5-22-2006

The Influence of Flooding on Contributions of Spartina Alterniflora Roots to Salt Marsh Soil Volume in a Field Setting

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THE INFLUENCE OF FLOODING ON CONTRIBUTIONS OF *SPARTINA ALTERNIFLORA* ROOTS TO SALT MARSH SOIL VOLUME IN A FIELD SETTING

A Thesis

Submitted to the Graduate Faculty of the
University of New Orleans
in partial fulfillment of the
requirements for the degree of

Master of Science
in
Geology

by

Daniel P. Gill

B.S. The Ohio State University, 2003

May, 2006

Acknowledgements

The research presented here would not have been possible without the involvement of many individuals.

First and foremost, I am grateful for the untiring input from my committee of advisors including Dr. Mark Hester, Dr. Mark Kulp, and most notably Dr. Denise Reed. The doors were always open to their offices which I readily entered to unleash any number of concerns, as well as receive feedback on methodologies, analyses and drafts.

The collection and processing of data was not always the most pleasant of experiences, yet the contributions of Reggie Graves, Matt Kaller, Justina Horan, Matt Weigel, and Dana Watzke-Bishara were able to fulfill and exceed my needs in the field. Back in the lab, the statistical know-how of Jonathon Willis was critical to this research, and the time he afforded me is greatly appreciated.

I owe added thanks to Dr. Hester and his lab for affording me use of equipment and lab space without a second thought, as well as, Dr. William Busch who was equally generous with lab space and equipment. I am indebted to Dr. Brian Perez for generously allowing access to water level data obtained at Bayou Chitigue, as well as, to Sirel White for providing unique solutions to my technology woes.

A great deal of gratitude is due to all the folks at LUMCON's Marine Center who accommodated all my needs during my four week marathon of sample collection and analysis in the aftermath of hurricanes Katrina and Rita.

A special thank you is required for Laura Dancer who not only aided in the field after hurricanes Katrina and Rita, but also tolerated my never-ending storm of supply orders, paperwork submissions, and mailing needs (which can be sizable when one has relocated to Ohio).

The ever-increasing love and support of Nicole (my wife), parents, brother, friends and colleagues provided a level of sanity and perspective that was needed during many a stressful night. This research was supported by funds from the US Geological Survey Patterns and Processes of Subsidence across the Mississippi River Delta Plain, Louisiana grant, award number 04ERAG0068.

To all of these people, and any that I have unintentionally overlooked, I offer a deep and heartfelt thank you.

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Abstract

Rapid rates of coastal wetland loss in Louisiana are widely recognized. One important question of wetland sustainability is how volumetric contributions of roots to wetland soils vary under the influence of different hydrologic regimes.

The research presented here specifically investigates the spatial and temporal relationships among the specific gravity of live roots, soil chemistry, and flooding regime for the macrophyte *Spartina alterniflora* Loisel. in natural, salt marsh, field settings located across southeastern coastal Louisiana. The results of this research propose the existence of a stress-tolerance threshold (beyond which root specific gravity modifications are observed), and highlight the importance of micro-scale factors over macro-scale regional characteristics in determining environmental stresses and the subsequent impact on root specific gravity. A conceptual model is developed linking the interactions of relevant environmental variables, root specific gravity, and the idea of a stress-tolerance threshold.

Chapter One: Introduction

1.1 Context

Coastal wetland loss in Louisiana is occurring at a rapid pace and wetland sustainability has become an issue of paramount importance. Rates of loss vary temporally and spatially along coastal Louisiana. Substantial efforts have been made toward quantifying land loss data largely relying on the comparison of historical maps, aerial photography, and satellite imagery (see Gagliano et al., 1981; Britsch and Dunbar, 1993). Regional rates of loss steadily increased during the 1900s until peaking sometime during the late 1950s to the early 1970s at approximately 39 to 42 mi^2 annually (Gagliano et al., 1981; Britsch and Dunbar, 1993). Following this peak in land loss, rates declined until the early 1990s at which point a stabilized value of approximately 24 mi^2 per year was reached (Britsch and Dunbar, 1993). Recent efforts associated with the Louisiana Coastal Area (LCA) Ecosystem Restoration Study established that the land loss trend of approximately 24 mi^2 per year was maintained from 1990 through 2000 (Barras et al., 2003). Localized estimates of loss range from negative values where land is actually building, as is currently the case in Atchafalaya Bay (Delaune et al., 1987; Barras et al., 2003), to upwards of approximately 2 mi^2 per year within the Empire U.S. Geological Survey quadrangle located within the Modern delta lobe of the Mississippi River (Britsch and Dunbar, 1993).

With historic increases in human activity, causes of land loss are often grouped into two categories: natural and anthropogenic. Natural causes consist of such processes as subsidence, compaction, erosive wave action, and fault displacement (Penland et al., 1990). Anthropogenic factors include canal dredging and associated spoilbanks that alter the natural hydrology of these systems, flood-control levee structures, and subsurface fluid withdrawal, e.g. oil, gas, and water (Penland et al., 1990; Morton et al., 2003). These processes are not mutually exclusive. Typically, multiple factors operate in conjunction with one another making it difficult to quantify individual contributions to land loss although attempts have been made (see Turner, 1997; Day et al., 2000; Penland et al., 2000; Gosselink, 2001; Turner, 2001; Day et al., 2001; Morton et al., 2003).

The processes involved with coastal land loss and their interactions operate on a range of spatial and temporal scales. Investigating these processes across their appropriate scales provides a more complete understanding of these relationships. The processes that this research focuses on and their respective scales are shown on Figure 1.1.

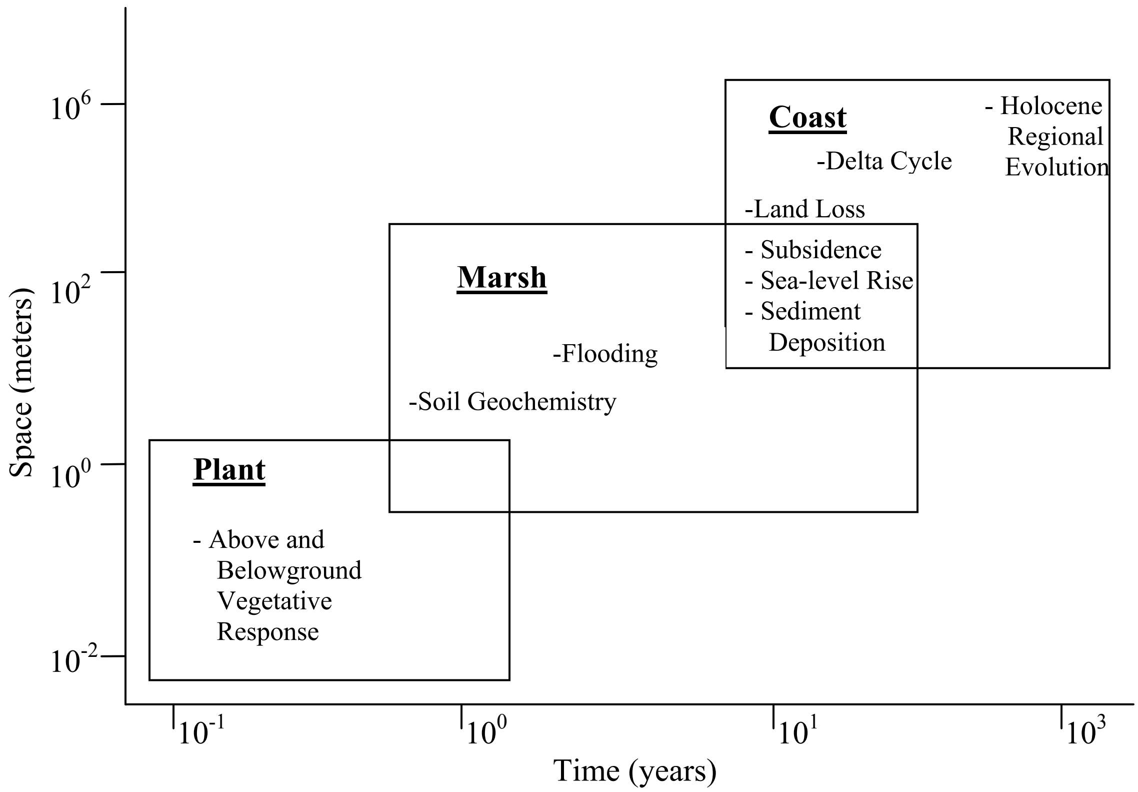


Figure 1.1: Relevant spatial and temporal scales of observation.

