Why do Cattails (Typha spp.) Dominate Wetlands on the Western Great Plains

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16. Abstract

Cattails are among the most widespread and abundant plant species in wetlands throughout the northern temperate zone.. Many marshes are affected by road construction requiring compensatory mitigation through the restoration and/or creation of wetlands. Since the goal of most mitigation projects is to replace the type of wetland lost, understanding how to create and restore wetlands that are dominated by species other than cattail, and that will not eventually be invaded by cattail is critical to agencies and individuals involved in compensatory mitigation.

This research addresses two major questions: (1) does the establishment of vegetation by the planting of nursery grown stock provide any short-term or long-term resistance to the invasion of cattails in newly created wetlands, and (2) is it possible to determine the hydrogeologic niche of cattail, so that sites that are not conducive to cattail invasion can be created. Specifically we wanted to understand whether competition with other species of marsh plants at several different water depths affects cattail growth. We also wanted to identify a suite of hydrologic and geologic factors that naturally limit cattail growth. These objectives were addressed in two separate field studies during the 1998 growing season on the eastern plains of Colorado.

Implementation

The results of this study recommend that cattail invasion can be limited, at least in the short term, by competition with other tall wetland species such as soft-shoot bulrush and prairie cordgrass. Management of hydrological site conditions can further discourage cattail invasion by flooding sites to a depth of 50 centimeters in the early summer, followed by varying water levels as much as possible throughout the growing season. Hydrologic management in controlling cattails will be most effective when the salinity in the wetland is kept as high as possible.

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INTRODUCTION

Cattails (*Typha* spp.) are among the most widespread and abundant plant species in wetlands throughout the northern temperate zone (Mitsch and Gosselink, 1993). Cattails dominate marsh wetlands that have seasonal standing water in glaciated prairies (van der Valk and Davis 1978), along the margins of the Great Lakes (Robb 1989), in California basins (Hofstetter 1983) and many other areas. Cattail often form dense, highly productive monospecific stands. The success of cattails has been linked to its abundant, aerially dispersed seed that can germinate under a wide range of environmental conditions (Stewart et al. 1997, Lombardi et al. 1997). Cattail rhizomes develop quickly and grow long, allowing the rapid spread of clones (D'Amico 1996). Cattails also have very high photosynthetic efficiency, fixing approximately 4 to 7% of the photosynthetically active radiation received, a rate similar to the most efficient crop plants (Mitsch and Gosselink 1993). Cattails also reach their photosynthetic peak and maximum growth rate very early in the growing season (Dykyjova and Kvet 1978), allowing it to grow when few other perennial species are active. Cattails are also highly invasive, for example the cattail invasion into the sawgrass (*Cladium jamaicense*) marshes of the Florida Everglades is well documented (Davis and Ogden 1994).

Marshes are the most common and widespread wetland type on the Great Plains in the central United States, and in many intermountain basins throughout the West. Many marshes are affected by road construction requiring compensatory mitigation through the restoration and/or creation of wetlands. Since the goal of most mitigation projects is to replace the type of wetland lost, understanding how to create and restore wetlands that are dominated by species other than cattail, and that will not eventually be invaded by cattail is critical to agencies and individuals involved in compensatory mitigation.

Our research addresses two major questions: (1) does the establishment of vegetation by the planting of nursery grown stock provide any short-term or long-term resistence to the invasion of cattails in newly created wetlands, and (2) is it possible to determine the hydrogeologic niche of cattail, so that sites that are not conducive to cattail invasion can be created. Specifically we wanted to understand whether competition with other species of marsh plants at several different water depths affects cattail growth. We also wanted to identify a suite of hydrologic and geologic factors that naturally limit cattail growth. These objectives were addressed in two separate field studies during the 1998 growing season on the eastern plains of Colorado.

STUDY SITES

The effect of competition on cattail growth was studied at the State of Colorado Department of Transportation's constructed wetland just east of Limon, in eastern Colorado (Figure 1). The mean annual precipitation at Limon is 39 cm. The study wetland is a series of five shallow ponds that receive some ground water but are filled largely by water pumped from an adjacent stream.

The effect of hydrologic and geologic factors on cattail growth was studied at ten wetland complexes in eastern Boulder County (Figure 2). Mean annual precipitation at the Boulder climate station is 48 cm. The wetlands chosen for study are those typical of the western Great Plains, including natural playas, marshes, reservoir margins, constructed wetlands, and abandoned gravel pits (Table 1).

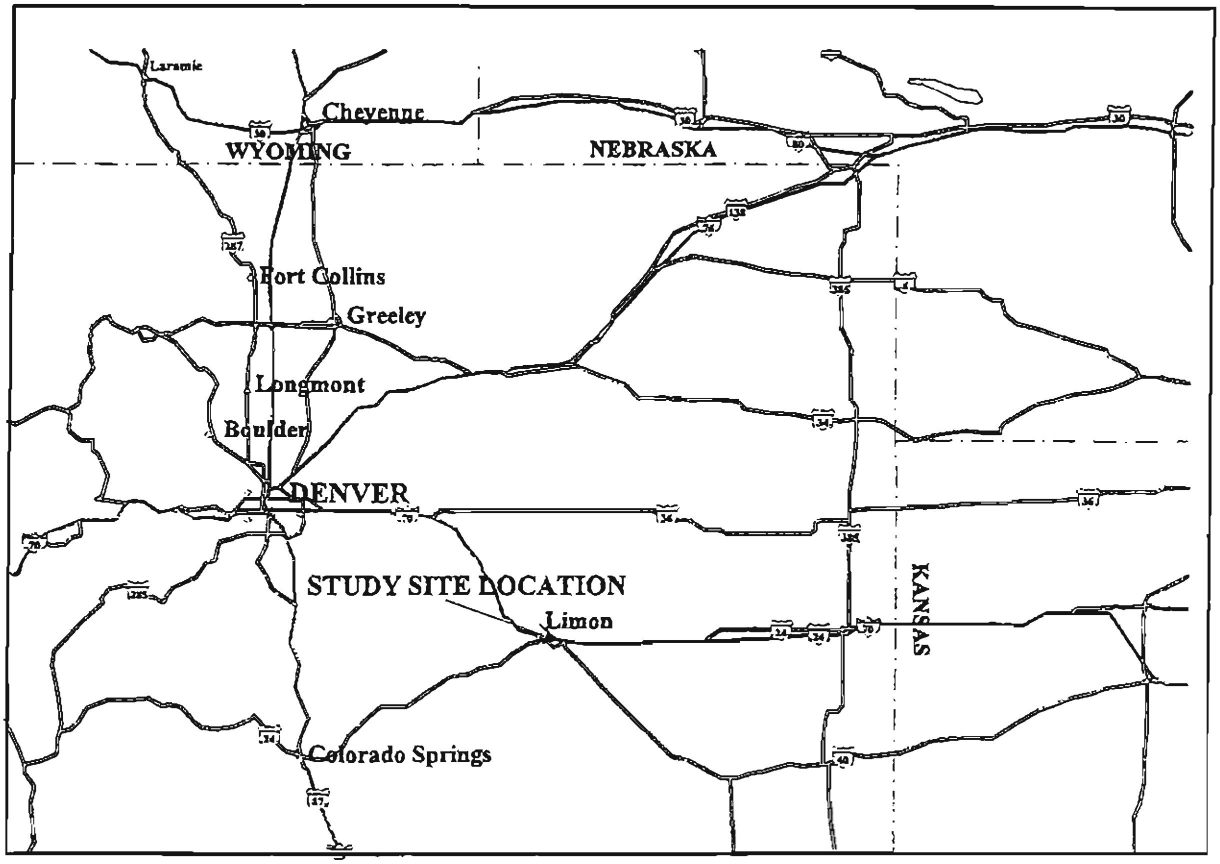

Figure 1. Location of study site for competition study. Study was conducted in a constructed wetland in Limon in eastern Colorado.

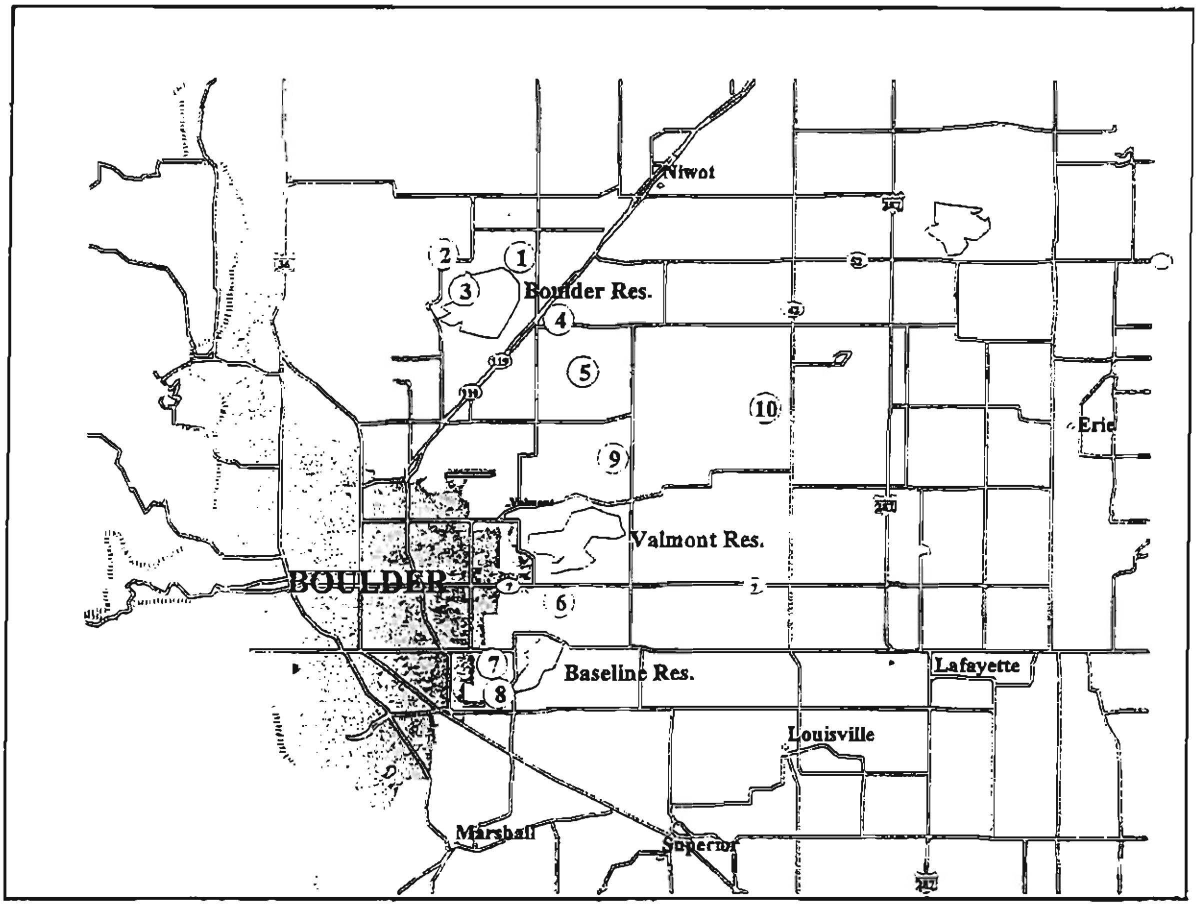

Figure 2. Locations of study sites in Boulder County, Colorado. Sites are indicated by numbered circles. Key to sites: 1.Coot Lake, 2. Dry Creek Pond, 3. Boulder reservoir, 4. Eleocharis playa, 5. Twin Lakes marsh, 6. Sombrero Marsh, 7. Kentucky property, 8. Boulder Recreation Center, 9. Sawhill Ponds, 10. Culver property.

Table 1. Summary descriptions of wetland sites used for study of hydrologic and geologic controls on cattail occurrence.

