RESOURCE ALLOCATION PATTERNS AND PHENOTYPIC VARIATION IN THE ENDANGERED TEXAS WILDRICE (*ZIZANIA TEXANA*, POACEAE)

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ABSTRACT

Zizania texana Hitchc., an endangered macrophyte endemic to the upper 4.9 km of the San Marcos River, Hays County, Texas was Federally listed in 1978 after the species experienced a population decline between about 1940 and 1967. Recent interest in restoration has focused attention on the need for a better understanding of the species' response to a variety of microhabitats. This study documents biomass allocation patterns in three microhabitats over 7 months. Current velocities ranged from 0.0–0.010 m/s in the slow site, 0.038–0.142 m/s in the moderate site, and 0.250–0.369 m/s in the fast site. Plants were harvested from each site, on seven occasions, washed, separated into roots, submersed leaves, and reproductive culms with associated leaves and inflorescences, then dried and weighed. At the end of the study, mean total biomass of plants grown in the fast site was 28.42 gdw vs 4.24 gdw for plants grown in the slow site. Resource allocation patterns differed among sites and two distinct phenotypes were apparent. One phenotype, associated with relatively higher current velocities, had higher net productivity, a well-developed root system, and allocated proportionally more biomass to non-reproductive organs (49.2% gdw root biomass in fast site vs 24.8% gdw root biomass in slow site). A second phenotype, associated with relatively slower flowing water, had lower net productivity and allocated proportionally more biomass to reproductive organs (22.1% gdw reproductive culm in fast site vs. 65.0% gdw reproductive culm in slow site). Because of lower productivity and the potential for loss from herbivory to a significant proportion of the plant in slower flowing water, a microhabitat with relatively low current velocity would not be recommended for restoration purposes.

RESUMEN

Zizania texana Hitchc., un macrófito en peligro, endémico de los 4.9 km superiores del río San Marcos, Hays Co., Texas se incluyó en la lista Federal en 1978 después que la especie experimentase una reducción poblacional entre 1940 y 1967. El interés reciente en la restauración ha prestado atención a la necesidad de una mejor comprensión de la respuesta de la especie a una variedad de microhábitats diferentes. Este estudio documenta los modelos de situación de biomasa en tres microhábitats durante 7 meses. Las velocidades normales variaron entre 0.0–0.010 m/s (el sitio lento), 0.038–0.142 m/s (en el sitio moderado), y 0.250–0.369 m/s (en el sitio rápido). Las plantas se cosecharon de cada microhábitat, en siete ocasiones, se lavaron, separaron las raíces, las hojas sumergidas, y los cúlmenes reproductores con las hojas e inflorescencias asociadas, luego se secaron y pesaron. A final del estudio, la biomasa total media de plantas del sitio rápido fue 28.42 gdw contra 4.24 gdw para plantas del sitio lento. Los modelos de recursos difirieron significativamente entre los diferentes sitios y fueron aparentes dos fenotipos claros eran. Un fenotipo asociado con velocidades actuales relativamente más altas, tenía una productividad neta más alta, un sistema radical bien desarrollado, y colocó proporcionalmente más biomasa en órganos vegetativos (49.2% de peso seco de biomasa de raíz en el sitio rápido contra 24.8% de peso seco de biomasa de raíz en el sitio lento). Un segundo fenotipo,

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asociado con agua de corriente relativamente más lenta, tuvo una productividad neta más baja y colocó proporcionalmente más biomasa en los órganos de reproductores (22.1% de peso seco de biomasa en cúlmenes reproductores en el sitio rápido contra. 65.0% de peso seco de biomasa en cúlmenes reproductores en el sitio lento). A causa de tasas bajas de productividad y la pérdida potencial debida a los herbívoros en una proporción significativa en el agua de corriente más lenta, este tipo de microhábitat no se debería recomendar para las restauraciones.

INTRODUCTION

Trade-offs between reproductive allocation and vegetative allocation with changes in environmental conditions have been reported by Harper and Ogden (1970); Hickman (1975); van Baalen, et al. (1990); Dunn and Sharitz (1991); Madsen (1991) and Neill (1993). Environmental factors associated with allocation trade-offs include substrate, nutrient availability, and water depth (Idestam-Almquist & Kautsky 1995; Blanch et al. 1999; Lorenzen et al. 2001; Vretare et al. 2001). Little information is available on current velocity and its affect on allocation patterns in macrophytes although numerous studies have identified current velocity as an important factor influencing macrophyte distribution, photosynthesis and growth (Nilssen 1987; Chambers et al. 1991; Madsen & Søndergaard 1983; Power 1996a). The work reported here was undertaken to document resource allocation patterns in the endangered *Zizania texana* Hitchc. over seven months in three different habitat types differing in current velocity and pH.

