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Factors influencing cattail abundance in the northern Everglades

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Abstract

Since the early 1900s, the Everglades have been influenced by anthropogenic actions including altered hydrology and increased nutrient loading. In the northern Everglades an apparent effect of these disturbances has been the development and proliferation of dense cattail (*Typha* spp.) stands in areas previously dominated by sawgrass (*Cladium jamaicense* Crantz) and sloughs. Cattail cover, soil nutrient concentrations, topography and fire history were determined for the Holey Land and Rotenberger Wildlife Management Areas, located in the northern Everglades. These data were analyzed using multiple regression to assess the relative influence of fire, hydrology and soil nutrients on cattail abundance. Holey Land and Rotenberger were overdrained over recent decades which resulted in soil compaction and nutrient accumulation, illustrated by increased soil bulk densities and elevated nutrient storage. Average bulk densities were 0.13 g cm^{-3} for Holey Land and 0.22 g cm^{-3} for Rotenberger. Average total P (TP) stored in the surface 10 cm of soil in Holey Land and Rotenberger were 7 and 13 g m^{-2}, respectively. In contrast, Everglades soils uninfluenced by nutrient enrichment and with less severe overdrainage have bulk densities of 0.07 g cm^{-3} and TP storage of 4 g m^{-2}. Typically, elevated soil P concentrations have been considered a primary factor influencing cattail growth and distribution in the Everglades. With the apparent absence of P limitation in Holey Land and Rotenberger, cattail abundance was influenced by either fire or hydrology. Forty-six percent of the variation of cattail cover in Holey Land was explained by elevation, indicating that increased water depth and duration of flooding have a

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significant impact on cattail expansion. In Rotenberger, fire was the most influential factor, explaining 57% of the variation in cattail cover. Hydrology was the second most important factor limiting cattail abundance. Published by Elsevier Science B.V.

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1. Introduction

The plant communities of the Everglades developed within a subtropical, rain-driven system. The resultant plant community is adapted to many environmental conditions including periodic fire, fluctuating hydroperiod, and low nutrient (specifically phosphorus) conditions (Craighead, 1971; Steward and Ornes, 1983; Cohen, 1984). During the beginning of this century the Everglades was impacted by the construction of an extensive system of canals and levees, built to meet flood control and water storage needs of the growing urban and agricultural development. These activities resulted in alterations in hydrology and water quality of the Everglades (Walters et al., 1992; Light and Dineen, 1994; McIvor et al., 1994). One effect of hydrologic management has been the conversion from an open, flowing system with water broadly distributed, to a compartmentalized system consisting of a mixture of both drained and impounded areas (Fennema et al., 1994). In drained areas the water table has been lowered by > 2 m (Wade et al., 1980). The overdrainage of the area likely contributed to the large number of severe fires that were recorded throughout the 20th century: 1926, 1928, 1937, 1943, 1945–1947, 1951, 1952, 1962, 1965, 1971, and 1973 (Davis, 1943; Craighead, 1971; Hofstetter, 1984). Many of these fires were intense, burning the top layers of peat, and in some places burned down to the underlying limestone (Craighead, 1971). Where peat burning fires (muck fires) occurred in sawgrass marshes the vegetation changed to aquatic plants in ponds and sloughs (Craighead, 1971).

In the Water Conservation Areas (WCA), which are impounded areas within the northern Everglades, the effect of altered hydrology has, in some sections, been increased water depths and extended hydroperiod (South Florida Water Management District, 1992; Richardson et al., 1994). These hydrologic changes have significantly affected the vegetation community composition. Vegetation shifts within the northern Everglades have been particularly evident along canals and near inflow structures where monospecific stands of sawgrass and sloughs have been converted to vegetative communities dominated by cattail (Richardson et al., 1990; Davis, 1994; Rutchey and Vilchek, 1994; Jensen et al., 1995). Several field and laboratory studies demonstrate that *Typha domingensis* Pers., the dominant species of cattail in the Everglades, is well adapted to the increased water depths and extended hydroperiods (Grace, 1987, 1988). In contrast, although sawgrass can survive complete submergence for approximately six weeks (Lynch, 1942; Wade et al., 1980), field observations suggest that sawgrass is adversely affected by deeper water (Toth, 1987, 1988). Direct comparisons between sawgrass and cattail have been limited; however, a recent study suggests that cattail will outcompete sawgrass in deeper waters (Newman et al., 1996).