Site name	Description
1. Boulder Reservoir	1. Primary water supply reservoir for City of Boulder.
2. Coot Lake	2. Abandoned gravel pit north-east of Boulder Reservoir. Owned and maintained as Open Space land by City of Boulder Parks.
3. Eleocharis Playa	3. Salt flat (playa) type wetland with intermittent standing water during periods of rainfall. Dominated by spikerush (*Eleocharis palustris*).
4. Dry Creek Pond	4. Constructed pond on Dry Creek, which flows into Boulder Reservoir. Inflow and outflow points are controlled by subsurface drains.
5. Twin Lakes	5. Groundwater fed cattail marsh on the north side of Twin Lakes. Wetland was formerly larger, but development has encroached on wetland margins.
6. Boulder Recreation Center	6. Constructed marsh type wetland comprising a strip of land between S.Boulder Recreation Center and South Boulder Creek. Wetland surface is graded to create varied topography with water levels at or close to the surface in depressions and below the surface for most of the year in higher areas.
7. Sombrero Marsh	7. Groundwater fed saline marsh with permanent standing saline water.
8. Kentucky Property	8. Constructed wetland site with freshwater wet meadow conditions.
9. Culver Property	9. Abandoned gravel pits under ownership of City of Boulder Parks. Gravel pits are recharged by seepage from Boulder Creek, so that water levels are high during early summer but drop rapidly as the river level drops. Emergent macrophytes fringing most of the ponds.
10. Sawhill Ponds	10. Series of abandoned gravel pits now owned and maintained as a natural area by City of Boulder Parks. Gravel pits are inundated year round, creating freshwater marsh-like conditions with emergent macrophytes fringing open water up to 2m deep.

METHODS

Effect of Competition on Cattail Growth at the Limon Wetland Bank

In the winter of 1996-1997 and the spring of 1997, the study wetland basins were graded and filled with water by CDOT. Several of the basins were chosen to plant wetland species grown from seed in a commercial nursery. Plants were installed on approximately 45 cm (18 inch) centers in monospecific patches. Five plant species, three-square bulrush (*Schoenoplectus pungens*), soft-stem bulrush (*Schoenoplectus lacustris*), spikerush (*Eleocharis palustris*), prairie cordgrass (*Spartina pectinata*) and alkali bulrush (*Bobloschoenus maritimus*) grew particularly well and by late summer 1997 these species had spread to cover the ground in the zones where they were planted. Each of the five species was planted in a distinct water depth as follows: soft-stem bulrush at 15 cm water depth, alkali bulrush at 10 cm depth, three square bulrush at approximately 5 cm depth, spikerush at 2 cm water depths, and prairie cordgrass in saturated sites with no standing water.

In August 1997, we established 105 experimental plots, fifteen in each of the five main species patches described above, and 30 control plots. Ten control plots were established at each of three water depths: 0, 10 and 20 cm. Into each plot we transplanted a single section of terminal cattail rhizome approximately 15 cm in length with one shoot, transplanted from an adjacent wetland. Control plots were established by introducing a similar cattail propagule into sites where planting had not occurred. The species transplanted was narrow-leaf cattail (*Typha angustifolia*), the most common species in the study area.

All plots were identified by a metal post and a unique number on an aluminum tag. Plots were visited regularly during the fall of 1997 and summer of 1998 and a few cattail transplants that died during the winter of 1997-1998 were replaced in early spring 1998. In early October 1988 we quantified cattail growth in a 0.25 m^2 plot centered around the site of the cattail rhizome transplant. Within this plot we clipped all cattails at their base to determine aboveground cattail biomass (M_C). The clipped material was first air dried, then oven-dried at 105 C for 24 hours and biomass weighted. We also clipped all other vegetation (M_V) occurring within each plot. Cattail shoot density (D_C), maximum cattail shoot height (H_C) and maximum height of other vegetation (H_V) were also measured at each plot. Four of the treatment plots within stands of *B. maritimus* and one plot within a stand of *S. lacustris* could not be located when the clipping was done, and were not included in the analysis.

We tested for differences in the response variables (M_C, D_C, H_C and M_T) among treatments and controls using Analysis of Variance (ANOVA) and multiple comparisons. All statistical analyses were performed using the SAS statistical software package (SAS Institute, 1989). ANOVA was used to test null hypotheses that all of the treatments and controls had similar cattail biomass, height, and shoot density versus the alternative hypothesis that at least one treatment or control was significantly different from the others. Prior to analysis the data were checked to ensure that the assumptions of ANOVA were met using the procedures available in the SAS statistical package (SAS Institute, 1989). Biomass and stem density were log normally distributed and had unequal variances between treatments so they were log transformed prior to analysis. A value of one was added to all biomass and density data so that zero values could be log transformed. Stem height data were normally distributed and had approximately equal variances so they were not transformed. All plots were considered to be independent because they were well separated in space.

If results of the ANOVA indicated that the alternative hypothesis was true and differences among treatments or between one or more treatments and at least one control occurred, then multiple comparison tests were performed to determine which of the treatment-control and treatment-treatment combinations were different from each other. Multiple comparisons were used as opposed to pre-planned comparisons because all possible treatment-control, and treatment-treatment comparisons were of interest for the study. The multiple comparison method used was the Bonferroni technique, which provides a high level of protection against Type I statistical errors, but it is also less likely to detect significance in a comparison (Ott, 1993). A Type I error occurs when a difference between two populations is identified as being significant even though it is actually due to chance. Bonferroni's method protects against Type I errors by controlling both the experiment wise and comparison wise error rates. The analysis was conducted using alpha (α) values of 0.05, 0.01, and 0.001.

Hydrologic and Geologic Factors affecting cattail abundance

In May 1998, 259 study plots were established in eastern Boulder County wetlands. The study wetlands ranged in size from less than 1 acre (0.4 ha) to over 500 acres (220 ha). Each study plot consisted of a representative 1 m^2 area either within a stand of cattails or around the margins of a cattail stand. Around lakes and ponds, stands were arranged in transects perpendicular to the shoreline, extending from the inner to the outer edge of cattails. Wherever possible monospecific stands were used to avoid the potentially confounding effect of interspecific competition.

A network of 86 wells and 14 staff gages installed at the study sites in May 1998 were used to measure water levels approximately weekly during the growing season from May through September. Water levels in the plots were determined by extrapolating from the nearest monitoring point, assuming a horizontal water surface. For each plot water level data were used to determine the maximum and minimum water levels, the range in water level, and the duration of standing water during the summer of 1998. At sites around ponds and lakes the slope, aspect and fetch were measured to assess the effect of shoreline disturbance due to wave action. The electrical conductivity (EC) of water at each site was measured in mid July 1998 using a Hach electrical conductivity meter so that the effect of salinity on cattail occurrence could be determined.

In early October 1998, the density of live cattail shoots and the height of the tallest live stem in a 0.25 m^2 plot within each stand were recorded to provide a measure of the total cattail biomass. The influence of each of the hydrologic and geologic variables on cattail density and stem height was assessed separately using scatter plots and regression analyses.

RESULTS

Effect of Competition on Cattail Abundance

Total above ground biomass of all species (M_T) for all plots ranged from 74.7 g/m^2 to 1917 g/m^2, with a mean of 614 g/m^2 (Table 2). Mean total biomass for the three sets of control plots was lower than for any of the treatments (Figure 3). The lowest total biomass was in the 20 cm water depth control (C_{20}), where the mean was 375 g/m^2. The 0 cm and 10 cm water depth controls (C_0 and C_{10}) had mean biomass totals of 487 and 455 g/m^2 respectively. All of the treatment plots had similar total biomass, ranging from a mean of 598 g/m^2 in *Schoenoplectus*

Table 2. Summary statistics for competition study. Controls: C_0 = water depth of 0 cm, C_{10} = water depth of 10 cm, C_{20} =water depth of 20 cm. Treatments: BOB MAR = *Bobloschoenus maritimus*, ELE PAL = *Eleocharis palustris*, SCH LAC = *Schoenoplectus lacustris*, SPA PEC = *Spartina pectinata*, SCH PUN = *Schoenoplectus pungens*. Variables: M_C = above ground biomass of cattails, M_V = above ground biomass of all other vegetation, M_T = total above ground biomass (sum of M_C and M_V). D_C = density of cattail stems (per square meter). H_C = maximum height of cattail stems (cm), H_V = maximum height of other vegetation (cm).

Control C_0 (0 cm water depth)

Variable	N	Mean	SD	Range
M_C (g)	10	487	241	209-983
M_V (g)	10	0	0	0- 0
M_T (g)	10	487	241	209-983
D_C (m^{-2})	10	74.4	48.1	16-168
H_C (cm)	10	139	22.9	102-169
H_V (cm)	10			

Control C_{10} (10 cm water depth)

Variable	N	Mean	SD	Range
M_C (g)	10	455	112	273-623
M_V (g)	10	0	0	0-0
M_T (g)	10	455	112	273-623
D_C (m^{-2})	10	55.2	24.9	28-88
H_C (cm)	10	140	7.28	131-151
H_V (cm)	0	.		

Control C_{20} (20 cm water depth)

Variable	N	Mean	SD	Range
M_C (g)	10	375	131	201-628
M_V (g)	10	0	0	0-0
M_T (g)	10	375	131	201-628
D_C (m^{-2})	10	29.2	12.4	16-48
H_C (cm)	10	145	14.2	129-169
H_V (cm)	0	.	.	.

Treatment BOB MAR (*Bobloschoenus maritimus*)

Variable	N	Mean	SD	Range
M_C (g)	11	115	67.0	24.0-263
M_V (g)	11	578	253	203-1009
M_T (g)	11	693	243	331-1092
D_C (m^{-2})	11	10.9	6.71	4-24
H_C (cm)	11	152	31.1	102-192
H_V (cm)	11	129	24.5	100-175

Treatment ELE PAL (*Eleocharis palustris*)

Variable	N	Mean	SD	Range
M_C (g)	15	97.9	90.8	5.36-285
M_V (g)	15	533	131	322-803
M_T (g)	15	631	178	327-1019
D_C (m^{-2})	15	13.6	6.90	4-28
H_C (cm)	15	118	30.3	68.0-166
H_V (cm)	15	81.0	32.2	49.0-146

Treatment SCH LAC (*Schoenoplectus lacustris*)

Variable	N	Mean	SD	Range
M_C (g)	14	23.3	23.7	0-89.5
M_V (g)	14	670	380	281-1631
M_T (g)	14	723	384	286-1652
D_C (m^{-2})	14	6.86	3.66	4-16
H_C (cm)	14	120	43.0	60.0-202
H_V (cm)	14	169	26.7	127-230

Treatment SPA PEC (*Spartina pectinata*)

Variable	N	Mean	SD	Range
M_C (g)	15	37.4	41.4	0.00-151.5
M_V (g)	15	748	551	3.64-1896
M_T (g)	15	785	546	74.7-1917
D_C (m^{-2})	15	15.2	12.0	4-44
H_C (cm)	15	79.2	24.2	36.0-122
H_V (cm)	15	168	23.8	138-213

Treatment SCH PUN (*Schoenoplectus pungens*)

Variable	N	Mean	SD	Range
M_C (g)	15	73.6	66.8	7.40-230
M_V (g)	15	524	243	38.1-970
M_T (g)	15	598	276	79.2-1122
D_C (m^{-2})	15	10.7	5.16	4-20
H_C (cm)	15	143	28.8	93-191
H_V (cm)	15	131	25.6	77-173

