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## ***Habitat characterization of Texas wild-rice (*Zizania texana* Hitchcock), an endangered aquatic macrophyte from the San Marcos River, TX, USA***

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### ABSTRACT

1. The habitat of Texas wild-rice (*Zizania texana* Hitchcock), known only from the spring-fed upper San Marcos River in Central Texas, was classified in terms of physical and chemical conditions, depth, current velocity, associated aquatic macrophytes, and substrate composition.

2. Randomly selected transects in sites with and without Texas wild-rice were evaluated during May, August and January 1994–1995. Physical and chemical conditions (temperature, dissolved oxygen, specific conductance, pH) were found to be nearly constant and uniform both among transect types and sampling dates. Chemical analysis of the substrate likewise showed few differences among transect types. Turbidity was found to be significantly different among transect types on only one sampling date ( $K_{\alpha_{0.05}} = 0.60$ ;  $p = 0.009$ ), but even non-significant levels of turbidity may present biologically significant impacts to wild-rice plants.

3. Differences in substrate particle size were highly significant ( $K_{\alpha_{0.05}} = 0.71$ ;  $p = 0.001$ ) with Texas wild-rice occupying sites having moderately coarse to coarse sandy soils (73%) compared with the moderately fine to fine clay soils found at non-rice sites (82%). However, no significant differences were found in organic matter content among rice and non-rice transects (= 2.09 and 2.56%, respectively).

4. Texas wild-rice was found primarily in shallow areas of the river (< 1 m) and at higher current velocities than those of non-rice sites ( $\geq 0.46 \text{ m s}^{-1}$  and  $\leq 0.22 \text{ m s}^{-1}$ , respectively).

5. Texas wild-rice appears to be more commonly associated with other native species rather than exotic species. Mean percentage composition of exotic macrophytes did not exceed 29% in areas where Texas wild-rice grew, but they accounted for nearly 47% of the composition in areas where rice did not grow.

6. The results of this study will allow for reliable and accurate identification of the remaining suitable habitat of Texas wild-rice in the San Marcos River for possible reintroduction and development of management plans.

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KEY WORDS: Texas wild-rice; *Zizania texana*; endangered species; habitat characterization

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## INTRODUCTION

Texas wild-rice (*Zizania texana* Hitchcock) is an aquatic perennial grass (Poaceae) occurring only in the clear, thermally constant spring waters of the upper San Marcos River above its confluence with the Blanco River, and primarily within the city of San Marcos, Hays County, TX, USA. The species is anemophilous and produces an emergent inflorescence, though it is most commonly observed in the submerged state with its long, ribbon-like leaves that sway with the stream flow. Due to its single small population, and to significant threats from cessation of spring-flow, habitat alteration, introduction of non-native species, and urbanization (Bowles and Arsuffi, 1993), Texas wild-rice was placed on the US federal endangered species list in 1978 (US Fish and Wildlife Service, 1978, 1996).

When first described (Hitchcock, 1933), Texas wild-rice was noted as being abundant in the San Marcos River, including its irrigation waterways and Spring Lake (an impoundment of the spring source) (Watkins, 1930; Silveus, 1933). Since that time, the species disappeared from Spring Lake and irrigation ditches, and its distribution in the San Marcos River also has decreased due to dam construction, siltation, erosion, aquatic vegetation removal, stream channelization, and introductions of exotic species (Terrell *et al.*, 1978). Subsequent to its extirpation from Spring Lake, wild-rice was reintroduced into the lake near its outfall (Power, 1996a).

Options for recovery are limited, owing to the restricted range and decreased abundance of this species (US Fish and Wildlife Service, 1996). In addition to alleviating various threats, reintroduction eventually may be necessary for full recovery of this species. Carefully chosen sites will be required, and habitat characteristics, while generally known based on the extant distribution of the species, require a higher degree of specification (US Fish and Wildlife Service, 1996). For example, Silveus (1933) stated that the species was found growing in the swiftest currents at some distance from the bank rather than along the stream margins as he expected, but neither current velocities nor exact locations of the rice were recorded. Likewise, in his study of Texas wild-rice, Vaughan (1986) gave a general overview of the geology, soils and vegetation of the San Marcos River, but he provided few specific habitat details. Various experimental studies also have been done to delimit habitat parameters for Texas wild-rice. However, most of these studies have been conducted under artificial conditions outside the currently occupied habitat of Texas wild-rice, or under modified conditions. These include several studies by Power and others who have looked at substrate, oxygen concentration, depth, current velocity, and associated vegetation (Vaughan, 1986; Power and Fonteyn, 1995; Power, 1996a,b,c). However, critical comparisons of sites occupied and not occupied by Texas wild-rice in the natural habitat have not been conducted previously. The purpose of the present study was to obtain an accurate habitat profile of Texas wild-rice in its native habitat.

