EARLY DEVELOPMENT OF WETLAND PLANT AND INVERTEBRATE COMMUNITIES: EFFECTS AND IMPLICATIONS OF RESTORATION

A Thesis

by

MATTHEW D. BERG

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2006

Major Subject: Rangeland Ecology and Management

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Approved by:

Co-Chairs of Committee,	X. Ben Wu Steven G. Whisenant
Committee Member,	Frances Gelwick
Head of Department,	Steven G. Whisenant

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ABSTRACT

Early Development of Wetland Plant and Invertebrate Communities: Effects and Implications of Restoration. (August 2006)

Matthew D. Berg, B.S., Texas A&M University at Galveston

Co-Chairs of Advisory Committee: Dr. X. Ben Wu
Dr. Steven G. Whisenant

Loss of wetland habitats across the nation is staggering and continues, especially in urbanizing areas. Thus, wetland restoration has become a priority. However, questions remain regarding system function and biotic communities. We studied a constructed floodplain wetland complex near Dallas, Texas. We sought to improve understanding of wetland ecosystem development under the influence of different approaches to wetland restoration in an urbanizing landscape. In the wetland complex, 10 constructed sloughs, approximately 70m by 15m, were designated for this study. Our experiment monitored the establishment of aquatic plant and invertebrate communities under different experimental conditions. In 5 sloughs, 5 native perennial hydrophyte species were transplanted in blocks in each slough, with the remaining 5 sloughs unplanted. Portions of each slough were caged to determine the effects of protective caging. Using $1m^2$ caged and neighboring uncaged areas as quadrats, we sampled vegetation and the invertebrate community over two years to determine the effects of restoration treatments on the communities.

Slough planting did not result in statistically different levels of plant cover. However, invertebrate abundance was greater in planted sloughs, and plant composition was different, comprised more of perennial species in planted sloughs than in unplanted sloughs. Caging did not have an effect on plant or invertebrate communities. However, changes due to time resulted in significant increases in plant cover and invertebrate abundance and shifts in community composition. Four of 5 transplanted species were emergent growth forms. Emergent cover and the remaining species, *Potamogeton nodosus*, a floating-leafed plant, accounted for invertebrate community variation. Transplanted emergent species did not fare well, though other emergent species did colonize the site, along with widespread coverage by submerged *Najas guadalupensis*. *Potamogeton* spread rapidly, colonizing unplanted sloughs, and this will likely affect community development across the site. Plant and invertebrate richness values were low, likely due to hydrological extremes and the short period of time since construction. Water level fluctuations resulted in plant communities dominated by obligate wetland plants, though drought stress took a toll on survival of plants and invertebrates in late summer. Community development and system function were dependent mostly upon time and hydrology.

To those who enjoy exploring moist ground and muddying their boots in a marsh, those who appreciate the solitude of a wetland at dawn…

ACKNOWLEDGEMENTS

Without much help, this work would have been impossible. I thank Gary Dick, Michael Smart, Dian Smith, Joe Snow, and the people at LAERF for their invaluable knowledge regarding wetland vegetation and their assistance in growing and maintaining the plants for the study. I am grateful to Ram Lopez, Steve Reagan, Kurt Sewell, Krista Thomas, and LAERF for their labor in constructing protective cages and transplanting vegetation. I thank Matt Simmons for his perspective on wetland function and cooperation on site visits. I also appreciate Feng Liu, Humberto Perotto, and Chen Yue for their cooperation and support in research. I extend thanks to Steve Whisenant for his time and valued experience and Fran Gelwick for her long hours and technical expertise in ecological analysis and research design. I am forever grateful to Ben Wu for his assistance, insight, encouragement, and motivation in ecological research. Without your help, these studies would have remained in the planning stages. Thanks for your long hours and rigorous ethic, both professionally and personally, in caring for your students. Finally, I would like to thank Jeff Harrison, Lori Jones, Ben Naylor, and friends and family for their consistent support and comfort outside the lab and classroom, without which, it would have been nearly impossible to complete these last few years.

TABLE OF CONTENTS

Page

CHAPTER Page

LIST OF FIGURES

FIGURE Page

LIST OF TABLES

CHAPTER I

INTRODUCTION TO WETLAND RESTORATION

For millennia, wetlands have been focal points for human settlement, with their resources and products meeting vital needs of human inhabitants in communities around the globe (Tiner 1999, Mitsch 2005). Though these systems connect upland and aquatic habitats, they are distinct from each, with characteristic species and processes that are not found elsewhere.

Though wetlands have proven extremely valuable to civilization, through both direct or indirect use, they have been considered wastelands in some locations at different times in history. As such, they have been targeted for conversion to drier upland areas able to meet more aims of human development. Following the resulting degradation of surrounding areas and loss of valuable services and products exclusively found in wetlands, the perception of these areas started to change. It is now recognized that wetlands perform many invaluable functions, including water quality improvement, erosion minimization, floodwater abatement, shoreline stabilization, habitat, nutrient cycling, recharging of groundwater, and sites of cultivation for many critical agricultural products (Mitsch and Gosselink 1986, Tiner 1999).

This thesis follows the style of Wetlands.

As public recognition of the value of wetlands increased, legislation in the form of the Federal Clean Water Act began to address issues of wetland protection. Though it was an important first step, it allowed some continued development of certain wetlands. As wetlands became a topic of controversy, guidelines were required to define and identify wetlands in order to delineate their area and regulate exploitation of important habitat and system function. Various federal and state organizations have created criteria for the delineation of wetlands to meet this need. However, wetlands are difficult to define due their variability and the presence of countless types of wetlands across the globe. Many attempts have been made to develop a common definition, but there has been no universal standard to date (Mitsch and Gosselink 1986, Tiner 1999). A national goal of "no net loss" of wetlands has been in place for over a decade. Progress has been made in wetland protection, but the function of wetland systems is not yet completely understood. To complicate this situation, the "no net loss" goal allows for mitigation wetlands to replace natural wetlands lost to development, agriculture, and other causes. Fierce debate remains regarding the effectiveness of this replacement, and demand for knowledge of processes in natural, restored, and created wetlands is ever increasing.

Though wetland protection is the most desired option, there is a continuing need for improving the ability to restore and create wetlands to replace those that have been lost in the past, and some loss will likely continue in the future, though at reduced rates well below historic levels (Mitsch 2005). Most current restoration efforts focus on the establishment of vegetation structure, but fully functioning wetland habitats require much more than plant cover. New developments are underlining the critical nature of hydrology and unseen processes of nutrient cycling and soil activity. One necessity is to treat wetland restoration projects as experiments, with each attempt contributing to the body of science (Grayson et al. 1999, Kentula 2000). Research has demonstrated that very real constraints play a tremendously important role in the development of restored wetlands, and proper planning with an understanding of system dynamics, utilization of a landscape/ecosystem perspective, and implementation of clear and obtainable goals is crucial for the long-term success of wetlands restoration (Ehrenfeld and Toth 1997, Race and Fonseca 1998, Ehrenfeld 2000, Kentula 2000, Choi 2004, Simenstad et al. 2006).

CHAPTER II

EFFECTS OF TRANSPLANTING, PROTECTIVE CAGING, AND TIME ON INITIAL WETLAND PLANT COMMUNITY DEVELOPMENT

INTRODUCTION

Wetlands and associated habitats perform multiple functions in the landscape and their direct and indirect effects are important, both locally and far removed from the wetland itself. Appreciation for their ability to provide critical habitat, mitigate floods, abate stormwater, recharge aquifers, improve water quality, and increase aesthetic appeal of the landscape (Mitsch and Gosselink 1986, Noon 1996) has grown in recent years. In recognition of their critical levels of loss, both historically and in contemporary times, wetlands are increasingly being created and restored, both in the United States and abroad. These wetlands are created for various purposes, including legally obligatory mitigation, recreation, wildlife habitat enhancement, wastewater and stormwater treatment, and others (Mitsch et al. 2005). Though wetland creation and restoration projects are rapidly becoming more common and larger in scope, the science behind the discipline is still quite new, and many questions remain regarding the proper approaches and effects of different practices (Zedler 2000).

One of the most commonly created wetland classes includes emergent freshwater marshes. One difficulty with applying a uniform approach to their creation is that they constitute an extremely diverse group of wetland types (Mitsch and Gosselink 1986). Freshwater marshes show significant variation in dominant species, hydrology, soils, and seasonality both in large geographic regions but also among wetlands separate by short distances. Since these wetlands are very distinct, each project must take into account the environmental conditions and landscape context of the specific location when planning restoration or creation efforts.

Predicting long-term dynamics in developing wetlands is very difficult (Zedler and Callaway 1999, Kellogg and Bridgham 2002, Hughes et al. 2005). Since there is significant uncertainty intrinsic in wetland restoration and creation and gaps in scientific knowledge remain, it is critical to employ experimental investigation during project implementation. This will both increase the likelihood of success in the individual wetland site and will contribute to the growing body of scientific knowledge regarding the patterns and processes at work in new wetlands.

An issue of great importance in wetland restoration is that of vegetation dynamics and succession (Noon 1996, Simenstad et al. 2006). Natural freshwater wetlands are highly dynamic in nature (van der Valk 2005), showing significant shifts in plant cover and species composition at multiple time scales, due to disturbance, periodic changes, or both factors. Changing conditions allow growth of different plant species, resulting in changes of wetland organization and function. Certain species may either facilitate or suppress colonization by other macrophyte species, drastically altering wetland succession. Such changes can affect nutrient cycling, primary production, habitat quality, soil formation, and many other wetland processes. Depending on landscape context and other factors, created and restored wetlands have been shown either structurally or functionally to fall all along a continuum of similarity to targeted reference wetlands and even amongst each other (Wilson and Mitsch 1996, Malakoff 1998, Zedler and Callaway 1999, Campbell et al. 2002, Mushet et al. 2002, Heaven et al. 2003, Seabloom and van der Valk 2003, Zampella and Laidig 2003, Balcombe et al. 2005b, Spieles 2005), demonstrating the highly variable response of wetland development to site conditions.

Commonly used approaches to wetland plant restoration include (1) total reliance on self-design, whereby a remnant seed bank or other plant material source (including introduction by humans) provides propagules which are ‘selected’ by conditions in the wetland and contribute differentially based on life history traits or survival requirements and (2) human design or ‘botanical engineering’ of highly-planned projects using transplanted vegetation preselected from a pool of available species and introduced into somewhat tightly controlled conditions. The action of wetland self-design has important implications in newly created wetlands, due to the lack of an established seed bank and the difficulty of dispersal for many wetland species (Noon 1996). However, in locations that do have remnant vegetation or in which vectors of dispersal are present, self-design alone is often adequate for reestablishment of vegetation (Mitsch and Wilson 1996, Mitsch et al. 1998, Luckeydoo 2002). The value of wetland self-design and the necessity of human design have been debated (Mitsch et al. 1998, Streever and Zedler 2000), but the utilized approach is largely dependent on past land use and current conditions, with complete self-design and complete ‘designer wetland’ approaches likely representing opposite endpoints of a continuum of wetland design options. Self-design will almost always exert strong selective pressure in wetland development, and this should be utilized in the practice of restoration.

Within the setting of a newly created wetland complex, our objective was to investigate the effect of different wetland planting approaches on the early development of plant communities. We investigated the hypotheses (1) that planting of created wetlands with different species results in hydrophyte communities that are distinct in cover and composition from those left to natural colonization processes alone, (2) that protective caging of transplant stock increases initial survival and affects plant communities at small scales, and (3) that transplanted and colonizing plant communities show significant temporal changes in the initial years of development. Knowledge gained in comparing transplanting and self-design approaches could then be applied to other local wetlands in a similar landscape context, and conclusions regarding initial wetland dynamics would contribute to the understanding of wetland ecology in other regions as well (Noon 1996).

METHODS

Study Site

The wetland site is located in Garland, Texas, USA, 27 km northeast of Dallas on the edge of a rapidly expanding metropolitan area (32°94’N, 96°59’W). From the early 1970s, the City of Garland disposed of solid waste at the Castle Drive Municipal Landfill prior to its closure in the fall of 2002. Over the course of years of management, a large 31 ha depression adjacent to the landfill and bordering a riparian area was excavated for soil as the landfill grew and was ultimately capped with clay. The riparian corridor follows Rowlett Creek and is part of a 3,143 ha watershed flowing into Lake Ray Hubbard, a large multiuse reservoir approximately 2.5 km downstream, ultimately contributing to the Trinity River. Fragments of bottomland hardwood forest remain in the area, dominated by *Quercus* spp. and *Ulmus* spp., though forested areas locally are limited to a narrow buffer along Rowlett Creek itself, and hackberry (*Celtis laevigata* Willd.) and green ash (*Fraxinus pennsylvanica* Marsh.) are characteristic of more disturbed areas (Nixon et al. 1991). Although the site lies within the Blackland Prairie ecoregion (Omernik 1995), the site itself is largely characterized by the hydrology, vegetation, and soils resulting from its low position in the landscape and its consistent disturbance. In the excavated depression, the surface soil has been removed mechanically, to more than 5 m in some areas. Heavy clays showing high shrink-swell potential, and partially weathered marl dominate the remaining soil. As periodic floodwaters from the creek rose and fell in the unvegetated basin, several disturbance-specialist plant species, including black willow (*Salix nigra* Marsh.), creeping primrose-willow (*Ludwigia repens* Forst.), and common cattail (*Typha latifolia* L.), had started to colonize the area. Extreme fluctuations in water level corresponding to the hydrology of an urbanizing area posed a significant obstacle to widespread revegetation. However, more desirable wetland macrophytes were present, including arrowheads (*Sagittaria* spp.) and burrhead (*Echinodorus spp.*), indicating the presence of at least a small seed bank or other mechanism of colonization and necessary conditions for hydrophyte establishment.

To establish a wetland complex with the potential for serving multiple purposes as mitigation bank, research site, and recreation area, heavy machinery was utilized to contour the depression, creating topographic variation in the form of shallow (~1.5-2 m) elliptical sloughs interspersed with 2.5 m ridges and surrounded by an oxbow lake 3 m in depth at its deepest point. A shallow water table maintains water levels in the sloughs, though elevated areas become quite dry in summer and extended periods without precipitation. Large berms created during site manipulation remain in place and cause the site to retain in-basin rainfall and runoff from surrounding upland areas.

Various measures involving major manipulation and maintenance of soil and plant communities have been proposed to establish wetland vegetation near landfill sites (Simmons 1999), but these are most often unsustainable, do not replicate natural or reference site conditions, and require intensive management. Therefore, alternative wetland restoration strategies focusing on the establishment of desirable native vegetation were formulated and incorporated into the study.

Study Design

Wetland Design

Using the constructed wetland complex as the basis for the experiment, 10 sloughs were designated for inclusion in a comparative study to determine the response of plant community dynamics under different methods to wetland restoration. Sloughs were chosen based on their relative similarities in soil, orientation, elevation and thus hydroperiod. Ten of the designated sloughs were randomly assigned a plant or non-plant status, with 5 sloughs each designated for planting and controls. Each of the planted sloughs was subdivided into 5 blocks, each of which would be planted with one common wetland plant species. These 5 species were randomly assigned in a randomized complete block design. This use of clustering of transplanted conspecifics has successfully been used in revegetation efforts in the past to improve initial survival and increase subsequent resilience in the face of herbivory. These “founder” populations can then provide sources of native plant materials for colonization of remaining areas of wetland habitat (Smart et al 1996).