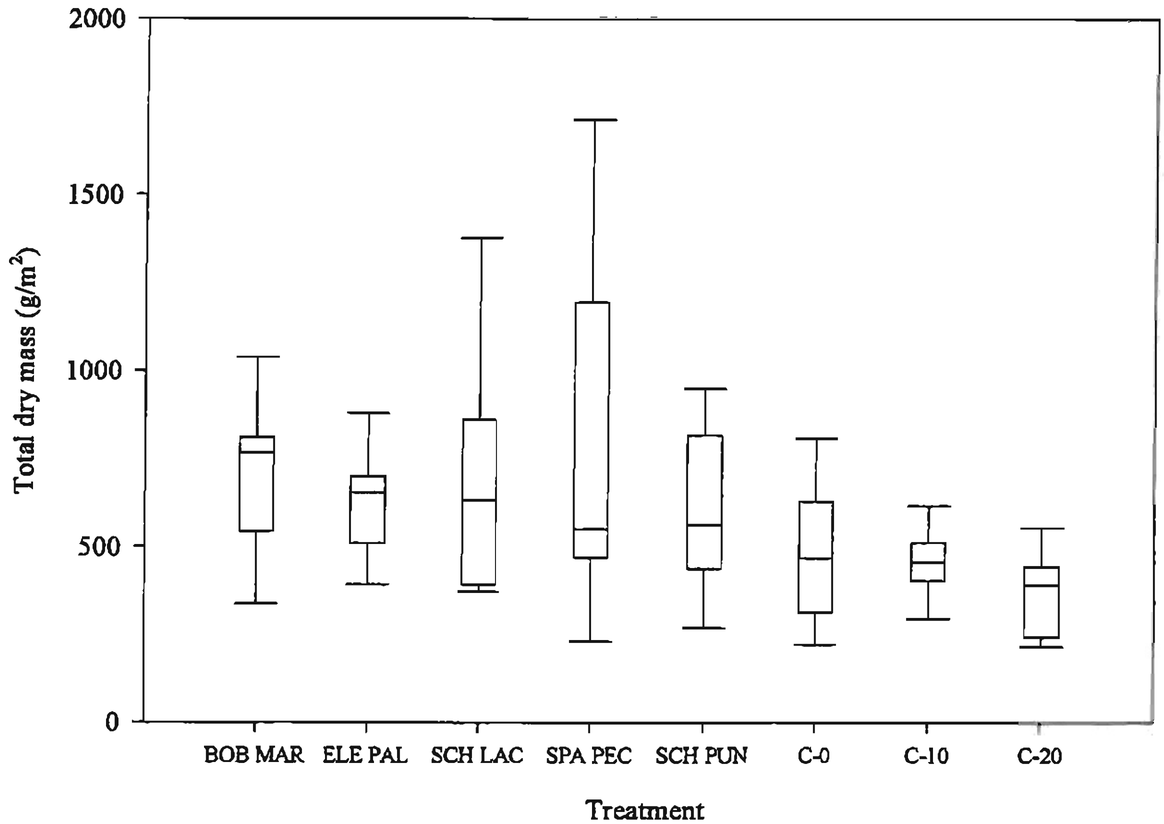

Figure 3. Box plots of total biomass for each treatment and control. Key to abbreviations: BOB MAR = Bobloschoenus maritimus, ELE PAL = Eleocharis palustris, SCH LAC = Schoenoplectus lacustris, SPA PEC = Spartina pectinata, SCH PUN = Schoenoplectus pungens, C-0 = Control with 0cm water depth, C-10 = Control with 10 cm water depth, C-20 = Control with 20 cm water depth. Box extends from 25th to 75th percentiles. Line inside box denotes median value. Vertical lines extend from 10th to 90th percentiles.

pungens stands to 785 g/m^2 in *Spartina pectinata* stands. The ANOVA for total biomass indicated that there were no statistically significant differences between any treatment and control, or between treatments (P = 0.0615, Table 3).

Cattail biomass (M_C) ranged from 0.004 to 983 g/m^2, with a mean of 181 g/m^2 (Table 2). The ANOVA for cattail biomass indicated that at least one treatment or control was significantly different from the others (P < 0.001, Table 3). All three controls had much higher cattail biomass than any of the treatments, indicating a strong treatment effect (Figure 4). The controls were not significantly different from one another based on the results of the multiple comparison analysis (Table 4).

Of the five treatments, the lowest cattail biomass occurred in *Schoenoplectus lacustris* plots ranging from 3.1 to 90.5 g/m^2, with a mean of 23.3 g/m^2. Total cattail biomass was also low in *Spartina pectinata* plots, ranging from 0.0 to 151.0 g/m^2 with a mean of 37.4 g/m^2. Both the *S. lacustris* and *S. pectinata* treatment plots had cattail biomass that was significantly different than all three controls (P < 0.001) (Table 4). Cattail biomass in these two treatments were not significantly different from each other.

In spikerush (*Eleocharis palustris*) plots, cattail biomass ranged from 5.4 to 285 g/m^2, with a mean of 97.9 g/m^2. In three-square bulrush (*Schoenoplectus pungens*) plots cattail biomass ranged from 7.4 to 230 g/m^2 with a mean of 73.6 g/m^2. Both the *Eleocharis palustris* and *Schoenoplectus pungens* treatments were significantly different from all three controls (P < 0.001) (Table 4). The highest cattail biomass among the treatment plots occurred in alkali bulrush (*Bobloschoenus maritimus*) stands, ranging from 25.0 to 263.0 g/m^2, with a mean of 115 g/m^2. The *B. maritimus* treatment was significantly different from the 0 cm and 10 cm water depth

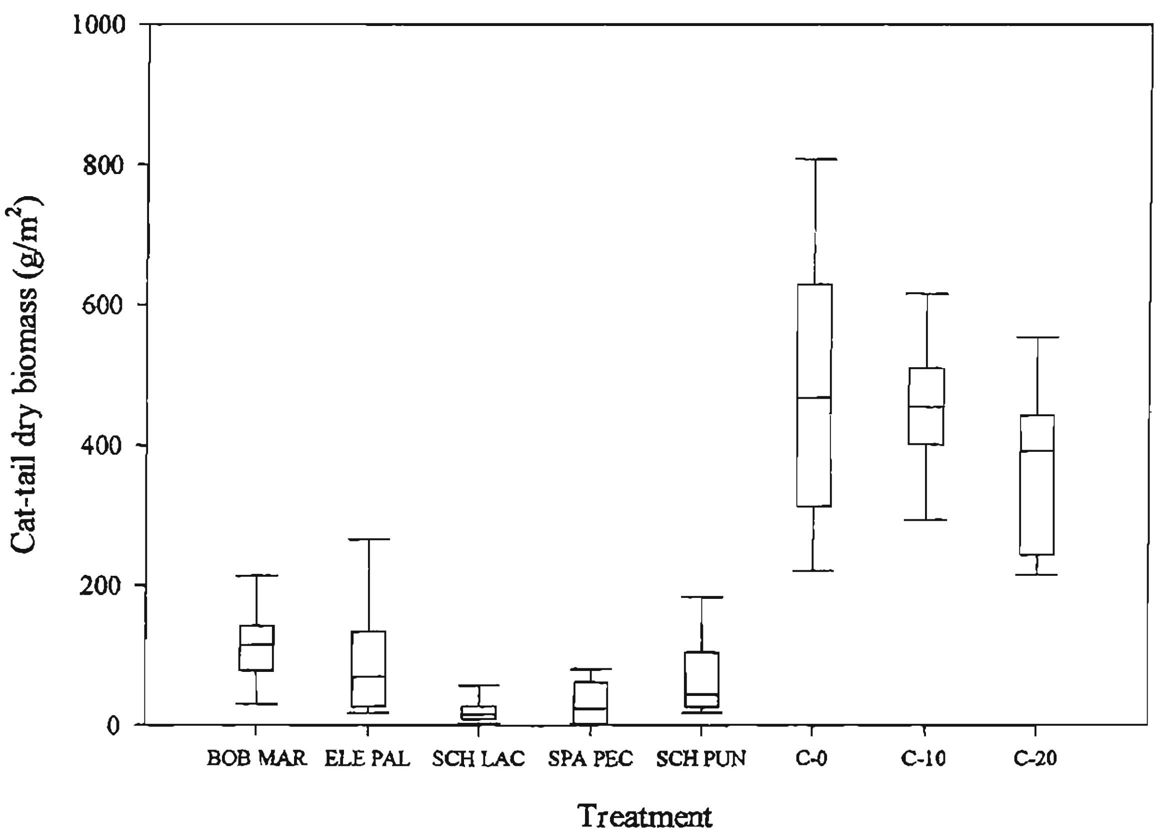

Figure 4. Box plot of total cattail biomass for each treatment and control. Key to abbreviations: BOB MAR = Bobloschoenus maritimus, ELE PAL = Eleocharis palustris, SCH LAC = Schoenoplectus lacustris, SPA PEC = Spartina pectinata, SCH PUN = Schoenoplectus pungens, C-0 = Control with 0cm water depth, C-10 = Control with 10 cm water depth, C-20 = Control with 20 cm water depth. Box extends from 25th to 75th percentiles. Line inside box denotes median value. Vertical lines extend from 10th to 90th percentiles.

Table 3. Summary statistics for ANOVAs. Abbreviations: DF= degrees of freedom, C.V. = coefficient of variation, Root MSE= root mean square error.

Dependent Variable: LOG(M_T)

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	7	0.725	0.104	2.01	0.0615
Error	92	4.73	0.051		
Corrected Total	99	5.46			

R-Square	C.V.	Root MSE	LOG(M_T) Mean
0.133	8.31	0.227	2.73

Dependent Variable: LOG(M_C)

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	7	29.4	4.20	24.33	0.0001
Error	92	15.9	0.173		
Corrected Total	99	45.3			

R-Square	C.V.	Root MSE	LOG(M_C) Mean
0.649	22.06	0.415	1.88

Dependent Variable: LOG(D_C)

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	7	10.5	1.506	23.26	0.0001
Error	92	5.96	0.065		
Corrected Total	99	16.5			

R-Square	C.V.	Root MSE	LOG(D_C) Mean
0.639	21.67	0.254	1.17

Dependent Variable: H_C

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	7	52944	7563.4	9.48	0.0001
Error	92	73401	797.8		
Corrected Total	99	126344.8			

R-Square	C.V.	Root MSE	H_C Mean
0.419	22.267	28.246	126.85

Table 4. Results of multiple comparisons for a) dry cattail biomass (H_C), b) cattail density (D_C), and c) cattail height (H_C). 0= not significant at alpha= 0.05, * = significant at alpha=0.05, ** = significant at alpha = 0.01, *** = significant at alpha = 0.001. See table 2 for definition of treatment abbreviations.

a) Dry biomass of cattails (grams/square meter)

	C_0	C_{10}	C_{20}	SPA PEC	ELE PAL	BOB MAR	SCH PUN	SCH LAC
C_0	-							
C_{10}	0	-						
C_{20}	0	0	-					
SPA PEC	***	***	***	-				
ELE PAL	***	*	***	*	-			
BOB MAR	*	***	*	***	0	-		
SCH PUN	***	***	***	*	0	***	-	
SCH LAC	***	***	***	0	**	***	0	-

b) Density of cattails (stems per square meter)

	C_0	C_{10}	C_{20}	SPA PEC	ELE PAL	BOB MAR	SCH PUN	SCH LAC
C_0	-							
C_{10}	0	-						
C_{20}	0	0	-					
SPA PEC	***	***	*	-				
ELE PAL	***	***	*	0	-			
BOB MAR	***	***	**	0	0	-		
SCH PUN	***	***	**	0	0	0	-	
SCH LAC	***	***	***	0	0	0	0	-

c) Height of cattails (cm)

	C_0	C_{10}	C_{20}	SPA PEC	ELE PAL	BOB MAR	SCH PUN	SCH LAC
C_0	-							
C_{10}	0	-						
C_{20}	0	0	-					
SPA PEC	***	***	***	-				
ELE PAL	0	0	0	**	-			
BOB MAR	0	0	0	***	0	-		
SCH PUN	0	0	0	***	0	0	-	
SCH LAC	0	0	0	**	0	0	0	-

controls ($P < 0.05$), but it was not significantly different from the 20 cm water depth control ($P > 0.05$) even though the mean differed by a factor of two.

Cattail shoot density (D_C) for all plots ranged from 4 to 168 shoots/m^2 with a mean of 28 shoots/m^2 (Table 2). Cattail shoot density was positively correlated with cattail biomass ($R^2 = 0.64$), so the results of the ANOVA and multiple comparison tests were similar to those for cattail biomass. The ANOVA indicated that at least one of the treatments or controls was significantly different from the others (Table 3). The three controls all had much higher shoot densities than any treatment (figure 5). The highest occurred in the 0 cm water depth control, where shoot density ranged from 16 to 168 shoots/m^2, with a mean of 74.4. In the 10 cm water depth control, shoot density ranged from 28 to 88 shoots/m^2 and had a mean value of 55.2 shoots/m^2 while in the 20 cm water depth control it ranged from 16 to 48 shoots/m^2 and had a mean of 29.2 shoots/m^2. For the 0 cm and 10 cm water depth controls all treatment-control comparisons were significant at $P< 0.001$, indicating a large difference between these controls and all of the treatments (Table 4). The 20 cm water depth control was also significantly different from all treatments but the level of significance was lower; only the *Schoenoplectus lacustris* treatment was different at $P < 0.001$. *B. maritimus* and *S. pungens* were different at $P < 0.01$, while *E. palustris* and *S.pectinata* were different at $P < 0.05$.