## METHODS

Transects were selected for study from the San Marcos River, Hays County, TX above its confluence with the Blanco River during May and August 1994, and January 1995 (Figure 1). This reach of the river represents the known historic distribution of Texas wild-rice. Transects were distinguished as those having Texas wild-rice (rice transects) and those without Texas wild-rice (non-rice transects), with 15 transects of each type being sampled for each sampling period. Because only a single population of Texas wild-rice is known, rice transects were selected from areas in the river where Texas wild-rice was growing. This was accomplished by assigning each wild-rice plant a reference number, randomizing those numbers, and then selecting the 15 transects in order of occurrence following randomization. Transects were considered as the area intersecting the rooted zone of the rice plant(s) in a straight line from bank to bank perpendicular to the current. Multiple rice plants grew in some transects. To select non-rice transects, the river was divided into 30 m increments, from Spring Lake to its confluence with the Blanco River (approximately

11 km total distance), and transects were randomly selected from among these divisions using the same process described for rice transects. Non-rice transects were considered as a straight line from bank to bank perpendicular to the current at the mid-point of those sections selected for study. If Texas wild-rice was found growing in a selected non-rice transect, that transect was excluded from study and another

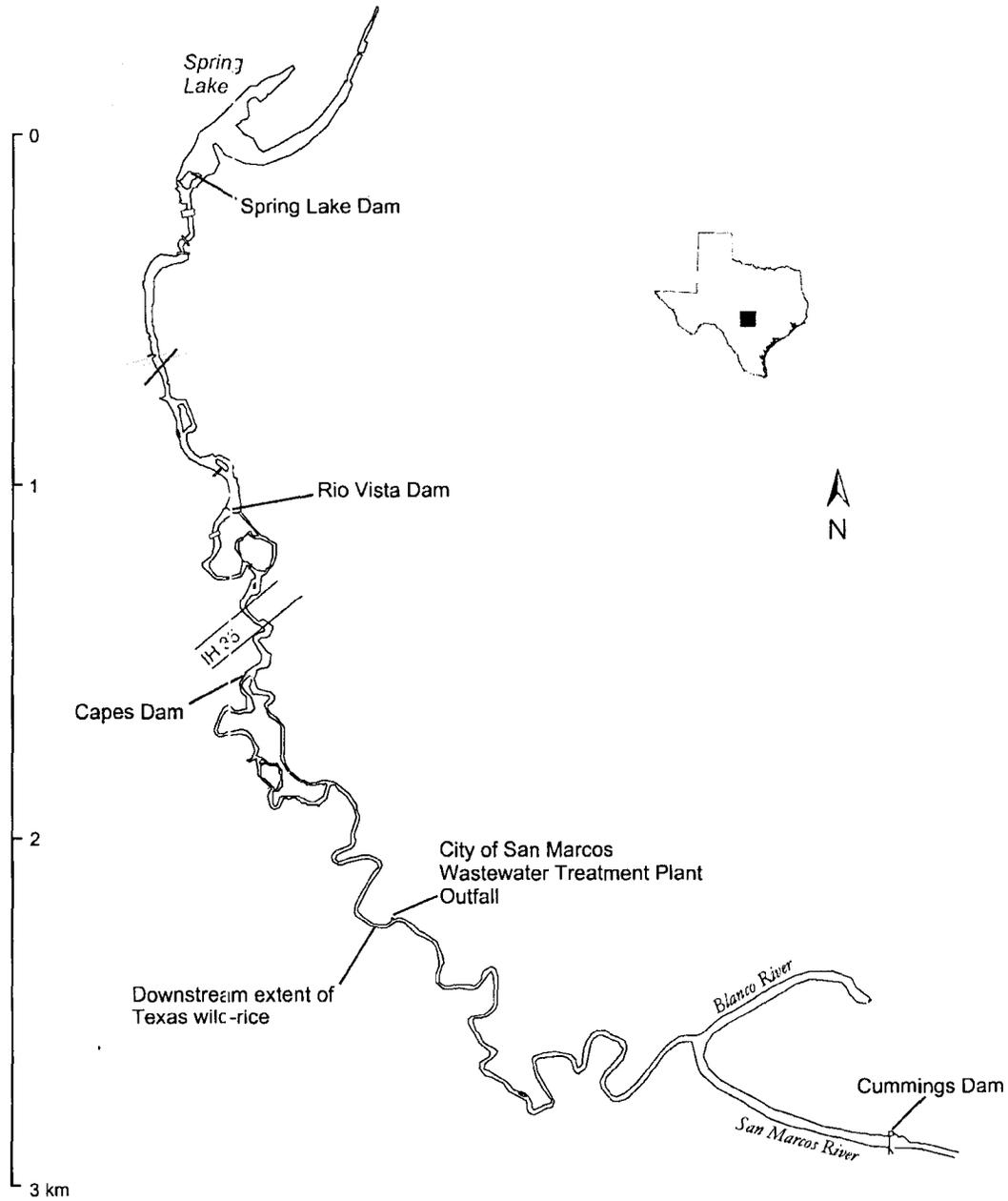


Figure 1. Map of the upper San Marcos River, Hays County, TX.

randomly selected transect was chosen for study. Channel widths of transects from upstream to downstream were variable, due to man-made and natural variations in channel morphology. However, mean transect widths were similar for rice and non-rice transects (16.7 and 18.5 m, 20.0 and 22.7 m, 17.2 and 15.3 m for the May, August and January sampling dates, respectively).