In the summer of 2003, with the cooperation of the U.S. Army Corps of Engineers Lewisville Aquatic Ecosystem Research Facility (LAERF), 6 small watertight wooden aboveground nurseries were constructed as grow-out ponds for transplant materials. Harvesting several hundred individuals of different species from on-site cultures at LAERF, plants were moved to the constructed nurseries and allowed to grow through the summer months and develop rootstock. Submerged plants were potted in wetland soil harvested on-site and maintained at water levels of approximately 0.75 m, and emergent plants were potted in topsoil and maintained at approximately 0.2 m water depth, according to plant requirements. Plants used included American pondweed (PW) *Potamogeton nodosus* Poir., broadleaf arrowhead (AH) *Sagittaria latifolia* Willd., bull-tongue arrowhead (BT) *Sagittaria lancifolia* L., flatstem spikerush *Eleocharis compressa* Sullivant, squarestem spikerush (SR) *Eleocharis quadrangulata* (Michx.) Roemer & J.A. Schultes, swamp smartweed (SW) *Polygonum hydropiperoides* Michx., and creeping burrhead *Echinodorus cordifolius* (L.) Griseb. Except for *Potamogeton*, a floating-leaf submerged plant, all plants are considered emergent species and are found in shallow areas of wetlands. All plants were potted as single stems and fertilized with ammonium sulfate and were watered using alum-treated water from the adjacent Corps of Engineers reservoir Lewisville Lake. Plants lost through mortality from heat stress and transplant stress were replaced in the initial two week period following relocation. Due to high losses and low vigor of *E. cordifolius* and *E. compressa*, these species were removed from the initial planting list, leaving the remaining species for the transplanting effort.

After one year of growth, the plants were moved approximately 40 km to the Garland site from transplanting in June 2004. The 5 selected species were introduced into the randomly assigned species blocks using the input and assistance of LAERF staff and volunteers. Stems were planted at 0.15, 0.3, and 0.45 m below estimated mean water level at a horizontal spacing of 1 m and a vertical spacing of approximately 0.3 m on the slough slopes. Multiple planting depths were implemented in order to accommodate plant survival through predicted water level fluctuations during the year, most notably summer drawdown. Blocks were planted with approximately 25 individuals per species, and unplanted buffers of 10 m were left between species to eliminate edge effects.

Within each species block, plants located centrally with respect to the flanking buffers were designated as paired plots for comparison of plant cover. The southernmost of the paired plots was enclosed in a fencing structure to minimize herbivory and mechanical disturbance of the plants and their roots. Cages were manually constructed from commercially available 14 gauge welded steel wire of 2” by 4” mesh cut to form cages 1.8 m x 0.6 m x 0.3 m in height and enclosed on all sides except the bottom, in order to avoid damaging plants during installation. These cages and adjacent uncaged marked areas of identical size served as quadrats covering just over 1 m^2 each. Quadrats were also established in unplanted sloughs as controls, with three cages and adjacent uncaged areas distributed equidistant from each other in a manner similar to that employed in planted sloughs.

Quadrat Scale

A series of quadrats were established within the protective cages and in neighboring uncaged areas in the planted sloughs and in the unplanted sloughs (Figure 2.1). Vegetation cover was sampled in late summer, approximately coinciding with maximal vigor and coverage (Matthews et al. 2005). Aerial cover was documented by visual estimate for each species. Species were also grouped by growth form, including emergent, floating-leaf, and submergent hydrophytes, and species longevity was noted for comparison of annual and perennial cover components. Presence or absence of a floating algal mat was also noted, with its total cover estimated where present. Transplant species, caging, and date were considered treatment variables. In the field, $n = 6$ research quadrats were placed in each of 5 unplanted sloughs and $n = 10$ quadrats constructed in each of 5 planted sloughs, for a total of $n = 80$ annually sampled quadrats.

Plot Transect Scale

To document the vertical dynamics of the hydrophyte community, short 3m transects were also established and centered on mean water level. Lines were positioned through each uncaged quadrat resulting in transects in both unplanted and planted

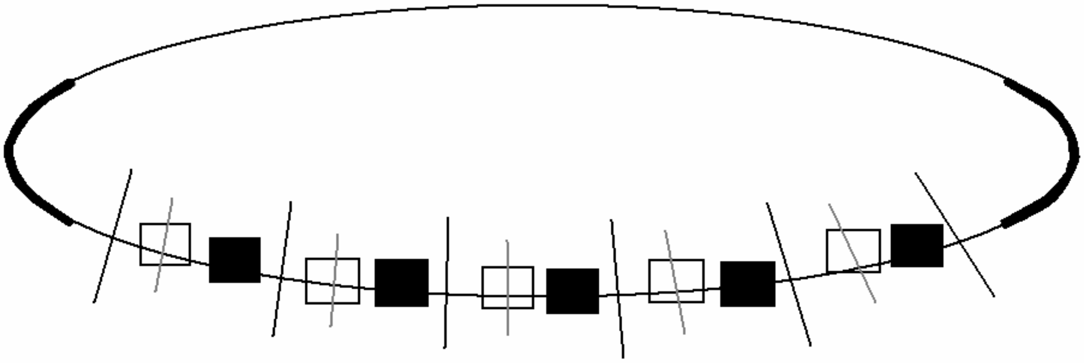


Figure 2.1. Wetland sampling design. Planted slough depicted, with longer lines separating species blocks. In each of 5 blocks, caged (closed rectangles) and uncaged (open rectangles) $1m^2$ quadrats were established for vegetation sampling. 3m transects were established through each uncaged quadrat to monitor vertical spread of transplanted and colonizing vegetation. 10m transects were also established on slough ends along the longitudinal axis (bold lines). Planted sloughs had aged and uncaged quadrats for each of 5 species blocks; unplanted control sloughs contained 3 caged and 3 uncaged quadrats randomly placed along the slough shoreline.

sloughs. Along these transects, percent cover of the hydrophyte canopy was estimated for each species along the vertical gradient, extending from below permanent water to near the slope break at the top of the sloughs. Similar to the prevalence index of Spieles (2005), an average “wetness value,” or wetland indicator status index (WIS index) was determined for transects by obtaining the regional wetland indicator status for each species and awarding a score from 0 for upland species to 10 for obligate species, with all intermediate status values scored separately. For example, a FACW species would receive a score of 8, with a FACW+ receiving a 9 and a FACW- receiving a 7. Index scores were weighted by proportional cover by individual species. Average wetness values were used to determine upslope expansion and development of the wetland plant community. Algal mat cover was not considered in this calculation. To monitor this vertical spread of wetland vegetation, transects were installed at $n = 3$ sites and $n = 5$ sites within unplanted and planted sloughs, respectively.

Slough Scale

To investigate effect of transplanting hydrophytes on the developing plant community at the level of a whole slough, at a larger scale and further removed from transplants themselves, a disjunct transect was established at the ends of the major axis of the sloughs. One 10 m segment was placed at each end, resulting in a 20 m transect for the entire slough. Along these transects, vegetation cover was estimated, with component macrophytes identified by species and classified by plant growth form. The slough transects were located up to 20 m from planted plots and did not cross portions of sloughs receiving transplanted vegetation. An average WIS Index was again calculated to determine colonization by hydrophytic vegetation. At the level of whole sloughs, each of the sloughs was sampled with one transect 20 m in total length for $n = 5$ in both unplanted and planted sloughs.

Statistical Analyses

Sampling was conducted in late summer in 2004 and 2005 in quadrats and plot and slough transects. Statistical analyses of plant cover were performed using repeated measures MANOVA procedures in SPSS 12.0 (Norusis 2004) to identify differences among species planting treatment, caging treatment, and sampling date. In comparisons of effects of transplant species on resulting total cover and species composition, the Student-Newman-Keuls method for multiple comparisons was used where applicable. Statistical significance was assumed at $p = 0.050$ for all analyses.

RESULTS

Quadrat Scale

Transplant Species

While total cover increased dramatically in the two years of this study ($p < 0.0001$), though with a high degree of variability (16.7% ± 2.7 year 1, 47.0% ± 3.1 year 2; plant cover given as mean ± S.E.), differences in total cover between each planting treatments (five transplant species and no-planting) were not significant ($p = 0.11$). However, the composition of cover did differ between planting treatments (Figure 2.2). Macrophyte species richness was significantly different ($p < 0.0001$), with unplanted quadrats showing fewer species than any of the transplanted quadrats. Though an increase in species richness did occur over the course of the study ($p < 0.0001$), values were remarkably low across both years and all planting treatments, with most quadrats having only 1-2 species in the 2004 and transplanted quadrats with 2-3 species by the 2005. Transplanted species were somewhat widespread in all planted treatments in 2004, but colonizing species were dominant in unplanted sloughs in the same year and in all planting treatments in 2005 (Figure 2.3).

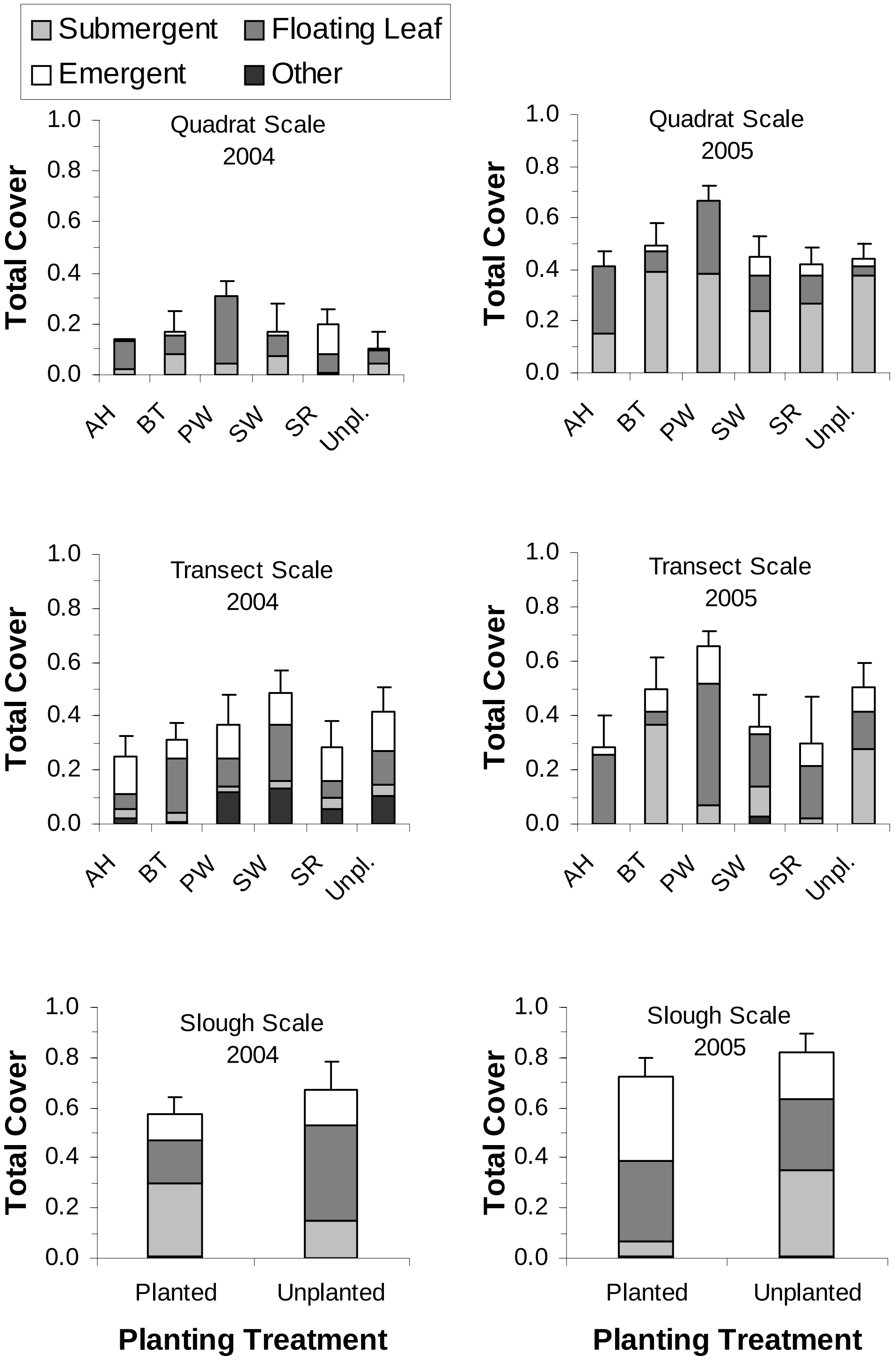


Figure 2.2. Community structure by planting treatment. Values given as means ± S.E. AH indicates plot planted with *S. latifolia*, BT *S. lancifolia*, PW *P. nodosus*, SW *P. hydropiperoides*, and SR *E. quadrangulata*. Unpl. indicates unplanted control plots. Floating-leaf cover had become widespread even in 2004, and submergent cover was the dominant structure in 2005. Non-wetland obligate species (other) largely disappeared by 2005.