The largest scale is the 'coast' scale which concerns regional activities (e.g. delta lobe switching, see Figure 1.1). Decades or centuries of data are required to make generalizations at this scale. The 'marsh' scale is concerned with local activities such as erosion and flooding. Years or decades of data are necessary for analyses at this scale. The smallest scale is the 'plant' scale focusing on individual plants and their reactions to modifications in environmental conditions. Months or years of observation can provide an understanding of the processes operating at this scale.

This introductory chapter establishes the setting, and describes in more detail the spatial and temporal scales of interest to the research presented here. Previously conducted research relevant to this study is also presented in this section, which concludes by stating general hypotheses to be investigated. The next chapter discusses the methodology employed during this study including study sites, specific hypotheses to be tested, experimental design, and field and laboratory techniques for sample collection, processing, and analysis. The hypotheses posed are then revisited in chapter three as results are presented and discussed. A final chapter summarizes the findings of this study with concluding remarks.

1.2 Background of Coastal Louisiana

According to current theories of delta cycle dynamics, which describe the natural processes influencing delta lobe construction and degradation, coastal regions of a delta plain associated with an active river channel will build land seaward as a regressive sequence (Woodroffe, 2002). Coupled with this constructive phase of the delta cycle is the development of many geomorphic features including: bay fills, overbank splays (Coleman, 1988), and extensive marsh platforms (Mitsch and Gosselink, 2000). The reactivation of this cycle occurred along coastal Louisiana approximately 3000 to 7000 years ago as sea-level became relatively stable after a steady rise driven by glacial meltwater input (Kolb and Van Lopik, 1958; Fisk, 1944; Curray, 1960; Frazier, 1967). This stabilization allowed for the formation of a deltaic plain consisting of five to seven delta lobe complexes in southeastern Louisiana (Fisk, 1944; Kolb and Van Lopik, 1958; Frazier, 1967; Penland et al., 1991b).

The continued productivity of the delta plain is highly dependent on the accumulation of two major sediment types, inorganic and organic (Gagliano et al., 1981; Reed, 1990; DeLaune and Pezeshki, 2003). Sediment deposition in these systems is governed by the interactions among hydroperiod, sedimentation, and vegetative growth (Reed, 1990). The deltaic structures of southeastern Louisiana were deposited from sediment associated with the Mississippi River, the largest river in North America with respect to discharge and sediment load (Coleman, 1988; Mossa, 1996).

Initially, regression is the result of mineral sediment deposition delivered from a nearby river system. Following this accumulation of substrate, tidal inundation and storm events provide additional inorganic sediment inputs (Reed, 2002). Coastal Louisiana is a microtidal region with an approximate mean tidal range of 0.43 m (Coleman and Wright, 1975). Reed (1989) determined that this limited tidal range does not account for the majority of inorganic sediment input to marshes. Instead, moderate frequency occurrence storm events are responsible for the greater part of mineral sediment deposition (Reed, 1989).

The establishment of marsh ecosystems on these mineral substrates causes organic inputs of peat and roots to become increasingly important to land maintenance, while mineral sediments continue to play a significant role during periodic flood events (Reed, 2002). However, the specific role of organic contributions remains poorly understood. In determining marsh accretion rates in coastal Louisiana, Hatton et al. (1983) noted an approximately constant mass of organic carbon in all the soils they tested. This finding begs an answer as to whether or not volume of organic matter was also constant. Various research efforts have noted seasonal fluctuations – or the absence of – with respect to biomass allocation between above and below-ground structures (Schubauer and Hopkinson, 1984; Dame and Kenny, 1986; Reed and Cahoon, 1992). While investigating a salt marsh system in Georgia, Schubauer and Hopkinson (1984) noted seasonal fluctuations in biomass allocation for the species *Spartina alterniflora* that was not present for the same species in the Louisiana salt marsh system examined by Reed and Cahoon (1992). Also in Louisiana marshes, White et al. (1978) and Reed and Cahoon (1992) showed that below-ground biomass and standing crop production varied during two sample seasons. Reed and Cahoon (1992) also found that elevation had fluctuating levels of influence on below-ground biomass production during two years of sampling. In a laboratory-scale study conducted on macrophytes native to the Florida Everglades, Edwards et al. (2003) found that plants exposed to a water depth of 54 cm produced less total biomass and greater aboveground biomass relative to belowground when compared to plants exposed to a water depth of 7 cm. Conflicting results obtained by independent researchers and variations in influential significance of a single variable acquired in one study confirm the need for further research to properly understand the function of organic matter with respect to accretion.

The inputs of inorganic and organic sediments work to balance the affects of erosion on the marsh platform surface and relative sea-level rise (RSLR). RSLR consists of the combined influences of global and local factors contributing toward local changes in sea-level elevation. Global factors are governed by eustatic sea-level fluctuations primarily arising from thermal expansion of ocean waters and glacial meltwater entering the ocean while local factors consist predominantly of subsidence. Southeastern Louisiana is characterized by measured rates of relatively high RSLR. Using radiometric dating techniques, Frazier (1967) calculated a rate of RSLR of 1.4 mm/yr during the last 425 years. The overwhelming influence of subsidence acting on geologically young alluvial deposits gives rise to contemporary RSLR rates ranging from 9.3 to 23 mm/yr during the last century (Penland and Ramsey, 1990; Morton et al., 2002; Morton et al., 2003). Given that land loss occurs temporally on the order of years to decades (see Figure 1.1), the more recent and higher rates prove to be more relevant to this research.

As a delta lobe continues to build seaward, the active river channel will eventually become hydraulically inefficient. At this time, the river will avulse, or switch channels, in favor of a more efficient route to the ocean where the cycle of delta lobe progradation and degradation will repeat.

The influences and feedback mechanisms of marsh vegetation described above often slow or reverse the events of delta lobe deterioration and land loss associated with abandoned river channels. Nevertheless, delta degradation will occur if the actions of subsidence and erosion overwhelm the processes of accretion (Penland et al., 1991). This results in the reworking of sediments causing land loss, as well as the creation of such features as barrier islands and offshore shoals (Penland et al., 1988).

For the duration of the current sea-level stillstand, the net relationship between delta lobe construction and degradation outlined above has been one of general progradation for the Louisiana delta plain (Gagliano et al., 1981). However, the recent actions of humans during the last century operating in conjunction with a regionally high rate of RSLR have worked to reverse this trend (Gagliano et al., 1981; Britsch and Dunbar, 1993; Penland et al., 1990). This turnaround has grave implications on the benefits provided by this marsh system which include, storm protection, wildlife habitat and nursery, and water purification.

Organized restoration efforts to stop, and ideally reverse, coastal land loss in southeastern Louisiana began during the 1990s. Current strategies, outlined in the Coast 2050 plan, seek to alleviate this problem by restoring specific ecosystem functions on a regional landscape scale. The plan recognizes the importance of incorporating ecological aspects of the system into attempts at achieving surface accretion, gradients of diversity, and the maintenance of system linkages (see Reed and Wilson, 2004 for a detailed discussion). The value of the inherent ecological processes of these systems with respect to restoration is gaining increased recognition.

This has resulted in a large inflow of scientific research seeking to elucidate the interactions among processes affecting subsidence and RSLR. A significant component of these interactions is the role of flooding. Subsidence and RSLR result in increased levels of flooding compromising the sustainability of marshes. As a result, the maintenance of marsh ecosystems is critically dependent on vertical accretion to counteract the influence of subsidence and RSLR. Successful marsh restoration, therefore, requires an understanding of the impact of flooding on contributions to vertical accretion.

1.3 Marsh-Scale Interactions

1.3.1 Contributions to Accretion

The existence of marshes on sedimentary deltaic formations increases the stability of the system through several feedback processes, the results of which are contributions to accretion. The presence of vegetation increases frictional resistance to surface-flow of sediment-rich floodwaters passing through the system (Darke and Megonigal, 2003; Nuemeier and Ciavola, 2004). The consequence is a decrease in water velocity. At diminished rates of flow, these flood-waters may no longer be able to maintain their initial load of mineral sediment in suspension causing deposition on the marsh surface. Also, the vertical erosive capacity of flowing surface water is lessened by this reduction in flow velocity (Nuemeier and Ciavola, 2004). Senescent aboveground biomass will also fall to the marsh surface providing a second, though less significant due to storm and tidal flushing, influx of substrate. Below the ground surface, root and rhizome production provide substantial contributions toward maintaining an ideal surface elevation for vegetation within the tidal range (Nyman et al., 1990). Marsh substrates often consist of greater than 35% to 70% organic matter (Cavatorta et al., 2003; DeLaune and Pezeshki 2003). While investigating a marsh complex in California, Culberson et al. (2004) determined that measured rates for the deposition of sediments originating outside the system were unable to maintain the surface elevation. They concluded that local organic productivity supplied the necessary substrate source. Belowground structures also work to bind sediments together limiting the erosive effects of waves and flood waters (van Eerdt, 1985).