Zizania texana is an endangered macrophyte endemic to the San Marcos River, Hays County Texas (U.S. Fish & Wildlife Service 1995). It commonly occurs midchannel in swiftly flowing water. Terrell et al. (1978) and Poole and Bowles (1999) provide thorough descriptions of the habitat for *Z. texana*. Threats to the species include reduced spring flow from the source aquifer due to overpumping of ground water for human use, competition and herbivory by nonnative plant and animal species, and absence of sexual reproduction in the wild, along with other human impacts including alteration of historic hydrologic patterns from dams located along the river and within the watershed, and recreational use (U.S. Fish & Wildlife Service 1995).

Under flowing water conditions, *Z. texana* produces long ribbon-like, submersed leaves and emergent culms, each with a terminal, wind pollinated inflorescence; however, sexual reproduction is nearly absent in the wild (U.S. Fish & Wildlife Service 1995). Historical accounts suggest this was not always the case. Photographs depicting fully developed inflorescences and verbal accounts suggest recruitment by seed occurred (Silveus 1933). More recent descriptions of floral structures and floral development by Emery and Guy (1979), and Power (1996b; 1997) indicate that sexual reproduction is most likely limited by environmental factors rather than cytological factors. It is not well understood why fully developed, emergent inflorescences are rare in the wild, although drifting mats of floating vegetation and herbivory play a role (Power 1996b, c). The species produces asexual clones (tillers) which form at the nodes of reproductive culms and it is assumed that tiller production is the primary mechanism for recruitment of new individuals in the wild (U.S. Fish & Wildlife Service 1995).

Zizania texana has two distinct phenotypes under wild and cultured conditions. When grown in the wild, *Z. texana* is primarily submersed and tends to be a long lived perennial plant. Under cultivated conditions, *Z. texana* is primarily emergent, reproductive, and short lived (Terrell et al. 1978 and pers. observ.). Information on plant response to environmental conditions, gains importance given the endangered status of the species and the need for restoration of the habitat as outlined in the Recovery Plan for the species (U.S. Fish & Wildlife Service 1995). Adequate restoration protocols cannot be developed without a thorough understanding of the response of *Z. texana* to a variety of conditions found in its historic range.

METHODS AND MATERIALS

This research project was carried out in Spring Lake on the Southwest Texas State University (SWT) campus. Spring Lake is an impoundment formed by a dam and spillway originally constructed across the San Marcos River in 1849. The dam and spillway are approximately 750 m downstream from the San Marcos Springs.

Study plants were obtained by germinating captive grown seed in the lab. Seedlings were then transplanted to 15 cm plastic pots, lined with small plastic bags and filled with sediments collected from one location in the study site in Spring Lake. Pots were placed in an outdoor cement raceway on the SWT campus and seedlings were allowed to grow for about 6 weeks. Water was supplied by an artesian well from the source aquifer for Spring Lake and the San Marcos River. In March 1995, potted plants were transplanted into three sites in Spring Lake and one site in the outdoor raceway on the SWT campus. This was a nested design with plants nested in plots and plots nested in sites. There were three replicate plots at each site. Each replicate plot had 36 potted plants for a total of 432 plants. All plants were protected from herbivores with 1 m^3, floating exclosures constructed of polyvinyl chloride (PVC) pipe and 2.5 cm wire mesh. Initially, four plants were harvested to obtain baseline biomass values for the newly transplanted individuals. The study design called for harvesting four plants from each replicate plot on nine separate occasions. However, during the study period some plants were lost to herbivory and some plants were washed away by the current. As a result, plants were harvested from each replicate plot on six dates, May 3, June 1, June 30, July 27, September 1, and October 16. At each harvest, plants were selected at random. Sediment was washed from plant roots, then plants were divided into vegetative parts, reproductive parts, and roots. Vegetative parts were defined as submersed leaves and reproductive parts were defined as reproductive culms with associated leaves, inflorescences, seeds, and tillers. Plants were then dried at 65°C for at least 48 hours and weighed to the nearest 0.01 g. Data are reported as means plus-minus standard error.