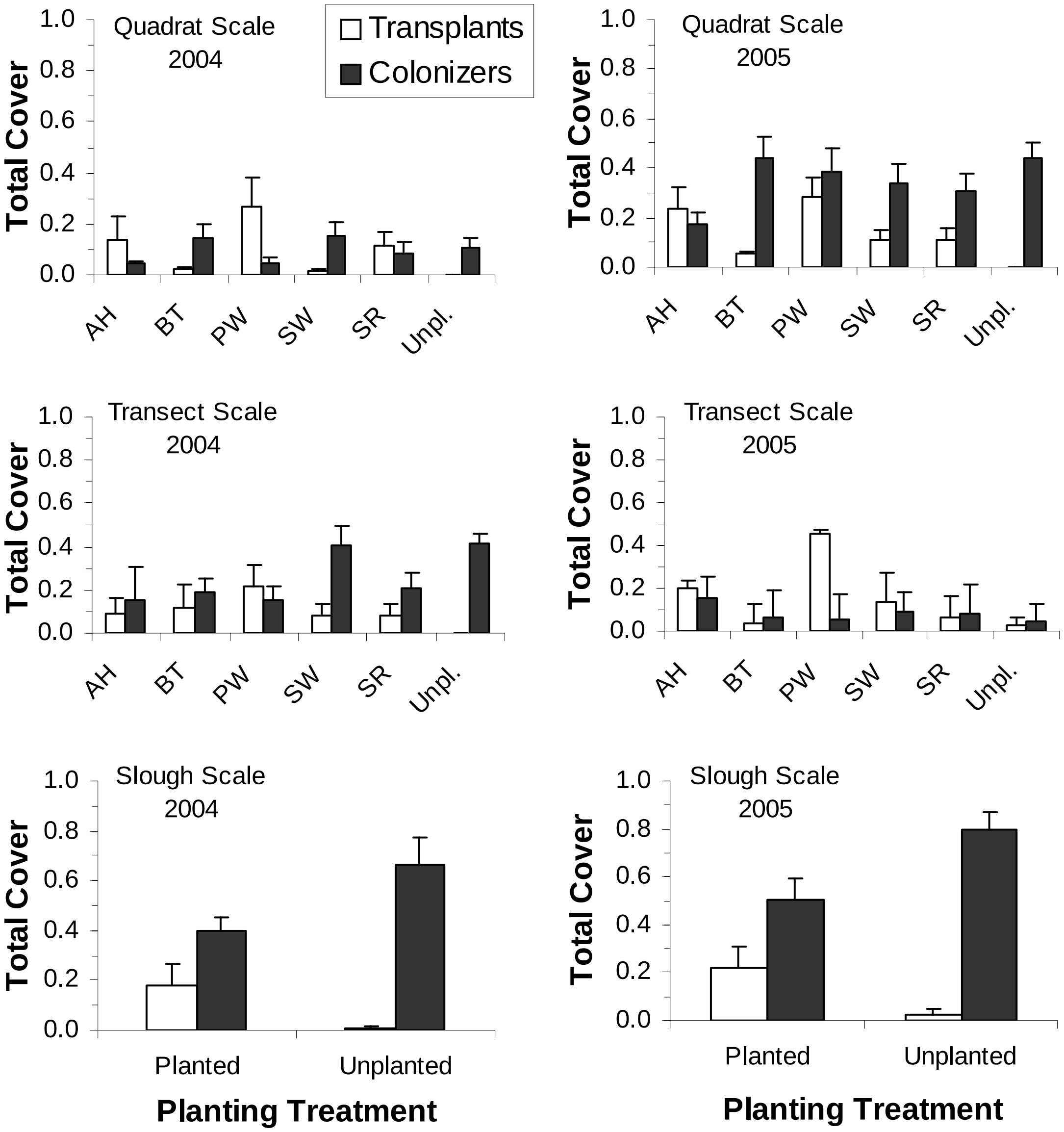


Figure 2.3. Percent cover by transplanted species and colonizing species as a proportion of total plant cover in different planting treatments. Values given as means ± S.E. AH indicated planting with *S. latifolia*, BT *S. lancifolia*, PW *P. nodosus*, SW *P. hydropiperoides*, and SR *E. quadrangulata*. Increases in transplant cover were largely due to *P. nodosus*. Large increase in colonizer cover in quadrats was due to spread of *Najas*. Loss of colonizers in transects largely a result of mortality among facultative species.

Quadrat cover by submersed vegetation, comprised of a dense matrix of *Najas guadalupensis* (Spreng.) Magnus and *Chara* spp., differed with year ($p < 0.0001$) but was not significantly different between planting treatments ($p = 0.36$). Though minimal in the initial year of study (4.4% ± 1.5), the *Najas-Chara* growth covered 32.1% ± 3.5 of quadrat area by the end of 2005 and constituted the majority of growth by colonizing species. Cumulative cover by all annual species was not significant between treatments, though sampling date did have an effect ($p < 0.0001$).

Surprisingly, emergent plant cover did not change over time ($p = 0.89$), though it did vary significantly with planting treatment ($p = 0.03$). *S. latifolia*, *S. lancifolia, P. nodosus, P. hydropiperoides*, and *E. quadrangulata* were not detected outside of quadrats in which they were planted. Cover by each species was remarkably low (< 1.5%), even after two years of growth. In fact, transplanted *S. latifolia* had completely disappeared from its plots by the end of the second year of study. A locally abundant emergent, *Typha latifolia*, was rare in 2004 but had grown in total cover to ~2% in the second year, and was present across planting treatments ($p = 0.79$).

Cover by floating-leafed vegetation became a major component of total cover over the course of study and was significant between planting treatments ($p = 0.005$). *Ludwigia repens* Forst. was common along slough borders in both years (5.1% ± 1.4 2004, 3.5 % ± 0.7 2005), though it did not differ between planting treatments ($p = 0.53$). *P. nodosus* spread rapidly and was present in five of six planting treatments three months after planting and all treatments but unplanted quadrats by 2005. Cover was significant between years ($p = 0.003$). Though it was common in many other planting treatments, cover remained much higher ($p < 0.0001$) in plots initially planted with the species (26.5 ± 16.1 2004, 28.0% ± 12.1 2005). It was also common in plots planted with *S. latifolia*.

By the second year of study, a floating algal mat had developed along the border of the sloughs on the site. Cover by this mat was significant between treatments ($p < 0.0001$), with unplanted quadrats showing the lowest values. *E. quadrangulata* quadrats contained nearly 20% algal cover, while unplanted quadrats had none.

Caging

The use of protected sloughs had little effect on the initial survival and spread of both transplanted species and colonizing species. Total cover was not significantly different between caging treatments ($p = 0.09$), nor was species richness ($p = 0.36$). One primary area of concern in the wetland restoration, success of transplanted emergent species, showed no effect with caging (*S. latifolia* $p = 0.57$, *S. lancifolia* $p = 0.91$, *P. hydropiperoides* $p = 0.12$, *E. quadrangulata* $p = 0.14$). *P. nodosus* was not significant ($p = 0.71$), nor was cover by the submersed *Najas*-*Chara* matrix ($p = 0.30$) or the floating algal mat ($p = 0.13$).

Plot Transect Scale

Transplant Species

As at the scale of the sampled quadrats, the time had a larger effect ($p < 0.0001$) on total cover than did the planting treatments ($p = 0.84$). Total cover along transects increased from 36.9% ± 4.1 in 2004 to 62.2% ± 4.7 by 2005. This trend of the importance of time over treatment also held for most measures of the plant community at the transect scale. While species richness increased but remained low among the quadrats, the same measure actually decreased ($p < 0.0001$) along transects, from 2.7 ± 0.2 in 2004 to 1.6 ± 0.2 in 2005. Only transects in plots planted with *P. nodosus* showed no change, remaining constant at ~ 2 species.

The average Wetland Indicator Status Index for the transects was not significantly different between planting treatments ($p = 0.53$), but did increase over time ($p = 0.03$). Index scores of 8.8 ± 0.3 (corresponding to slightly drier than FACW+) increased to 10.0 ± 0.0, near complete dominance by wetland obligates species (Figure 2.4).

As in the quadrats, submersed cover increased dramatically between years ($p = 0.01$) but was not significantly different between planting treatments ($p = 0.10$). As much of the length of the transects fell above the water level, cover by the Najas-Chara matrix was lower than in quadrats. However, submersed cover (3.67% ± 1.8 2004, 17.5% ± 3.9 2005) still contributed to the increase in total cover.

Cover by emergent species showed no significant difference between planting treatments (p = 0.75) and actually showed a minimal (p = 0.14) decrease between years (12.7% ± 1.8 2004, 7.9% ± 1.9 2005). Cover due to transplanted species was very low (< 1%) or absent in most cases. However, individuals of transplanted species, whether from

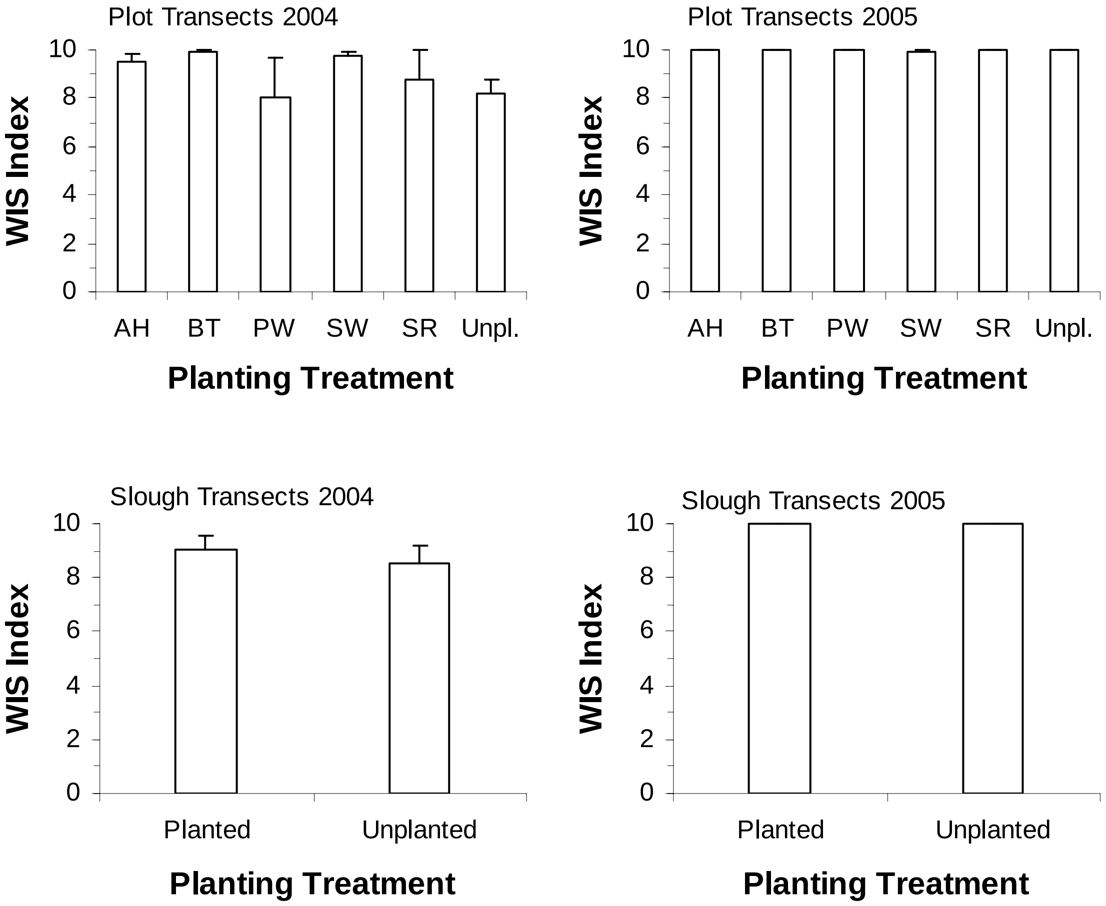


Figure 2.4. Wetland Indicator Status Index under different planting treatments. Values given as means ± S.E. AH plots planted with *S. latifolia*, BT *S. lancifolia*, PW *P. nodosus*, SW *P. hydropiperoides*, and SR *E. quadrangulata*, respectively. Although significant cover by facultative wetland and facultative upland species was present in 2004, all plots were completely dominated by wetland obligate species in 2005.

transplanted stock or colonizing plants, were found in treatment plots in addition to the plot planted with that species. *S. latifolia* and *S. lancifolia* were found on multiple transects outside their transplanted plots, but were still low in frequency. *T. latifolia*, as it did at the quadrat scale, increased (p = 0.04) over the course of the study, from 0% in 2004 to 1.8% ± 0.8 in 2005, but was not significantly different between treatments (p = 0.11). *Cyperus erythrorhizos* Muhl., an annual colonizer that was common in many wet areas in the first year (3.2% ± 1.0) was rare by 2005 (0.4% ± 0.3). Though the decrease was significant between years (p = 0.046), planting treatment did not have an effect (p = 0.38). One species rare at the quadrat scale, *Leersia hexandra* Sw., contributed more to cover at the transect scale (6.0% ± 1.3 2004, 4.8% ± 1.6 2005). This species was not significantly different between sampling date or planting treatment.

Though total cover by floating-leafed vegetation was not significantly different between years (p = 0.051) or planting treatment (p = 0.66), its component species showed different trends. *L. repens* was nearly constant between all levels at nearly 8% cover. However, *P. nodosus* increased between years (p = 0.01) and differences between planting treatments were significant (p = 0.004), with plots planted with *P. nodosus* itself retaining highest cover.

The algal mat was also present along portions of multiple transects in 2005. As it did among quadrats, algal cover was significantly different between planting treatments (p = 0.002), with unplanted plots again among the lower values. Unplanted transects had nearly 0% algal cover, while planted S. latifolia plots had consistently high coverage, over 40%. Planted *P. nodosus* plots had low algal cover in quadrats and transects (approximately 10%), more nearly resembling unplanted plots than those treated with other transplant species.

Chamaecrista fasciculata (Michx.) Greene, a colonizing facultative upland annual species frequently found on upslope portions of transects, showed no significant differences between treatments (p = 0.53) but declined (p = 0.04) from 3.3% ± 1.6 in 2004 to 0% in 2005.

Slough Scale

Planting Treatment

At the slough scale, total macrophyte cover was not significantly different between planted and unplanted sloughs (p = 0.14) or between years (p = 0.28). Plant cover at this scale (62.6% ± 7.2 2004, 77.3% ± 6.4 2005) was also somewhat higher than among both quadrats and transects. Species richness was also roughly equivalent between years (p = 0.60) and planting treatment (p = 0.12). Overall across both years, the increased scale of measurement translated into slightly increased richness over smaller scales. However, these values were still very low (4.8 ± 0.5 2004, 5.1 ± 0.4 2005). By the end of 2005, however, species richness values that were nearly identical between planting treatments (approximately 4.8 species per transect) had begun to diverge somewhat, with planted sloughs harboring slightly higher numbers of species (6.2 ± 0.2) than unplanted sloughs (4.0 ± 0.4).

Among sloughs, increases in WIS Index values between years were minimal (p = 0.06). However, trends were almost identical to those at the plot transect scale. With some facultative species present in 2004, scores were 8.8 ± 0.5. The plant community was almost entirely dominated by obligate hydrophytes by the second year of growth (10.0 ± 0.0), however, after the die-off of upland and inundation-intolerant species. The introduction of transplanted vegetation had no effect (p = 0.65) on the average WIS Index of species at the slough level.

As at other scales, slough-level submersed cover showed significant differences between years (p = 0.03). However, the *Najas-Chara* matrix was not significantly different between unplanted and planted plots (p = 0.11), though differences became more apparent in 2005, with unplanted sloughs at 33.8% ± 15.3 compared to 5.8% ± 5.7 in planted sloughs. The patchy nature of submersed cover at the site contributed to very high levels of variability between transects.

Total emergent vegetation was not significantly different with date (p = 0.85) or planting treatment (p = 0.73). Though *S. latifolia* and *S. lancifolia* were found in both planted and unplanted sloughs, transplanted species were present at very low levels. Much of the emergent cover was comprised of *L. hexandra*, *C. erythrorhizos*, and *T. latifolia*, species found in both planting treatments. Likewise, none of these colonizing emergent species was significantly different between years, with initial establishment occurring in 2004 and little expansion observed by 2005.

Floating-leafed vegetation was a major component of slough macrophyte cover. While it did not differ with planting treatment (p = 0.22) or date (p = 0.49), cumulative cover of 22.1% ± 6.6 in 2004 and 30.2 % ± 6.1 in 2005 made *L. repens* and *P. nodosus* the dominant hydrophytes at the slough scale. *L. repens* was common in both years (15.9 % ± 5.9 in 2004, 19.0% ± 6.9 in 2005) and comparable between planted and unplanted sloughs. *P. nodosus* was present in some unplanted sloughs by 2005 at slightly lower levels than in planted sloughs (p = 0.6). In contrast with measurement at smaller scales, *P. nodosus* did not differ between years (p = 0.52). By 2005, floating cover was dominated by *L. repens* in unplanted sloughs (25.8% ± 13.0 versus 12.1% ± 4.9 in planted sloughs) and by *P. nodosus* in planted sloughs (19.9% ± 8.9 versus 2.2% ± 0.0 in unplanted sloughs).