1.3.2 Factors Influencing Frequency and Duration of Flooding

The frequency and duration of flooding experienced by a marsh system are influenced by a multitude of factors. Mendelssohn and Morris (2000) provide and excellent summary regarding the effect of proximity to tidal channels shown in Figure 1.2. As stated by these authors, the frequency of flooding decreases while waterlogging, or prolonged saturation, increases with increasing distance from a tidal channel. Reed and Cahoon (1992) established the importance of microtopographic marsh elevation with regard to hydroperiod. Their results, obtained in a coastal marsh of Louisiana, showed that a difference in elevation as small as 4 cm provided significant differences in flooding duration. Other natural factors impacting flooding regime include tidal range, climate, and fluctuating seasonal conditions (Mitsch and Gosselink, 2000).

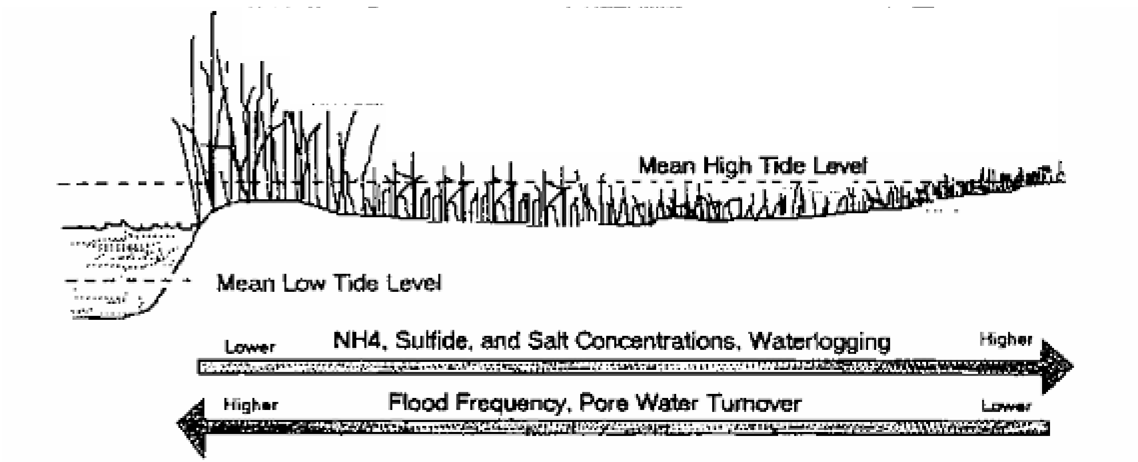


Figure 1.2: Effects of proximity to a tidal channel on flooding characteristics (modified from Mendelssohn and Morris, 2000)

The activities of humans also contribute to variations in flooding characteristics. Ecosystem modifications, such as dams, levees, and spoilbanks, affect hydrological dynamics by reducing tidal exchanges while increasing soil waterlogging (DeLaune et al., 2003). DeLaune et al. (2003) also illustrated the potential positive impacts associated with increased flooding from freshwater diversions. These authors suggested that the input of freshwater “reduces the mineral sediment requirement for growth of marsh vegetation” (p. 659). The exploitation of this relationship promotes marsh vegetation growth helping to reduce or reverse rates of land loss. Figure 1.3 illustrates the impacts of hydrologic modifications.

Warren and Niering (1993) recognized that alterations in soil geochemistry resulting from increased flooding and waterlogging give rise to shifts in marsh vegetative communities. In their examination of a marsh complex in Connecticut, they determined that flood-stressed population changes consisted of the replacement of *Spartina patens* and *Juncus gerardi* with forbs and stunted *S. alterniflora.* They observed that the resultant vegetative communities exhibited decreases in primary productivity, sediment trapping, peat production, and accretion. These hindrances reduce the sustainability of a marsh ultimately leading to land loss.

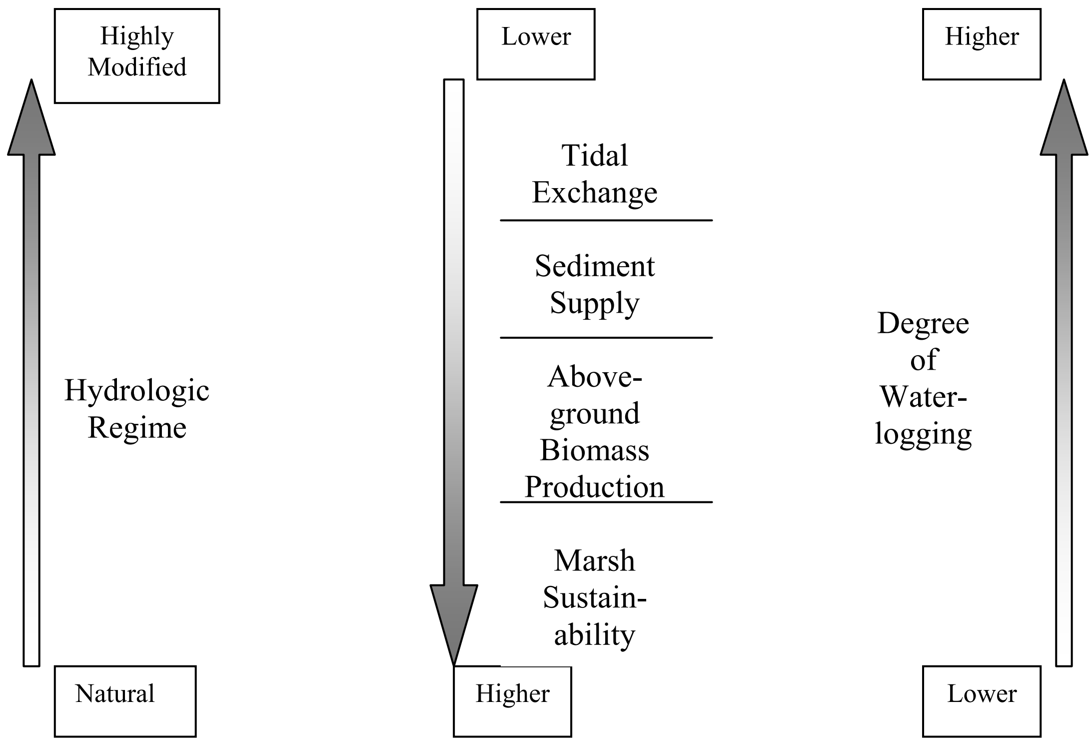


Figure 1.3: Impacts of modifications to the natural hydrologic regime of a marsh.

1.3.3 Conditions Resulting from Increased Flooding

Increased levels and durations of flooding, caused by the factors described above, result in various marsh system alterations. Previous research efforts have determined that increased waterlogging correlates with decreased sediment supply and increased salinity (DeLaune et al., 2003). Hypoxic conditions have also been shown to accompany soils flooded at 3 to 5 cm above the soil surface (Koch and Mendelssohn, 1989). In addition, a resultant decrease in redox potential (Eh) increases levels of reduced inorganic compounds such as sulfides, ammonium, and ferrous bearing molecules (Mendelssohn and McKee, 1988; Koch and Mendelssohn, 1989; Pezeshki et al., 1991; Mendelssohn and Morris, 2000). Jackson et al. (1981) and Pezeshki et al. (1991 and 1993) demonstrated that increased soil concentrations of ethylene may also be observed.

1.3.4 Flooding Effects on Marsh Vegetation

Depending on the frequency and duration, flood-waters can provide positive or negative influences on marsh vegetation. Burdick and Mendelssohn (1987) and Burdick (1989) showed in several experiments that increased levels of flooding duration and waterlogging resulted in the decrease of specific gravity for *S. patens* roots. This may correlate to increased root volume which suggests increased contributions to accretion. These authors, however, were expressly using specific gravity measurements as an indirect indicator for aerenchyma production and did not specifically explore the volumetric implications regarding accretion. Burdick (1989) also showed that heightened levels of flooding duration increased root mortality suggesting that an optimal flooding regime exists for individual species.

According to a study conducted by Jackson et al. (1981) focusing on *Zea mays*, increased ethylene concentrations were found in flooded wetland soils resulting from increased ethylene production in the roots of marsh vegetation. Their results also suggested that an increased level of ethylene reduces vegetative growth by slowing root extension, and inhibiting leaf extension and seminal root elongation. In an attempt to mitigate the impacts of ethylene *Z. mays* improved aeration by increasing adventitious root development and aerenchyma formation. An increased level of oxygen within roots diminishes anaerobic metabolic demands, a process that results in the production of ethylene. Results obtained by Pezeshki et al. (1991, 1993) showed that decreased Eh levels enhanced aerenchyma formation and root porosity in *S. patens*. These impacts reduced the photosynthetic activity of this species despite the morphological root changes. Maricle and Lee (2002) used image analysis software to render digital images of live root cross-sections for *S. alterniflora* and *S. anglica*. They determined that exposure to flooded soil conditions also resulted in increased aerenchyma formation in the species *S. alterniflora*. However, they measured no subsequent effect on oxygen transport. They concluded that increases in aerenchyma worked to reduce the volume of respiring tissue, thereby decreasing metabolic demands. Again, these authors were specifically interested in the effects of ethylene on anatomical root structure, specifically aerenchyma formation. Examining total volume fluctuations of roots was outside the scope of their study.