The treatment with the lowest shoot density, *S.lacustris* also had the lowest cattail biomass. Shoot density for this treatment ranged from 4 to 16 shoots/m^2 and had a mean value of 6.7 shoots/m^2, more than 4 times less than the mean of the corresponding 20 cm depth control. Stands of *B. maritimus* and *S. pungens* also had relatively low shoot densities. The *B. maritimus* stands had shoot densities that ranged from 4 to 24 shoots/m^2 with a mean of 10.9 shoots/m^2,

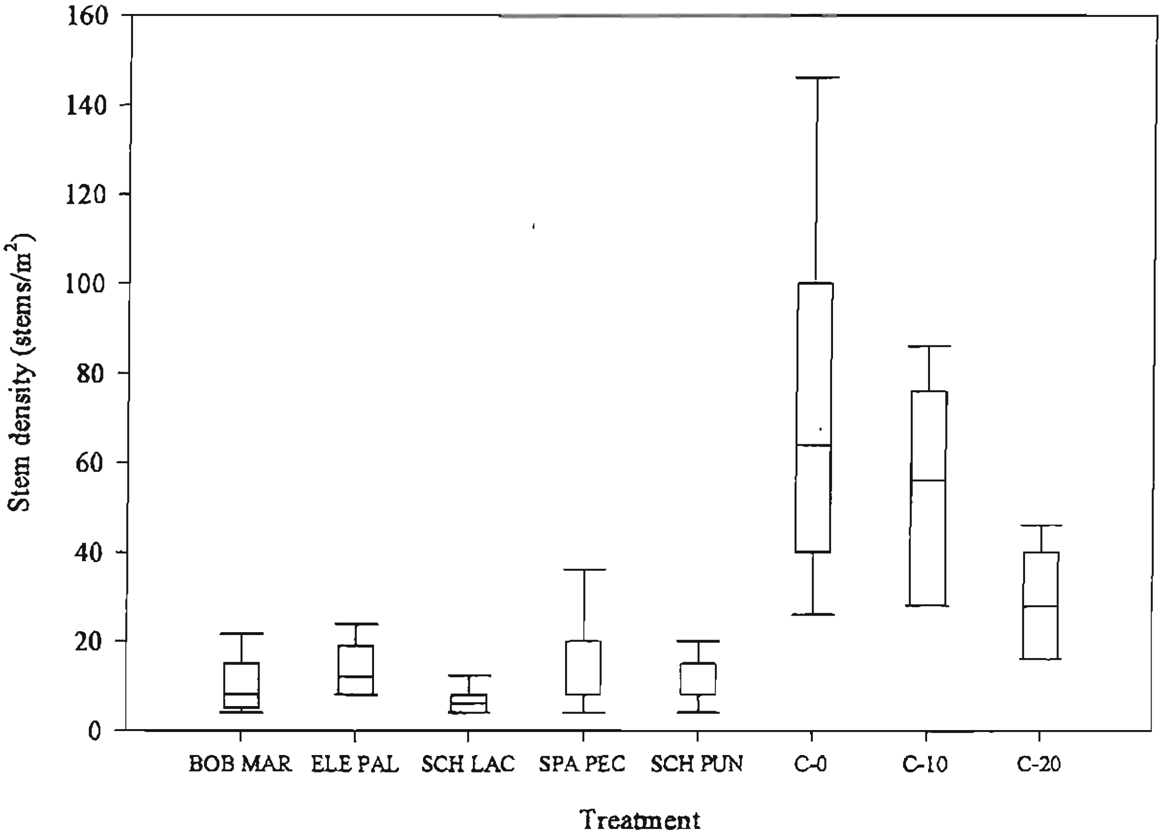

Figure 5. Box plots of cattail stem density for each treatment and control. Key to abbreviations: BOB MAR = Bobloschoenus maritimus, ELE PAL = Eleocharis palustris, SCH LAC = Schoenoplectus lacustris, SPA PEC = Spartina pectinata, SCH PUN = Schoenoplectus pungens, C-0 = Control with 0cm water depth, C-10 = Control with 10 cm water depth, C-20 = Control with 20 cm water depth. Box extends from 25th to 75th percentiles. Line inside box denotes median value. Vertical lines extend from 10th to 90th percentiles.

while *S. pungens* stands had densities that ranged from 4 to 20 shoots/m^2 with a mean of 10.7 shoots/m^2. All three of the treatments, along with the *S. pectinata* treatment were significantly different from all three of the controls at $P < 0.001$. The *E. palustris* treatment was also significantly different from the 0 cm and 10 cm water depths at $P < 0.001$, while the level of significance for the comparison with the 20 cm water depth control was $P < 0.01$. Overall, the results showed that while the three controls were similar, they were significantly different from all of the treatments.

Cattail shoot height (H_C) for all plots ranged from 36 to 202 cm with a mean of 127 cm. Shoot height was not correlated with cattail biomass or shoot density ($R^2 = 0.17$ and 0.07, respectively). The results of ANOVA indicated that at least one of the treatments or controls was significantly different from the others at $P< 0.001$ (Table 3). Shoot heights in the three controls were similar (Figure 6). Mean shoot heights for the 0 cm, 10 cm and 20 cm water depth controls were 139, 140 and 145 cm respectively, none of which was significantly different (Table 4). Shoot height in the *B. maritimus* treatment was slightly larger than in the controls; the mean shoot height was 152 cm, but there were no significant differences between this treatment and the controls. The *S. pungens* treatment had a mean shoot height almost identical to the controls, 143 cm, while the other three treatments had lower mean shoot heights. The lowest mean shoot height of 79 cm was recorded in the *S. pectinata* treatment. Shoot height for this treatment was significantly different from all of the other treatments and controls at a significance level of 0.001 (table 4). Statistically significant comparisons were also identified for two of the other treatments; *S. lacustris* and *E. palustris* were both significantly different from *S. pungens* ($P < 0.05$), *B.maritimus* ($P < 0.01$) and the 20 cm water depth control ($P < 0.05$).

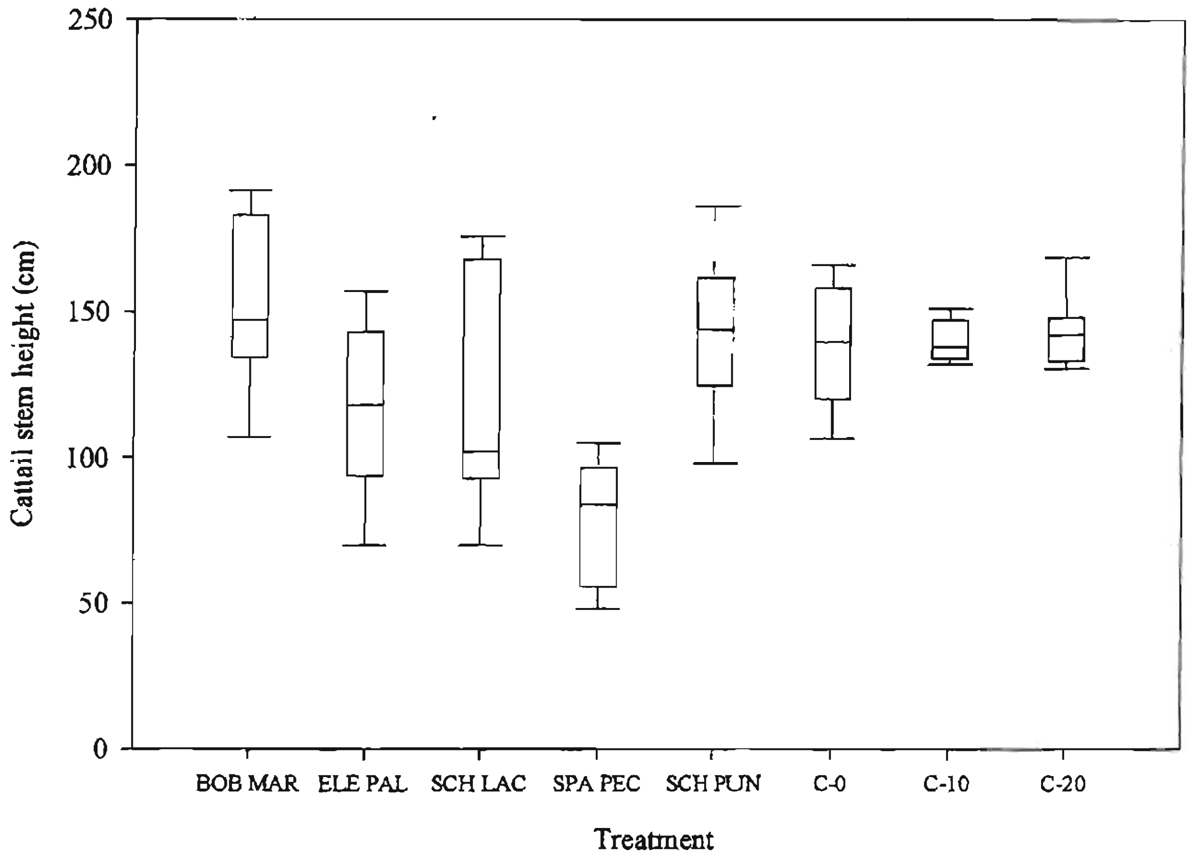

Figure 6. Box plots of cattail stem height for each treatment and control. Key to abbreviations: BOB MAR = Bobloschoenus maritimus, ELE PAL = Eleocharis palustris, SCH LAC = Schoenoplectus lacustris, SPA PEC = Spartina pectinata, SCH PUN = Schoenoplectus pungens, C-0 = Control with 0cm water depth, C-10 = Control with 10 cm water depth, C-20 = Control with 20 cm water depth. Box extends from 25th to 75th percentiles. Line inside box denotes median value. Vertical lines extend from 10th to 90th percentiles.

Hydrologic and Geochemical Factors Affecting Cattail Abundance

Of the 259 stands for which data were collected, 155 contained cattails. The other 104 stands were just beyond the edges of cattails stands and were used to define the limits of cattail distribution. For stands containing cattails, shoot density ranged from 4 to 164 shoots/m^2 with a mean of 38 shoots/m^2. Shoot height ranged from 48 to 270 cm with a mean of 140 cm. These values are consistent with the measurements of shoot density and height in the controls at the Limon study site.

Each of the ten study sites had distinctive hydroperiod characteristics created by the relative influence of groundwater vs. surface water on the site hydrologic regime. The water level in Boulder Reservoir was highest in mid- to late-June as the reservoir is used for agricultural water storage. As water was released the reservoir water level dropped. By late summer the water level was ~1.4 m lower than it was in June (Figure 7). This was the largest water level fluctuation measured at the study sites. Water levels in the other lake sites, Coot Lake, Sawhill Ponds and the lake on the east side of the Culver Property, rose in the early part of the summer and then remained fairly stable (Figures 8, 9 and 10). However, in the smaller ponds at Sawhill Ponds and the Culver Property water levels dropped from a seasonal maximum in early June, and many went dry by August (Figures 9 and 10). At Dry Creek pond the water level fluctuated from week to week in response to varying creek inflows. The highest water levels occurred in the early summer and over the entire season the pond water level fluctuated by approximately 25 cm (Figure 11). Sombrero Marsh was flooded in the early part of the summer, but water levels dropped rapidly and the flooded area receded to the marsh center (Figure 12). However, in early

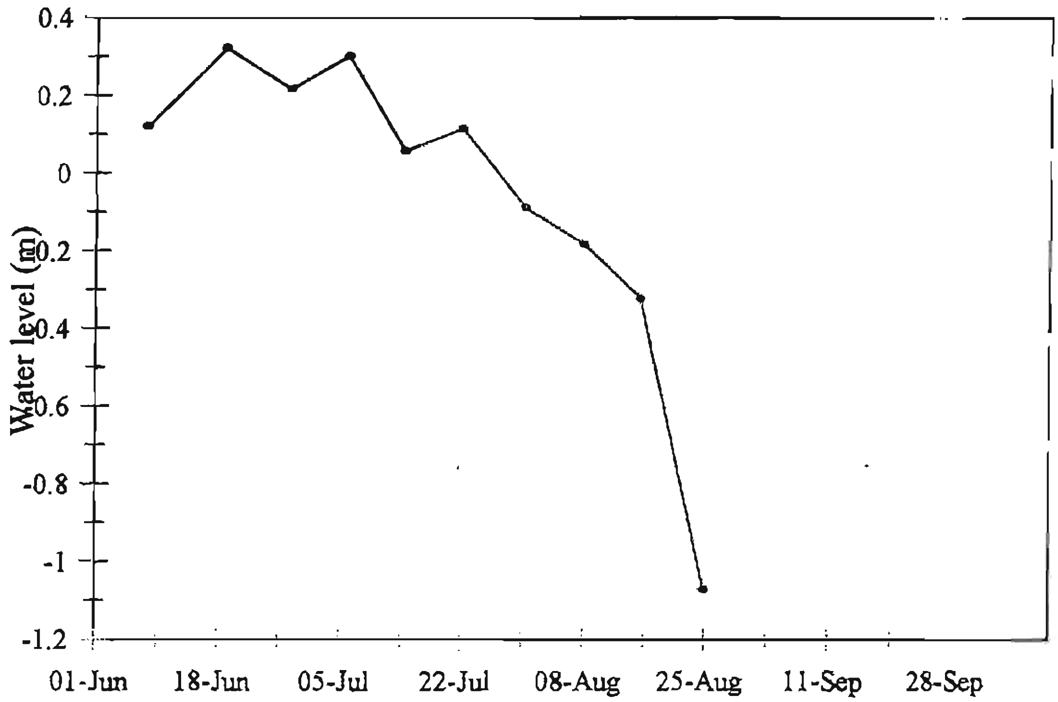

Figure 7. Representative hydrograph for Boulder Reservoir site. 1 June - 30 September 1998. Water level dropped below staff gage after 25 August.