In addition to the differences in hydrologic adaptations of cattail and sawgrass, available evidence suggests that these species also have different nutrient requirements

(Toth, 1987, 1988; Davis, 1991; Koch and Reddy, 1992). Historically, nutrient supply to the Everglades was provided primarily through rainfall (Davis, 1943; Parker, 1984); thus, the native vegetation was selected for low nutrient requirements (Steward and Ornes, 1983). Increased nutrient loading to the area has produced elevated nutrient concentrations in both the surface water and the soils. Studies indicate that sawgrass growth is adapted to low nutrient environments and in the Everglades sawgrass is P-limited. The addition of P to sawgrass resulted in increased biomass or increased P uptake in both field and greenhouse enrichment experiments (Steward and Ornes, 1975, 1983; Craft et al., 1995). In contrast, cattail species are frequently indicators of disturbed and nutrient-rich environments (Dykyjova and Kvet, 1978; Grace and Harrison, 1986; Keddy, 1990).

Studies of plant invasions have repeatedly shown that the combination of disturbance and altered habitat conditions promote the displacement of native vegetation by introduced or formerly restricted species (Groves and Burdon, 1986; Mooney and Drake, 1986). In the Everglades, disturbance due to muck fire, alteration of hydroperiod, and increased nutrient inputs have all been implicated as factors that can affect the development and proliferation of cattail stands in areas previously dominated by sawgrass (Toth, 1987, 1988; Davis, 1991; Herndon et al., 1991; Urban et al., 1993). The objectives of this paper are: (1) to describe the invasion of cattails into an area of the northern Everglades, i.e., Holey Land and Rotenberger Wildlife Management Areas and (2) to develop a hypothesis of the relative importance of fire, soil nutrients and hydrology in cattail proliferation in the Everglades.

2. Study areas

The study areas encompass Holey Land and Rotenberger Wildlife Management Areas, both located in the northern Everglades. Holey Land is a 14,000 ha, predominately sawgrass marsh. During World War II and the Korean War, the southern portion of the area was used as a bombing range, hence the name ‘Holey’. Currently, no physical evidence of this disturbance is discernable from viewing the surface or topography of the area. However, the area has been degraded by decades of overdrainage, muck fires, and invasion by upland plant species. Holey Land was historically comprised of sparse to dense sawgrass marshes with scattered shrub thickets and sloughs (Davis, 1943). After a period of 30 yrs, the plant community had changed significantly (Cornwell and Hutchinson, 1974). Cornwell and Hutchinson (1974) classified the vegetation into four major communities: old field–weed association with scattered shrubs (44%), sawgrass prairie (30%), shrub association (*Sambucus/Myrica/Baccharis/Salix*) (20%), and deeply burned and/or barren areas (6%). Overdrainage also caused much of the topography of Holey Land to change due to oxidation and subsidence of organic peat soils. These events created conditions favorable for muck fires that have further changed the topography by causing localized areas of even lower elevation. To restore the natural Everglades habitat of Holey Land, a restoration project consisting of a levee system, culverts and pumps was constructed and completed in late 1989. Water now enters Holey Land from a pump at the northwest corner and exits the area through three gated culverts in the southern levee. Following the implementation of the pumping, approximately 80% of Holey Land surface area is inundated >9 months a year.

In contrast, Rotenberger has not been impounded to restore hydroperiod and primarily receives all water inputs through rainfall. The hydroperiod of this 12,000 ha wetland is driven by regional weather patterns. Water levels are typically ≤ 0.3 m throughout the year, with a 5–8 month hydroperiod. The dominant vegetation within Rotenberger is sawgrass. Other vegetation communities include cattail stands, scattered small tree islands, *Myrica cerifera* (wax myrtle) and *Panicum* spp. Two sections along the eastern edge were farmed and sawgrass grows in rows in this area. These two sections were excluded from any analyses.

3. Methods

3.1. Cattail cover

The boundaries of the cattail areas within each of the study areas were delineated using a helicopter and Loran. The percent cover of cattail from 1992 to 1994 was determined by aerial sampling. The delineation was conducted in two phases. In the first phase all cattail stands in the two areas were located by systematically traversing the entire area. Latitude and longitude coordinates were taken at all extensive areas (>8 ha) of cattail growth. After completing the initial survey each of the areas was mapped by collecting latitude and longitude coordinates along their perimeters. The following day these areas were revisited and the perimeter locations were verified.