While investigating the impact of increased flooding on *S. alterniflora*, studies by Mendelssohn et al. (1981), Koch and Mendelssohn (1989), and Koch et al. (1990) determined that sulfide accumulation inhibited nitrogen uptake and anoxic metabolic pathways decreasing biomass production. Mendelssohn and McKee (1988) arrived at similar conclusions in a field study that involved transplanting streamside swards of *S. alterniflora* into the more waterlogged inland section of a marsh. Interestingly, reverse transplantations alleviated stresses, stimulating increased levels of growth as measured with respect to aboveground biomass.

1.4 Research Needs

Previous research efforts have identified several noteworthy relationships. The hypoxic and geochemical soil conditions arising from increased and prolonged flooding lead to (1) initial increases in anaerobic metabolic activity followed by inhibition of energy production, (2) reduced aboveground biomass production, (3) decreased nutrient uptake, (4) increased aerenchyma formation, and (5) decreased specific gravity of roots. At the same time, the majority of prior research treats organic matter on a mass basis. Those that do examine specific gravity and porosity variations are primarily lab-scale experiments or refrain from quantifying total organic volume fluctuations. The association of decreased biomass with decreased specific gravity, and hence increased volume, lends further support to the importance of volume-based field measurements of organic production when concerned with vertical land building, which is quantified by the volume of soil produced not by the weight of that soil. Figure 1.4 establishes a proposed conceptual model of the interactions relating flooding to root volume. The construction of this model is based on the previous lab-scale research concerning such species as *S. alterniflora, S. patens, S. anglica, Z. mays,* etc. presented above, though the results obtained during this study specifically focus on natural stands of *S. alterniflora*. The signs for the arrows simply indicate whether the relationship between boxes is directly or inversely proportional. For example, a negative sign between marsh surface elevation and flooding duration indicates that as surface elevation increases flooding duration decreases and vice versa.

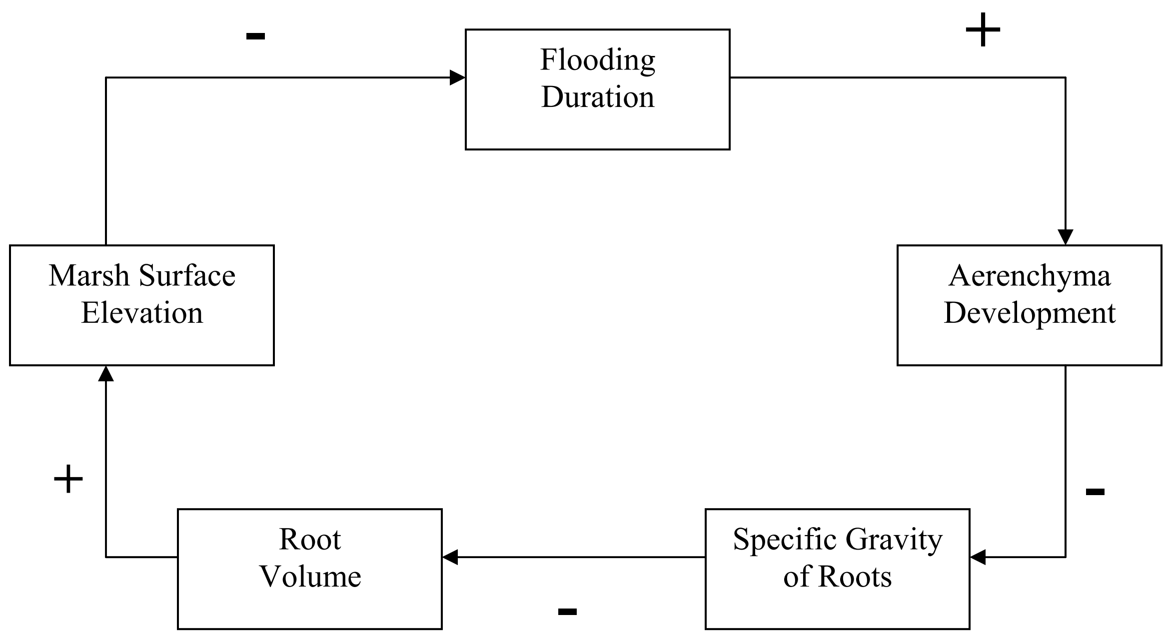


Figure 1.4: Hypothesized conceptual model relating flooding regime, root specific gravity, and accretion in a natural salt marsh.

The research presented here seeks to determine the applicability of the lab-based conceptual model (Figure 1.4) to natural field settings by investigating the process interactions among % time of flooding duration, environmental stresses, and live root specific gravity. Landscape variability was examined spatially and temporally to gain further insight regarding the impacts of variations in rate of RSLR, freshwater input, season, flooding regime, and soil biogeochemistry.

It was hypothesized that differences in regional characteristics at the coast-scale of observation, such as rate of RSLR and land loss (see Figure 1.1), would correlate to predictable modifications of live root specific gravity. Marshes in regions experiencing relatively higher rates of RSLR and land loss (e.g., Terrebonne Basin) were expected to experience greater flooding durations and associated environmental stresses, such as lower soil redox potential and higher sulfide concentrations, than marshes in areas with lower rates of RSLR and land loss (e.g., St. Bernard delta lobe). As suggested in the proposed conceptual model of Figure 1.4, a possible vegetative response to greater flooding stresses is to decrease the specific gravity of live roots through increased aerenchyma production, thereby, possibly increasing root volume and marsh surface elevation assuming that root biomass is constant. Thus, regions with higher rates of

RSLR and land loss would have roots with lower specific gravity values when compared to regions with lower rates of RSLR and land loss.

Accumulation of sulfide within marsh soils has been reported to significantly reduce root biomass of *S. alterniflora* (Koch and Mendelssohn, 1989). As a result, it was reasoned that higher rates of RSLR and land loss, which are hypothesized to be indicators of such stresses as sulfide concentration and flooding duration, would correspond to decreased belowground biomass production leading to lower soil organic matter content. Having reasoned that increased environmental stress is expected to correspond to lower soil organic matter content as well as lower root specific gravity values it follows that marsh soils with lower organic matter contents should also contain roots having lower specific gravity values. For example, it is anticipated that the higher rates of RSLR and land loss observed in the Terrebonne Basin (as noted by Britsch and Dunbar, 1993; Barras et al., 2003) will correlate to greater environmental stresses, soils with lower organic matter content and roots with lower specific gravity values than would be found in the St. Bernard region which experiences relatively lower rates of RSLR and land loss.

Ultimately, what is proposed here is that in order to maintain an ideal surface elevation within a tidal regime vegetation attempts to maximize the volume of soil occupied by roots. This may be accomplished in two ways, either by producing more roots which individually occupy less volume or by producing roots which occupy greater volumes though in less quantity.

Finally, it was hypothesized that temporal variations in environmental stresses would directly correlate to alterations of root specific gravity values (i.e., increasing stresses through time would result in lower specific gravity values and vice versa). As noted in Figure 1.1, weeks, months, or years of data are required to make generalizations at the plant-scale of observation. Time constraints associated with a master’s thesis research project permitted sample collection during a single growing season for this study.

Chapter Two: Methodology

2.1 Study Sites

The selection of site locations was guided by several characteristics. First, it was desired to locate sites in regions that were expected to experience different flooding regimes. Using regional trends for rates of relative sea-level rise (RSLR) and land loss as indicators of flooding regime, sites were located to allow for the comparison of a region with high flooding durations (e.g., Terrebonne Basin) with a region that experienced low flooding durations (e.g., St. Bernard delta lobe). Secondly, to investigate temporal variations it was desired to locate a site that experienced a significant fluctuation in environmental stresses through time. Ultimately, this study was conducted at three locations within the Mississippi River delta plain along the southeastern coast of Louisiana (see Figure 2.1). All sites selected exhibited monotypic stands of *Spartina alterniflora* that constituted at least 90% of the vegetative cover as noted by visual inspection.