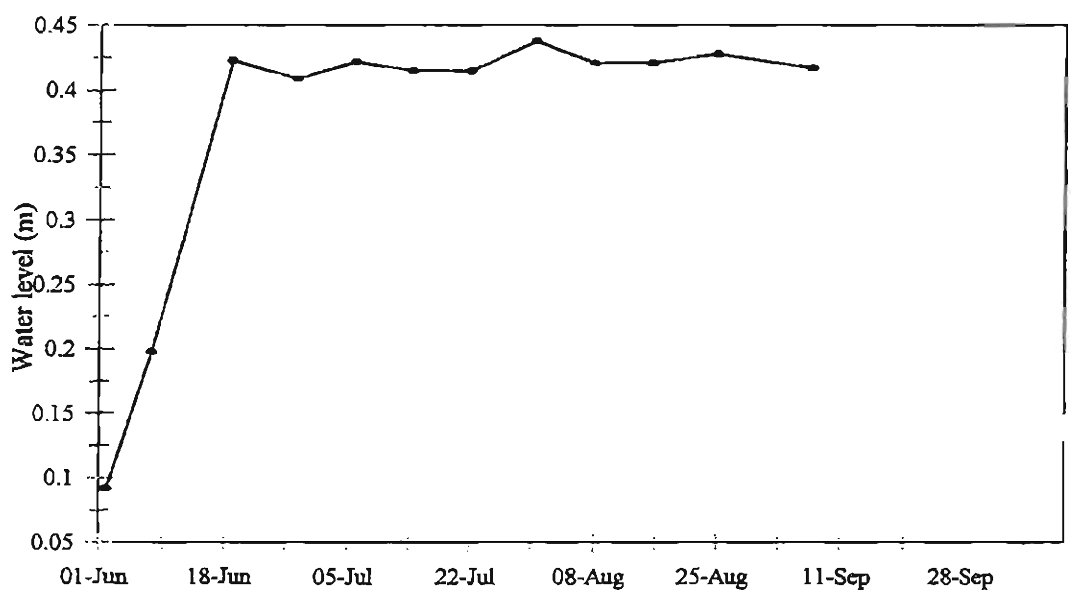

Figure 8. Representative hydrograph for Coot Lake site. 1 June - 30 September 1998.

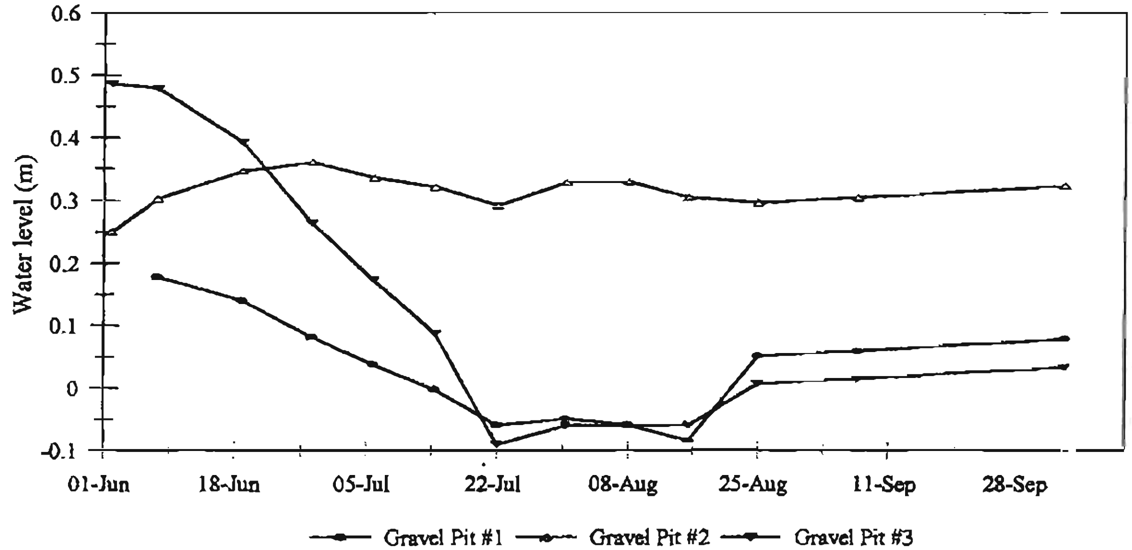

Figure 9. Representative hydrograph for Sawhill Pond sites. 1 June - 30 September 1998.

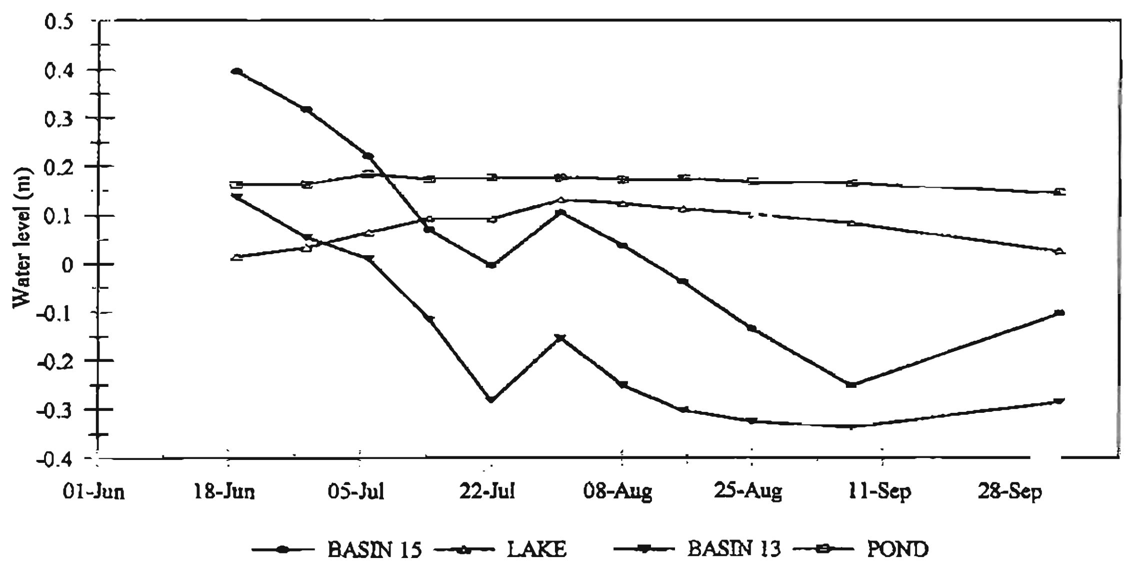

Figure 10. Representative hydrographs for study sites at Culver property. 1 June - 30 September 1998.

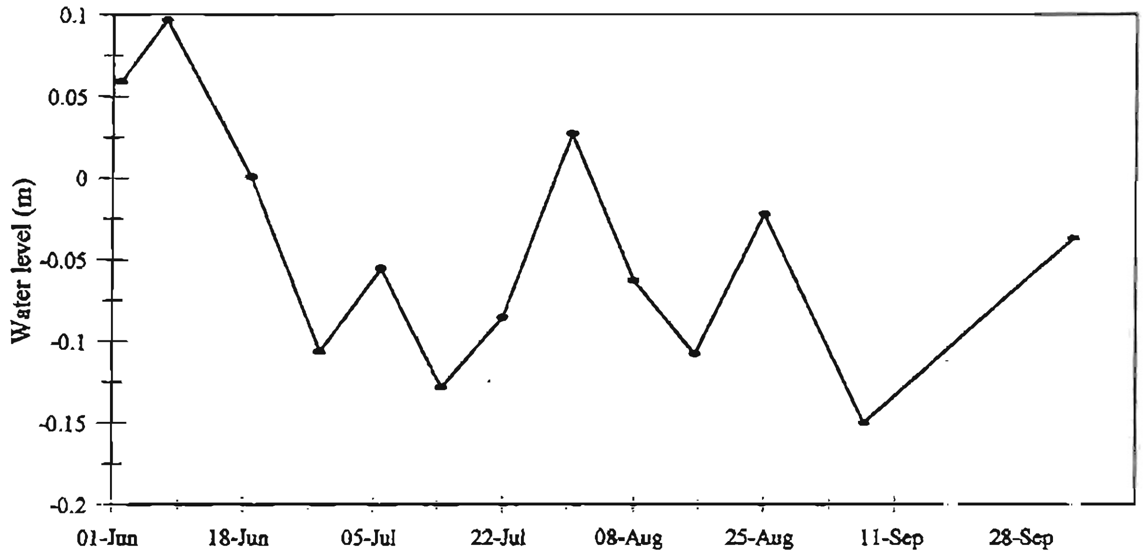

Figure 11. Representative hydrograph for Dry Creek Pond study site. 1 June - 30 September 1998.

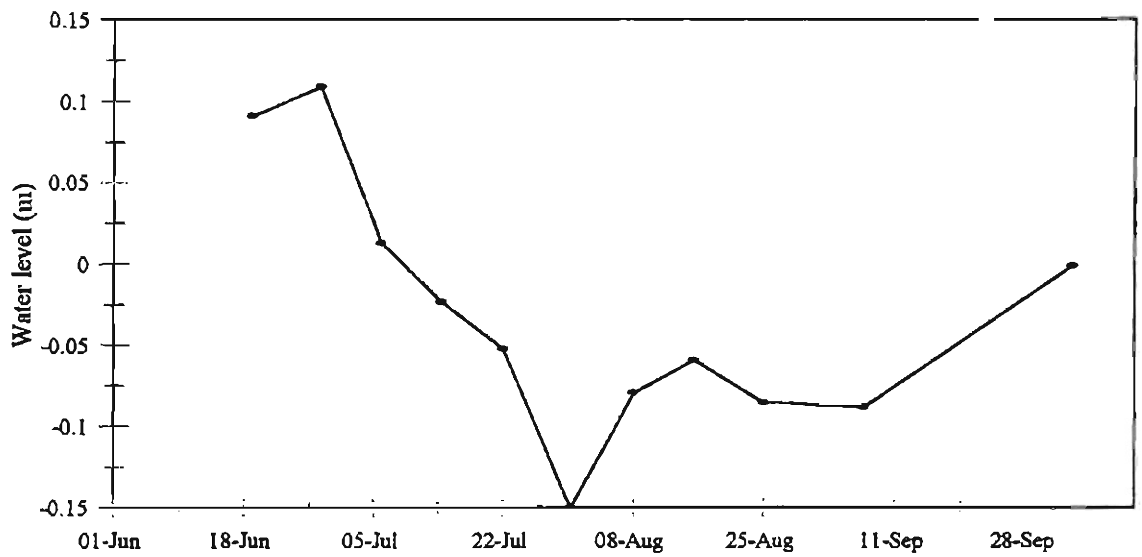

Figure 12. Representative hydrograph of water levels at Sombrero Marsh study site. 1 June - 30 September 1998.