At each transect sampled, the static physical and chemical conditions (dissolved oxygen concentration, conductivity, pH and temperature) were determined using a calibrated Hydrolab Scout<sup>®</sup> 2 with one set of readings being taken per transect. Water samples for turbidity analysis were collected in clean glass 50 ml bottles at three locations (mid-, left- and right-channels) for each transect sampled. Turbidity was measured in the laboratory with a turbidity meter (HF Scientific, Inc.<sup>®</sup>, DRT-15CE) on the same day that water samples were collected in the field. The three readings were pooled for each transect.

Depth and current velocity were measured at 1 m intervals across the entire width of the river channel at each transect using a calibrated, top-setting wading rod and a Marsh–McBirney<sup>®</sup> velocity meter using the methodology of Buchanan and Somers (1980) and Gordon *et al.* (1992). For depths less than 0.8 m, mean column velocity for each transect interval was determined at  $0.6 \times$  the depth, and, for depths greater than 0.8 m, mean column velocity was estimated as the average of the velocity readings taken at  $0.2 \times$  and  $0.8 \times$  the depth. Velocity and depth readings were then averaged for each transect. At each wild-rice plant found growing in rice transects, depth and current velocity were measured at the rooted zone using these same techniques. The total number of rice plants measured for each sampling date was 36 (May), 44 (August) and 24 (January), respectively.

Aquatic macrophyte composition was determined at 1 m increments along each transect within an approximate 0.5 m transverse band along the mid-line of each segment. Macrophyte composition, based on visual observation, was recorded as the relative percentage of each species occupying the total area of the transect band. Macrophyte species identifications were according to Correll and Correll (1975).

In the spring of 1995, substrate samples were taken from the river bed at one location for each of 15 randomly selected rice transects and from three locations each (mid-, right- and left-channel) for the 15 randomly selected non-rice transects using a Wildco<sup>®</sup> hand-operated (5 cm diameter) benthic core sampler. For rice transects, cores were taken adjacent to the upstream side of the rooted zone of wild-rice plants sufficiently close as to get a representative sample of the substrate, but not close enough to uproot or damage the plants. For each sample, the corer was pushed into the substrate until it would no longer move downward. Substrate samples were placed in clean plastic bags in the field, labelled, and returned to the laboratory where they were dried. Dried substrate samples were analysed for chemical composition, particle size, and assigned to standard soil classifications by the Soils Testing Laboratory at Texas A&M University, College Station, TX.

Comparative, parametric statistics could not be properly employed in the analysis of the data collected due to the inherent difficulties of sampling a single population from one ecosystem. Because Texas wild-rice is represented by a single population from only one stream, pseudo-replication and lack of independence among samples were constraints of data analysis (Hurlbert, 1984). However, because the primary concerns of this study were the distribution functions associated with rice and non-rice transects, the Kolmogorov–Smirnov goodness-of-fit test ( $\alpha = 0.05$ ) was employed where applicable to test for differences between transect types (Conover, 1980; Sokal and Rohlf, 1981).

## RESULTS

### Physical and chemical parameters

Physical and chemical conditions in the San Marcos River were found to be uniform, both among sampling dates and transect types, as a result of the strong influence of spring flows (Figure 2). These data