The second phase of the cattail mapping process used an aerial point-sampling scheme. At an elevation of 213 m, a 4×5 grid of cross hairs spaced at 4 cm intervals (20 intersections of cross hairs per grid) was held parallel to the ground. An observer looked through the grid and the number of points landing on cattails, sawgrass, willow and openwater were recorded. Two hundred points were recorded within each of the defined cattail areas. Points were recorded by two observers, resulting in a total of 400 points per area. The percent cover estimate error was calculated as the difference between the two observer estimates divided by the value of the lowest observer estimate. Over 75% of the total estimated hectares of cattail had observer estimates differing by less than 5%. Holey Land cattail cover data for 1990 and 1991 were obtained from Gilbert (1991).

3.2. Soil nutrients

Soil samples were collected at 36 and 31 sites in Holey Land and Rotenberger, respectively. A polyvinyl chloride (PVC) coring tube (10 cm i.d.) was slowly driven at least 30 cm into the soil using a sledge hammer. The surficial 0–10 cm soil sections were removed from the coring tube, placed in plastic bags on ice, and transported to the laboratory. Samples were stored at 4°C until analyzed. A subsample of soil was weighed and dried at 70°C for 72 h or until a constant weight was obtained. Bulk density was determined. Ash content was determined by combusting the dried samples at 550°C in a muffle furnace. Total P was determined from acid-digested samples (Methods 365.4 and 365.2 of the US Environmental Protection Agency, 1983). Total N and TC were determined from finely ground soil samples using a Carlo-Erba NA 1500 C–N–S analyzer (Haak-Buchler Instruments, Saddlebrook, NJ). Phosphorus extracted with HCl (1:50 soil to solution ratio) was used as an estimate of the inorganic pool of P. One half gram of air dry soil was extracted with 1 M HCl for 3 h, then filtered through a 0.45 μm membrane filter. The filtrate was analyzed for inorganic P (Method 365.1 of the US Environmental Protection Agency, 1983). In this study plants are surveyed based on area, so soils data are corrected for bulk density and analyzed on an areal basis (g m^{-2}) unless otherwise stated.

3.3. Elevation, water depth and hydroperiod

Two representative continuous recording stage gauges were selected in Holey Land and Rotenberger to estimate average annual water depths.

Elevation was determined by extensive water depth sampling in both areas. Six surface water depths were measured at each intersection along a 0.5 min latitude/longitude grid. Sampling sites were determined to ± 0.05 minutes to allow for drift in Loran readings. Totals of 1176 and 894 water depths were taken at 196 and 149 sites in Holey Land and Rotenberger, respectively. A flat surface water slope was assumed and ground elevations were obtained by subtracting the six-point average water depth from the corresponding stage gauge reading. These elevations were compared to historic stage gauge readings to estimate the length of time water levels were aboveground (i.e., hydroperiod).

3.4. Fire

Fire is typically separated into two groups, surface, i.e., vegetation burns, versus peat or muck fires when the soil is also burnt. Surface wild fires occur almost annually, while muck fires are more intensive and less frequent causing a greater and longer lasting disturbance to the vegetative community. Only muck fires were considered in this study. Maps delineating muck burned areas since 1981 were digitized. These maps were originally developed during aerial reconnaissance trips to monitor wildfire status. The approximate position was documented through comparisons with surrounding landmarks (e.g., canals, levees, water gauges).

3.5. Statistical analyses

Ash content, bulk density, TP, TN, HCl Pi and percent cattail cover were log-transformed to normalize the data and obtain homogeneous variances before statistical analyses. A value of one was added to each cattail percent cover value prior to transformation to avoid the creation of missing values following log transformation of zero values. Elevation and presence or absence of muck fires were not transformed.

Soils data were collected at 36 and 31 sites in Holey Land and Rotenberger in 1993 and 1994, respectively. Vegetation data from the same years and same sites as the soil samples were used for statistical analyses. All data were analyzed using SAS, version 6.09 (SAS institute Inc., 1989). Correlations were obtained using Pearson correlation coefficients. Multiple regressions were run using the option to determine the r^2 of all possible regression models.

4. Results

4.1. Cattail cover

Cattail cover within Holey Land increased each year from 1990 to 1994 (Fig. 1). The initial invasion in 1990 was in isolated areas, but by 1993 over 25% of the marsh interior consisted of 10% or greater cattail (Fig. 2). Cattail density also increased over time, manifested as increased percent cover in existing cattail areas (data not shown). Cattail spread in Rotenberger was relatively slow, increasing from 930 ha in 1992 to 1200 ha in 1994, compared to an increase from 570 to 2200 ha in Holey Land over the same time period. To compare with other well-documented cattail invasions in the Everglades, the rate of spread was contrasted with that observed in WCA 2a (Fig. 1). The initial rate of cattail increase in Holey Land was more rapid than that observed in WCA 2a. Cattail cover in WCA 2a and Holey Land increased exponentially with time, with r^2 of 0.99 and 0.95, respectively (Fig. 1).