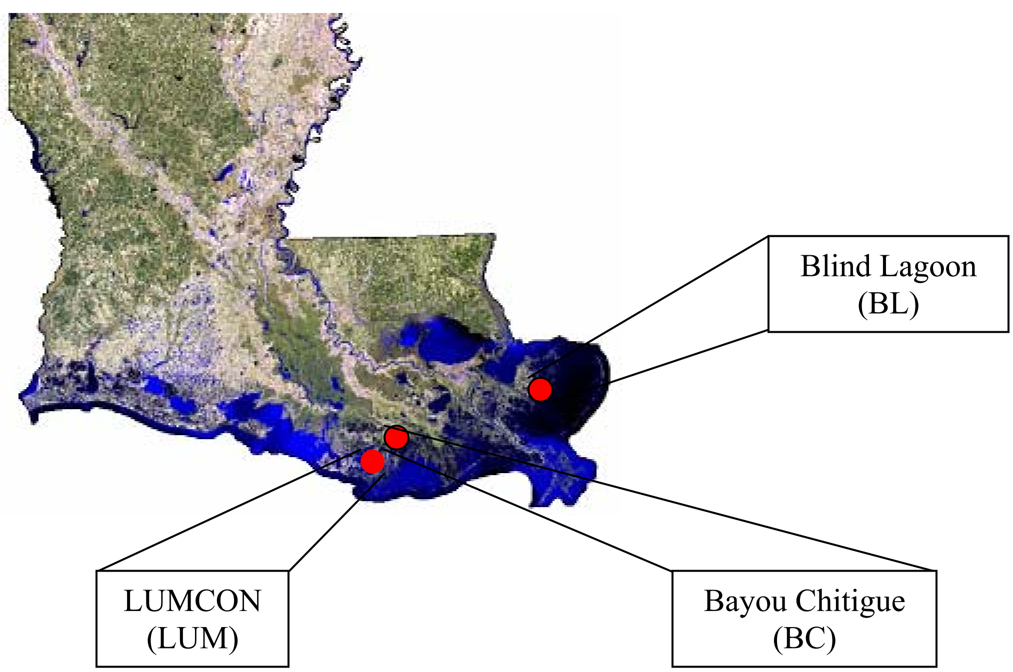


Figure 2.1: Approximate location of field sites along the southeastern coast of Louisiana.

Two of the sites were situated in Terrebonne Basin. Marsh establishment in this region originated with the deposition of the Lafourche delta lobe of the Mississippi River delta complex. The area is characterized by relatively high rates of subsidence and sea-level rise contributing to a relatively high rate of RSLR, which in this region has been approximated at 1.09 cm/yr (Penland and Ramsey, 1990). Relatively high rates of land loss are also characteristic of this area. Land loss rates in this region are estimated at 9.4 sq. mi/yr during 1978 to 2000 (Barras et al., 2003). The vegetation in these salt marshes is largely dominated by the macrophyte *S. alterniflora* while communities of *Juncus roemericanus* and *Distichlis spicata* are also present.

Due to its close proximity to the Louisiana Universities Marine Consortium (LUMCON) Marine Center in Cocodrie, LA the first sample site is referred to hereafter as the LUM site (see Figure 2.1). Located west of Bayou Petit Caillou, the LUM site experiences a significant freshwater input from the nearby Houma navigation canal during spring. The monitoring station located at the LUMCON Marine Center maintains a record of salinity values. These data illustrate the general trends of fresh- and saltwater influence at the LUM site (see Figure 2.2). It was hypothesized that the nature of the freshwater input at LUM would provide insight concerning the impacts of temporal fluctuations in environmental stresses.

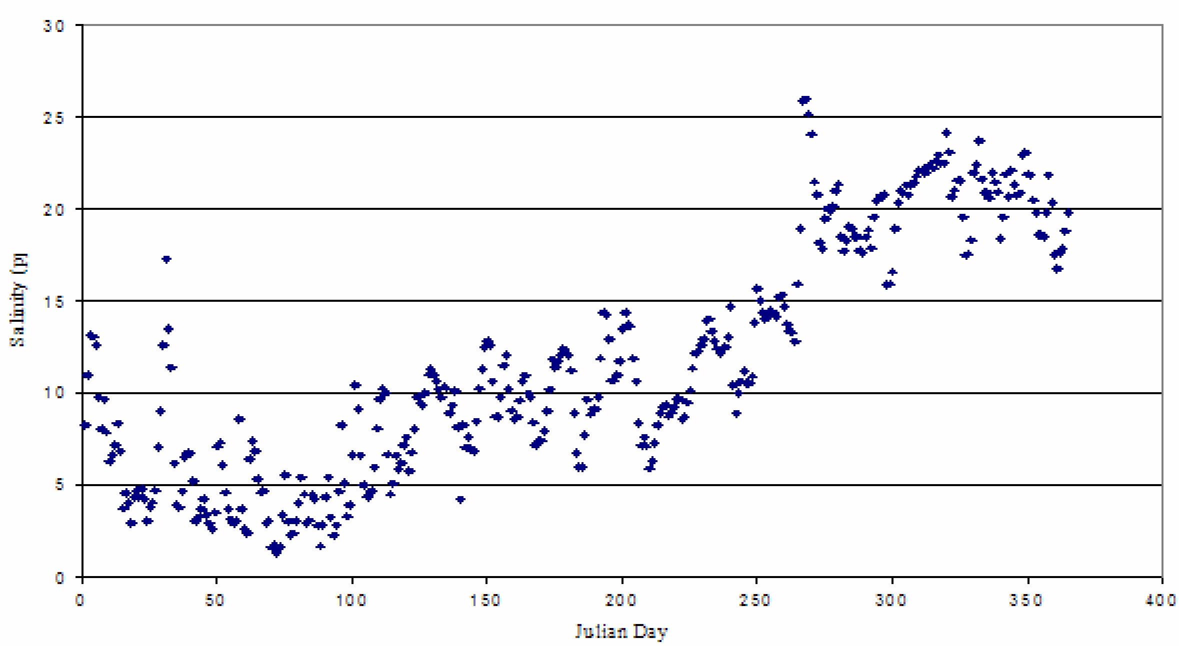


Figure 2.2: Average daily salinity values at LUM for 2005 (reported by LUMCON Marine Center).

The second site in the Terrebonne Basin was located east of Bayou Petit Caillou near a hot spot of marsh loss along Bayou Chitigue resulting in its being named the BC site (see Figure 2.1). It was believed that the high rates of RSLR and land loss in this region would relate to a relatively high degree of flooding duration at this site.

The final site was located in St. Bernard Parish within Breton Sound. Marsh development in this area occurred in conjunction with the deposition of the St. Bernard delta lobe of the Mississippi River delta complex. This region is more stable than the Terrebonne coastal marshes with relatively lower rates of subsidence, sea-level rise, and land loss. This results in a lower rate of RSLR, with estimates ranging between 0.36 and 0.45 cm/yr for this area (Penland and Ramsey, 1990). Rates of land loss for the St. Bernard region are approximated at 4.5 sq. mi/yr from 1978 to 2000 (Barras et al., 2003). The vegetation composition of these marshes primarily consists of *S. alterniflora*, *J. roemericanus*, and *D. spicata*. This sampling location was located in close proximity to a natural open water body, Blind Lagoon, whose name was also adopted for the site. Hereafter, this site will be referred to as the BL site (see Figure 2.1). Table 2.1 highlights the key differences and similarities among the three sites.

Table 2.1: Regional characteristics of the sampling site locations (citations are located within the text).

Site ID	Rate of RSLR	Relative Rate of Land Loss	Presence of Substantial Freshwater Input
LUM	~ 1.09 cm/yr	~ 9.4 sq. mi/yr	During Spring
BC	~ 1.09 cm/yr	~ 9.4 sq. mi/yr	No
BL	~ 0.36 – 0.45 cm/yr	~ 4.5 sq. mi/yr	No

2.2 Hypotheses

Collecting data from BC, BL, and LUM allowed for the testing of several hypotheses concerning process interactions and impacts of landscape variation. The research presented here sought to address the following hypotheses:

H1: Increased percent time of flooding duration results in decreased specific gravity of live roots for *S. alterniflora*.

H2: Flooding and associated stresses will be greater at BC than at BL correlating to lower root specific gravities for BC.

H3: The percent organic matter of the soil will be lower at BC than at BL corresponding to lower root specific gravities for BC.

H4: Flooding and associated stresses will be greater at BC than at LUM correlating to lower root specific gravities for BC.

H5: The percent organic matter of the soil will be lower at BC than at LUM corresponding to lower root specific gravities for BC than LUM.

H6: As a result of the diminished influence of benefits derived from the waning freshwater input at LUM, stresses will increase from the first sample session in May to the third sample session in November. This will correlate to root specific gravities that progressively decrease from May to November.