On nine occasions between May 1995 and October 1995 pH, water depth, and current velocity were recorded in each replicate plot, in each site. Current velocity was measured with a Marsh McBirney Model 201 portable water current meter and calculated as the average velocity at 20%, 60%, and 80% depth. The four sites differed in mean current velocity and were identified as follows: slow (raceway), no flow, moderate and fast.

RESULTS

Plants in the no flow site in Spring Lake were lost to herbivory, probably by crawfish, prior to the second harvest and this site was dropped from the study.

Water depth, current velocity, and pH at the remaining sites were recorded at the study sites eight times between May and October (Table 1). In the slow site, mean water depth was 0.71 m (±0.03) mean current velocity was 0.001 m/s (±0.004), and pH ranged from 7.50 to 7.68. In the moderate site, mean water depth was 0.88 m (±0.06), mean current velocity was 0.090 m/s (±0.048), and pH ranged from 7.23–7.26. In the fast site, mean water depth was 0.85 m (±0.07), mean current velocity was 0.290 m/s (±0.076) and pH ranged from 7.16–7.28.

Plants in all study sites increased in size during the study period (Fig. 1). At each harvest, fast site plants had the greatest root, submersed leaf, and total net biomass, furthermore, data from the September harvest showed mean net total biomass of fast site plants was an order of magnitude greater than mean net total biomass of slow site plants (34.05 g vs. 3.66 g).

Number of submersed leaves increased in all sites during the study period, however fast site plants produced six times as many submersed leaves as slow site plants. At the end of the study period, mean number of submersed leaves in fast site plants was 18.0 (± 1.414) while mean number of submersed leaves in slow site plants was 3.0 (± 0.211).

Reproductive culms were present in every harvest between 1 June 1995 and 16 October 1995. Culm number was greatest during the September harvest in plants grown in the fast site with 2.9 (± 0.380) culms/plant. For plants grown in the slow site, number of culms was greatest in the October harvests with 1.6 (± 0.159) culms/plant. (Fig. 2).

Biomass allocation to plant roots and reproductive culms varied through time and among sites (Fig. 3). The proportion of biomass allocated to roots increased from 27% in March at the beginning of the study to 49% in October in plants grown in the fast site. In contrast, the proportion of biomass allocated to roots decreased from 27% at the beginning for the study to 25% at the end of the study in the slow site.

Plants in all sites produced similar numbers of culms, however biomass allocation varied greatly among sites. In October, culm biomass constituted over

TABLE 1. Means and ranges for environmental factors in two sites (Moderate and Fast) in Spring Lake and one site (Slow) on the SWT campus. Data were collected on nine separate days between May 1995 and October 1995.

	Slow	Moderate	Fast
Depth (m)			
mean (sd)	0.71 (±0.03)	0.88 (±0.06)	0.85 (±0.07)
range	0.69–0.75	0.87–0.91	0.80–0.87
Current velocity (m/s)			
mean (sd)	0.001 (±0.004)	0.090 (±0.048)	0.290 (±0.076)
range	0–0.010	0.038–0.142	0.250–0.369
pH			
range	7.50–7.68	7.23–7.26	7.16–7.28

half of total plant biomass in slow site plants (65%; culm number = 1.6±0.159), in moderate site plants, 48% of total net biomass was culm biomass (culm number = 1.7±0.129 and fast site plants allocated only 22% of total net biomass to reproductive culms (culm number = 2.25±1.591).

The proportion of biomass allocated to submersed leaves was similar among sites even though the number of leaves varied among sites. In October, submersed leaf biomass was 29% of total biomass in the fast site (leaf number = 18±1.414), 15% of total biomass in the moderate site (leaf number = 5.3±1.862), and 28% of total biomass in the slow site (leaf number = 3±0.211).

DISCUSSION

In this study, plants exhibited markedly different growth patterns among study sites. Net total biomass accumulated over the study period was an order of magnitude greater in plants grown in water flowing between 0.146–0.442 m/s compared with plants grown in water flowing between 0–0.01 m/s. Net biomass accumulation in individual plant organs (roots, submersed leaves, and reproductive culms) also was greater in fast flowing water compared with slow flowing water. Submersed leaf biomass was 18 times greater in fast site plants compared with slow site plants and 4.5 times greater compared with moderate site plants. *Zizania texana* exhibited a similar response to flowing water in other studies (Power 1996a, b).