4.2. Soil nutrients

The surface soils of both wildlife management areas are peat with a varying amount of inorganic material with average ash contents of 28.6 and 18.8% for Holey Land and

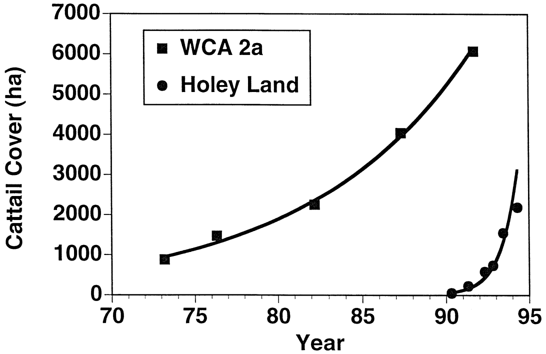
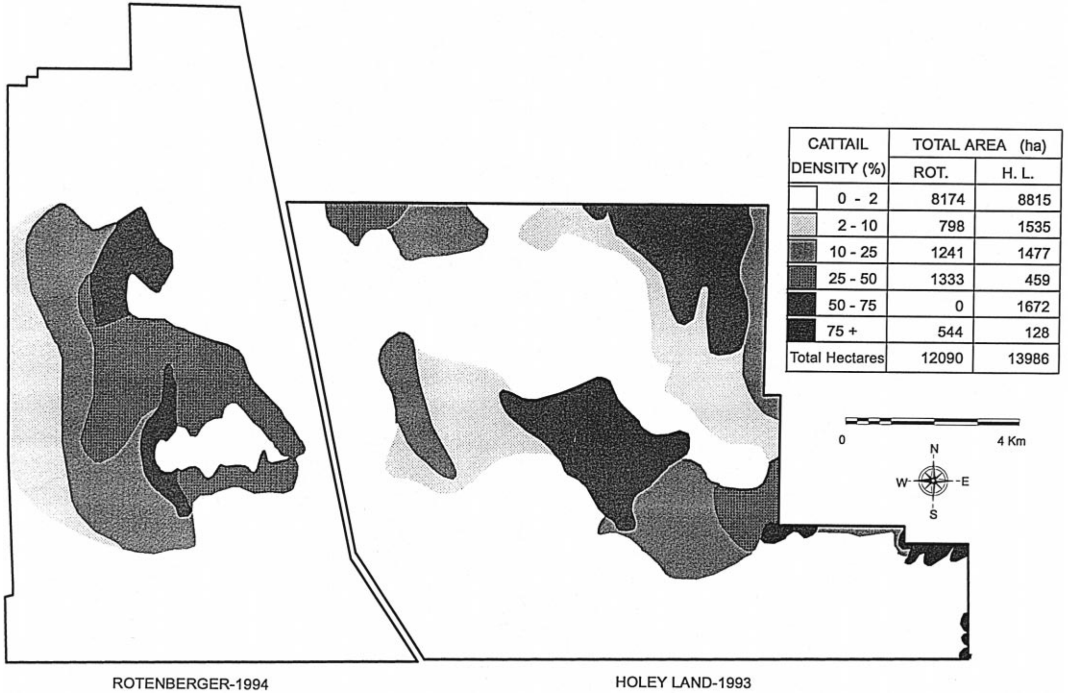


Fig. 1. Increase in cattail abundance over time in Holey Land and WCA 2a (WCA 2a modified from Jensen et al., 1995).



ROTENBERGER-1994

HOLEY LAND-1993

CATTAIL DENSITY (%)	TOTAL AREA (ha)	
	ROT.	H. L.
□ 0 - 2	8174	8815
░ 2 - 10	798	1535
▒ 10 - 25	1241	1477
▓ 25 - 50	1333	459
■ 50 - 75	0	1672
■ 75 +	544	128
Total Hectares	12090	13986

Fig. 2. Cattail distribution (percent cover and total area) in Rotenberger in 1994 (ROT) and Holey Land in 1993 (H.L.).

Table 1
Physicochemical properties of Holey Land and Rotenberger Wildlife Management Area soils (mean ± SE)

Site	N	Bulk density ($g\ cm^{-3}$)	Ash content (%)	Total C ($g\ kg^{-1}$)	Total N ($g\ kg^{-1}$)	Total P ($mg\ kg^{-1}$)	HCl Pi[a] ($mg\ kg^{-1}$)
Holey Land	36	0.131 ± 0.01	28.6 ± 3.3	403 ± 16	25.5 ± 1.1	543 ± 53	299 ± 53
Rotenberger	31	0.216 ± 0.02	18.8 ± 1.4	475 ± 8	32.9 ± 0.5	594 ± 26	101 ± 13

[a] HCl-extractable inorganic P.