2.3 Experimental Design

It was decided that twelve plots would be laid out at each of the three study sites in an attempt to balance the desire to capture variability within data sets and the ability to feasibly process collected samples before live root integrity was compromised. Using a split-plot design, the plots were arranged in two transect zones parallel to the shore of the closest tidal creek. The first transect, plots 1 through 6, was located along the natural levee of the nearby channel, while the second transect, plots 7 through 12, was located within the inner marsh zone, an area of relatively lower elevation. The streamside and inner marsh placements of these two zones followed a flooding gradient within each site allowing for further investigation into the impacts of hydroperiod variation (refer to Figure 1.2 and the accompanying discussion in chapter 1 concerning the effects of proximity to a tidal channel on flooding characteristics). Two distinct height forms of *S. alterniflora* are found along the Gulf of Mexico coast. As noted by Mendelssohn and Morris (2000), streamside stands are generally taller than those found further inland. Visual inspection of the plant community at the sampling sites allowed for transect placement within the desired region of the marsh according to stand height. Surveying the elevation of the sites allowed each plot to be placed so that fluctuations in plot elevation were minimized within a given zone. All site surveys were conducted using a KERN quick-set level placed upon a stationary tripod and a telescoping rod accurate to one centimeter. The elevation of each corner of all twelve plots at BC, BL, and LUM was determined in this fashion using the surveyed elevation of the respective water level sensor (discussed in section 2.4.1) as a local datum. Figure 2.3 illustrates the plot layout at the BL site (plot layout maps for BC and LUM are located in the appendix).

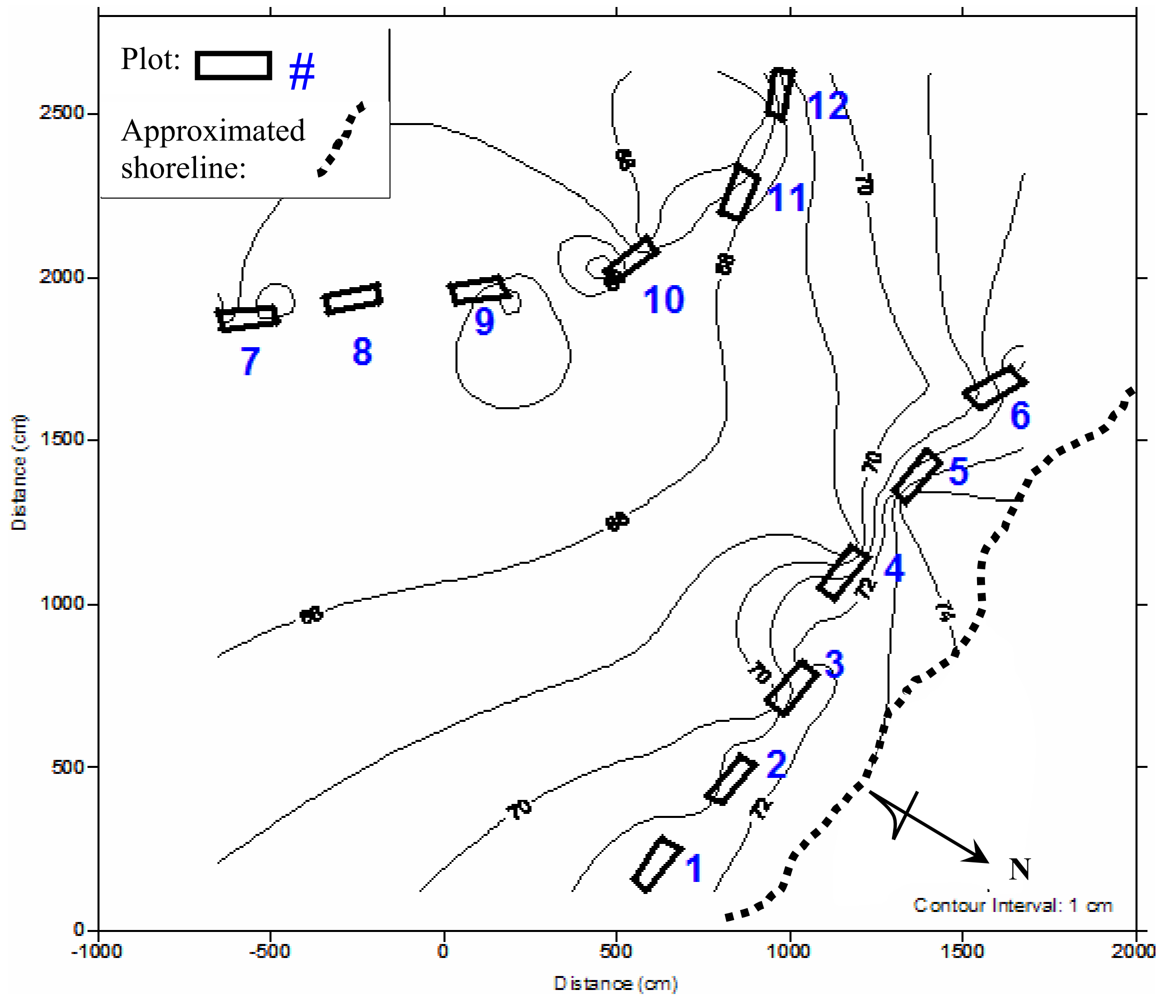


Figure 2.3: Surfer 8 plot of map view of BL plot layout using surveyed elevation of respective water level sensor as a local datum.

Each plot is 50 cm x 150 cm and is divided into three subplots (see Figure 2.4). The labels within each subplot refer to the time of sampling for that area. Subplot I was sampled during 5/24/05 – 6/6/05, subplot II was sampled during 8/17/05 – 8/23/05, and subplot III was sampled on 11/29/05. The assigned subplot labels were randomly selected for each plot. Soil organic content and live root specific gravity measurements were taken from each subplot at the assigned time.

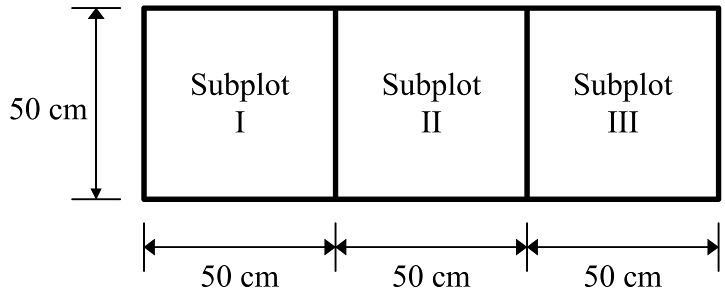


Figure 2.4: Map view of a single plot (I: May sampling; II: August sampling; III: November sampling).

The occurrence of hurricanes Katrina and Rita resulted in the loss of soil organic content data collected during the August sampling session from sites BC, LUM, and BL. In addition, the root specific gravity data from the August sampling session was lost for sites BC and BL. The storms also negatively impacted the accessibility of BL and instrumentation located at BC. This prevented sampling these two sites during the third session in November.

2.4 Field and Laboratory Methods

2.4.1 Flooding Regime

Water level elevation was determined using water level gauges located at each of the sampling sites. Differences in elevation between the plot and the water level through time allowed for calculation of approximate flooding durations. Recognized sources of error associated with this method of determining hydroperiod include the influence of ponding, fluctuations in surface water runoff rates, and variations in hydraulic conductivity of the soil.

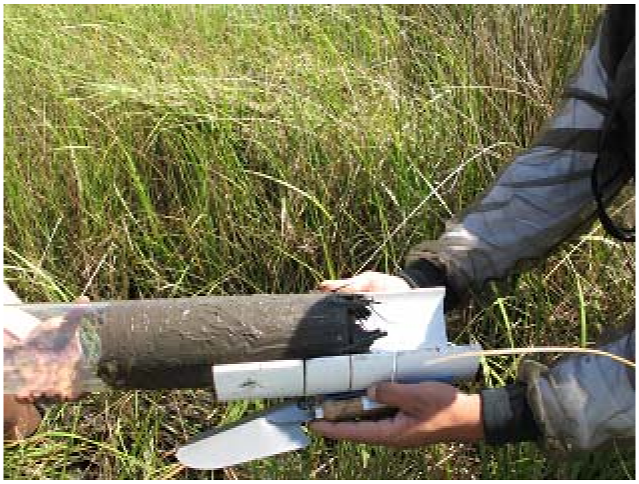
A Keller series 169 submersible pressure transducer and a Campbell Scientific CR10X datalogger were installed at the BL site on April 20, 2005. Calibration of the sensor was performed prior to installation at BL to ensure the accuracy of recorded data. The datalogger was affixed to a wooden post which was then driven into the marsh platform approximately thirty feet from the nearest tidal creek. The pressure transducer was fastened to a ten foot section of PVC pipe which was inserted into the bed of the nearby tidal creek at a location where the sensor would remain submerged at all times. Once installed, the elevation of the sensor was surveyed and adopted as the local datum for the plot elevations at the BL site. A length of cable connected the sensor to the datalogger. The cable was protected with a sleeve of flexible hose and buried just below the marsh surface.