August the water level recovered considerably following several days of rain which included one day with 4.3 cm (1.7 in) of precipitation.

Water levels at the Kentucky property, Twin Lakes, and Boulder Recreation Center sites were closely controlled by shallow groundwater. At Twin Lakes and Kentucky Property sites water levels rose in early June, dropped in July and then rose again in August in response to rainfall (Figures 13 and 14). Water levels were more stable at the Boulder Recreation Center wetland probably due to the proximity of Boulder Creek which may control ground water levels (Figure 15). The driest site was the *Eleocharis* playa which is maintained entirely by precipitation ponding on a clay layer just below the soil surface. This site had up to 38 cm of standing water in the early summer, but by the end of June the site was dry (Figure 16).

The highest water levels during 1998 for all 155 cattail stands was 48 cm above the soil surface to 108 cm below the soil surface, with a mean of 7 cm below the soil surface. Shoot density exhibited a unimodal relationship with maximum water depth, indicating both an upper and a lower limit with a central maximum (Figure 17). In plots where the maximum water depth height (H_{max}) ranged from 0 to 10 cm of standing water shoot densities were generally >30/m^2. In stands where H_{max} was greater than 20 cm in depth shoot density was generally less than 20/m^2. Cattails were not found in sites where the maximum depth of standing water exceeded 50 cm, suggesting that a periodic maximum water depth greater than 50 cm prevents the growth of cattails. Shoot density also was lower in sites with deeper depths to the water table below the soil surface. There were very few sites with cattails where the maximum water level was more than 50 cm below the surface.

Minimum water depth for all sites with cattails ranged from 25 cm above the soil surface

Figure 13. Representative hydrograph for water levels at Twin Lakes study site. 1 June - 30 September 1998.

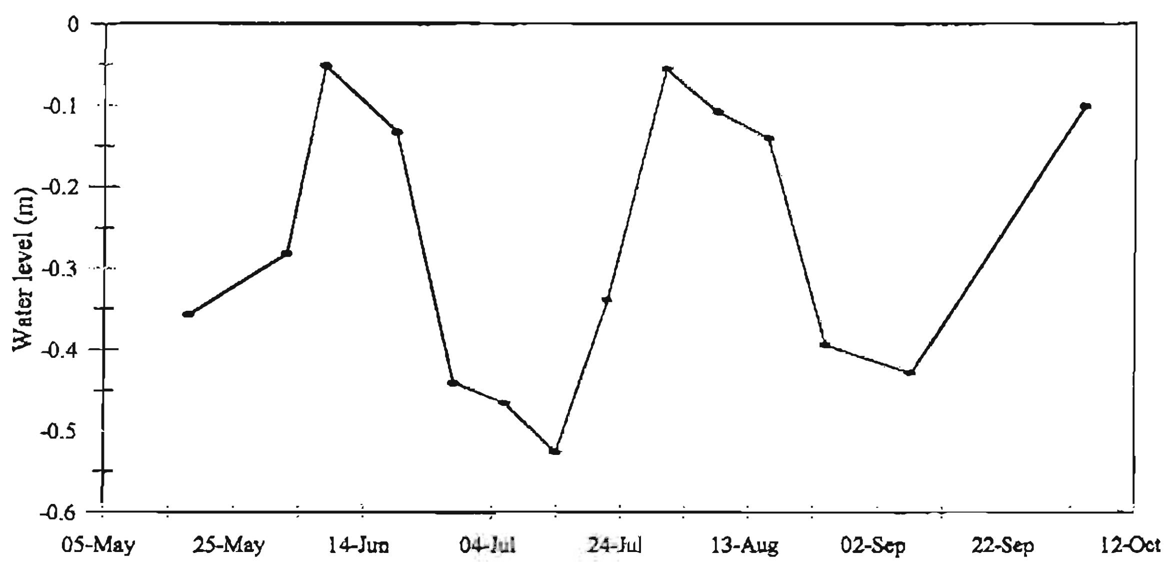

Figure 14. Representative hydrograph of water levels at Kentucky Property. 1 June - 30 September 1998.

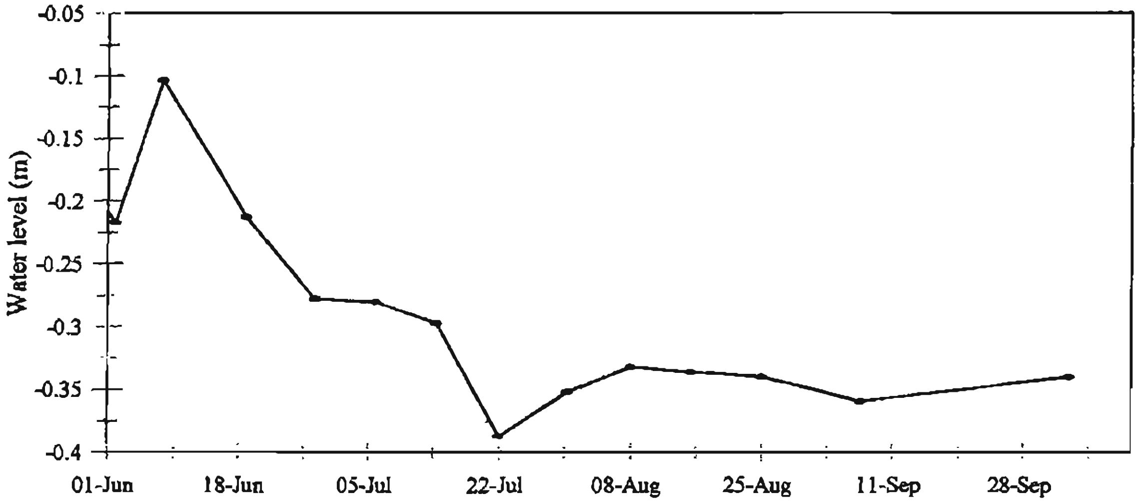

Figure 15. Representative hydrograph of water levels at Boulder Recreation Center study site. 1 June - 30 September 1998.

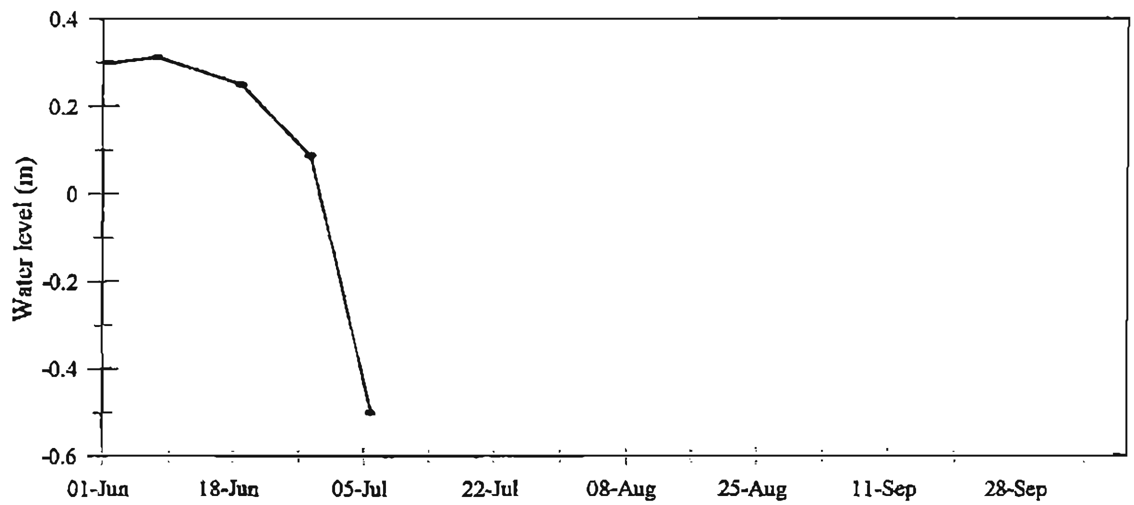

Figure 16. Representative hydrograph of water levels at Eleocharis playa, 1 June - 30 September 1998.

to 148 cm below the soil surface with a mean of 45 cm below the soil surface. The relationship of shoot density to minimum water depth was unimodal, although the trend was not as distinct as it was for maximum water depth. There was little difference in shoot density for stands with minimum water levels between 10 cm above and 50 cm below the soil surface (Figure 18). However, stands with minimum water levels more than 70 cm below the soil surface had lower shoot densities, and very few sites were found with cattails where the minimum water level was more than 100 cm below the surface. Thus, seasonal water levels more than 100 cm below the soil surface appears to limit cattail occurrence. Shoot densities were also low where the minimum water level was greater than 10 cm above the surface, but this probably reflects the collinear relationship between minimum and maximum water levels (i.e. sites with a high maximum water level also tend to have a high minimum water level).

The seasonal fluctuations in water levels for all sites supporting cattails ranged from 0 to 80 cm with a mean of 39 cm. The water level at Boulder Reservoir fluctuated by 1.4 m, but there were cattails in areas with the largest stage change. Cattail shoot density was inversely related to the seasonal range in water levels in a stand, *ie.* the highest shoot densities occurred at sites with the smallest annual fluctuation. Shoot densities of up to $40/m^2$ were recorded at sites where the range in water levels was between 0 and 10 cm (Figure 19). For sites with a seasonal water level fluctuation of between 70 and 80 cm shoot densities were generally less than $5/m^2$. No sites were found with cattails when the seasonal variation in water depths was more than 80 cm. These results indicate that cattails occur where water levels are relatively stable, and fluctuating water levels may inhibit the development and persistence of cattail populations.

The duration of standing water at sites with cattails ranged from 0 to 121 days (out of a

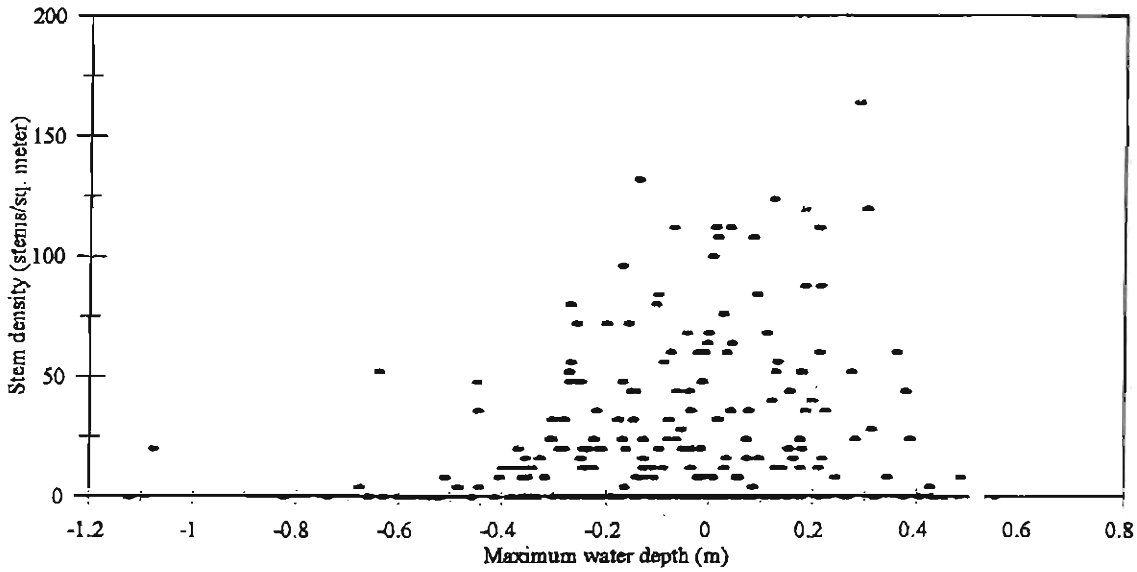

Figure 17. Relationship of stem density to maximum water depth for all study sites.