Rotenberger, respectively (Table 1). As anticipated based on the higher ash content, Holey Land also had a higher concentration of inorganic P. In contrast, the bulk density of Rotenberger soils was 1.6 times greater than the bulk density of Holey Land soils. Concentrations of total C, N and P were similar in both areas (Table 1). Total P concentrations of Holey Land and Rotenberger soils were similar to those measured in the WCA (Table 2). In contrast, following correction for bulk density and soil depth Holey Land and Rotenberger had elevated TP and inorganic P concentrations compared to the WCA (Table 2).

4.3. Elevation, water depth and hydroperiod

Holey Land elevation ranged 2.7 to 4 m NGVD. A distinct low point was associated with the muck burnt area in the northeast corner. In contrast, the elevation range for Rotenberger, 3.4 to 3.8 m NGVD, was much narrower. Average water depths recorded from two representative points in each of the marsh interiors are shown in Fig. 3. Prior to a change in the Holey Land water regulation schedule in 1990 and continuous pump operation in 1991 typical water depths during the wet season were less than 0.2 m. These depths were similar to those observed in the unimpounded, rain-fed Rotenberger. Following the Holey Land water schedule change, typical water depths in Holey Land exceeded 0.6 m throughout the wet season. The northeast corner of Holey Land was

Table 2
Comparison of TP concentrations and TP storage in surface soils (0–10 cm) in the northern Everglades (mean ± 1 SE)

Site	N	Bulk density ($g\ cm^{-3}$)	TP ($mg\ kg^{-1}$)	TP ($g\ m^{-2}$)	HCl Pi[a] ($mg\ kg^{-1}$)	HCl Pi ($g\ m^{-2}$)
Holey Land	36	0.131	543 ± 53	7.38 ± 0.95	230 ± 53	4.36 ± 0.91
Rotenberger	31	0.216	594 ± 26	13 ± 1.28	101 ± 13	2.15 ± 0.35
WCA 1	90	0.064	540 ± 40	3.75 ± 0.48	165 ± 18	1.14 ± 0.18
WCA 2a	74	0.068	671 ± 48	4.54 ± 0.39	223 ± 21	1.54 ± 0.18
WCA 3	101	0.131	461 ± 20	5.47 ± 0.31	160 ± 8	1.97 ± 0.18

[a] HCl-extractable inorganic P.

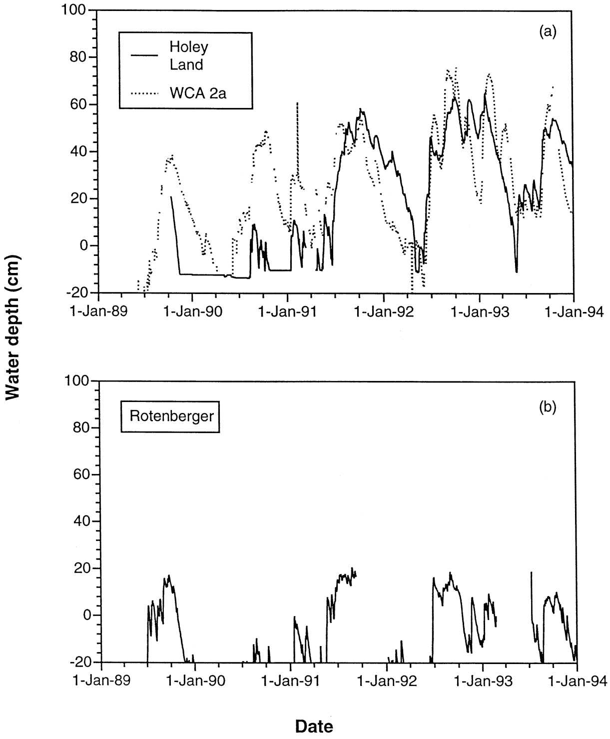


Fig. 3. Typical water depths measured using stage recorders in (a) Holey Land and WCA 2a, and in (b) Rotenberger.

ponded and experienced water depths in excess of 1 m. Shallower water depths were observed in the southwest and southern portions of the area.

The extent of inundation was different for both areas (Table 3). Over 80% of Holey Land's area was inundated for > 9 months a year during 1991–1993. In contrast, < 1% of Rotenberger's area was inundated for > 9 months. Rotenberger typically experienced a 5–8 month hydroperiod over 81% of the area.