Flowing water has been shown to influence macrophyte photosynthetic rates (Westlake 1967; Smith & Walker 1980; Madsen & Sondergaard 1983), distribution (Fonseca & Kenworthy 1987; Nilssen 1987); and growth (Chambers et al. 1991). Plants occur in a range of current velocities and there is considerable variability in optimum flow rates for macrophytes. Chambers et al. (1991) found an inverse relationship between biomass and current velocity between 0.01–1.0 m/s. Nilssen (1987) found species richness reached a peak at about 0.3

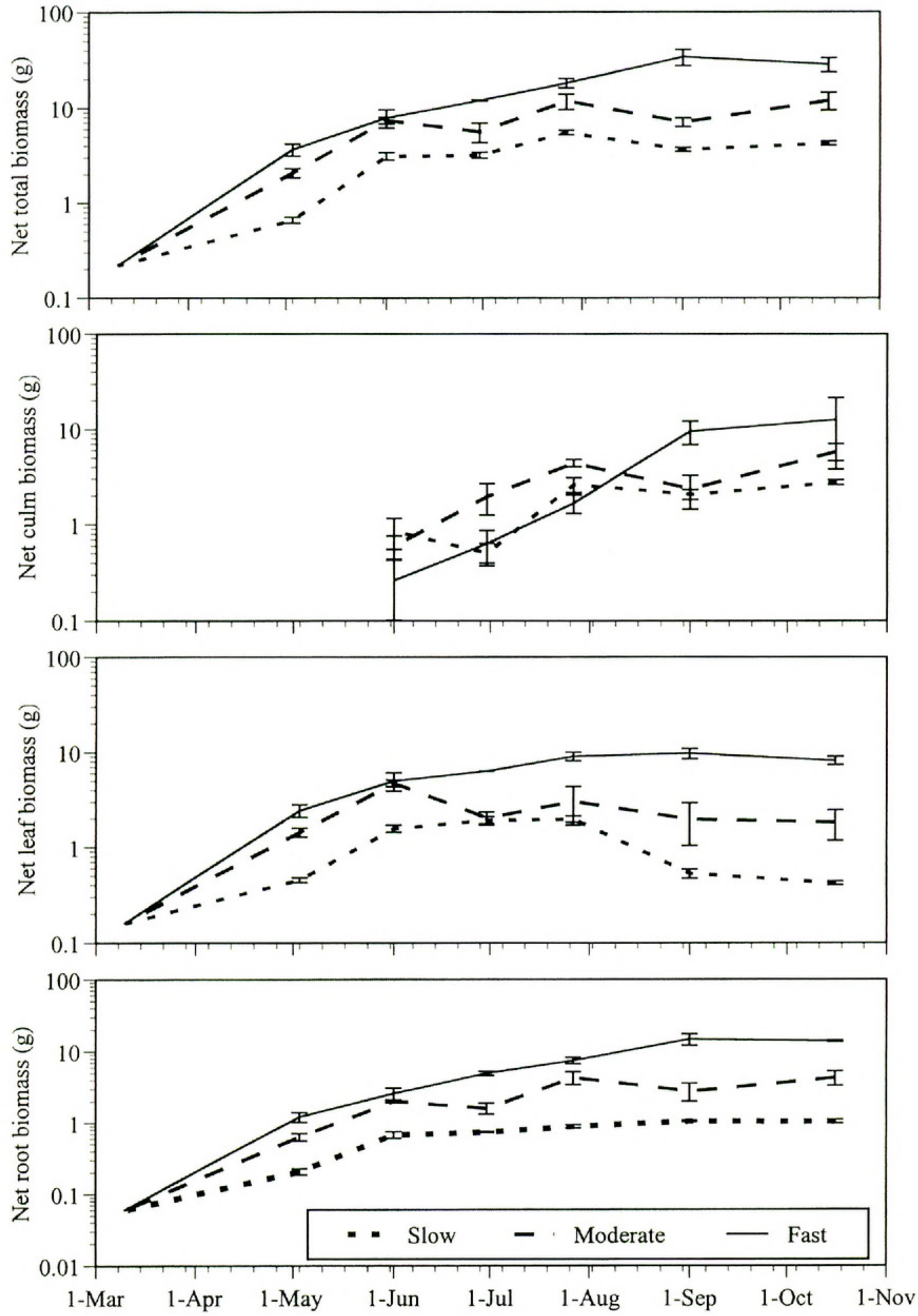

Fig. 1. Growth by potted *Zizania texana* over 7 months from two sites in Spring Lake (fast and moderate sites) and one site at Southwest Texas State University (slow site). After 7 months, plants grown in the fast site had the greatest net root, net leaf, net culm, and net total biomass compared with the other two sites. Points on graph represent the mean ± standard error.