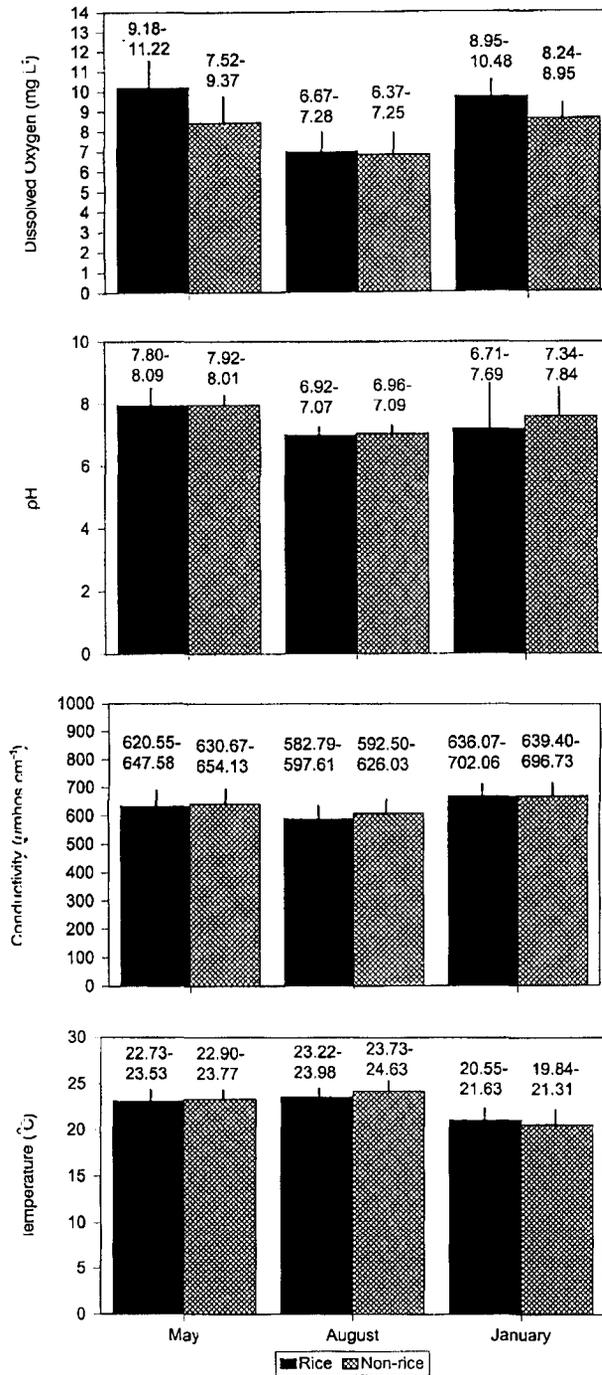


Figure 2. Physical and chemical parameters (+1 S.D.) measured for transects supporting and not supporting growth of Texas wild-rice in the upper San Marcos River, Hays County, TX. Numbers above the bars represent 95% confidence intervals.

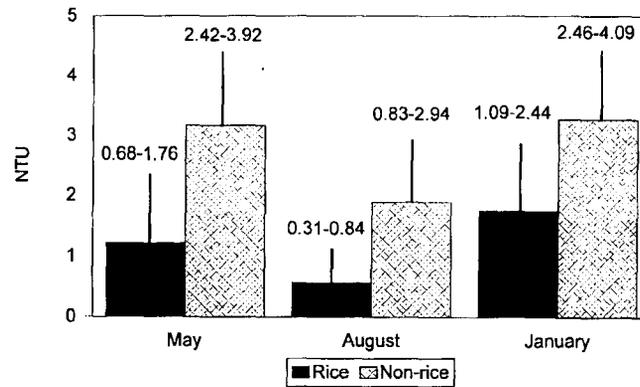


Figure 3. Turbidity (+1 S.D.) in nephelometric turbidity units (NTU) for transects supporting and not supporting growth of Texas wild-rice in the upper San Marcos River, Hays County, TX. Numbers above the bars represent 95% confidence intervals.

were consistent with those of previous water quality studies on the river (Groeger *et al.*, 1997). Few significant differences were observed among physical and chemical parameters between rice and non-rice transects among sampling dates. Moreover, these differences may not be biologically significant. For example, dissolved oxygen concentrations were found to be significantly different between rice and non-rice sites during January ( $K\alpha_{0.05} = 0.57$ ;  $p = 0.002$ ), but in each instance, mean dissolved oxygen concentration for both types of transect were within 20% of the temperature-dependent saturation concentration (Groeger *et al.*, 1997). Likewise, significant differences among conductivity measurements in May and August and temperature during August ( $K\alpha_{0.05} = 0.53$ ;  $p = 0.028$ ) were not large. Turbidity was significantly higher ( $K\alpha_{0.05} = 0.60$ ;  $p = 0.009$ ) for non-rice transects compared with rice transects during May (Figure 3), but the maximum turbidity recorded for any sampling date was low and did not exceed 5.6 NTU. Groeger *et al.* (1997) reported turbidity estimates from the upper San Marcos River similar to those reported here. The higher mean turbidity of the non-rice transects probably relates to some being downstream from the outfall of the San Marcos Wastewater Treatment Plant. Although relatively low and not statistically significant, increased turbidity in downstream areas was visibly apparent during field investigations, and in general the bottom of the stream could not be seen.

### Substrate analysis

Chemical analysis of the substrate samples showed few differences between rice and non-rice transects (Table 1), and some of those differences (i.e. salt, Ca, Mg,  $\text{SO}_4$ ) may not be biologically significant (Wetzel, 1975). However, the most interesting differences observed were in concentrations of potassium (K), iron (Fe), and copper (Cu), all of which were significantly higher for the non-rice transects. It is unknown why these particular values were higher for non-rice transects though they may relate to water quality changes associated with urban and agricultural run-off and the discharge of San Marcos Wastewater Treatment Plant.