Algal mat cover was significantly different between years (p < 0.0001). Also, this growth of algae was very different between planting treatments (p = 0.001), with mat coverage of 1.3% ± 1.3 in unplanted sloughs and 16.1% ± 2.6 in planted sloughs, both in 2005.

DISCUSSION

Planting and Assembly Rules

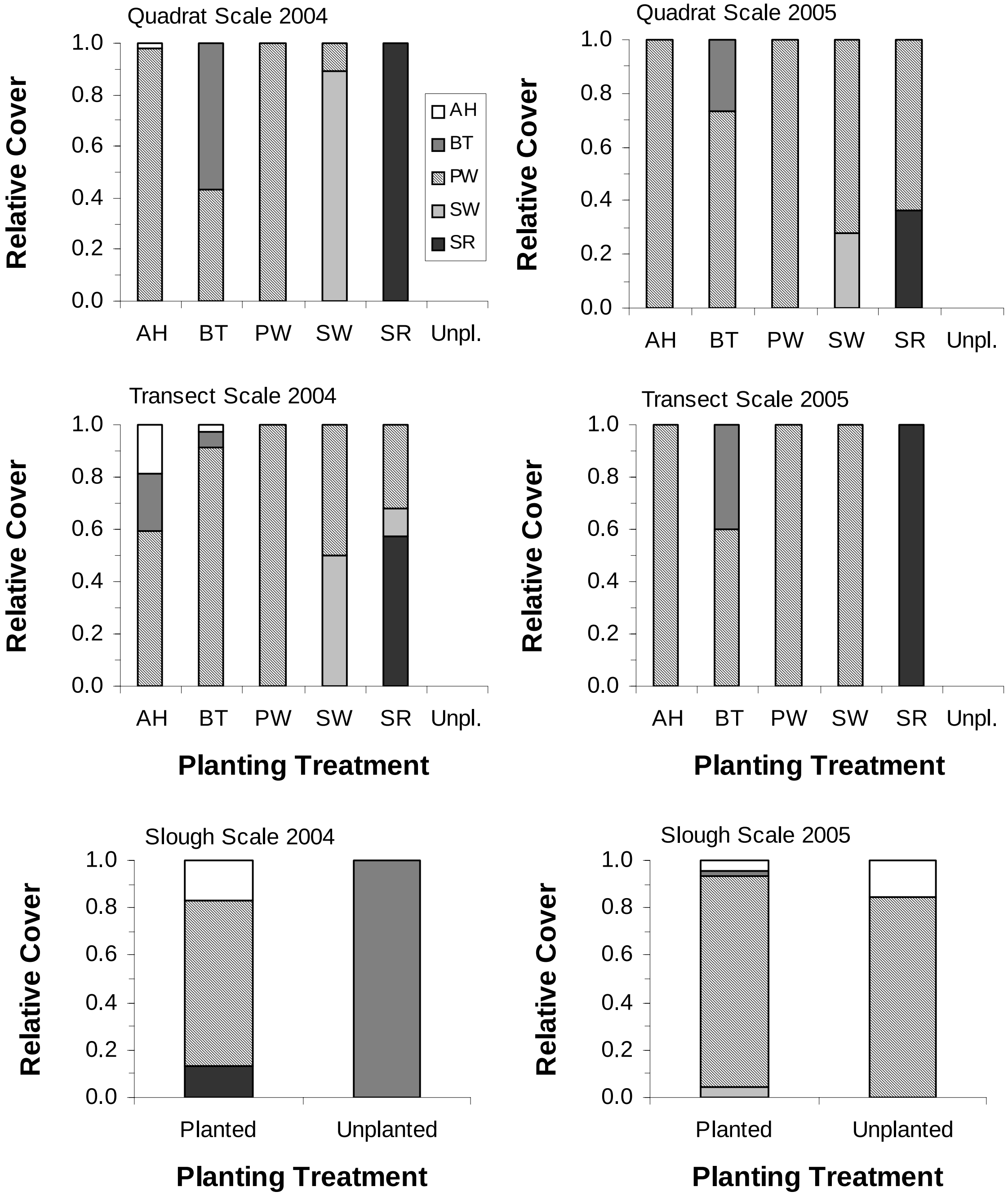
Use of different planting treatments did have an effect on the establishment and development of wetland plant communities. While total cover was comparable across all planting treatments at all scales, the composition of that cover and the identity of the dominant species under different treatments may have lasting impacts on system function (Callaway et al. 2003).

Many factors affect the dynamics of wetland plant communities, particularly in the years immediately following many wetlands creation and restoration projects, and a proper understanding of these factors is necessary when planning a plant community on a previously vacant site. As proposed by Keddy (1999), the trajectories of wetland plant communities are largely determined by species pools, filters on establishment, and plant traits. By introducing transplant stock, the pool of available species is expanded by virtue of overcoming potential dispersal limitations, and such approaches are preferred in certain unpredictable environments and when using species with certain life history traits (Keddy 1999, Whisenant 1999). Environmental filters select certain species based on certain abiotic factors, though biotic factors such as facilitation and competition are also important, and plants whose traits require or tolerate these conditions will survive (Keddy 1999). Assuming the transplanted stock display the necessary the necessary traits, the developing plant community will likely include both introduced materials as well as colonizing individuals of other members of the local species pool.

Individuals of transplanted species and their congeners (especially *Sagittaria* spp. and *Polygonum* spp.) were present on site in very low densities prior to restoration efforts. However, large-scale soil disturbance likely removed or buried most of these plants. Reappearance by these species following treatment was observed outside restoration plots, as was establishment of other common wetland species, but it was not determined whether this was a result of reproduction of transplanted stock, regrowth from the residual seed bank, or introduction by other means, including stormwater inputs and waterfowl (Charalambidou and Santamaria 2005). As plants were present initially, dispersal was not a limiting factor in the presence of these species in the wetland complex. Low frequencies, whether due to reduced seed densities or conditions that were only marginally favorable to the establishment of these species, were enhanced by the introduction of mature plants through transplanting efforts. In addition, species that were not present at the site before restoration (*E. quadrangulata*, *P. hydropiperoides*, and *P. nodosus*) and which may have been limited by dispersal into the wetland, became an important component of the plant community by increasing the available members of the local species pool.

In our study, the response of developing wetland plant communities was distinct between planted and unplanted sloughs, and results indicate initially very different structure in the initial years of wetland restoration. The use of transplants in appears to have resulted in minor differences in total cover but significant differences in species richness and dominance. Introduction of plant material into selected plots altered the community structure of those plots. While unplanted plots displayed coverage dominated by *L. repens* and *N. guadalupensis*/*Chara* spp., cover by transplanted emergent and floating species played a larger role in each of the planted plots, with *P. nodosus* comprising a large portion of cover even outside its own plots (Figure 2.5). Though most of the species transplanted were emergent species (with the exception of *P. nodosus*), much of the cover in planted plots was floating-leafed vegetation.

The apparent high mortality and lack of growth among planted emergent species in the sloughs may significantly impact future trends in the plant community. Emergent species are important primary producers in inland freshwater marshes (Mitsch and Gosselink 1986), and struggles of these species may inhibit the development of characteristically complex food webs and functional pathways. Pezeshki et al. (2000) found that moderate-duration (maximum 42 days) preconditioning through flooding prior to transplant efforts had no effect on plant survival and performance among emergent species *Panicum hemitomon* Shult. and *Sagittaria lancifolia* once in the field. However, a combination of preconditioning and fertilization of transplants resulted in species-dependent increased performance. Our study utilized transplants preconditioned off site under high water conditions for one year. It is possible fertilization increased growth of these transplants, at least initially. However, this was likely through an increase in production of belowground biomass. Even by the end of 2004, many transplants, most notably *Sagittaria* and *Polygonum*, had shed much of their photosynthetic structure, and few if any leaves remained on the majority of the plants.


Quadrat Scale 2004

Quadrat Scale 2005

Transect Scale 2004

Transect Scale 2005

Slough Scale 2004

Slough Scale 2005

Figure 2.5. Relative cover by transplant species (colonizing species excluded) in each treatment plot. AH represents *S. latifolia*, BT S. *lancifolia*, PW *P. nodosus*, SW *P. hydropiperoides*, and SR *E quadrangulata*, respectively. Under nearly all treatments, except planting with *E. quadrangulata*, *P. nodosus* became the dominant transplant species by 2005 and was present to a limited extent even in unplanted plots. Emergent transplants typically showed either no change in cover or mortality after one year.

However, by the beginning of 2005, the remaining rootstock produced a flush of new aboveground growth. It is likely that among transplants, most of the energy went to production of rootstock in preparation for growth in the following year, rather than leaf production and photosynthesis in the year of planting. With expected benefits of fertilization, it is puzzling that emergent cover remained very low. However, planting at low densities has been shown to have only a minimal effect on developing plant communities (Kellogg and Bridgham 2002), and our site may follow the same trend.

Interestingly, a floating algal mat in 2005 was found to be significantly greater in planted plots than in unplanted control plots. Fertilization meant to enhance macrophyte growth likely contributed to a spatially variable bloom of algae (Wu and Mitsch 1998). Almost no algal cover was found in unplanted sloughs at all scales. This cover by algae likely affected spread of macrophyte cover. As algae benefited from the lingering effects of transplant fertilization, growth was concentrated around planted areas. Despite periodic storms, the floating mat was observed to be physically held in place by plant stems, both of transplants and senesced stems of inundated annuals from the previous year. Dense floating mats were observed to be associated with sparse cover by transplants, creating a feedback mechanism. Dense transplant growth retained algal cover, potentially shading out new growth under the slough water surface. Such a pattern of algal dominance in early succession has been observed elsewhere and may initially lead to suppression of emergent and submergent macrophytes (Yallop and O’Connell 2000). Lack of macrophyte growth also likely meant increased available nutrients for algal uptake. Where much of the fertilization was partitioned in macrophyte growth, absence of algae led in increased dominance by hydrophytes. We suspect that over time, the nutrients resulting from fertilization will be exhausted and macrophytes will outcompete algae (Lougheed et al. 2004), limiting future algal blooms. Additionally, and probably more important to emergent plant growth was the duration and severity of flooding very likely played a role in diminished emergent cover.

Watershed urbanization has been shown to result in increased proportion of overland flow, resulting in alteration of timing and intensity of inputs to associated wetlands, and changes in base flow characteristics, depending on landscape context and regional climate (Owen 1999, Rose and Peters, 2001, Wissmar et al. 2004, White and Greer 2005, Roy et al. 2006). The Garland, Texas area has experienced rapid suburban expansion in recent years as agricultural lands are converted to housing and additional development, and this has altered the flow patterns and channel morphology of Rowlett Creek. The resulting amplification of hydrological impacts on the wetlands over the course of this study was significant, with intense seasonal floods and drying in summer months.

Hydrology is often an important determinant of wetland plant communities (Weiher and Keddy 1995, Keddy 1999), and the effect of urban hydrology may potentially act as a stringent filter in the assembly of species in the developing plant community on site. As originally designed, the wetland complex, located adjacent to Rowlett Creek, would contain both inlet and outlet structures to allow passage of floodwaters through the system. However, earthen berms constructed during excavation were never removed. This resulted in a largely enclosed depression that is removed from all but extreme floods and retains water from floods, runoff, and direct rainfall for much longer and at far greater depths than anticipated. The growth form and life history strategies of plants had a major role in the development and expansion of the wetland plant community in this context. Emergent species, especially transplanted plants, showed very little development outside the immediate area of transplantation. Rhizomatous expansion and growth from tubers accounted for most of the development of *Eleocharis* and *Sagittaria*.

Urbanization and associated hydrological patterns have had significant effects on growth and function of emergent wetland vegetation elsewhere (Kleppel 2004). Under relatively narrow water level fluctuations, growth and diversity of emergent vegetation is actually enhanced by allowing periodic soil oxidation for germination and expansion of new plants (Kellogg and Bridgham 2002, Coops et al. 2004). Low levels of flooding may also result in increases in wetland species richness and improved wetland functioning (Fennessy et al. 1994, Engelhardt and Ritchie 2002), underscoring the value of hydrologic variability within relatively restricted ranges. In our wetland, periodic high water allowed germination of species such as *Sagittaria latifolia* at slightly higher elevations than depths which initially received transplants. However, evapotranspiration resulted in significant summer drawdown, causing widespread drought stress and loss of aboveground biomass in many individual plants stranded above the receding water level. Alternatively, when plants sprouted and began to spread at the new lower water levels, fall and winter rains flooded the site, raising water levels up to 2m in some locations, submerging emergent plants to depths beyond their tolerance. This rapid and extreme increase of water depths likely impeded gas exchange, arrested root processes ad germination, and in some cases, increased depth to such an extent that photosynthesis was no longer possible (Pezeshki et al. 2000). Widespread mortality of wetland plants has been shown to occur with significantly lesser flooding (Pezeshki et al. 2000, Fraser and Kairnezis 2005), and this likely favors plant species with special strategies including annual life cycles and reproduction by fragmentation.

These fluctuations in water level did allow for colonization by several annual species. In 2004, many of these plants were facultative or facultative upland species, including *Chamaecrista fasiculata* and *Iva annua* L, which took advantage of barren substrate following construction and colonized the site in very high densities. However, unseasonably high rainfall and cool temperatures the remainder of the year led to higher water levels and mortality of species not adapted to hypoxic or saturated soil conditions. Water level has been shown to be a critical factor in the development of vegetation at the interface between aquatic and terrestrial habitats (Hudon 2004), and this was observed in our site. The overall increase in affinity for hydric soils among the species represented in the plant community is reflected in the increase in the WIS Index for the site and corresponds with findings of other studies (Fennessy et al. 1994). Upland and peripheral species were drastically reduced or disappeared altogether, while wetland obligates almost completely dominated the site in 2005.

Though hydrological variability hindered the growth and survival of obligate emergent and facultative species, it likely represented a factor significantly favoring the proliferation and dominance of *P. nodosus.* Establishment of most emergent species in wetlands initially depends on germination, though vegetative reproduction increases in importance thereafter and as water levels rise (Smith et al. 2002). While emergent species showed some expansion in 2004, *P. nodosus* had already spread rapidly, and by 2005 showed extensive coverage in planted sloughs. *Potamogeton* growth occurred primarily through rhizome extension; vegetative propagation independent of germination requirements. Additionally, much of the expansion of *Potamogeton* resulted from mechanical disturbance, which removed portions of fragile stems and leaves from the parent plant. These detached sections were then transported by wind and deposited along the slough shore. Locally, prevailing winds are southerly in summer and northerly and westerly in winter. As the sloughs are primarily arranged along this axis of wind direction, this provided a mechanism for transport and expansion. Fragments deposited by wind quickly rooted and began to spread, acting as source colonies for further plant propagation. As water levels fluctuated seasonally, translocated plants were able to colonize new areas throughout the slough as submerged areas experienced drawdown in dry periods of the year. Due to this translocation and the flexible, floating nature of this species, *Potamogeton* was also able to remain its photosynthetic structures at the water line, enduring the periodic stress of drastically increased water depths. Remants of colonizing Individuals of this species were found far above the mean water level, indicating an ability to adapt to hydrologic variability and colonize new substrate.