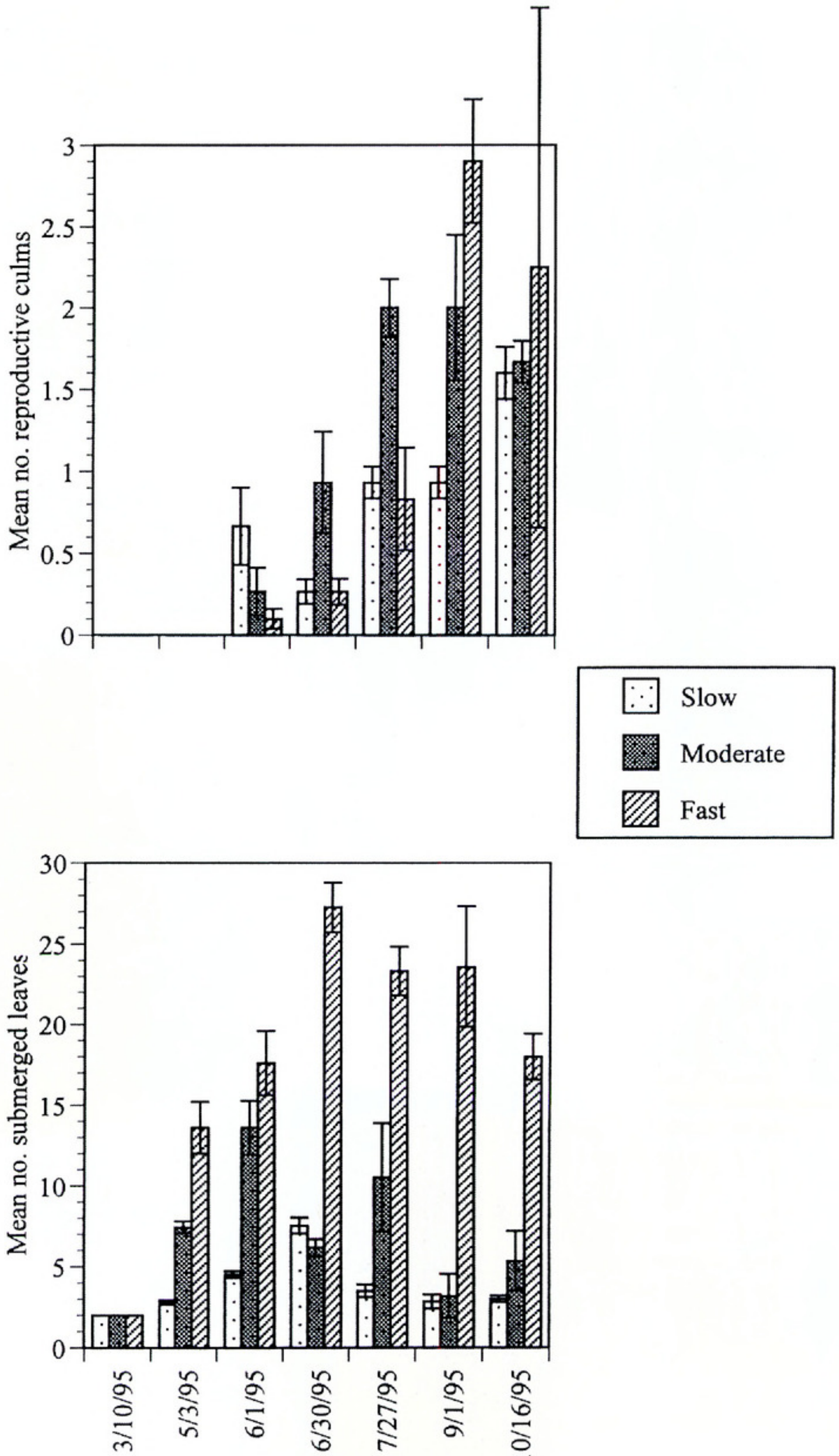

FIG. 2. Number of submersed leaves and reproductive culms from potted *Zizania texana* harvested over 7 months from two sites in Spring Lake and one at Southwest Texas State University. Plants grown in fast flowing water produced more submersed leaves and reproductive culms compared with plants grown in slow flowing water. Vertical bars represent ± standard error.