Differences in the physical composition of the substrate between rice and non-rice transects were considerable (Figure 4). While no significant differences were found in the organic matter content of the substrate between types of transects among sampling dates, rice transects had more than twice the amount of sand compared with non-rice transects (69.53 and 30.73%, respectively;  $K\alpha_{0.05} = 0.67$ ;  $p < 0.001$ ). By comparison, non-rice transects had more than twice the amount of clay and silt (37.29 and 31.47%, respectively;  $K\alpha_{0.05} = 0.71$ ;  $p < 0.0001$ ) than rice transects (18.67 and 11.80, respectively;  $K\alpha_{0.05} = 0.71$ ;  $p < 0.0001$ ). This pattern is also evident in the soil classification analysis (Table 2). Texas wild-rice grew

in predominantly moderately coarse to coarse sand-based soils (73.34%) while non-rice transects were largely moderately fine to fine clay-based soils (82.22%). Indeed, 40% of the non-rice core samples analysed were classified as clay. Organic matter content did not exceed 4.5% for any transect sampled.

### Depth and velocity

Rice transects were found to be predominantly shallow (1 m) and with considerably higher current velocities compared with non-rice transects where water depth was greater (1.7 m) and the current velocities were lower (Figures 5 and 6). However, non-rice transects generally were found to be strongly dissimilar from conditions observed for rice transects. Mean water depth for rice transects and individual rice stands among sampling dates ranged from 0.72 to 0.80 m and 0.75 to 0.83 m, respectively, compared with 1.76 to 1.85 m for non-rice transects. Mean current velocities among sampling dates ranged from 0.38 to 0.93 m s<sup>-1</sup> for rice transects compared with 0.46 to 1.01 m s<sup>-1</sup> for individual rice stands and 0.09 to 0.22 m s<sup>-1</sup> for non-rice transects. Individual rice stands were not significantly different from the mean conditions of the transects in which they occurred ( $p \geq 0.92$ ). However, individual rice stands were significantly different with respect to mean current velocity compared with non-rice transects ( $p \leq 0.03$ ) except during January when these transect types were not found to be significantly different ( $K\alpha_{0.05} = 0.47$ ;  $p = 0.08$ ).

Table 1. Soil chemistry analysis of substrate samples taken from rice and non-rice growing areas of the San Marcos River, TX<sup>a</sup>

Parameter <sup>b</sup>	Rice transects ( $n = 15$ )	Non-rice transects ( $n = 45$ )	$K^c$	$p$
pH	7.91 (S.D. = 0.25) (7.77–8.04)	7.85 (S.D. = 0.19) (7.79–7.91)	0.24	0.51
Salt <sup>d</sup>	966.67 (S.D. = 475.34) (703.43–1229.90)	703.33 (S.D. = 286.12) (617.37–789.29)	0.33	0.16
NO <sub>3</sub>	12.67 (S.D. = 16.51) (3.52–21.81)	6.51 (S.D. = 9.97) (3.51–9.50)	0.22	0.63
P	73.67 (S.D. = 22.80) (61.34–86.29)	85.53 (S.D. = 32.41) (75.79–95.27)	0.24	0.51
K	95.80 (S.D. = 75.68) (53.89–86.29)	163.64 (S.D. = 61.67) (75.79–95.27)	0.64	0.0002*
Na	116.87 (S.D. = 52.27) (87.92–145.81)	119.33 (S.D. = 70.38) (98.19–140.49)	0.18	0.87
Ca	19 173.20 (S.D. = 205.67) (19 059.30–19 287.09)	19 502.35 (S.D. = 272.84) (19 420.38–19 584.32)	0.51	0.0056*
Mg	959.80 (S.D. = 233.94) (830.25–1089.35)	1129.51 (S.D. = 350.44) (1024.22–1234.79)	0.40	0.05*
Zn	4.85 (S.D. = 3.77) (2.76–6.94)	6.71 (S.D. = 5.04) (5.20–8.23)	0.27	0.40
Fe	45.97 (S.D. = 28.18) (30.36–61.58)	89.05 (S.D. = 29.91) (80.06–98.03)	0.60	0.0006*
Mn	5.37 (S.D. = 4.43) (2.52–7.82)	5.98 (S.D. = 3.15) (5.04–6.94)	0.35	0.12
Cu	1.22 (S.D. = 0.79) (0.78–1.65)	1.83 (S.D. = 0.64) (1.58–2.07)	0.35	0.12
SO <sub>4</sub>	1555.78 (S.D. = 326.29) (1375.08–1736.48)	1343.97 (S.D. = 256.94) (1266.78–1421.16)	0.51	0.0056*

<sup>a</sup> Values are means with S.D. and 95% confidence intervals indicated in parentheses.