A monitoring station was already functional at the LUMCON Marine Center prior to the start of this study. Included in the list of parameters monitored by this station is water level, which is reported using NAVD88 as the datum. The site elevation survey at LUM allowed the water level reported with respect to the NAVD88 datum by LUMCON to be converted with respect to the local sensor elevation. This conversion of datums provided actual water height values with respect to the water level sensor. Knowing both the actual water height and the surveyed plot elevations at LUM with respect to the sensor elevation allowed for the calculation of flooding duration at this site.

Water level data at the BC site were recorded using an Infinities USA, Inc Model 220 Ultrasonic water level datalogger maintained by the US Geological Survey (USGS) prior to the start of this study. Water level data was recorded with respect to a local datum. The site elevation survey at BC allowed for the application of the water level data reported by the USGS monitoring station.

2.4.2 Collection and Analysis of Soil Cores

Soil cores were collected from all subplots during the appropriate sampling session. Cores 10 cm in diameter were taken using a piston-type Hargis corer to a depth of 15 cm from the marsh surface (Hargis and Twilley, 1994). A sharp blade at the end of the corer allows for insertion into the soil with minimal compaction (see Figures 2.5 and 2.6).



Figures 2.5 (left) and 2.6 (right): The Hargis corer and a soil core within the Hargis corer.

Following extraction, cores were extruded onto a tray in the field (as shown in Figure 2.6). Using a hacksaw, cores were then divided equally into three 5 cm segments corresponding to the soil depths 0 – 5 cm, 5 – 10 cm, and 10 – 15 cm from the marsh surface. Each of these segments were cut into equal halves, placed in sample bags, and kept on ice until being placed in a refrigerator at 3-4^{0}C to maintain the integrity of the live roots and await further processing. One of the halves of each 5 cm core segment was used to determine the organic content of the soil. The other half of each core segment was used to analyze the specific gravity of the live roots.

2.4.2.1 Percent organic matter of substrate

Water content of the soil was determined for half of each 5 cm core segment. Each of these samples was weighed on a scale accurate to one tenth of a gram. They were then placed in an oven to dry at 60^{0}C until all moisture was removed and a constant weight measurement could be obtained. The sample was then reweighed. Subtracting this value from the weight obtained prior to drying provided the weight of the water within a sample.

Following analysis for water content, samples were ground into a powder using a mortar and pestle. Organic matter content of a given sample was determined using the loss on ignition (LOI) procedure guidelines established by Heiri et al. (2001).

Crucibles were cleaned, dried, and weighed. A portion of the homogeneously powdered sample was placed into a crucible and reweighed. This was repeated in triplicate for each sample. Care was taken to maintain uniformity of sample size within the crucibles. The samples were placed into a muffle oven for four hours at 550^{0}C. Samples were then removed from the oven and allowed to cool to room temperature at which time they were reweighed. The percent organic matter of a given sample was determined using Equation 1:

$$LOI_{550} = ((DW_{60} – DW_{550}) / DW_{60}) * 100 \qquad (1)$$

Where, LOI_{550} is the organic matter content of the sample given as a percentage, DW_{60} is the dry weight of the sample prior to combustion, and DW_{550} is the weight of the sample following combustion.

2.4.3 Root Specific Gravity

The half of each core segment not used for analysis in section 2.4.1.1 was used to determine the specific gravity of the live roots within that segment. All sediments were gently rinsed away from the roots. Live roots were then segregated from dead roots according to color, transparency, and tensile strength. Live roots tend to be white, opaque, and more elastic when compared with dead roots (Rodgers et al., 2004). All sediment and detritus was thoroughly rinsed from the live roots, which were then gently patted dry. Specific gravity of these roots was then determined using a pycnometer, a glass flask of standardized volume with a glass stopper ensuring accurate volume measurement (see Figure 2.7), according to the method described by Burdick (1989).

To determine the specific gravity of a substance, a pycnometer is first filled with water and weighed. With a density of 1 g/cm^3, using water simplifies calculations. The substance with the unknown specific gravity (in this case the roots) is then placed in the pycnometer displacing a certain volume of water. The pycnometer is then reweighed. Volume remains constant and cancels out of the calculation. Knowing the two mass values and the density of water allows for the determination of the density of the unknown. The unknown specific gravity can then be calculated from the ratio of these two densities.

By definition, Equation 2 then relates volume to specific gravity:

$$SG = \rho_s / \rho_{water} = m_s / (V_s * \rho_{water}) \qquad (2)$$

Where, SG is the specific gravity of a given substance (in this case the live roots), ρ_s is the density of that substance, m_s is the mass of that substance, V_s is the volume of that substance, and ρ_{water} is the density of water (1 g/cm^3). From the above relationship it can be determined that a decrease in specific gravity requires an increase in volume when all other variables remain constant.

Figure 2.7: A pycnometer filled with water and live roots.

A clean 25 ml pycnometer was filled with deionized water and weighed. 0.1 to 0.3 g of live roots were then rinsed clean, gently pat dry, weighed and placed in the pycnometer which was also dried (to ensure water not contained within the pycnometer was not included in the measurement) and reweighed. Care was taken to minimize altering root volumes while patting dry (as could have occurred if applied pressure was too great). Specific gravity of the roots was determined according to Equation 3:

$$SG = R / (P + R - PR) \qquad (3)$$

Where, SG is the specific gravity of the live roots, R is the mass of the live roots, P is the mass of the water-filled pycnometer, and PR is the mass of the pycnometer containing roots and water.

2.4.4 Collection and Analysis of Interstitial Pore Water

All interstitial pore water measurements were taken during the first sampling session in close proximity to, but not actually within, respective plots. Readings taken include soil redox potential (Eh), sulfide concentration, pH, and Salinity.

Eh measurements were taken in triplicate at each plot. Measurements were taken at 2 cm and 15 cm depths below the soil surface using brightened platinum electrodes and a reference calomel electrode (+244 mV was added to the meter reading to obtain Eh). Probes were allowed to equilibrate (~10 – 15 minutes) prior to taking a reading.

Sulfides, pH, and salinity were collected with the aid of an interstitial pore water sipper apparatus (McKee et al., 1988; Kaller, 2003). The interstitial sipper setup, shown in Figure 2.8, consists of a syringe connected to a perforated plastic tube. This tube was inserted 15 cm below the surface of the marsh to collect pore water present in the active root zone. A suction cup located 15 cm from the end of the perforated tube ensured that the tube was consistently inserted to the desired depth and minimized surface flood waters, when present, from being collected. Samples were taken within 0.25 m of the core location discussed in section 2.4.2.

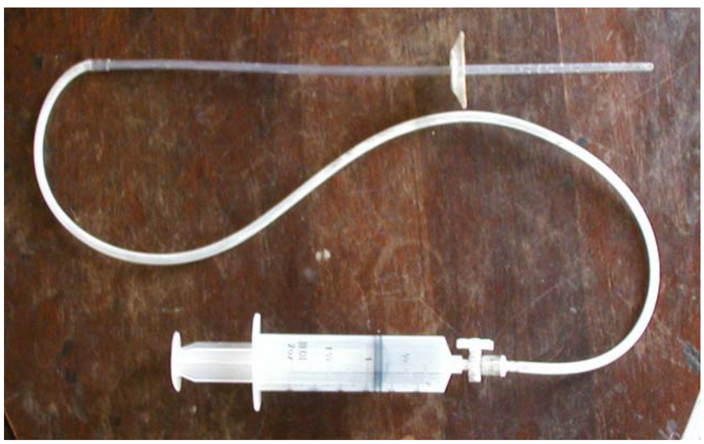


Figure 2.8: The interstitial pore water sipper apparatus.

An initial 5 ml of pore water was used to rinse the syringe prior to the collection of samples at each plot. 3 ml of pore water were then extracted and placed in a vial containing an equal volume of antioxidant buffer. The samples collected in this manner were kept at room temperature and processed within 24 hours for sulfide concentration. Sulfide standards were prepared in the laboratory using 0.75 g of sodium sulfide crystals and 25 ml of antioxidant buffer. This solution was brought to a volume of 100 ml with deoxygenated water that had been bubbled through with nitrogen for ten minutes. Performing serial dilutions with this solution provided standards with sulfide concentrations of 1000 ppm, 100 ppm, 10 ppm, 1 ppm, and 0.1 ppm. A calibration curve was constructed from the Eh values obtained from these standards. Eh values of the samples collected in the field were determined and plotted along the calibration curve to determine sulfide concentration. Sulfide values were ascertained using a Hanna

Instruments model HI 9025 microcomputer pH/mV meter and Corning high-stability reference sulfide probe. The probe was rinsed with deionized water between measurements to eliminate cross-contamination of samples.