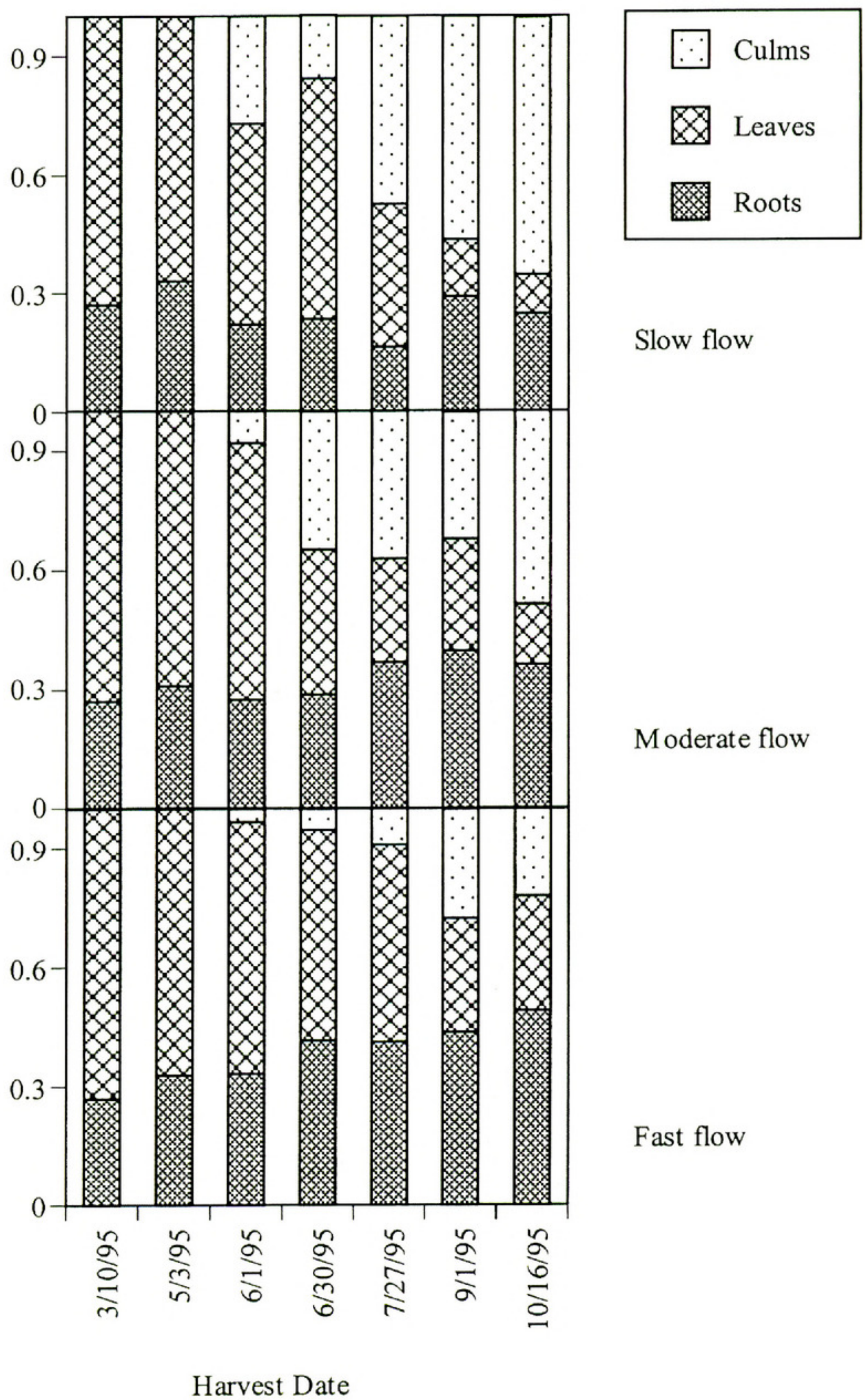

Fig. 3. Proportional allocation of plant mass to roots, leaves, and reproductive culms when grown under three current velocities over 7 months. Biomass allocation to plant roots and reproductive culms varied among sites. There was little difference in the proportion of plant mass allocated to submersed leaves among sites.

m/s along a current gradient from 0.04–1.23 m/s, with some species growing in current velocities greater than 1 m/s. Many species occur in slower current velocities, while fewer species are specialized to withstand the forces of velocities over 0.3 m/s. Apparently, *Z. texana* with smooth, ribbon-like leaves is one of few species able to withstand velocities over 0.3 m/s. Poole and Bowles (1999) found wild *Z. texana* stands primarily in current velocities > 0.46 m/s and the current velocity tolerance range for *Z. texana* exceeds 1.0 m/s; from this study however, it was not possible to identify a maximum or an optimum current velocity for growth.