4.4. Fire

Holey Land was impacted by severe muck fires in 1981, 1982, 1984, and 1989. The largest muck fire occurred in 1981 and encompassed 2200 ha in the northeast corner and burnt the surface 2 to 56 cm, with remnant soil only 5 cm above bedrock in some places. Areas which were ponded year round tend to correspond to the areas burned by muck fire.

Four muck fires were documented in Rotenberger. Over the last 20 yrs only two were greater than 100 ha and these occurred in 1981 and 1994. The 1981 muck burn encompassed 2088 ha in the interior of Rotenberger marsh.

Table 3
Duration of inundation in Holey Land and Rotenberger Wildlife Management Areas

Period of Inundation (months)	Percent area affected, 1991–1993	
	Holey Land	Rotenberger
12	0.01	0
11–12	45.24	0
10–11	23.79	0
9–10	12.41	0.76
8–9	9.70	7.80
7–8	4.66	31.53
6–7	2.36	19.98
5–6	0.56	29.21
4–5	0.68	7.92
3–4	0.13	2.09
2–3	0.22	0.70
1–2	0.10	0
0–1	0.14	0

4.5. Statistical analyses

Pearson correlation coefficients were used to suggest trends between the variables measured in this study (Table 4). Cattail cover was negatively correlated with elevation in both Holey Land and Rotenberger, −0.68 and −0.65, respectively. Positive correlations were found between cattail cover and months of inundation. Cattail cover was also positively correlated with the presence of muck fire; correlation coefficients were 0.45 and 0.75 for Holey Land and Rotenberger, respectively. Generally, weaker correlations were obtained with soil parameters. Cattail cover was correlated with both forms of P and ash content in Holey Land but cover was only correlated to HCl Pi in Rotenberger. In both areas, elevation was negatively correlated with muck fires.

Table 4
Correlation matrix for selected variables in soils of Holey Land and Rotenberger Wildlife Management Areas

Variable	Elevation	Muck fire	Ash content	Bulk density	Total P	Total N	HCl Pi[a]	Months[b]
Holey Land								
Cattail cover	−0.68	0.445	0.612	0.421	0.426	NS	0.520	0.540
Elevation		−0.576	−0.481	NS	−0.359	NS	−0.432	−0.772
Muck fire			NS	NS	0.341	NS	0.366	NS
Ash content				0.609	0.776	−0.417	0.922	0.445
Rotenberger								
Cattail cover	−0.648	0.754	NS	NS	NS	NS	0.451	0.605
Elevation		−0.598	NS	NS	NS	NS	NS	−0.976
Muck fire			NS	NS	NS	NS	NS	0.601
Ash content				0.827	0.824	0.702	0.589	NS

[a] HCl-extractable inorganic P.
[b] Period of inundation.
NS = not significant.

Regression analyses of the two datasets showed that cattail cover was explained by different factors in the two sites. The best significant one- and two-factor models were:

Holey Land

$\ln(\text{cattail cover} + 1) = -1.88 \cdot \text{elevation} + 22.23 \qquad r^2 = 0.46$

$\ln(\text{cattail cover} + 1) = -1.39 \cdot \text{elevation} + 0.93 \ln(\text{ash content}) + 13.99 \qquad r^2 = 0.57$

Rotenberger

$\ln(\text{cattail cover} + 1) = 2.28 \cdot \text{muck fire} + 0.38 \qquad r^2 = 0.57$

$\ln(\text{cattail cover} + 1) = 1.73 \cdot \text{muck fire} - 2.00 \cdot \text{elevation} + 24.75 \qquad r^2 = 0.63$

Fifty seven and 63% of the variation in cattail cover is thus explained by two factors in Holey Land and Rotenberger, respectively. The number of months of inundation, elevation and fire was the best three variable model for the Rotenberger data.