P. nodosus is presently the dominant species in planted sloughs, and given time, will likely colonize unplanted sloughs as well. Similar trends by *Potamogeton* spp. have been documented at sites in many regions, with typical species of pondweeds contributing >50% of aquatic plant biomass in some studies (Kennison et al. 1998, Engelhardt and Kadlec 2001). Though dominance has been linked to mechanisms such as eutrophication (van den Berg et al. 1999, Cristofor et al. 2003, Hudon 2004) and disturbance by wind-related stress (Havens et al. 2004), rapid expansion and dominance by *Potamogeton* is also often associated with extremes in hydrology, both drawdown and periodic high water (Capers 2003, Combroux and Bornette 2004, Turner et al. 2005). In many cases, *Potamogeton* in highly variable and dynamic systems can quickly dominate other macrophytes through its rapid growth and its ability to reproduce by seed, rhizome extension, and fragmentation.

Over the course of the study, dense growth of submersed *Najas guadalupensis*/*Chara* spp. was widespread in all plots, regardless of planting treatment. Both species are annuals with high rates of reproduction via seeds (*Najas*) or spores (*Chara*) and are common in shallow lakes with high visibility. Soil introduced with transplants had high densities of *Najas* seed, a measure utilized by LAERF in restoration projects to encourage rapid cover of bare substrate. Sediment stabilization by the anchoring action of many fibrous roots in *Najas*, increases in water clarity resulting from reduction of water currents by both *Najas* and *Chara*, and nutrient retention in submerged tissues often affect establishment of other macrophytes in shallow lakes (Kufel and Kufel 2002, Nõges et al. 2003, Schutten et al. 2005). As these submersed plants are held to be somewhat transitional in nature in shallow lakes, it is anticipated that they will eventually be outcompeted by more desirable macrophytes through succession over time, though *Chara* may likely continue in importance (Smart et al.

1996, Havens et al. 2004). Initially, however, *Najas* will likely impact system processes through rapid generation of biomass. Dense growth of submersed *Najas*/*Chara* clumps filled the entire water column in many plots, from the substrate to the water surface, resulting in several kg/m^2 of plant material in the slough shallows. At these densities and under current conditions, competition with floating-leafed and germinating broad-leafed emergent plants will likely result in dominant coverage of submersed cover in portions of many sloughs. Some quadrats with near complete coverage of submersed cover were found to have low levels of cover by other hydrophytes. High densities may result in diminished spread by floating-leafed vegetation and less available substrate for colonization and expansion by emergent vegetation and may also suppress competition through allelopathy (Gross et al. 2003). Vigor of perennial vegetation found in dense clumps of submersed vegetation was qualitatively observed to be lower than among individuals in areas with reduced *Najas*/*Chara* cover, possibly demonstrating competitive stress.

Temporal Effects on Community Development

While planting did have a significant effect on the plant community, the passage of time also had a profound impact on the makeup of developing hydrophyte associations. By 2005, the site was dominated by submersed *Najas guadalupensis* vegetation, with *Potamogeton nodosus* forming a major component of plant cover in planted sloughs. Life history strategies encouraging rapid growth and high rates of reproduction likely contributed to the increasing dominance of both species. Interestingly, species richness values differed on scale of study, with quadrats increasing in species present, while transects showed a significant decline. Regardless of trend, species richness was very low both in quadrats and along transects, with only 1-3 species/m^2. However, this may an artifact of using small quadrats and relatively short transects in sampling. Though each individual plot contained very few species, the sloughs as a whole were more species rich. The number of species represented in all quadrats and transects was actually somewhat higher (Table 2.1), and additional species were present in the site but not found in sampled plots.

Dispersal limitations likely explain the current paucity of other typical regional hydrophytes, though these may be introduced in time through colonization processes. Migrating waterfowl are seasonally abundant on the site, and have been shown to transport small seeds of certain wetland emergent and submersed aquatic species as well as oogonia of Charophyte algae in other areas (Holt Mueller and van der Valk 2002) Charalambidou and Santamaria 2005). The cumulative effect of large numbers of birds in successive seasons may contribute significantly to an influx of propagules and species into the wetland over time. Likewise, transplanting was partially able to overcome this dispersal obstacle for some species, and resulted in higher numbers of species in planted areas than in unplanted controls. Additionally, among the transplanted species, only *Sagittaria lancifolia* and *Sagittaria latifolia* were believed to have been present prior to transplanting. The removal of topsoil likely removed the majority of wetland plant propagules, diminishing the seed bank and reducing the pool of colonizers from within the site. Created and restored wetlands recovering from intense disturbance often face this obstacle, and species richness often increases over time, but this is dependent upon dispersal vectors (Luckeydoo et al. 2002). Through establishment of transplanted vegetation,

Table 2.1. Species present in sample plots. Though richness in quadrats and along transects themselves was low, the number of species present in the wetland was higher, and many of these were wetland obligates.

Species	Indicator Status
Alternanthera philoxeroides (Mart.) Griseb.	OBL
Ambrosia trifida L.	FAC
Ammannia coccinea Rottb.	OBL
Chamaecrista fasciculata (Michx.) Greene	FACU-
Cyperus erythrorhizos Muhl.	OBL
Eleocharis acicularis (L.) Roemer & J.A. Schultes	OBL
Eleocharis compressa Sullivant	FACW
Eleocharis quadrangulata (Michx.) Roemer & J.A. Schultes	OBL
Iva annua L.	FAC
Leersia hexandra Sw.	OBL
Ludwigia repens J.R. Forst.	OBL
Najas guadalupensis (Spreng.) Magnus	OBL
Panicum dichotomiflorum Michx.	FACW
Pluchea odorata L. Cass.	OBL
Polygonum hydropiperoides Michx.	OBL
Polygonum lapathifolium L.	FACW-
Populus deltoides Bartr. ex Marsh.	FAC
Potamogeton nodosus Poir.	OBL
Sagittaria lancifolia L.	OBL
Sagittaria latifolia Willd.	OBL
Salix nigra Marsh.	FACW+
Sesbania exaltata (P. Mill.) McVaugh	FACW-
Sesbania vesicaria (Jacq.) Ell.	FAC+
Symphyotrichum subulatum (Michx.) Nesom	OBL
Typha latifolia L.	OBL

created wetlands have, in some cases, species richness values that actually exceed those of unplanted restored wetlands and even reference wetlands (Heaven et al. 2003), though species composition is often dominated by early-successional or facultative upland species. By 2005, introduction of other hydrophytes locally had resulted in increased species richness in areas that received transplants. Transplanting can boost species richness initially, and this may be sustained by increased subsequent propagule production (Kellogg and Bridgham 2002).

Another significant barrier to higher species richness and diversity was the fluctuation of water levels in the site. Quadrats were primarily located just below the mean water level, resulting in somewhat stable inundation for much of the year. However, transects spanned the slough slope from water depths of approximately 0.5m to elevations of 0.5m above mean water levels.

Over time, transplants such as *P. nodosus* spread between planting treatments, and a few colonizing species, including *Leersia hexandra*, began to appear in low numbers in quadrats. *L. hexandra* is common in broadleaf freshwater marshes and its rhizomatous growth allows rapid colonization and expansion in newly flooded substrate in areas near preexisting wetlands (Wetzel et al. 2001), and other species with similar growth strategies will likely colonize the site in the future. *Najas* became present in nearly all plots, increasing richness slightly in the quadrats. While obligate wetlands plants increased in the quadrats, the loss of facultative species resulted in the overall decline in transect richness. In 2004, peripheral wetland species including *Iva annua*, *Pluchea odorata* (L.) Cass., and *Polygonum lapathifolium* L., were common along drier upslope portions of slough shores, and dense stands of *Chamaecrista fasciculata* were found slightly higher. These warm season annuals were able to quickly colonize the new substrate and were widespread by early summer 2004. The typical summer pattern of dry, weather allowed continued dominance of these species in many areas. However, by fall and winter 2004, uncharacteristically high rainfall and seasonal reductions in evapotranspiration combined to drastically increase the water level in the wetland complex. Upland and facultative plants were inundated, and almost no open ground remained above water until late spring. The annual facultative species experienced complete mortality under the increased water levels. While larger slough transects captured more species, there were still only 3-4 species/20m transect. Interestingly, planted sloughs increased in species richness while unplanted soughs declined in number of species present. As among plot transects, we suspect alternating flooding and desiccation caused mortality of some species that initially colonized the site in 2004, resulting in the loss of several facultative species. However, transport of uprooted and detached transplant fragments likely also contributed to local increases in species richness as viable propagules from elsewhere in the transplanted sloughs were deposited on slough shores by wind and wave action. *Sagittaria* spp. tubers were observed to resprout and expand via rhizomatous growth after deposition through this process.

While the seasonal variations in hydrology may increase the hydrophytic character of the site, the highly variable nature of local hydrology and resulting frequent and intense disturbances may cause a periodic ‘resetting’ of the site, resulting in dramatic changes between alternate states (Kennison et al. 1998, Yallop and O’Connell

2000, Didham et al. 2005) and increasing the importance and dominance of annuals and opportunistic species. Periodic inundation resulted in harsh environmental conditions that favored neither wetland obligates or upland vegetation (Figure 2.6). It is likely that the plant community will be dominated by short-lived opportunistic ruderal species and species that tolerate or adapt to extreme variation in water levels, such as *P. nodosus* and *Typha* spp. (Fennessy et al. 1994, Weiher and Keddy 1995, Giovannini and da Motta Marques 1999). Perennial vegetation must tolerate these hydrological regimes are will be forced to rely on annual colonization as conditions allow (DeBerry and Perry 2004). This may prove to be problematic, as disturbance-prone conditions often enhance performance of invasive species and early colonizers that may suppress growth of desirable native species (Farnsworth and Meyerson 2003, Hager 2004, van der Valk 2005). Such extremes are initially stressful on plant community formation, resulting in periodic loss of species and biomass (McKinstry and Anderson 2003, Turner et al. 2005), but sustained drying may actually benefit the site in the long run, allowing germination and enhancing soil nutrient cycling. Additionally, perennial wetland obligates can survive dry conditions for periods of over a year and will respond with fluctuations in plant distribution and community composition upon reflooding (Hudon 2004, van der Valk 2005), though this response assumes healthy macrophyte growth or at least a viable seed bank is present on the site (Liu et al. 2006). Though minimal flooding and drawdown can be beneficial, the current hydrologic regime in the wetlands is much more characterized by flooding than drying, and this stress may prove difficult to overcome for all but floating-leaf and submersed aquatic vegetation.

Figure 2.6. Extreme water level fluctuations will likely have a large impact on developing wetland plant communities. The views are of the same location from different perspectives, both in 2005. At top, note high water, drowned upland vegetation, and algal mats found in late spring. By late summer, water levels had receded, exposing fish spawning pits and resulting in severe soil cracking.

Time and proximity to seed source have been shown to be important determinants of wetland plant colonization (Reinartz and Warne 1993, Onaindia et al. 2001, Luckeydoo et al. 2002), but even as seeds are dispersed into the wetland, they must be able to survive highly variable conditions (Liu et al. 2006). Increases in species richness may stabilize, not due to establishment of high successional perennial species as observed by Parikh and Gale (1998), but rather due to extreme environmental conditions that represent a barrier to macrophyte survival. Emergent freshwater marshes are also somewhat uncommon in north Texas, and geographic isolation from other wetlands may prevent dispersal of some typical wetland plant species in the region (McKinstry and Anderson 2003). Land use of surrounding areas may further affect and suppress species richness by altering propagule availability and dispersal vectors (Houlahan et al. 2006). If this barrier proves in surmountable, further transplants of additional species may be required in the future and may improve wetland function (Callaway et al. 2003). However, the location of the wetland within the floodplain of Rowlett Creek may diminish the effect of isolation and increase the likelihood of dispersal of propagules into the sloughs (Matthews et al. 2005). One potential factor that may improve survival by an increased number of species the topographic heterogeneity and increased wetland edge habitat created as part of mechanical manipulation of the wetland. Species richness among ponds and sloughs has been correlated with pond perimeter (Matthews et al. 2005) and increases in environmental heterogeneity (Brooks et al. 2005). Diversity of wetland obligates is largely tied to emergent species, plants often found in a fringe around open water. The creation of multiple sloughs increases this available fringe, and topographic heterogeneity may allow the continued presence of wetland fringe vegetation even in periods of high water, maintaining the potential habitat required for high species richness. Nevertheless, the small size of individual sloughs themselves may result in low levels of stable, interior wetland habitat, which could limit the establishment of some sensitive species (Matthews et al. 2005).

Another factor that may affect wetland development is that urban wetlands are often hydrogeomorphically atypical to regional wetlands (Cole and Brooks 2000, Kentula et al. 2004). Such disparity in environmental conditions between local wetlands may limit dispersal and survival of colonizing plants, even from nearby sources (Grayson et al. 1999), leading change in system function (Ehrenfeld 2004). The nature of drainage on the site and fluctuating hydrological regimes will likely lead to highly dynamic seasonal patterns of plant cover (Smith et al. 2002), with marked differences between summer and winter species and abundance patterns. Riverine floods have been shown to act as both a disturbance and a vector for plant colonization (Assini 2001), but only when both inflow and outflow are permitted will this propagule source be realized. The current lack of stability in environmental conditions will preclude establishment of sensitive perennial species and will probably lead to a landscape comprised largely of open water habitat and bare ground, though annual species will likely colonize many areas in warm months. This highly transitional nature will likely impact formation of wetland soils and alter succession trajectories. Constant saturation and drying cycles may not only decrease plant growth and resulting organic matter inputs, but may also stress the soil microbial community and inhibit proper soil processes. A lack of sediment and nutrient inputs into the system from riverine floodwaters will probably further prohibit plant growth and colonization.

Much focus is placed on the long-term succession and vegetation dynamics of wetland sites, but noticeable changes occur on much shorter time scales. Particularly among algae and submersed vegetation, changes in biomass may occur over periods of weeks and even days (Hudon 2004). While fluctuations among existing plant populations will occur over time, until an outlet is installed on the site, seasonal succession pathways due to extreme water level changes will likely play a very significant role on the site and may drastically affect long-term succession (Smith et al. 2002) as seasonal extremes cause widespread mortality and prevent germination of colonizing plants (Wetzel 2001, van der Valk 2005). Additionally, since lack of outflow magnifies hydrological fluctuation, seasonal variation and interannual climate change may also act as a filter on species establishment and community composition (Singer et al. 1996, Zedler and Callaway 1999, Hudon 2004, Johnson et al. 2005, Toth 2005). While seasonal fluctuations played an important role in the pattern of developing vegetation, the duration and intensity of inundation of the site was markedly different between years, with summer 2005 water levels averaging 0.5m higher than the corresponding period in 2004 and taking more than a month longer than the previous year to return to mean water levels. Such fluctuations likely present significant stress to many plants, and the interaction of seasonal and annual climate patterns will likely inhibit many desirable species from colonizing the site beyond a single growing season. Crisman et al. (2005) document the difficulty in establishing wetland macrophytes under rapid drawdown and reflooding regimes, and phytoplankton and cyanobacteria often become the dominant means of primary production in such circumstances.