Zizania texana exhibits phenotypic variation in response to current velocity. One phenotype, associated with relatively higher current velocities, has higher net productivity, a well-developed root system, and allocates proportionally more biomass to nonreproductive organs. A second phenotype, associated with relatively slower flowing water, has lower net productivity and allocates proportionally more biomass to reproductive organs. Plants face a tradeoff between the need for a well-developed root system to anchor plants in potentially unstable sediments, the need for submersed leaves with which to photosynthesize, and the need for emergent stems for reproduction. In this study, the proportional allocation to nonreproductive organs (roots and submersed leaves) decreased with decreasing current velocity as the proportional allocation to reproductive organs increased. Apparently there is a trade-off in favor of submersed organs in faster flowing water.

Other factors directly and indirectly influenced by current velocity may play a role in net biomass accumulation in plant organs. They include herbivory, deposition of debris and sediments on leaves interfering with metabolic processes, colonization of leaves with epiphytes, and the plant's inability to utilize HCO_3^- and its dependence on CO_2 as an inorganic carbon source (unpublished data). Ribbon-like submersed leaves of *Z. texana* are adapted to withstand the forces of flowing water and can reduce carbon limitation by exploiting flowing water habitat where boundary layer surrounding leaves and diffusion distances for CO_2 are reduced, and leaves are continually bathed with carbon rich water. In contrast, in slower flowing water, photosynthesis by submersed leaves of *Z. texana* is carbon limited and few submersed leaves are produced. Emergent reproductive culms with associated emergent leaves most likely are not carbon limited because culms obtain CO_2 from the atmosphere where CO_2 is more readily available owing to the higher diffusion rate and current velocity in air relative to water (Madsen & Sand-Jensen, 1991; Denny 1993).

Increased proportional allocation to emergent reproductive organs in relatively slower flowing water concurs with observations of captive grown *Z. texana* when grown in current velocity ≈0.015 m/s in which plants allocate a greater proportion of biomass to reproductive organs and typically set seed and senesce after one growing season. This is similar to *Z. palustris* and *Z. aquatica*, annual species which commonly occur in shallow water along the margins of lakes and streams (Ferren & Good 1977; Weir and Dale 1960). The importance of having leaves and flowers above the surface of the water may be due to CO_2 limitation in submersed leaves. In relatively slower flowing water, gas exchange and photosynthesis may be insufficient to support vegetative organs and resources shift to emergent organs where CO_2 is plentiful.

Herbivory is a factor contributing to sexual reproductive failure in *Z. texana* (U.S. Fish & Wildlife Service 1995; Power 1996c). Plants growing in microhabitats with relatively slow flowing water and potentially over 60% of biomass allocated to reproductive parts, are especially vulnerable to herbivory by waterfowl. Microhabitats with conditions which would trigger a low productivity/high reproductive phenotype in the wild include back eddies and protected stream edges, emergent macrophyte beds, impoundments upstream from dams, and potentially, reduced springflows due to drought and overpumping of the source aquifer (the Edwards Aquifer) for human use. These microhabitats would not be recommended as possible *Z. texana* restoration sites.

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REFERENCES

Blanch, S.J., G.G. Ganf, and K.F. Walker. 1999. Growth and resource allocation in response to flooding in the emergent sedge *Bolboschoenus medianus*. Aquatic Bot. 63:145–160.

Chambers, P.A., E.E. Prepas, H.R. Hamilton, and M.L. Bothwell. 1991. Current velocity and its effect on aquatic macrophytes in flowing waters. Ecol. Applications 1:249–257.

Denny, M.W. 1993. Air and water: The biology and physics of life's media. Princeton University Press, New Jersey.

Dunn, C.P. and R.R. Sharitz. 1991. Population structure, biomass allocation, and phenotypic plasticity in *Murdannia keisak* (Commelinaceae). Amer. J. Bot. 78:1712–1723.

Emery, W.H.P. and M.N. Guy. 1979. Reproduction and embryo development in Texas wildrice(*Zizania texana* Hitchc.). Bull. Torrey Bot. Club 106:29–31.