<sup>b</sup> All values are expressed in ppm except pH and salt ( $\mu\text{mhos cm}^{-1}$ ).

<sup>c</sup> Kolmogorov–Smirnov goodness-of-fit test.

<sup>d</sup> Includes all salts present.

\* Significantly different ( $\alpha = 0.05$ ).

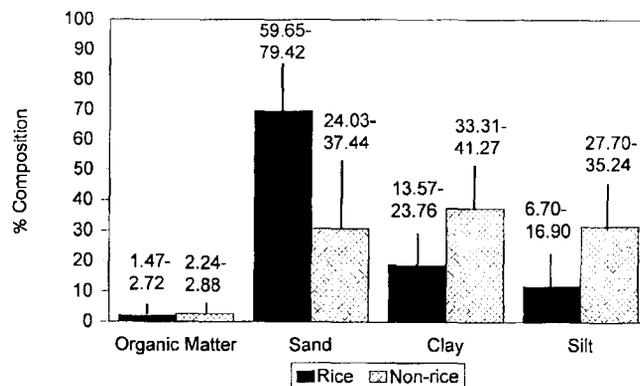


Figure 4. Mean percentage substrate composition (+ 1 S.D.) in transects supporting and not supporting growth of Texas wild-rice in the upper San Marcos River, Hays County, TX. Numbers above the bars represent 95% confidence intervals.

### Aquatic vegetation

In some transects, *Hydrilla* and *Egeria* grew together, often intermingled and occasionally in water up to 2.5 m deep. Without the use of SCUBA equipment these plants could not be identified with certainty. In addition, during this study one exotic species (*Hygrophila polysperma* Roxb.) was misidentified as a native species (*Ludwigia repens* Forst.) (Angerstein and Lemke, 1994). For these reasons, a statistical analysis of aquatic macrophyte data was not attempted. Instead, summaries of the mean percentage of each species occurring in rice and non-rice transects for each sampling date are presented in Table 3. While data on macrophyte composition could not be interpreted conclusively, a general trend is apparent based on an analysis of the summary statistics. Exotic macrophytes, particularly *Hydrilla verticillata* (L. f.) Royle and *Egeria densa* Planch., comprised a greater percentage of the total macrophyte population in non-rice transects than in rice transects. For rice transects on all sampling dates, exotic species (excluding the

Table 2. Classification of soils collected from rice and non-rice growing areas of the San Marcos River (after Brady, 1974)

Common name	Texture	Class name	% Occurrence	
			Rice transects (n = 15)	Non-rice transects (n = 45)
Sandy soils	Coarse	Sand	0	2
		Loamy sands	27	4
Loamy soils	Moderately coarse	Sandy loam	47	2
		Fine sandy loam	0	0
		Very fine sandy loam	0	0
	Medium	Loam	0	9
		Silt loam	0	0
		Silt	0	0
Clayey soils	Moderate y fine	Clay loam	13	13
		Sandy clay loam	7	11
		Silty clay loam	0	11
		Sandy clay	0	0
Clayey soils	Fine	Silty clay	0	7
		Silty clay	0	7
		Clay	7	40

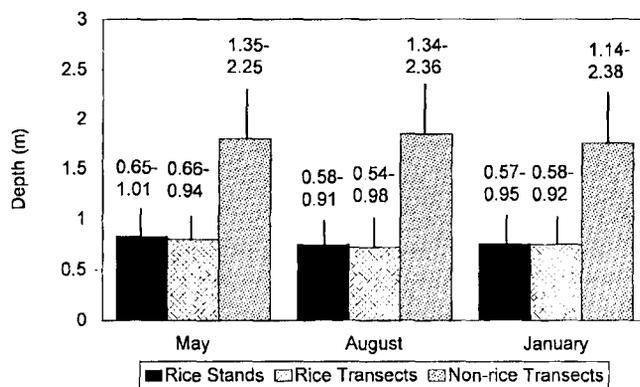


Figure 5. Mean (+ 1 S.D.) depth for individual rice stands and transects supporting and not supporting growth of Texas wild-rice in the upper San Marcos River, Hays County, TX. Numbers above the bars represent 95% confidence intervals.

*Ludwigia/Hygrophila* combinations) did not exceed 29%, but for non-rice transects, the total mean percentage of exotic species ranged from 43.94 to 46.75% among sampling dates. Conversely, native species of macrophytes were typically more abundant in the rice transects. While aquatic macrophyte composition in the non-rice transects contained a greater percentage of exotic species, the absence of wild-rice from these areas may be a function of the deeper, slow-flowing characteristics of these areas that favours growth of the former macrophyte assemblage rather than from direct competition with these species.