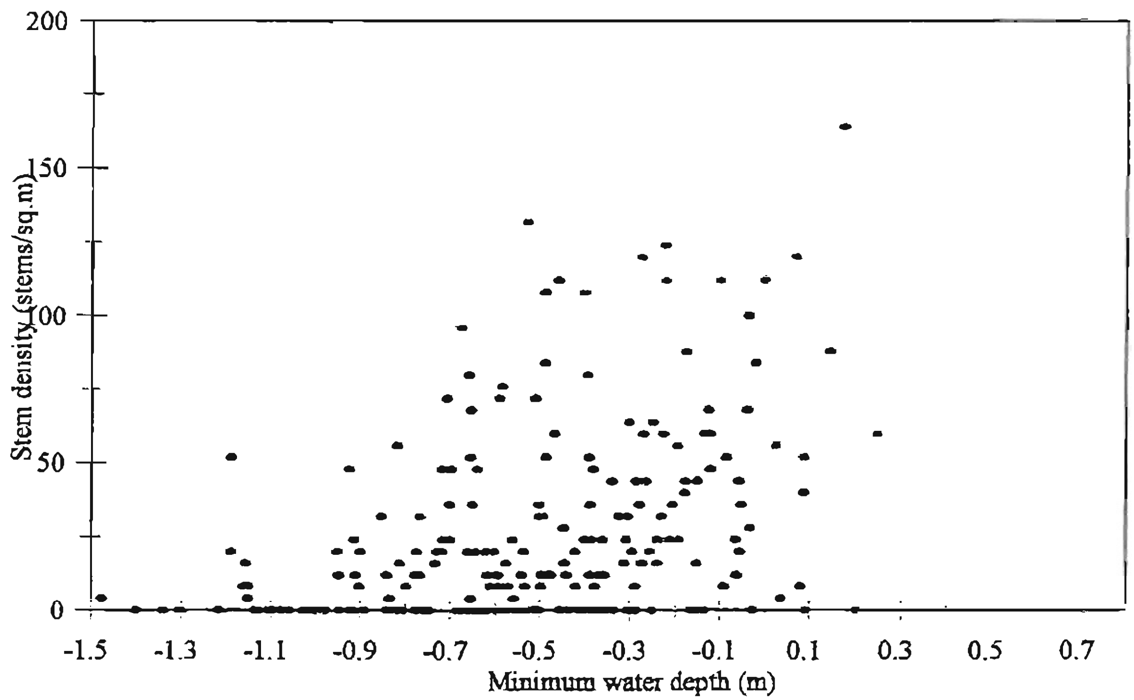

Figure 18. Relationship of cattail stem density to minimum water level for all sites.

possible 121 days) with a mean of 27 days. There was no obvious relationship between shoot density and the duration of standing water at sites. Shoot densities at sites without any standing water during the summer ranged from zero to over $30/m^2$, as did those where there was standing water all summer (Figure 20).

Most of the study sites had water with electrical conductivities (EC) between 200 and 2,000 μS/cm. Electrical conductivities in this range had little apparent effect on cattail shoot density (Figure 21). Much higher conductivity values were recorded at three sites: Sombrero Marsh, *Eleocharis* playa and Twin Lakes. At Sombrero Marsh the standing water in the marsh had an EC of approximately 10,000 μS/cm. Although cattails occur in a few localized areas on the edge of the marsh, they occurred only where water of lower salinity discharged into the marsh at storm drain outlets. Since the hydrologic conditions at Sombrero Marsh are appropriate for cattails to occur it appears that salinity prevents cattails from establishing in the main portion of the marsh.

At *Eleocharis* playa the EC of standing water early in the summer was approximately 3500 μS/cm. This site had standing water only in the early summer and soils became dry in mid summer. Thus, hydrologic conditions were inappropriate for cattails although salinity may also play a role in preventing cattails from establishing. The EC of standing water in cattail stands at the Twin Lakes site ranged from 1450 to 4450 μS/cm, with lower conductivity levels in wells at the southern end adjacent to a small reservoir and higher values in the low lying north end of the site. The conductivity gradient at this site is most likely due to mixing of relatively fresh water seeping from the reservoir with saline groundwater. Cattails only occur at the southern end of the site, indicating that conductivity is limiting the spread of cattails into the northern part. On the

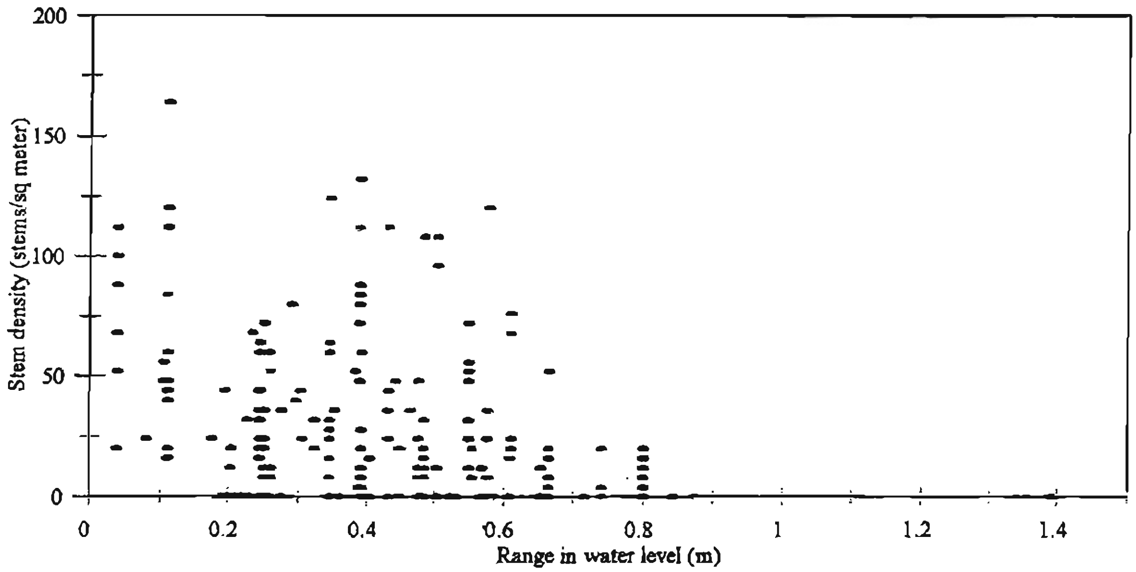

Figure 19. Relationship of cattail stem density to the range in water levels between 1 June and 30 September 1998.

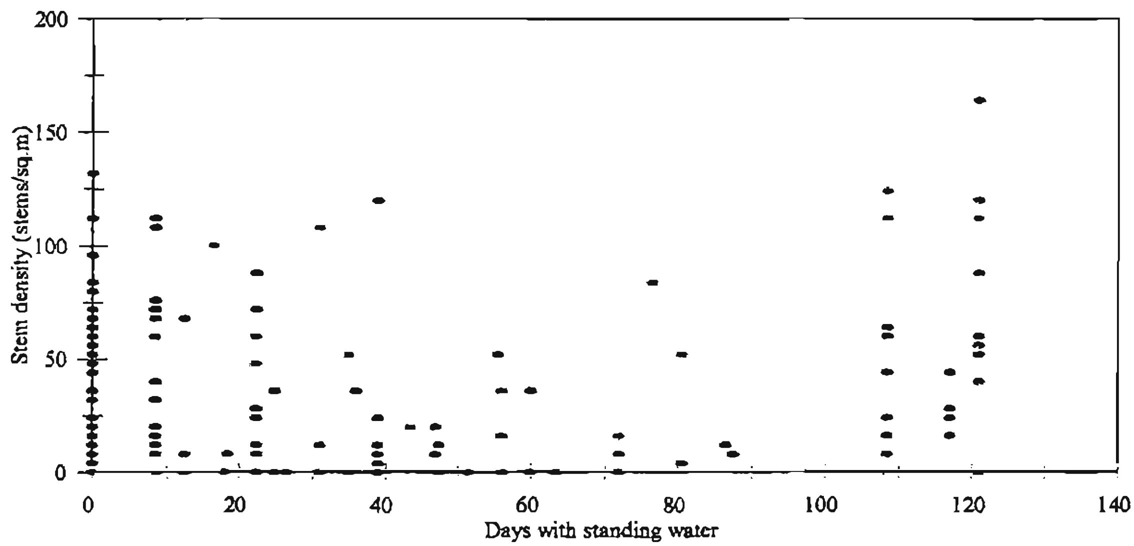

Figure 20. Relationship of cattail stem density to duration of inundation. Inundation duration measured as the number of days (out of a possible 121) when there was standing water at a site between 1 June and 30 September 1998.

basis of the EC data, the limiting conductivity for cattail occurrence is approximately 4000 μS/cm. Around the margins of reservoirs cattail shoot density was related to aspect and slope. Sites with cattails were found within all quadrants of the compass. However, the highest shoot densities were recorded at sites with an aspect between 290 and 315 degrees from north (approximately west to northwest) (Figure 22). The prevailing wind in the area is from the west, so higher cattail densities on the western sides of large water bodies is most likely due to sheltering from wave action. The effect of aspect was most obvious at Coot Lake where dense cattail-dominated marsh vegetation occurs on the western side of the lake, but is absent from eastern lake edges. When sites were divided into classes according to fetch length of greater than or less than 50 m, it was apparent that the effect of aspect is limited to larger water bodies with fetches of more than 50 m, and lake areas of > 0.5 acres. Cattail densities in smaller wetlands had no relationship with aspect.

The slope of the shoreline cattail stands ranged from 4 to 22 degrees. Shoot density decreased considerably as the slope of the shoreline increased beyond 10 degrees (Figure 23). Shorelines with slopes less than 10 degrees had shoot densities up to $40/m^2$, whereas shorelines with slopes greater than 10 degrees the maximum shoot density was $< 25/m^2$. Slope most likely influences shoot density by increasing the erosive power of waves hitting the shoreline, steeper slopes producing larger waves and more erosion. The effect of slope on shoot density was similar regardless of wetland size.

Fetch for all sites with cattails ranged from 15 to 410 m with a mean of 118 m. Fetch had no effect on shoot density for distances up to 400 m (Figure 24). The lack of an effect due to fetch is probably because the erosive power of waves depends largely on shoreline aspect.

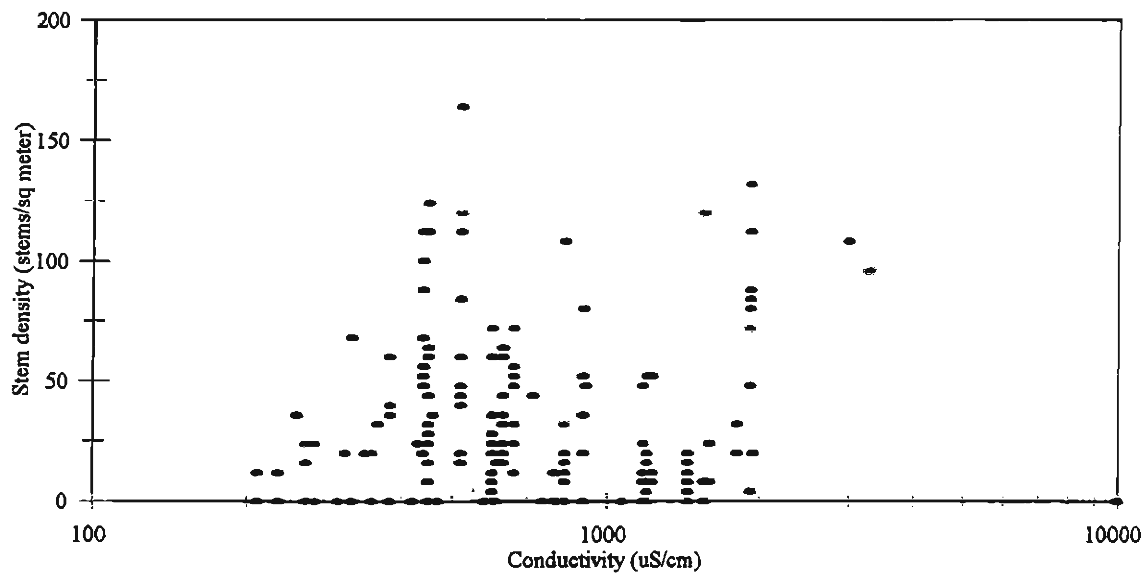

Figure 21. Relationship of cattail stem density to electrical conductivity for all sites.