Ferren, W.R. and R.E. Good. 1977. Habitat, morphology and phenology of southern wild rice (*Zizania aquatica* L.) from the Wading River in New Jersey. Bull. Torrey Bot. Club 104:392–396.

Fonseca, M.S. and W.J. Kenworthy. 1987. Effects of current on photosynthesis and distribution of seagrasses. Aquatic Bot. 27:59–78.

Harper, J.L. and J. Ogden. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. J. Ecology 58:681–698.

HICKMAN, J.C. 1975. Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense* (Polygonaceae). J. Ecology 63:689–701.

IDESTAM-ALMQUIST, J.and L. KAUTSKY. 1995. Plastic responses in morphology of *Potamogetonpectinatus* L. to sediment and above-sediment conditions at two sites in the northern Baltic proper. Aquatic Bot. 52:205–216.

LORENZEN, B., H. BRIX, I.A. MENDELSSOHN, K.L.MCKEE, and S.L.MIAO. 2001. Growth, biomass allocation and nutrient use efficiency in *Cladium jamaicense* and *Typha domingensis* as affected by phosphorus and oxygen availability. Aquatic Bot. 70:117–133.

MADSEN, J.D. 1991. Resource allocation at the individual plant level. Aquatic Bot. 41:678–86.

MADSEN, T.V. and M. SONDERGAARD. 1983. The effects of current velocity on the photosynthesis of *Callitriche stagnalis* Scop. Aquatic Bot. 15:187–193.

NEILL, C. 1993. Growth and resource allocation of whitetop (*Scolochloa festucacea*) along a water depth gradient. Aquatic Bot. 46:235–246.

NILSSEN, C., 1987. Distribution of stream-edge vegetation along a gradient of current velocity. J. Ecology 75:513–522.

POOLE, J. and D.E. BOWLES. 1999. Habitat characterization of Texas wild-rice (*Zizania texana* Hitchcock), an endangered aquatic macrophyte from the San Marcos River, TX, USA. Aquatic Conservation: Marine and Freshwater Ecosystems 9:291–302.

POWER, P. 1996a. Effects of current velocity and substrate composition on growth of Texas wildrice *(Zizania texana)*. Aquatic. Bot. 55:199–204.

POWER, P. 1996b. Direct and indirect effects of floating vegetation mats on Texas wildrice (*Zizania texana*). Southw. Naturalist 41:462–464.

POWER, P. 1996c. Reintroduction of Texas wildrice (*Zizania texana*) in Spring Lake: Some important environmental and biotic considerations. In: Proceedings from second southwestern rare and endangered plant conference: Rocky Mountain Forest & Range Experimental Station.

POWER, P. 1997. Moisture, seeds, and reproductive failure in Texas wildrice (*Zizania texana*). Southw. Naturalist 42:435–440.

SILVEUS, W. A. 1933. Texas grasses, classification and description of grasses. The Clegg Co., San Antonio, Texas.

SMITH, F.A and N.A. WALKER. 1980. Phtosynthesis by aquatic plants: effects of unstirred layers in relation to assimilation of CO_2 and HCO_3- and to carbon isotopic discrimination. New Phytol. 86:245–259.

TERRELL, E.E, W.P.H. EMERY, and H.E. BEATY. 1978. Observations on *Zizania texana* (Texaswildrice), an endangered species. Bull. Torrey Bot. Club 105:50–57.

U.S. FISH AND WILDLIFE SERVICE. 1995. San Marcos/Comal (revised) recovery plan. Albuquerque, New Mexico.

VAN BAALEN, J., W.H.O. ERNST, J. VAN ANDEL, D.W. JANSSEN, and H.J.M. NELISSEN. 1990. Reproductive allocation in plants of *Scrophularia nodosa* grown at various levels of irradiance and soil fertility. Acta Bot. Neerl. 39:183–196.

VRETARE, V., S.E.B. WEISNER, J.A. STRAND, and W. GRANÉLI. 2001. Phenotypic variation in *Phragmites australis* as a functional response to water depth. Aquatic Bot. 69:127–145.

Weir, C.E. and H.M. Dale. 1960. A developmental study of wild rice, *Zizania aquatica* L. Canad. J. Bot. 38:719–739.

Westlake, D.F., 1967. Some effects of low-velocity currents on the metabolism of aquatic macrophytes. J. Exp. Bot. 18:187–205.

Zar, J.H., 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.