Nevertheless, as submersed plants are shaded and potentially replaced by floating *Potamogeton*, this may have further significant impacts on the function of the aquatic system. Gas exchange in submersed vegetation releases oxygen to the surrounding water column with moderate rates of transfer to aquatic sediments, retaining much of the dissolved oxygen locally. However, floating-leafed vegetation gas exchange occurs at the water-air interface, releasing oxygen to the atmosphere and depleting dissolved oxygen (Caraco 2006). Additionally, while *P. nodosus* produces high levels of organic matter, it is the distribution of this growth that may affect the system. Submersed species, such as *Najas guadalupensis*, reinvest much of their organic matter output in sediments, through rootstock growth and deposition of plant material. Floating-leafed species often produce much higher levels of organic matter, but this is concentrated at the surface and in respiring aquatic tissues. During photosynthesis, organic matter is imported without oxygen, resulting in increased deficits of dissolved oxygen. As plants senesce, carbon is exported from *P. nodosus* communities and is transported greater distances than in systems dominated by submersed plants. *Najas* spp. have been shown to be unaffected by *Potamogeton* spp. competition (Agami and Waisel 1985), but if a shift in community structure does occur, such differences in plant physiology may have profound impacts on system function and the pattern of wetland vegetation (Caraco 2006).

Protective Caging

Protective caging was utilized upon recommendation by LAERF personnel and is widely utilized in wetland restoration and other projects involving the transplanting of wetland vegetation. Due to the potential for intense grazing pressure on sparsely planted introduced plant materials in the initial stages of restoration projects, mechanical structures minimizing access to plants themselves are a commonly used approach to increase initial survival. Many emergent species, including *Typha latifolia*, have been shown to suffer high rates of mortality after underwater cutting to simulate herbivory, and detrimental effects were compounded by variable flooding regimes (Mathis and Middleton 1999). As such, protection of transplanted emergent vegetation was a priority. Prior to planting, site inspection and test planting revealed the potential for herbivory by pond slider turtles *Trachemys* spp. and common carp *Cyprinus carpio* L. Mammalian herbivory was not anticipated. However, despite the possibility of plant disturbance, caging had almost no effect on plant survival.

While herbivory did not play a significant role, the structure of cages may have actually provided the basis for some of the vegetation patterns observed. Though not born out in statistical comparisons, cages did appear to provide a focal point for growth of floating-leafed and submersed vegetation. Though cages themselves did not harbor significantly higher levels of plant cover, growth around cages and in neighboring plots possibly obscured trends in plant community expansion which may have been an artifact of design and placement of cages. When sampling, we observed uncaged quadrats directly adjacent to caged quadrats to have somewhat higher *Najas* and *Potamogeton* cover than unsampled areas at greater distances from cages. While cover between sampled caged and uncaged plots was not significant, differences between uncaged plots near cages and uncaged areas removed from cages likely were. We suspect that cages served as protection not from herbivory and biological disturbance but from mechanical disturbance. Periodic storms and seasonal wind patterns dislodged some *P. nodosus* transplant fragments and transported them along the slough. Caged areas apparently trapped some of these fragments, and vegetative growth of translocated segments continued within and adjacent to cages. As cages and surrounding areas became 'hotspots' for this new vegetative growth, the increasingly dense vegetation produced a positive feedback mechanism by which cages and plant cover both reduced removal of plant material and increased retention of fragments from elsewhere in the slough. As structure increased capture and growth of submersed and floating-leafed cover, expansion continued in an approximately north-south axis, roughly corresponding to prevailing winds. *P. nodosus* and *N. guadalupensis* likely increased their dominance through this mechanism, as structure elsewhere on the sloughs was associated with elevated levels of each species. Terminal ends of sloughs along the north-south axis had much higher percentage cover by these species than did lateral shores of the same sloughs. As fragments were transported, they were carried by wind and wave energy until their movement was impeded. In ends of sloughs as well as cages, these areas became dense colonies of submersed and floating-leafed plants that spread outward along the shore and into uncaged plots. These founder colonies may serve as an important front for further expansion (Smart et al. 1996).

Though herbivory is not at present a driving force in our study site, its role may increase in the future as herbivores themselves colonize the site. As vegetation continues to become established in bare substrate, terrestrial organisms will likely move into the wetland to utilize developing resources in and around sloughs. Aquatic herbivores have already been observed to have moved into and dispersed across the site in association with periods of flooding. These organisms, particularly turtles, can influence plant community succession and dynamics as they selectively graze hydrophytes in sloughs. Common carp also affect growth of both submergent and emergent macrophytes (Lougheed et al. 2004, Tatrái et al. 2005) and may colonize the wetlands in the future. Though transplanted herbaceous species were not appreciably reduced by grazing pressure to date, woody colonizing species and saplings planted elsewhere in the wetland, including *Populus deltoides* Bartr. ex Marsh. and *Salix nigra,* suffered heavily from mammalian herbivory. If this grazing pressure shifts to emergent species, there may be profound effects on production and community composition, possibly degrading the system (Johnson Randall and Foote 2005). While the lack of herbivory on hydrophytes in our site was not a certainty beforehand, caging is often a critical preventative measure in the early stages of plant establishment.

Effects of Scale

One interesting trend in the data is the decrease of observable effects of transplanting with increased scale of examination. At the small scale of sampled quadrats, we found detectable differences in species richness, total cover by the all transplanted species as well as cover by each individual introduced species, and cover by emergent and floating-leafed plants. With the exception of *P. nodosus*, planted species were restricted to plots originally receiving transplant of that species, and no plants were found in unplanted sloughs. When transects were examined, total cover by all transplanted species was again significantly different between planting treatments. However, individual transplant species were present in such low densities that only *Potamogeton* showed significant effects between planted and unplanted sloughs. At the slough scale, even strong differences in *P. nodosus* between planting treatments disappeared. While none of the individual species were present in different quantities based on planting, the sum of all transplanted species remained significantly different, with planted sloughs retaining greater cover. Curiously, while cover by non-transplanted colonizing species was not different between planted and unplanted treatments in quadrats or transects, planting treatment resulted in significant differences in colonizer cover at the scale of whole sloughs. It is to be expected that a lack of transplanted vegetation presents open substrate and an available niche for colonizing species to fill, resulting in an inverse relationship between transplant and colonizer cover. However, it is interesting that this pattern was not observed at smaller spatial scales. One possible explanation offered by Kellogg and Bridgham (2002) is that lack of differences between planting treatments indicates rapid colonization during the process of succession. While this may be true at larger scales, similarities between treatments are largely a result of dominance by only one or two species in this site.

This overall trend of lack of significance between planted plots and controls in initial years poses serious questions about the future development of the system. Though Parikh and Gale (1998) observed only slight differences among perennial cover between restored and reference wetlands, responses between treatments in our wetland, rather than being a result of consistent high levels of growth, were instead tied to consistent lack of cover and richness. All treatments are far below desired perennial cover of observed nearby reference wetlands. As vegetation sampling yielded low estimates of species richness compared with the species actually present in the wetlands, perhaps the scale of observation plays a role in determining the effects of planting on community assembly. Will differences between plant communities arise and become more pronounced as transplanted vegetation undergoes expansion and reproduction, or will they remain dampened by slow transplant growth and roughly equivalent rates of colonization by additional species? Time will tell, but the answer most likely lies ultimately in site hydrology. Under current conditions of extreme water level fluctuation and associated plant stress, only plants adapted to such unstable conditions will expand in total coverage. Some transplanted species may not have life history traits necessary for survival in this environment, and this may lead to domination of the site by one transplanted species (*P. nodosus*), several species of pioneering warm season annuals, and a few hardy perennials, including *Typha latifolia* and possibly *Sagittaria* spp. Woody perennials that tolerate alternating periods of inundation and drying, such as *Salix nigra*, may also increase in importance in the wetland complex in the future. An almost identical pattern of colonization during drawdown by plants including *Polygonum lapathifolium*, *Cyperus* spp., and *Populus deltoides* has also been observed elsewhere (Hudon 2004) and may represent the future status of wetland vegetation dynamics in the sloughs.

CONCLUSION

We sought to determine the effects of using different species in transplanting efforts, protective caging of introduced plant materials, and the passage of time on the development of the plant community as part of a wetland restoration project. While introduced emergent species did not contribute significantly to community development, transplanted *Potamogeton nodosus* dominated the system and will likely affect community dynamics in the future. Unplanted sloughs were largely dominated by aggressive annuals after two growing seasons. Species richness was very low across the entire site, regardless of transplanting. Caging had no effect on plant cover or community composition but may prove to be a focal point for submersed and floating-leaf vegetation. Many of the significant changes at the species level were associated with the passage of time.

Though the dominance of *P. nodosus* and *N. guadalupensis* and colonization by annual species is likely to continue, there is a tremendous need for continued monitoring of the system well into the future. As seasonal and interannual fluctuations occur and more species are dispersed into the site, the composition and function of the wetland plant community will likely continue to fluctuate, and it would be very difficult to predict future vegetation succession. As conditions change, more plantings may be necessary, possibly including a more species-rich mix, which may improve wetland function and enhance the likelihood of at least a portion of those species being suited to environmental conditions in the wetland. Time and hydrology will remain critical.

CHAPTER III

AQUATIC MACROINVERTEBRATE COLONIZATION AND THE EFFECT OF VEGETATION STRUCTURE

INTRODUCTION

Wetlands are important habitats because they perform countless functions at the landscape scale (Mitsch and Gosselink 1986, Noon 1996) and have been greatly reduced in extent from historical levels. Various approaches to replacing these wetlands include construction of new wetlands as well as restoration of damaged or disturbed existing wetlands. Though wetland creation and restoration projects are rapidly becoming more common and larger in scope, the science behind the discipline is still quite new, and many questions remain unanswered regarding these approaches differences among the effects of such practices (Zedler 2000). Depending on landscape context and other factors, different studies have shown created and restored wetlands, either structurally or functionally, to vary along a continuum of similarity to their targeted reference wetlands and even to each other (Wilson and Mitsch 1996, Malakoff 1998, Zedler and Callaway 1999, Campbell et al. 2002, Mushet et al. 2002, Heaven et al. 2003, Seabloom and van der Valk 2003, Zampella and Laidig 2003, Balcombe et al. 2005a, Spieles 2005), thus demonstrating the highly variable and contextual responses of wetland development.

One key element in successful wetland restoration is the aquatic invertebrate communities that develop in project areas. Organisms representing a broad range of taxa play critical roles in system function of all wetland types (Brooks 2000, Craft 2000, Euliss et al. 2002). However, much uncertainty remains regarding the effects on the invertebrate assemblage and its dynamics during the initial years, depending on the approach taken in wetlands restoration. In mitigation wetlands, invertebrate communities sometimes replicate natural communities (Streever et al. 1996, Gleason et al. 2004, Stanczak and Keiper 2004, Balcome et al. 2005), but similarities depend upon various factors, including macroinvertebrate taxa (Hillman and Quinn 2002).

To improve our understanding of the development of aquatic invertebrate communities in restored wetlands, we sampled the invertebrate community in 10 sloughs (approximately 70 m x 15 m) in a restored wetland complex. Our objectives were to determine the change in invertebrate distribution and abundance (1) following initial transplantation of wetland vegetation, (2) in response to protective caging of transplanted vegetation, and (3) correlated species-environment relationships within developing wetland sloughs.

METHODS

Study Site

Following the closure in fall 2002 of a municipal landfill operated by the City of Garland, Texas, the adjacent land underwent major changes intended to create a research area for the study of wetland development in creation and restoration projects. Located approximately 27 km northeast of Dallas in northeast Dallas County (32°94’N, 96°59’W), the wetland research project is adjacent to an area experiencing rapid suburban development, and as such is subject to rapidly changing hydrological conditions. After nearly three decades of landfill operation, a large 31 ha borrow pit was excavated. The upper 3-5 m of removed soil was incorporated into, and used to cap, the old landfill area. In the borrow pit, the water table is quite high because it immediately borders Rowlett Creek. The creek is the main drainage in the 3,143 ha Rowlett Creek watershed, contributing to the Trinity River. Remaining forested riparian corridors, dominated by *Quercus* spp and *Ulmus* spp. (Nixon et al. 1991), have been significantly impacted based on observed channel features such as downcutting of the creekbed and active sloughing of stream banks. Within the borrow pit, eolian deposition and periodic (seasonal) floods had transported colonizing plant material typical of other disturbed local wetland sites, including *Typha latifolia* L., *Salix nigra* Marsh., and *Ludwigia repens* Forst. However, summer evaporation of water from dense clay soils having high shrink-swell potential had limited the development of plant cover.

In this setting, heavy machinery was used to increase topographic heterogeneity that would help to create a wetland complex of several sloughs, flats, ridges, and a large oxbow lake. Water level in these sloughs is maintained by groundwater and is augmented by increased local precipitation in spring and fall, to produce depths that range from 1 to 2 m throughout much of the year. Evapotranspiration during summer dry spells causes significant drawdown and a reduction of water levels. Occasionally, large rainfall events elevate water levels enough to temporarily connect the sloughs within the complex. Ten sloughs were designated for our investigation of the initial response of aquatic macroinvertebrate communities.

Study Design

In ten sloughs in the site, multiple-factor vegetation transplanting treatments were implemented to establish planted and unplanted experimental sloughs. In each of five sloughs, five wetland species were planted near the mean water level and arranged in species blocks: *Potamogeton nodosus* Poir., *Sagittaria latifolia* Willd., *Sagittaria lancifolia* L., *Eleocharis quadrangulata* (Michx.) Roemer & J.A. Schultes, and *Polygonum hydropiperoides* Michx. Each of these species is common to regional wetlands, widely used in revegetation efforts, and was preconditioned offsite at the U.S. Army Corps of Engineers Lewisville Aquatic Ecosystem Research Facility (LAERF). With the exception of *P. nodosus,* which was transplanted at slightly greater depths, all plants used are herbaceous emergent species. Within planted blocks grouped by species, both caged and uncaged quadrats were established to test the effect of protective caging on the survival and spread of our transplanted vegetation as well as colonizing hydrophytes. With five species, each planted slough contained five each of caged and uncaged subplots, one of each per transplanted species area. Cages were approximately 1m^2 and were constructed using 14 gauge welded steel wire with 5 cm x 10 cm mesh and anchored with 1.3 cm steel reinforcing bar to prevent the displacement of cages by animals and debris transported into and within the wetland during high water. Three caged and three uncaged quadrats were established in each of the five unplanted sloughs as controls for caging and transplanting effects.