DISCUSSION

Texas wild-rice appears to grow primarily in areas having high to moderate current velocities, shallow water approximately 1 m or less, and a coarse, sandy substrate with a relatively low organic matter content. Associated aquatic macrophytes in these areas consist largely of native species. This suggests that minimal conditions necessary for the establishment and growth of Texas wild-rice are similar to those conditions reported in this study. Conversely, areas not supporting stands of Texas wild-rice are typically deeper with slower current velocities and substrates consisting primarily of fine, clay-based soils. The composition of aquatic macrophytes in the non-rice areas was dominated by exotic species such as *Hydrilla*

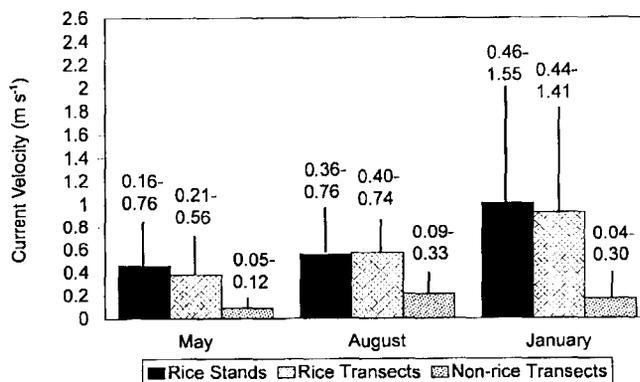


Figure 6. Mean current velocity (+ 1 S.D.) for individual rice stands and transects supporting and not supporting growth of Texas wild-rice in the upper San Marcos River, Hays County, TX. Numbers above the bars represent 95% confidence intervals.

Table 3. Mean percentage composition of aquatic macrophytes in belt transects in rice and non-rice growing areas of the San Marcos River, 1994–1995<sup>a</sup>

Species <sup>b</sup>	% Composition					
	May		August		January	
	Rice	Non-rice	Rice	Non-rice	Rice	Non-rice
<i>Cabomba caroliniana</i>	0.15	4.49	14.23	20.36	19.34	0.77
<i>Ceratophyllum demersum</i>	0.11	3.55	0	0	0	0
<i>Ceratopteris thalictroides</i> <sup>c</sup>	0	0	0	0	0	1.92
Chlorophyta	0.22	10.36	6.00	15.75	7.23	1.99
<i>Colocasia esculenta</i> <sup>c</sup>	5.33	10.42	3.28	7.88	13.32	12.33
<i>Cyperus</i> sp.	0	0	0	0	0.29	0
<i>Egeria densa</i> <sup>c</sup> / <i>Hydrilla verticillata</i> <sup>c</sup>	15.87	36.33	11.41	36.06	15.50	31.74
<i>Hydrocotyle umbellata</i>	0	0	0	0	6.47	0
<i>Ludwigia repens</i> / <i>Hygrophila polysperma</i> <sup>c</sup>	5.61	0.38	14.12	4.93	11.17	6.28
<i>Potamogeton illinoensis</i>	34.98	5.83	28.82	34.73	16.68	0
<i>Myriophyllum</i> spp. <sup>c</sup>	0	0	0	1.32	0	0
<i>Najas guadalupensis</i>	5.45	0	0	0	9.44	2.08
<i>Sagittaria platyphylla</i>	0.80	0	8.62	14.78	10.72	0
<i>Vallisneria americana</i>	15.58	0.71	21.68	2.62	9.39	0
<i>Zizania texana</i>	9.17	—	8.15	—	3.66	—

<sup>a</sup> Grand means of transect averages for each species. Transects read at 1 m intervals within an approximate 0.5 m band along mid-line of segment.

<sup>b</sup> Arranged in alphabetical order.

<sup>c</sup> Exotic species.

*verticillata* and *Egeria densa*. The three top-release dams present in the upper San Marcos River produce varying degrees of impoundment of the river channel. The extant distribution of Texas wild-rice in the San Marcos River apparently reflects the effects of such impoundment. Indeed, Texas wild-rice does not grow in those areas immediately behind dams where lentic conditions are approached.

The results of this study are in contrast to the conclusions of Power and Fonteyn (1995), who studied the effects of oxygen concentration and substrate on Texas wild-rice germination and seedling growth. Power and Fonteyn (1995) concluded that low oxygen levels trigger germination in anaerobic sediments and that clay-based sediments ultimately provide the most suitable medium for growth of Texas wild-rice seedlings. However, the study by Power and Fonteyn was done under laboratory conditions and did not address the broad range of natural conditions in the San Marcos River, the only natural habitat of Texas wild-rice. For example, they used deionized water that contained only limited nutritive value (Power and Fonteyn, 1995). In contrast, a broad range of nutrients were available in the sediments of the San Marcos River (Table 1) that could potentially influence growth of Texas wild-rice (Wetzel, 1975). Also, Power and Fonteyn (1995) used sterile sand containing virtually no organic matter and clay rich in organic matter taken from a man-made pond as the experimental substrates for their study. However, analyses of soils collected from the San Marcos River shows that organic matter content among sandy and clay soils essentially was the same.

