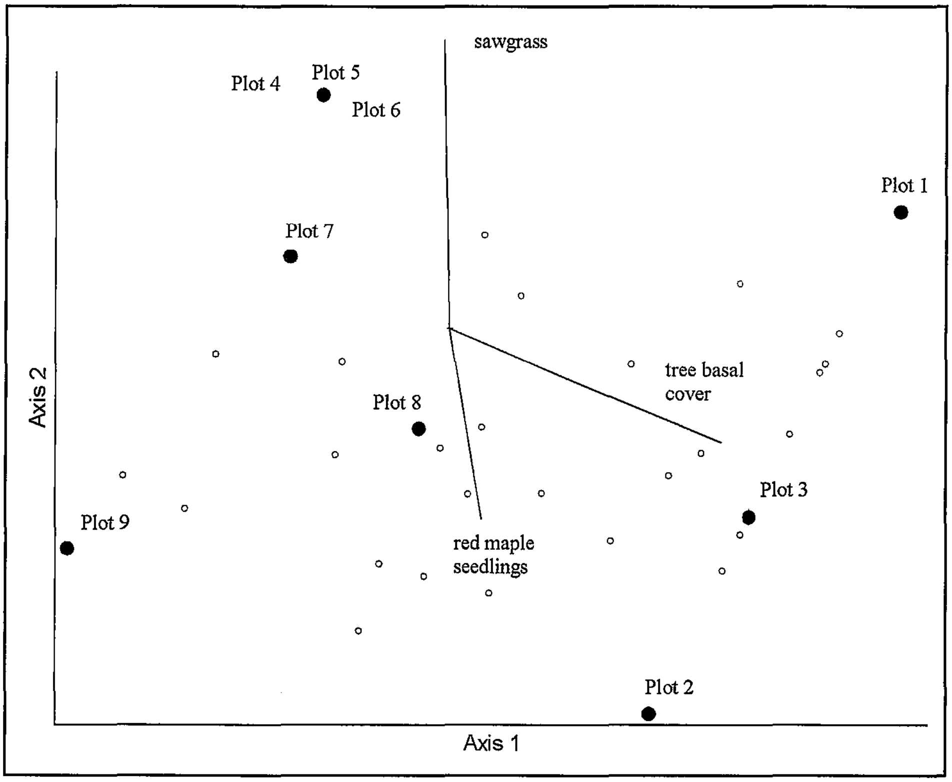

Figure 7. Nonmetric multidimensional scaling plot for understory vascular plant species within the MacKay Tract, Orlando, Florida. Lines indicate direction and strength of association with sawgrass tussocks, red maple seedlings and tree basal cover.

single fire (Lee et al. 2005). It is our hope that such management practices will be implemented before the isolated sawgrass wetland within the MacKay Tract changes permanently.

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Appendix. Understory plant species per plot in the MacKay Tract (spring 2007). Numbers indicated frequency in four 2 m diameter circular subplots. The correlation coefficient ($P < 0.001$) of species associated with the NMS ordination axes is indicated. Numbers in the heading identify the plots. T = total frequency across all plots.

	Tree canopy category by 2002											
	Intermediate			Low			High					
Species	1	2	3	4	5	6	7	8	9	T	Axis 1	Axis 2
Acer rubrum L. (seedlings)	3	4	4	2	0	0	4	4	4	25		-0.78
Arisaema triphyllum (L.) Schott	0	0	0	0	0	0	0	0	1	1		
Baccharis halimifolia L.	0	0	0	0	0	0	1	0	0	1		
Callicarpa americana L.	1	4	4	0	0	0	0	0	0	9	0.67	-0.68
Carex albolutescens Schwein.	4	2	4	0	0	0	0	0	0	10	0.92	
Carex sp.	4	0	0	0	0	0	0	0	0	4		
Centella asiatica (L.) Urb.	0	0	0	0	0	0	1	0	0	1		
Cladium jamaicense Crantz	4	0	4	4	4	4	3	3	0	26		0.78
Commelina diffusa Burm f.	3	0	2	0	0	0	0	0	0	5	0.82	
Cyperus sp.	2	0	0	0	0	0	0	0	0	2		
Cyperus surinamensis Rottb.	1	0	0	0	0	0	0	0	0	1		
Dichanthelium commutatum (Schult.) Gould	1	0	1	2	0	0	0	2	0	6		
Erechtites hieraciifolius (L.) Raf. ex DC.	2	3	2	0	0	0	0	4	2	13		-0.77
Eupatorium capillifolium (Lam.) Small ex Porter & Britton	1	4	4	0	0	0	3	3	4	19		-0.93
Galium tinctorium L.	4	3	4	0	0	0	0	3	0	14	0.89	
Hydrocotyle umbellata L.	4	4	3	0	0	0	0	2	1	14	0.84	
Hypericum sp.	0	1	0	0	0	0	0	1	1	3		-0.76
Juncus sp.	0	0	0	0	0	0	0	0	1	1		
Leucothoe axillaris (Lam.) D. Don	0	0	0	3	0	0	0	0	0	3		
Magnolia virginiana L.	0	0	0	0	0	0	0	0	3	3		
Mikania scandens (L.) Willd.	1	4	1	0	0	0	0	3	0	9		
Morella cerifera (L.) Small	0	1	1	0	0	0	0	0	1	3		-0.86