Macroinvertebrates were collected in late summer in 2004 and 2005. In each year, 10 quadrats (5 uncaged, 5 caged) were sampled in each planted slough, and 6 (3 uncaged, 3 caged) quadrats were sampled in control sloughs receiving no transplanted vegetation. Within each of these quadrats, we visually estimated percent total cover by each plant species (transplanted as well as colonizing species) and sampled vegetation and the water column collectively for aquatic macroinvertebrates. Using a hollow cylinder (30 cm diameter x 45 cm height), we enclosed a portion of the sampled quadrat, disturbed the substrate to suspend invertebrates in the water column, and collected them in a hand-held net with 1 mm mesh. After two minutes of sampling effort, the quadrat was considered exhaustively sampled when no additional macroinvertebrates were found. In caged quadrats, rebar anchors were temporarily removed and the cage was raised briefly to permit sampling and was immediately repositioned following macroinvertebrate collection. Invertebrates were collected and identified (to order or family as needed to distinguish among commonly reported wetland taxa; Brooks 2000) upon return from the wetland site.

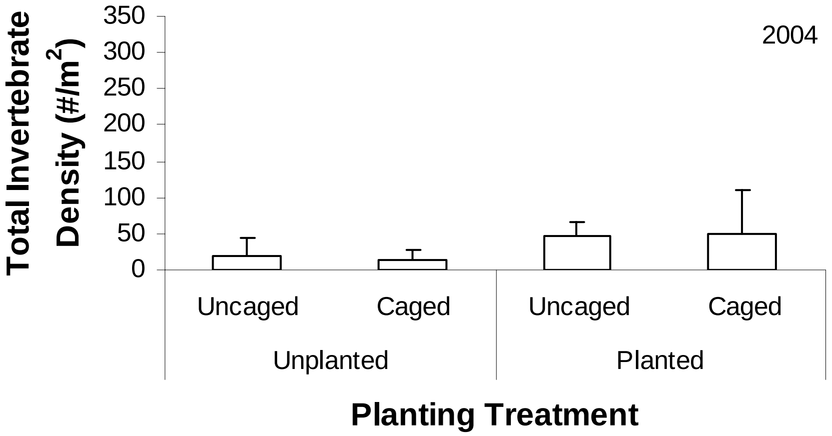
Statistical Analyses

Invertebrate counts were summed by caging treatment and slough and means were calculated for each cage treatment within each slough for comparisons between treatments. Statistical comparisons of total invertebrate abundance were performed with repeated measures MANOVA procedures using SPSS 12.0 (Norusis 2004). A significance level of $p = 0.05$ was used for statistical tests.

Counts of each invertebrate taxon were used in a correspondence analysis (CA) to determine environmental gradients related to plant cover components. We used canonical correspondence analyses (CCA) in CANOCO (Jongman et al. 1995) to quantify relationships between the invertebrate abundance matrix and a matrix of explanatory variables (including arcsine-transformed plant cover and environmental factors) related to our restoration transplanting treatments. Sampling date was utilized as a blocking variable to remove variation due to temporal replication within sloughs. Using Monte Carlo simulation (N = 499 permutations), we tested each variable for its significant ($p = 0.05$) contribution to the distribution of macroinvertebrate abundance in our samples. We also omitted variables having a high degree of mutlicollinearity (VIF > 3). To visualize their relationships, we used biplots of results for invertebrates, explanatory variables, and supplemental environmental variables (those variables having high VIF values but included in plots in order to visualize their relationships to other variables).

RESULTS

Overall, total invertebrate abundance was significantly different between unplanted and planted sloughs ($p < 0.0001$). Although these differences were not significant in 2004 ($p = 0.090$), they were significant in 2005 ($p = 0.002$) as abundance values diverged. Transplanted sloughs (228.9/m^2 ± 20.5, abundance given as mean ± S.E.) harbored greater numbers of individuals per sampled quadrat than did unplanted sloughs (99.0/m^2 ± 26.5) in 2005 (Figure 3.1). Additionally, the passage of time had a significant effect on total abundance ($p < 0.0001$), which increased by almost an order of magnitude across the two years. Whereas in 2004 some samples yielded no invertebrates, by 2005 samples in all sloughs contained multiple taxa, and many sloughs had over 100 individuals/m^2. The protective caging had no significant effect on macroinvertebrate abundance ($p = 0.542$), and comparable numbers of organisms were found in caged (32.7/m^2 ± 17.1 in 2004, 153.6/m^2 ± 47.2 in 2005) and uncaged plots (31.26/m^2 ± 20.4 in 2004, 174.36/m^2 ± 42.9 in 2005).



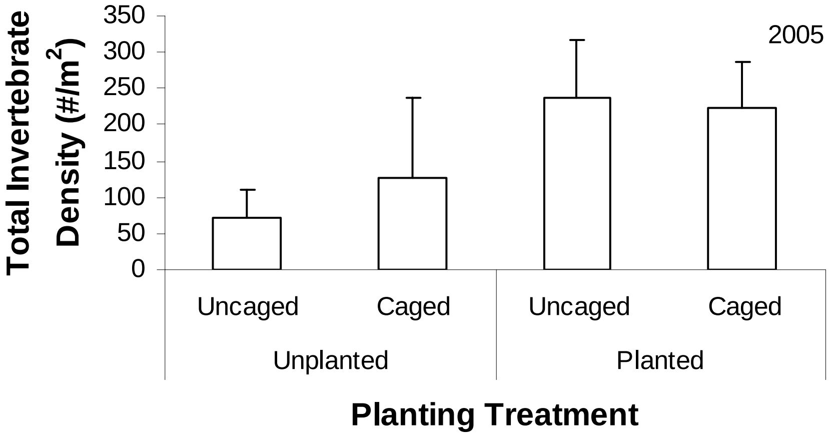


Figure 3.1 Total invertebrate abundance in each summer for caged and uncaged subplots within unplanted and planted wetland sloughs.

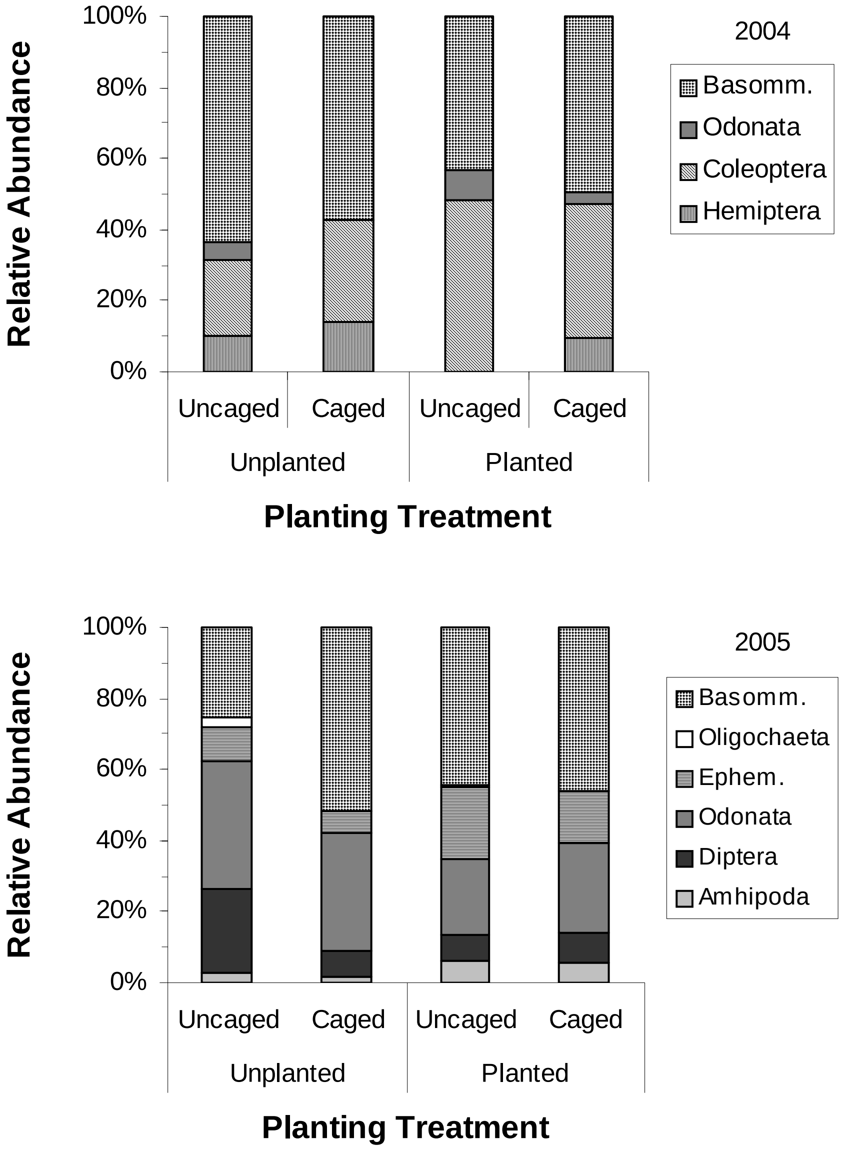


Figure 3.2. Invertebrate community composition in each summer for caged and uncaged subplots within unplanted and planted wetland sloughs. Plots in both years were generally dominated by snails and aquatic insect life stages, although the composition of insects changed dramatically between years.

As did invertebrate abundance, the composition of the macroinvertebrate community also changed between years but was not significantly affected by caging (Figure 3.2). While Basommatophoran snails (in the families Physidae and Planorbidae) were particularly common in all treatments in both years (approximately 50% of total invertebrates in 2004, 40% in 2005), the relative abundance of other taxa shifted dramatically. Odonates comprised 5-10% of invertebrates in 2004, but in 2005 had increased to approximately 30% in all treatments. Coleoptera and Hemiptera, somewhat common (30% and 10% of the total invertebrate abundance, respectively) in 2004, were almost entirely absent in 2005, but instead Ephemeroptera (15%), Diptera (10%), and Amphipoda (5%) were present. Trichoptera, Decapoda, and Hirudinea were present both years, but at very low frequencies, occurring in only one or two samples. Overall, the system was dominated in summer by snails and aquatic life stages of insects in both years. The CCA for slough invertebrates yielded a total inertia of 1.377, with axis I ($p = 0.006$) and axis II accounting for 28.0% of total species data variation, and of this, 87.7% was due to included environmental factors. CCA indicated *Potamogeton nodosus* cover, *Ludwigia repens* J.R. Forst. cover, emergent cover, and total invertebrate abundance were significantly related to invertebrate community variation along axis I, and emergent cover, total plant cover, and total invertebrate abundance were significant along axis II (Figure 3.3).

Restoration treatments of transplanting and protective caging of wetland vegetation were not significantly related to either axis, nor was cover by submersed vegetation. Therefore, these variables were fitted to the regression and plotted after the model for other environmental variables was determined, to visualize relationships. As indicated on the plot, submergent cover was statistically nonsignificant due to its strong negative correlation with emergent cover and positive correlation with total cover. Diptera and Oligochaeta were associated with low plant cover and low total invertebrate abundance. Amphipoda, Decapoda, and Trichoptera were associated with high values of cover by floating-leafed plants *P. nodosus* and *L. repens*. As most of the centroids of invertebrate data are clustered around the origin, this may indicate either a weak correlation with environmental data or a significant relationship with intermediate values along these gradients. We suspect that the relationships demonstrated are in fact weak correlations with environmental gradients, as both high and low extremes of plant cover data were present in sampling. However, intermediate cover values may provide both cover and freedom of movement where either would be unavailable among extremely dense or open vegetation. Overall, 68.0% of species data variation was due to covariance with sampling date, which was used as a blocking variable.

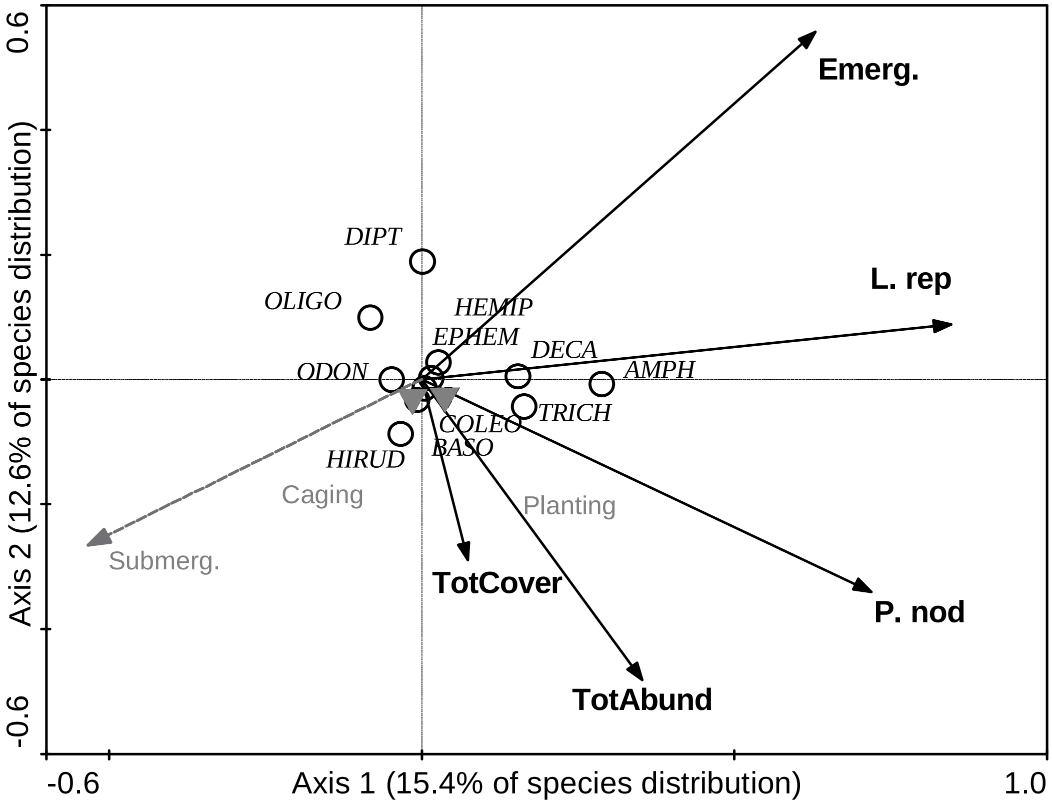


Figure 3.3. Canonical correspondence analysis (CCA) relating invertebrate community composition to plant cover components and wetland restoration treatments. Open circles indicate centroids of invertebrate distribution (AMPH = Amphipoda, BASO = Basommatophora, COLEO = Coleoptera, DECA = Decapoda, DIPT = Diptera, EPHEM = Ephemeroptera, HEMIP = Hemiptera, HIRU = Hirudinea, ODON = Odonata, OLIGO = Oligochaeta, TRICH = Trichoptera). Solid arrows indicate environmental vectors toward increasing values with longer arrows indicating broader range of variation in invertebrate data (Emerg. = emergent plant cover, L. rep. = *L. repens cover*, P. nod = *P. nodosus* cover, TotAbund = total invertebrate abundance, TotCover = total plant cover). Dotted arrows indicate insignificant supplemental environmental variables (submergent plant cover). Inverted triangles indicate insignificant nominal variables representing planting and caging treatments.

DISCUSSION

Aquatic invertebrates are a critically important but sometimes overlooked component of wetland ecosystems. They perform critical roles in the food web, act as primary consumers and decomposers, and often indicate healthy system function on a larger scale (Brooks 2000, Craft 2000, Euliss et al. 2002, Momo et al. 2006). While protective caging of transplanted vegetation did not affect the abundance of aquatic invertebrates in sloughs within the wetland complex, the introduction of transplants themselves did have a positive effect on total invertebrate abundance. There was a dramatic increase in macroinvertebrate abundance over the first two years of development of the newly restored wetlands. While neither transplanting or caging had a significant effect on invertebrate community assemblage, compositional change over time between the two years of the study may have profound impacts on system function in the future as the plant and invertebrate communities develop interdependently.