5. Discussion

Rotenberger is a rain-fed area with a typically reduced hydroperiod compared to other managed regions of the northern Everglades. Drier conditions increase the susceptibility of Rotenberger vegetation and soils to fire. The 1981 muck burn location is congruent with the area currently dominated by cattail, suggesting that fire is the dominant variable influencing cattail distribution in the Rotenberger landscape. This relationship between muck fire and cattail in Rotenberger is emphasized by the absence of cattail in the unburnt center of the 1981 muck fire area and the explanation of 57% of the variability in cattail cover in Rotenberger by muck fires. Fire can influence plant growth by changing many factors, including remobilization of soil nutrients, changing local topography and providing openings in the landscape. No significant correlation was observed between TP and muck burnt areas in Rotenberger and only a small correlation in Holey Land. This suggests that nutrients were not remineralized or did not remain at the site of remineralization. Muck burnt areas and elevation were inversely correlated in both Rotenberger and Holey Land indicating that fire may have resulted in lower surface elevations (Table 4). Depressions in the wetland landscape will become ponded and experience extended hydroperiods. In addition, the removal of surface vegetation and soil by fire provides an opening in the landscape (Craighead, 1971). Such a severe disturbance provides a competitive advantage to plants with rapid vegetative growth and aerial seed dispersal, such as cattail. In contrast, sawgrass has a slower expansion rate and the seeds are dispersed through water column movement.

In contrast to Rotenberger, the impoundment of Holey Land resulted in the conversion of the wetland from a rain-fed system with substantial dry periods to an impounded, almost continuously flooded, system. Holey Land experienced elevated water depths and extended hydroperiod when compared to both Rotenberger and WCA 2a. Such conditions provide a competitive advantage to *Typha domingensis* which has been shown to grow in water depths > 1.2 m for sustained periods (Grace, 1987, 1988). Recent experimental results also confirm that the combination of elevated nutrients and increased water depth will favor the growth of cattail over sawgrass in the Everglades (Newman et al., 1996). In addition, multivariate analysis of cattail growth in WCA 2a suggests that both nutrient enrichment and extended hydroperiod favor cattail proliferation (Urban et al., 1993). Holey Land data support these conclusions with 46% of the variation in cattail cover explained by a single variable, elevation. Emergent macrophytes can adapt to variations in water level but an extended increase in water depth, as observed in Holey Land, tends to drown out many species. Thus, an opening appears in the landscape providing an invasion opportunity for a rapid growing, responsive species such as cattail. Cattail invasion in Holey Land was initially associated with slough areas or other openwater environments (J. Shortemeyer, personal communication, Florida Game and Fresh Water Fish Commission, Naples, FL). It is anticipated that the rate of cattail expansion will decrease as the slough areas decrease and cattail competes with existing dense stands of sawgrass.

Throughout the northern Everglades cattail expansion is typically associated with water control structures, canals and areas of increased P concentrations (Richardson et al., 1990; Davis, 1994; Rutchey and Vilchek, 1994). The coincidence of hydrologic and nutrient impacts has fueled a debate over the relative importance of increased P loading versus altered hydrology on cattail expansion in this ecosystem (Davis, 1991, 1994; Richardson et al., 1994). The invasion of cattail into Holey Land coincided with both the impounding of the area and increased water supply from an adjacent canal system. Comparisons between cattail cover and water quality characteristics within Holey Land showed a significant correlation among all the nutrients making it difficult to examine individual effects (Smith, 1994). The P load associated with the increased water supply during the 2.5 yrs of pumping canal water into Holey Land was approximately 54 metric tonnes (Shih et al., 1992). However, the patchy nature of the cattail growth is not one which suggests a relationship between growth and inflow concentrations. Using average soil TP concentrations and bulk densities, TP storage within the surface 0–10 cm of soil was calculated. The mass of externally supplied TP is small compared to the 1017 metric tonnes TP stored within the surficial 0–10 cm of Holey Land soil, suggesting soil P may influence cattail distribution more than P loaded within inflow waters. In other areas of the northern Everglades strong relationships between soil P and cattail growth have been documented (Richardson et al., 1990; Davis, 1991; Koch and Reddy, 1992; Urban et al., 1993; DeBusk et al., 1994). Spatial analyses of the vegetation species, soil TP concentrations and topography of WCA 2a indicated that sawgrass will be replaced by cattail when soil TP concentrations exceed 650 mg kg^{-1} (Wu et al., 1997). Of the 36 soil sites in Holey Land, only eight had soil TP concentrations greater than the 650 mg kg^{-1} threshold proposed by Wu et al. (1997).