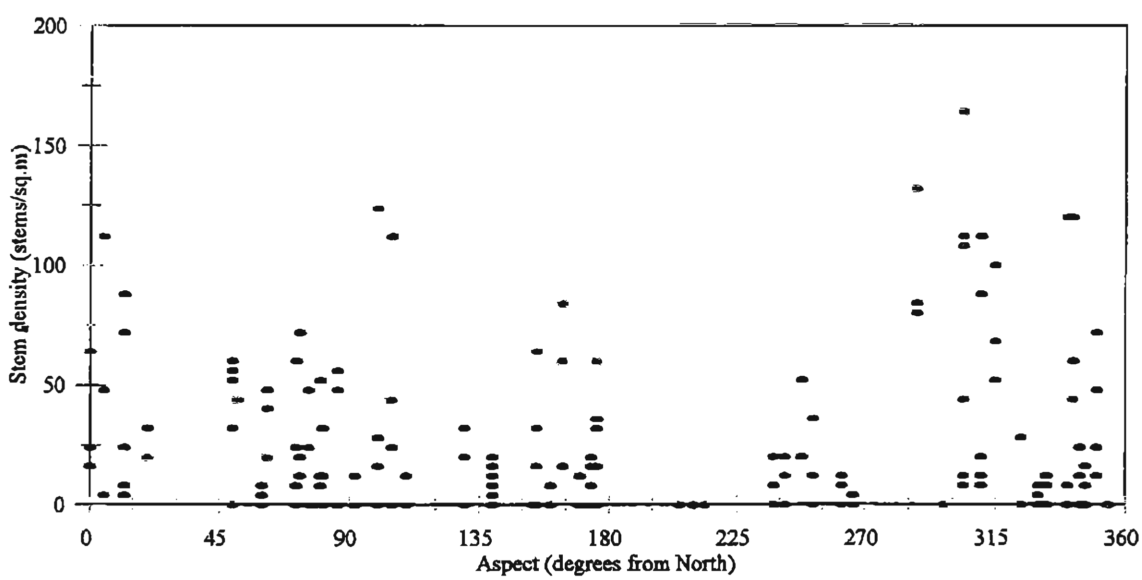

Figure 22. Relationship of cattail stem density to aspect of shoreline. Aspect measured as azimuth clockwise from north. Prevailing wind in Boulder County is from the west.

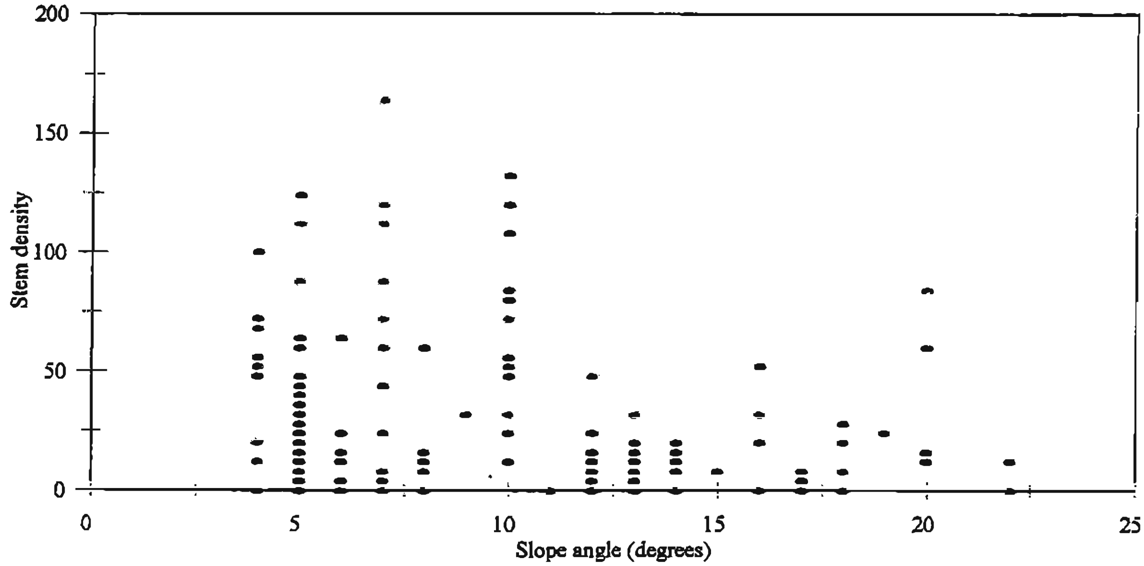

Figure 23. Relationship of cattail stem density to slope angle of shoreline in degrees measured from horizontal.

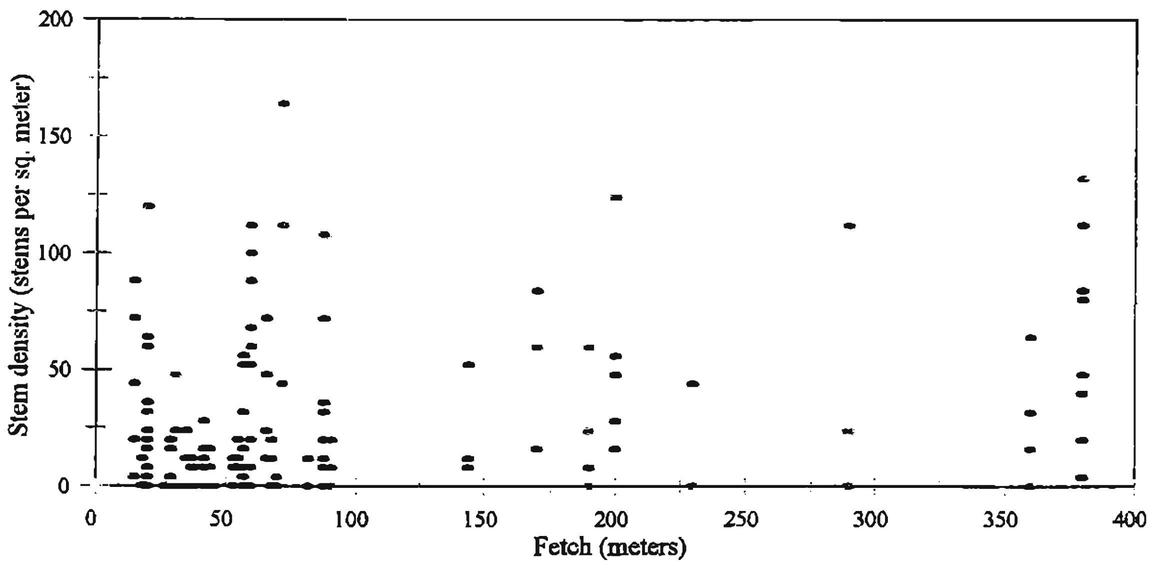

Figure 24. Relationship of cattail stem density to fetch (distance from opposite shoreline).

Sheltered, east facing shorelines are not as exposed to wave action even if the fetch is very large. At Boulder Reservoir the fetch was 1500 m and visual observation suggested that wave action on the shoreline was considerable. Shoreline erosion at this site is accentuated during the summer by powered water craft which generate waves even on calm days. Shoreline erosion due to wave action may be a factor limiting the development of cattails at this site.

No measured variable was related to shoot height. Consequently none of the relationships are presented graphically. Shoot height appears to be a poor predictor of the ecological response of cattails to environmental variables. Shoot density on the other hand provides a good measure of cattail productivity and biomass. This is consistent with the findings of the study at Limon, where we found shoot density was highly correlated with total stand cattail biomass.

DISCUSSION

The competition study at the Limon wetland clearly demonstrates that during the first year, cattail growth is limited by the presence of other plant species. The greatest effect occurred in stands of soft stem bulrush *(Schoenoplectus lacustris)* in deeper water areas. Comparison of cattail growth in the three controls indicated that there was a decrease in cattail biomass with increasing water depth suggesting that water depth as well as competition might have affected growth in the *S. lacustris* stands. However, the mean cattail biomass in stands of *S. lacustris* was approximately 1/16 that occurring in the corresponding 20 cm water depth control, indicating that for the water depths occurring at Limon, competition is by far the most important factor limiting cattail invasion.

The next most effective species limiting cattail growth was prairie cordgrass *(Spartina pectinata)*, which grows in sites with saturated soils, but without inundation. The mean cattail biomass for this treatment was approximately 1/13 that occurring in the corresponding control (C_0), which also indicates that competition has a greater effect on cattail growth than water depth.

In the two treatments that had the greatest effect in reducing cattail growth *S. lacustris* and *S. pectinata*, the mean maximum height of vegetation was greater than that of the cattails. In the other three treatments the mean cattail height was greater than that of the dominant vegetation. One of the less effective treatments, spikerush *(Eleocharis palustris)*, had much shorter mean shoot height than that of cattails in spikerush stands. This suggests that vegetation height may play a role in preventing initial cattail invasion, probably by reducing sunlight from reaching the transplanted shoots.

In a study of competition between *Typha angustifolia* and *Typha latifolia* in a eutrophic lake in Sweden, Weisner (1993) found that *T. angustifolia* had a competitive advantage because of its ability to grow taller shoots and thus complete more effectively for light. The results of the present study support the conclusion that cattails are most competitive against species with shorter shoots.

The results of the hydrologic and geochemical analysis provided valuable information about the environmental factors that affect the occurrence of cattails. Clearly, water depth is an important control on cattail occurrence. Cattails did not occur in any site where the annual maximum water depth was greater than approximately 50 cm. The preference of cattail for depths less than 80 cm has also been reported by Grace and Wetzel (1981). In other areas, such as the Florida Everglades, cattails can be found in water more than 1 m in depth (Newman et al., 1998). However, the shorter growing season on the western Great Plains and lower daily mean temperatures create cattail stands with shorter shoots, which may not be as tolerant of deeper water. In our study area a seasonal maximum water depth of 50 cm appears to limit cattails occurrence.

Another hydrologic factor that clearly had an effect on cattail growth was the annual range of water levels at a site. Cattail shoot density was highest in sites with stable water levels, and decreased as water level variability increased. However, the duration of inundation at a site appeared to have little effect on the growth of cattails. From this we conclude that stable water levels, rather than the consistent presence of standing water, seemed most favorable for cattail growth. Cattail invasion in the Florida Everglades is favored by impoundment and canal construction which stabilizes water levels (Newman et al., 1998). The results of the present study are consistent with these findings, and suggest that constructed and managed wetlands in eastern Colorado should be designed to create a fluctuating water levels if cattail invasion is to be discouraged.

Cattail establishment was inhibited in sites with wave action on the shoreline of reservoirs and ponds. Cattails clearly do best in sites with low angle shorelines that face east and south, while shorelines that face west and northwest may be scoured of plants where size of the pond allows fetch to be large enough to support wave development. Thus, the effect of aspect and slope angle on cattail occurrence is limited to larger ponds and lakes. In ponds less than approximately 0.5 acres in size these factors have little effect. Since many constructed wetlands are small, the potential for controlling cattail growth by designing for increased wave action is limited.

The presence of cattails is limited by water and soil salinity. At Sombrero marsh, cattails did not occur in areas with salinity of 10,000 $\mu S/cm^2$. More salt tolerant species such as alkali bulrush (*Bobloschoenus maritimus*) and three square bulrush (*Schoenoplectus pungens*) were abundant at this site. At the *Eleocharis* playa the potential for cattail invasion was limited by the high salinity and short hydroperiod. Saline wetlands are an important wetland type on the western Great Plains, but managing constructed wetlands to develop high concentrations of salt, while it would allow species other than cattails to occur, is not an easy task. It could be accomplished by creating and maintaining hydrologic connection with local saline groundwater systems, or creating a perched wetland which can be filled with brackish water (EC > 800 $\mu S/cm^2$). However, this could not be accomplished in most sites.

The two studies performed demonstrate that cattails are affected by competition with other species, as well as abiotic factors such as maximum site water depth, water level stability, salinity, and exposure to wind and waves. Cattail invasion can be limited, at least in the short term, by competition with other tall wetland species such as soft-shoot bulrush (*Schoenoplectus lacustris*) and prairie cordgrass (*Spartina pectinata*). The hydrologic conditions at a site may be managed so as to further discourage the invasion of cattails by flooding sites to a depth of more than 50 cm in the early summer and then by varying water levels as much as possible over the growing season. The effectiveness of hydrologic management in controlling cattails will be most effective when salinity in the wetland is kept as high as possible.

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