In a related study, Power (1996b) grew Texas wild-rice in pots placed in Spring Lake, and found that stem density was greater at current velocities of 0.40–0.49 m s<sup>-1</sup> when compared with lower velocities (< 0.24 m s<sup>-1</sup>). In addition, during an attempt to reintroduce Texas wild-rice into Spring Lake, Power (1996a) found that rice plants produced reproductive culms and fewer asexual tillers when grown in current velocities up to 0.345 m s<sup>-1</sup> and depths of 2 m or less. The individual plants transplanted under these conditions remain the only survivors in Spring Lake. These conditions are quite similar to those in which Texas wild-rice was found growing in the San Marcos River (e.g. Figure 6). Power (1996b) also found that Texas wild-rice exhibited a positive growth response, including having greater biomass and stem density

above ground, when grown in sandy clay, and a negative growth response when grown in gravel. By comparison, the soils analysis associated with wild-growing plants showed that most plants were growing in loamy sands and sandy loams. A proposed adaptation of Texas wild-rice to living in fast-flowing water is that plants may actually modify the substrate in their favour by increasing fine sediments and detritus deposition (Gregg and Rose, 1982; Power, 1996b). Such modification apparently results in fine sediments being retained within the plant stands, and coarse sediments around stands. Similarly, the results of this study show that, although rice plants grow in predominantly moderately coarse and coarse soils, there also are appreciable amounts of clay and silt associated with these substrates.

Present-day biologists do not have a clear understanding of the natural appearance and conditions of the San Marcos Springs before they were impounded more than 100 years ago. However, based on extant spring-flow (ca.  $4500 \text{ L s}^{-1}$  average daily flow), the volume of flow and current velocity of the upper San Marcos must have been quite high before impoundment and pumping demands were placed on the Edwards Aquifer, the source of San Marcos Springs (Bowles and Arsuiffi, 1993). Of the few historical accounts of the San Marcos Springs and River before impoundment, McClintock (1930) stated that 'These springs gush from the foot of a high cliff and boil up as from a well in the middle of the channel. . . the channel is here 40 yds wide, the water 15 or 20 feet deep, yet so strong is the ebullition [sic] of spring, that the water is thrown two or three feet above the surface of the stream. . . Large stones are thrown up, as you've seen grains of sand in small springs, it is unaffected by the driest season. . . It is about 60' wide and 3' deep on an average with a current [sic] of not less than 10 to 15 miles per hour.' Though anecdotal, the historical conditions described by McClintock (1930) for the upper San Marcos River (i.e. on average approximately 20 m wide, 1 m deep, and a maximum estimated current velocity of more than  $5 \text{ m s}^{-1}$ ) do not suggest a system dominated by silt and clay-laden benthic deposits. Even if some side-channel areas of the upper San Marcos River historically were marshy as some suspect, periodic spates and flash floods would have scoured deposits of silts and clays leaving behind heavier substrate particles, such as sand and gravel. However, during the 1970s, five small flood control dams were built in the upper San Marcos Watershed (Power, 1996b). These dams have altered the frequency and magnitude of historic flooding cycles as well as causing increased sedimentation in the river.

When one considers the historic abundance of Texas wild-rice throughout the upper San Marcos River (Silveus, 1933), the probable historical conditions of the river, and the extant distribution of the remaining stands of Texas wild-rice and their associated habitat conditions, a reasonably clear picture emerges that this species prefers relatively shallow water with moderate to fast current and a moderately coarse substrate. Moreover, the anemophilous nature of sexual reproduction for this species certainly supports this contention. Regrettably, the notion fostered by Vaughan (1986), that ideal growth conditions for Texas wild-rice are no longer present due to the numerous modifications made to the San Marcos River, may be correct. The present distribution of Texas wild-rice in the upper San Marcos River appears to be a function of the species being extirpated from downstream areas largely due to construction of dams and their associated negative impacts on stream structure and functioning. Factors such as increased sedimentation, turbidity and water depth, and decreased current velocities have produced habitat conditions unsuitable for the growth of Texas wild-rice throughout much of its historic range.

The results of this study allow reliable and accurate identification of the remaining suitable habitat of Texas wild-rice in the San Marcos River for possible reintroduction sites and development of a sound management plan to ensure the survival of this species. Efforts are currently underway to augment the existing population of Texas wild-rice in its natural habitat. A refugium stock of this species has been developed by the US Fish and Wildlife Service and is maintained at the San Marcos National Fish Hatchery and Technology Center in San Marcos, TX. Plants from this stock are selectively being reintroduced into the river on a trial basis in cooperation with the University of North Texas, Denton, TX. Reintroduction sites for wild-rice in this trial programme are being selected based on the habitat conditions identified in this study. However, at this time, no data are available as to the success of this reintroduction effort. A broader reintroduction programme will begin following a preliminary analysis of the pilot studies.

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