As bulk densities increase from 0.1 to 0.4 g cm^{-3} a linear increase in plant growth has been documented in other systems (DeLaune et al., 1979; Barko and Smart, 1986). When soil TP is corrected for bulk density and soil depth both Holey Land and Rotenberger have elevated soil TP compared to other areas of the Everglades (Table 2). This suggests that both Holey Land and Rotenberger have sufficient P to support cattail expansion and that is why other factors may have more influence on cattail expansion in these areas. However, macrophyte growth in unenriched areas of the Everglades is typically P limited (Steward and Ornes, 1975, 1983; Craft et al., 1995) and higher soil

TP (g m^{-2}) may have contributed to the greater initial growth rate of cattail in Holey Land relative to other regions of the northern Everglades (cf. Fig. 1). In contrast, Rotenberger is sufficiently dry most of the year that growth may be limited by water and the difficulty of invading dense stands of sawgrass. However, while developing this hypothesis it is recognized that the form of P in the soils will influence its bioavailability. Holey Land soils have inorganic P values two-fold higher than any of the other northern Everglades soils. Also, inorganic P is positively correlated with cattail cover. Inorganic P is directly taken up by higher plants and is readily available to support growth (Marschner, 1986). Organic P, the primary form of P stored in Everglades soils, requires remineralization to inorganic P before it can be utilized for growth. Elevated levels of inorganic P are also associated with the enriched cattail dominated zone in WCA 2a (DeBusk et al., 1994).

Combining the data from this study with literature published elsewhere we developed a hypothesis of the importance of fire, nutrients and hydrology in different regions of the Everglades. Hydrology and P have been shown to produce a combined advantage for cattail invasion (Newman et al., 1996). In Holey Land, which already has high TP storage, we hypothesize that hydrology is the primary factor influencing cattail growth (Fig. 4). Regression analysis suggests that following hydrology, ash content is the second dominant variable influencing cattail abundance. The ash content of soil is a reflection of both the mineral content and/or the fire history. The ash content is correlated with soil nutrient concentrations. Because inorganic nutrients are more readily available for plant uptake than organic forms, areas of higher ash content may have a

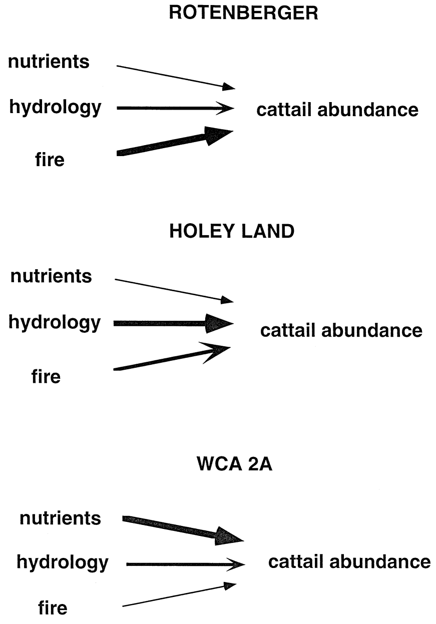


Fig. 4. Hypothesized relative importance of dominant variables influencing cattail abundance in the northern Everglades (the thicker the arrow the greater the relative importance).

higher nutrient availability. Nutrients were the third factor influencing cattail abundance (Fig. 4).

In contrast, Rotenberger is a rain-fed system, which does not support the interactive advantage of soil nutrients and deeper water which facilitates cattail invasion. Thus, we hypothesize that muck fire is the primary factor facilitating cattail invasion (Fig. 4). The ability of the area to burn is a function of hydrology. Elevation, an indication of hydrologic conditions, was the second most significant factor in the cattail cover model for Rotenberger and therefore may be the secondary controlling factor, with nutrients again coming third (Fig. 4).

For comparison, in an area which developed a nutrient gradient over time, cattail expansion in WCA 2a was shown to be controlled by soil TP concentrations (Wu et al., 1997). The area is impounded and does not have the same history of severe muck burns experienced by Holey Land and Rotenberger. Thus, we hypothesize that hydrology will be the secondary factor influencing cattail growth in WCA 2a (Fig. 4).

6. Conclusions

Comparisons of fire, nutrients and hydrologic effects on cattail growth in the northern Everglades marshes suggest that these interactions are site-dependent (Fig. 4). Overdrainage and the resultant soil oxidation facilitates accumulation of soil nutrients. It is hypothesized that because of existing elevated nutrient storage in the soils of Holey Land and Rotenberger, cattail growth there will principally be controlled by other factors. In the absence of nutrient limitation, cattail proliferation in Holey Land is controlled hydrologically. Thus, efforts to reduce the rate of cattail expansion should focus on reduced water depths, and potentially reduced hydroperiod. Cattail distribution in Rotenberger is primarily determined by historic muck fires. Increased hydroperiod in this area will reduce the potential for fire but may increase the potential for cattail invasion due to the high levels of TP in the soils. However, the relative importance and bioavailability of the inorganic component of the TP pool requires further study to test this portion of the hypothesis. This relationship is particularly significant in south Florida where efforts are being made to restore the hydroperiod of the managed Everglades.

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