continued

Appendix. Continued.

Species	Tree canopy category by 2002: Intermediate 1	2	3	Low 4	5	6	High 7	8	9	T	Axis 1	Axis 2
Osmunda cinnamomea L.	0	0	0	4	4	4	4	4	4	24	-0.91	
Oxalis debilis Kunth var. *corymbosa* (DC.) Lourteig	1	0	0	0	0	0	0	0	0	1		
Parthenocissus quinquefolia (L.) Planch.	0	0	1	0	0	0	1	2	2	6		
Polygonum spp.	4	1	3	0	0	0	3	2	0	13	0.71	
Ptilimnium capillaceum (Michx.) Raf.	3	0	0	0	0	0	0	0	0	3		
Quercus sp. (seedlings)	0	0	0	0	0	0	0	1	2	3		
Rubus sp.	0	4	2	0	0	0	1	0	4	11		-0.86
Rumex verticillatus L.	2	0	0	0	0	0	0	0	0	2		
Sabal palmetto (Walter) Lodd. ex Schult. & Schult. f.	0	0	1	0	0	0	0	0	0	1		
Saururus cernuus L.	1	0	1	0	0	0	0	0	0	2	0.81	
Scirpus cyperinus (L.) Kunth	1	0	0	0	0	0	0	0	0	1		
Smilax sp.	0	0	0	0	0	0	2	0	1	3		
Sphagnum spp.	0	0	3	1	0	0	0	3	2	9		
Thelypteris interrupta (Willd.) K.Iwats.	2	4	4	0	0	0	0	0	0	10	0.78	
Tillandsia recurvata (L.)L.	2	0	0	0	0	0	0	1	0	3		
Toxicodendron radicans (L.) Kuntze	1	0	0	0	0	0	0	0	0	1		
Typha sp.	0	2	0	0	0	0	0	0	0	2		
Vitis sp.	2	0	0	1	0	0	3	2	4	12		
Xanthosoma sagittifolium (L.) Schott	0	0	0	0	0	0	0	0	1	1		
unknown 1	0	2	0	0	0	0	0	0	2	4		-0.74
unknown 2	3	1	1	0	0	0	0	0	0	5	0.87	

continued

Appendix. Continued.

	Tree canopy category by 2002											
	Intermediate			Low			High					
Species	1	2	3	4	5	6	7	8	9	T	Axis 1	Axis 2
unknown 3	0	0	1	0	0	0	0	0	0	1		
unknown 4	0	0	0	0	0	2	0	0	0	2		
unknown 5	0	0	0	0	0	0	1	0	0	1		
unknown 6	0	0	0	0	0	0	1	0	3	4		
unknown 7	0	0	0	1	0	0	0	0	0	1		
unknown 8	0	0	0	0	0	0	0	2	0	2		
unknown 9	0	0	0	0	0	0	0	0	3	3		
unknown 10	0	0	0	0	0	0	0	0	1	1		
unknown 11	0	0	0	0	0	0	0	0	1	1		
unknown 12	0	0	0	0	0	0	0	0	1	1		
unknown 13	0	0	0	0	0	0	0	0	2	2		
Total	25	16	21	8	2	3	13	17	24			