Vegetation Effects

The extent of vegetation does have implications for system function. Expanding plant cover as a result of transplanting vegetation may provide important structure for emergence and metamorphosis of juvenile life stages (Figures 3.4 and 3.5) and may exclude some predators while providing grazing opportunities

Figure 3.4. Empty exoskeleton on emergent *Eleocharis quadrangulata* (Michx.) Roem. & Schult.after metamorphosis of dragonfly (Odonata) nymph.

Figure 3.5. Dense floating-leafed cover composed primarily of *Potamogeton nodosus* with *Ludwigia repens*. A well-developed vegetation canopy likely provided important potential for grazing and cover for some groups of aquatic invertebrates.

(Parsons and Matthews 1995), and many invertebrate groups are positively associated with organic matter (Spieles and Mitsch 2003). CCA analysis indicated floating cover by transplanted *Potamogeton nodosus* and colonizing *Ludwigia repens* were significant in explaining invertebrate variation, and high growth rates of both of these species may have significant implications for this site. Many other studies have concluded that floating cover is a significant factor in explaining invertebrate community variation and likely results in increased macroinvertebrate abundance (Parsons and Matthews 1995, van Duinen et al. 2003). Regardless of species identity, vegetation growth form and structure is strongly correlated with invertebrate community structure (van den Berg et al. 1997, Garono and Kooser 2001, Phillips 2003, Schindler et al. 2003, Bried and Ervin 2005, Kostecke et al. 2005, Hornung and Foote 2006), and plant species richness increases invertebrate richness (Nicolet et al. 2004). Increased production of organic matter may expedite soil formation and provide feeding opportunities, affecting invertebrate community development (Craft 2000, Flinn et al. 2005). However, most wetland invertebrates require heterogeneity of habitats to complete various life stages, so monotypic cover across the site will likely diminish taxonomic diversity if floating cover does come to dominate the sloughs.

Colonization and Hydrology

One critical determinant of aquatic macroinvertebrate assemblages in developing wetlands is that of dispersal through various vectors from other wetland areas off-site (Brady et al. 2002). This may occur via wind, floodwaters, or wildlife for different organisms (Charalambidou and Santamaria 2005). A potential factor initially affecting the invertebrate community may be the introduction of vegetation transplants themselves. Plants were collected at LAERF and preconditioned in constructed nursery ponds under fertilization and relatively constant water levels for one year to establish vigorous rootstock. Through collection from ponds in the facility, soil gathered along with plant stems was transferred during potting in submerged containers. This soil likely contained eggs and small numbers of various life stages of different macroinvertebrates. Over the course of growth in the nursery ponds, some of these organisms were observed to emerge and disperse, while others, particularly dragonflies (Odonata) were seen congregating around the ponds, likely utilizing them as small isolated wetlands for reproduction. As invertebrates differentially recruited and dispersed into the nursery ponds, they probably colonized the potted soil. Thus, when this substrate was introduced into the wetland site with the transplanted vegetation, some invertebrates were probably introduced as well, inoculating otherwise barren sloughs with low levels of aquatic organisms. Although these particular macroinvertebrates might also have colonized the site at a later time, this initial source of individuals may have accelerated recruitment of some taxa, especially those lacking an aerial life stage. Such introductions may not only increase species diversity but result in assemblages that more resemble those of established wetlands (Brady et al. 2002, Gleason et al. 2004). Interestingly, Brady et al. (2002) also found that such facilitated recruitment resulted in dominance by gastropod snails where plants were introduced, whereas control plots contained higher numbers of chironomid dipterans. This trend was also observed in our study, but was not distinguishable from correlation due to early establishment of cover as a result of transplanting.

Between the two years of sampling, substantial hydrological changes occurred due to both seasonal weather patterns and interannual climate variation. Large earthen berms remain in place around the site, acting as levees to prevent all but the most extreme flood flows from entering the site. However, the resulting enclosed depression in which the wetland site sits receives considerable in-basin rainfall and large volumes of runoff from surrounding upland areas. Though floods are excluded, the retention of rainfall and runoff results in water level fluctuations with storm events. These sharp increases in water level periodically increase connectivity between sloughs, potentially allowing dispersal between these ponds as high water allows. As drawdown occurs through seasonal evapotranspiration, re-isolation increases, so that sloughs become more independent their developmental trajectories can differ during the majority of the warm season (Painter 1999). These shifts may affect invertebrate communities by allowing temporary mixing of assemblages, introducing some organisms and resulting in exclusion of others. Seasonal succession of wetland invertebrates has commonly been observed in wetland communities (Gonzales Martinez and Valladares Diez 1996, van den Berg et al. 1997, Brooks 2000, Hillman and Quinn 2002), and likely occurred within the timeframe of our study, but the interval between sampling periods hindered its detection.

2004 was exceptionally cool and wet, resulting in relatively high water levels in sloughs throughout the year. Precipitation diminished in late 2005, resulting in drought-like conditions in many portions of the site, exposing previously submerged areas and lowering water levels in the site. One the one hand, flooding may slow colonization (Bedford and Powell 2005), and on the other, falling water levels may exclude those macroinvertebrates that are characteristic of open water while elevating the abundance and dominance of those utilizing the margins of wetland habitat. Drought conditions may also prevent invertebrates with extended life histories requiring longer hydroperiods from completing their life cycles (Tronstad et al. 2005), which may make biological assessment of wetland function particularly difficult (Wilcox et al. 2002). Between periods following intense storms and summer drought conditions, water level changes in excess of 2 m represented an extremely variable hydrology for this area. Cyclic shifts between seasonal weather patterns and wet and dry years greatly affect the macroinvertebrate assemblage, and this likely occurred in the wetland site. 2005 sampling occurred at the end of a wet period, and the invertebrate community was dominated by species more characteristic of open water. Brooks (2000) and Bedford and Powell (2005) determined that annual hydroperiod fluctuations were a major factor in determining invertebrate abundance and composition, though community assemblage was somewhat stable in the long-term, in contrast to our results. Though wet and dry cycles are natural in many wetland communities, the severity and duration of such cycles in our site may be a barrier to colonization and long-term survival of some taxa. The timing of alternating wet and dry periods is likely critical in determining invertebrate community composition, as such phases must coincide with the requirements of different life stages of invertebrates. If conditions are excessively wet or dry or the seasonality of these conditions does not match what is needed by a given invertebrate’s life cycle, life stages may not be completed.

The low overall taxonomic richness could be due to many factors: the short interval of time since wetland restoration, significant barriers to colonization and dispersal, or the large shifts in wetland hydrology. Most likely, some combination of these influenced the dynamics of the macroinvertebrate community. Though life stages of many aquatic invertebrates are highly mobile and permit rapid colonization and establishment in new habitat, invertebrate diversity and total abundance are typically low in newly created wetlands (Craft 2000, van Duinen et al. 2003). Those that do become established in new wetlands must be able to tolerate temporal variations in environmental conditions, and both richness and abundance can be greatly affected by hydroperiod (Corti et al. 1997, Leeper and Taylor 1998, Brooks 2000, Lillie 2003), although invertebrate communities are typically adapted in the long-term to hydrological variation (Leslie et al. 1997). Continued urbanization and land use change of the area surrounding the wetland may magnify hydrological extremes and both reduce invertebrate richness and alter community composition (Lundkvist et al. 2002, Freeman and Schorr 2004, Batzer et al. 2005, Moreno and Callisto 2006). Interestingly, total invertebrate abundance itself was highly correlated with invertebrate community composition. Those groups associated with the substrate (oligochaetes and dipterans) were negatively associated with total abundance, perhaps indicating dominance by these groups as a result of adverse water quality, soil conditions, or other factors. However, macroinvertebrates utilizing the water column or vegetation were associated with samples having a larger number of specimens. Thus, higher total abundance yielded a higher taxonomic richness through the addition of these latter taxonomic groups.

Predation

While periodic high water provides connection between sloughs and a means of dispersal for invertebrates across the site, this connection also provides a pathway for colonization by predatory fishes in the sloughs. Before major soil manipulation and construction of the sloughs, a small pond was present in the site and received overflow from Rowlett Creek during storm events. Black bullheads *Ameiurus melas* (Rafinesque), mosquitofish *Gambusia affinis* (Baird and Girard), sunfishes *Lepomis* spp., and largemouth bass *Micropterus salmoides* (Lacepède) have been consistently observed in wetland sloughs. However, their relative distributions are highly variable. As drawdown occurs, mortality increases more quickly among the fish population in drier sloughs, although these sloughs are recolonized in high water periods. Though all sloughs had observed surface water even in the driest periods, this concentration of prey and predators likely reduced abundance of some invertebrate taxa, both through loss of habitat and increased predation. Large numbers of small fishes, particularly juveniles, can consume large numbers of spatially-confined invertebrates, albeit to different degrees in different sloughs, but effects may not alter community composition (Corti et al. 1997, Batzer et al. 2000, Johansson and Brodin 2003, Blanco et al. 2004). Likewise, while waterbirds are seasonally abundant in the site, predation by these animals has been shown elsewhere to not contribute significantly to invertebrate community structure or overall abundance (Ashley et al. 2000). Caging was not strongly associated with in increased macroinvertebrate abundance. Despite the fact that mesh size allowed entry by most smaller (insectivorous) fishes while excluding larger adult piscivores, consumption and growth rates are lower for small fishes using the structure of plants as refuge than those in open water (Savino and Stein 1982, Maceina et al. 1991). The cages may also act as artificial cover, providing refuge for some of these fishes. Moreover, plant cover was not significantly greater in caged areas. However, dense plant cover would likely increase the difficulty of sampling in sites and may have resulted in underestimation of macroinvertebrate abundance.

Community Implications

Domination of sloughs by snails may be a reflection of current dominance of cover by submersed and floating vegetation (Parsons and Matthews 1995), and this may prove to be a factor in future development of slough systems. Grazing snails were observed in large numbers on bare substrates, and these patches of open substrate may be maintained by feeding and movement of crayfish and carp *Cyprinus carpio* (Linneaus), resulting in cloudy water in portions of the sloughs. Competition may suppress chironomid populations (Batzer et al. 2000) and wind-driven currents may also provide a feedback mechanism whereby locally increased turbidity inhibits growth and establishment of submerged vegetation, causing a dynamic patchy distribution of vegetation in the sloughs. Though dominance by the ubiquitous snails presently seems to indicate a lack of other taxa associated with bare substrate, the alternating patches and open areas eventually may provide niches for different macroinvertebrates, creating interior habitat in vegetation clumps, bare substrate, and edge habitat at the interface of the two and at low vegetation densities. Beginning in 2005, a submerged matrix of dense *Najas guadalupensis* (Spreng.) Magnus and *Chara* spp. dominated slough shallows in many portions of the site, and vegetation dynamics will likely continue to play a major role in structuring the invertebrate community. Marklund et al. (2001) found that very dense submerged growth excludes most insect groups but provides key habitat for snails. The continued importance of predatory invertebrates, including dragonflies, beetles, and true bugs, will also drive system structure. As grazers and invertebrates with various feeding strategies become more common, larger numbers of the predatory taxa may be supported, and this in turn may result in complex interactions with both the fish and plant communities.

CONCLUSION

We found that planting wetland sloughs resulted in increased wetland invertebrate abundance, though the planting treatment alone did not explain the variation in community structure. Plant cover accounted for much of the variation in abundance and distribution among the invertebrate assemblage, and emergent species cover and cover by floating-leafed species *Ludwigia repens* and *Potamogeton nodosus* were significant explanatory variables. While protective caging of vegetation did not result in significant differences in the invertebrate community, temporal variation resulted in increases in abundance and shifts in assemblage structure. As the invertebrate community will likely continue to be very dynamic and driven largely by hydrological conditions, complex seasonal and annual interactions will likely replace straight linear succession in the coming years. We recommend monitoring the macroinvertebrate assemblage following storm events and at shorter times intervals in order to track the community response to high water, resulting fish population dynamics, and changes in wetland vegetation. Collection of water quality parameters may also contribute to explanation of community dynamics.

CHAPTER IV

SUMMARY

The purpose of our study was to contribute to the level of understanding in the growing science of wetland restoration and management. We conducted a study to monitor the characteristics of vegetation and aquatic macroinvertebrate community development and test the effects of using different approaches to the restoration of wetland habitats. In a constructed wetland complex in Garland, Dallas County, Texas, we implemented multiple-factor restoration techniques involving transplantation of wetland macrophytes and the utilization of protective caging for transplants. We investigated the following hypotheses:

- Planting of restored wetlands using several species results in plant communities that differ from those left to colonization alone
- Protective caging of vegetation increases survival and spread of transplants and affects community composition
- Wetland plant communities show significant temporal changes during development
- Sloughs with transplanted vegetation have higher invertebrate abundance values
- Caging of vegetation results in higher levels of invertebrate abundance

As our final objective, we also determined correlated species-environment relationships between invertebrate data and measured values of plant cover and restoration treatments to explain variation in abundance and distribution among the invertebrate community assemblage.

Based on the vegetation study, planted and unplanted wetland sloughs did not show significant differences between plant cover values. However, the composition of the plant communities in both of these broad-level treatments was significantly different. Unplanted sloughs were dominated by annuals and fast-growing colonizing species that were not part of initial transplanting efforts. Protective caging had no significant effect either on plant cover or on community composition. Time was perhaps the most significant factor in wetland plant community development. Over the course of the study, plant cover increased dramatically and showed shifts in component species, with floating-leafed and submersed species spreading to cover a large portion of the site. Wetland obligates also became more prevalent, though this was mostly due to colonizing plant growth and the expansion of one transplanted species, *Potamogeton nodosus*. Species richness was low in all treatments, likely a result of adverse environmental conditions.

In the invertebrate study, wetland sloughs receiving transplanted vegetation did have higher levels of invertebrate abundance. Though unplanted and planted sloughs were similar in 2004, the abundance values diverged in 2005, with planted sloughs supporting much higher abundance levels. As with the plant community, protective caging did not result in significant differences in invertebrate abundance or invertebrate community composition. Though planting did result in higher invertebrate abundance, it was the composition of plant cover that better explained differences in invertebrate distribution and the components of the community assemblage. Cover by all emergent plant species and *Potamogeton nodosus* and *Ludwigia repens* (the latter two both floating-leafed plants) were significant explanatory variables. The use of planting and caging treatments themselves did not account for community composition. Again, the identity of plant cover species was more critical in determining effects among the invertebrate community.

Both the plant community and the aquatic macroinvertebrate community will likely continue to be very dynamic and driven largely by hydrological conditions, and complex seasonal and annual interactions will likely replace straight linear succession in the coming years. Composition of the developing communities will likely undergo frequent shifts with environmental conditions, especially among water levels in the wetland complex. With these frequent changes, wetland system function and community composition will be very difficult to predict. As such, frequent continuing monitoring is recommended as time and hydrology will be critical factors in the development of the restored wetland complex.

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