Following extraction of the sample to be tested for sulfide concentration, 10 ml of pore water were collected with the sipper apparatus to determine pH and salinity levels at each plot. The sample was placed into a 20 ml scintillation vial. Values of pH were established using a Hanna Instruments model HI 9025 microcomputer pH/mV meter, while salinity was determined with a YSI model EC 300 salinity meter.

2.4.5 Collection and Analysis of Aboveground Biomass

The procedure for collecting aboveground biomass is based on the guidelines set forth by Mack (2004). Aboveground biomass was collected from all subplots during the appropriate sampling session (refer to Figure 2.4). A 0.1 m^2 quadrat was laid down within the subplot. Hand shears were used to harvest to ground level all plants rooted within that 0.1 m^2 quadrat (see Figure 2.9).

Figure 2.9: Harvesting of aboveground biomass.

Harvested vegetation was then placed into paper sample bags and labeled. Sample bags were stored loosely to aid with drying until oven drying was able to take place. Oven drying consisted of placing the paper sample bag with its contents into an oven at 60^0C until all moisture was removed and a constant weight measurement could be obtained (approximately one week). Once dry, a sample bag and its contents were weighed on a scale accurate to one tenth of a gram. The sample bag was emptied and reweighed. Standing biomass was obtained by subtracting the bag weight from the total weight. Units were then converted to obtain a measurement for aboveground biomass in g/m^2.

2.4.6 Statistical Analyses

Statistically significant differences were determined using analysis of variance (ANOVA, proc GLM) as a split-plot design with geographic location serving as the main plots. This was performed using the SAS (Statistical Analysis System) software package. Unless indicated otherwise, a 95% confidence interval ($\alpha = 0.05$) was used with site location, sample depth, zone, and date of sampling serving as categorical variables. Significant variance of repeated sampling dates was adjusted using the H-F (Huynh-Feldt) correction factor. Linear regressions were used to investigate the relationships among % time flooded, root specific gravity, organic matter content of the soil, and redox potential using Microsoft EXCEL 2002.

Chapter Three: Results and Discussion

The data collected further established the intricate nature of process interactions for the wetland ecosystems investigated. Complex relationships existed spatially and temporally. While this has resulted in the development of further questions concerning wetland function, the data collected do provide valuable information regarding the hypotheses posed.

3.1 Process Interactions: Revisiting the Conceptual Model

Hypothesis 1: Increased percent time of flooding duration (% TFD) results in decreased specific gravity of live roots for *Spartina alterniflora*.

Explicitly, the string of logic statements under scrutiny is as follows:

- ↑ % TFD ➔ ↑ stresses on vegetation.
- ↑ Stresses on vegetation ➔ ↑ aerenchyma production within live roots.
- ↑ Aerenchyma development ➔ ↓ specific gravity values for these roots.

The acceptance of this hypothesis requires validation for each of these interactions.

3.1.1 Percent Time of Flooding Duration and Soil Redox Potential

Soil redox potential (Eh) serves as a measure of electron availability for metabolic processes within a solution. Oxygen is used as an electron acceptor during aerobic respiration at Eh levels between +700 and +400 mV (Mitsch and Gosselink, 2000). When oxygen becomes depleted from soils, as occurs with the onset of flooding, Eh drops as stocks of alternate terminal electron acceptors, such as nitrate (NO_3^-), ferric iron (Fe^{3+}) and sulfate (SO_4^{2-}), are utilized and reduced. Decreased Eh values correlate to increased stresses on vegetation, including diminished or depleted supplies of available oxygen and nitrogen, as well as, the accumulation of phytotoxins, most notably hydrogen sulfide accruing from the reduction of sulfate (Mendelssohn and Morris, 2000). Saturated soils deficient in oxygen are also associated with the accumulation of ethylene, a gas produced by vegetation, which has been shown to inhibit seminal root elongation and growth (Jackson et al., 1981).

Percent time of flooding duration (% TFD) was calculated for 28 days (d), 21 d, 14 d, 7 d, 3 d, and 1 d prior to each sampling date. Eh values were measured at 2 cm and 15 cm below the marsh surface at each plot. The correlation between Eh and % TFD was strongest when % TFD was computed for the 28 days prior to sample collection. Combining the data obtained from BC, BL, and LUM, and performing linear regressions provided R^2 values of 0.19 and 0.10 for Eh sampling depths of 2 cm and 15 cm respectively (see Figures 3.1 and 3.2). Carrying out the same analysis when samples taken from BC, BL, and LUM were plotted independently of one another increased R^2 values, which ranged from 0.28 to 0.89 (see Figures 3.3 and 3.4). The removal of a single data point outlier from Figures 3.3 (depicting Eh readings taken at 2 cm) and 3.4 (depicting Eh readings taken at 15 cm) improved this R^2 range to 0.58 to 0.91. Recognizing that this correlates to a 37 % and 30 % shift in significance (for the two plots respectively) and that the data from plot 6 at the LUM site was the outlier for both graphs supports omission of these points. The increase in R^2 values when sites are considered independently of each other suggests the important influence of site specific characteristics in addition to flooding duration, such as the relative size of terminal electron acceptor stocks, in determining soil Eh. It can also be noted from Figures 3.3 and 3.4 that, within sites, the inner marsh zones were always flooded for longer durations and, subsequently, were more reduced than the streamside zones. All slopes were negative reinforcing the trend that increased % time of flooding duration results in decreased soil Eh.

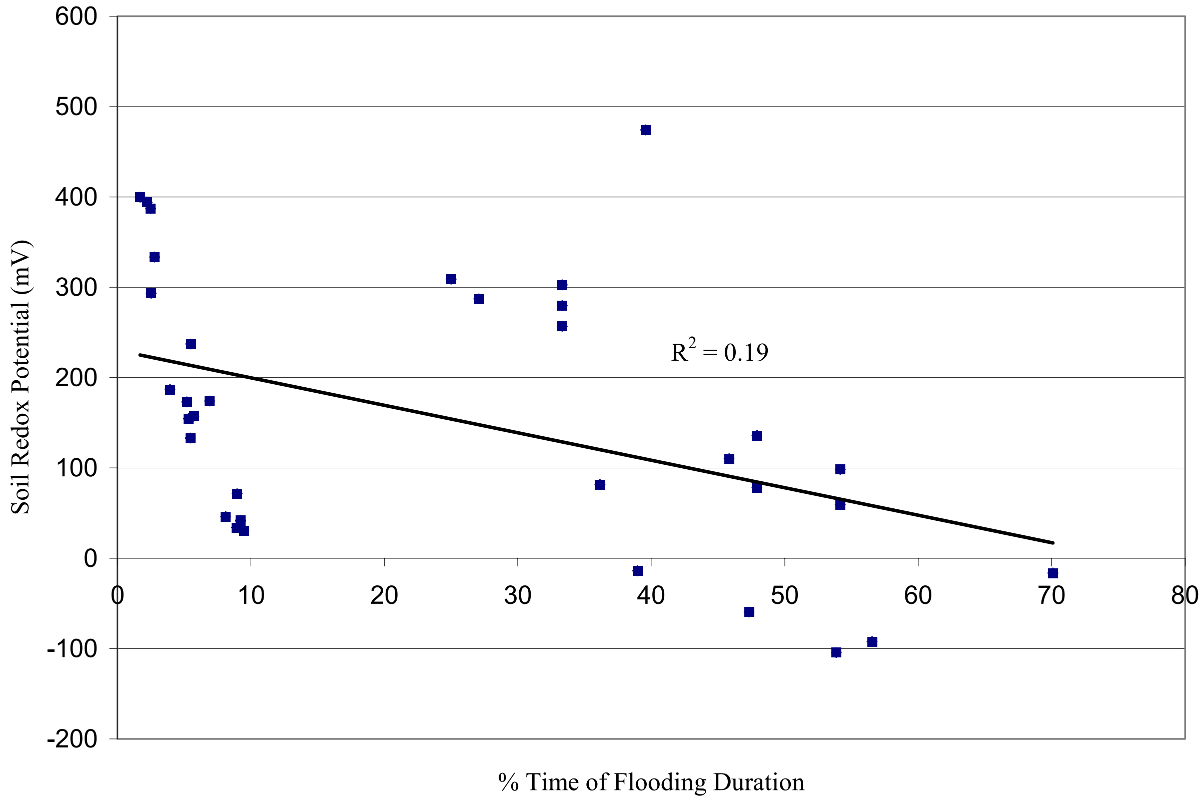


Figure 3.1: Eh values taken at 2 cm below the marsh surface versus % time of flooding duration calculated for the 28 days prior to the May sampling. Combined data set from BC, BL, and LUM. (n = 35).

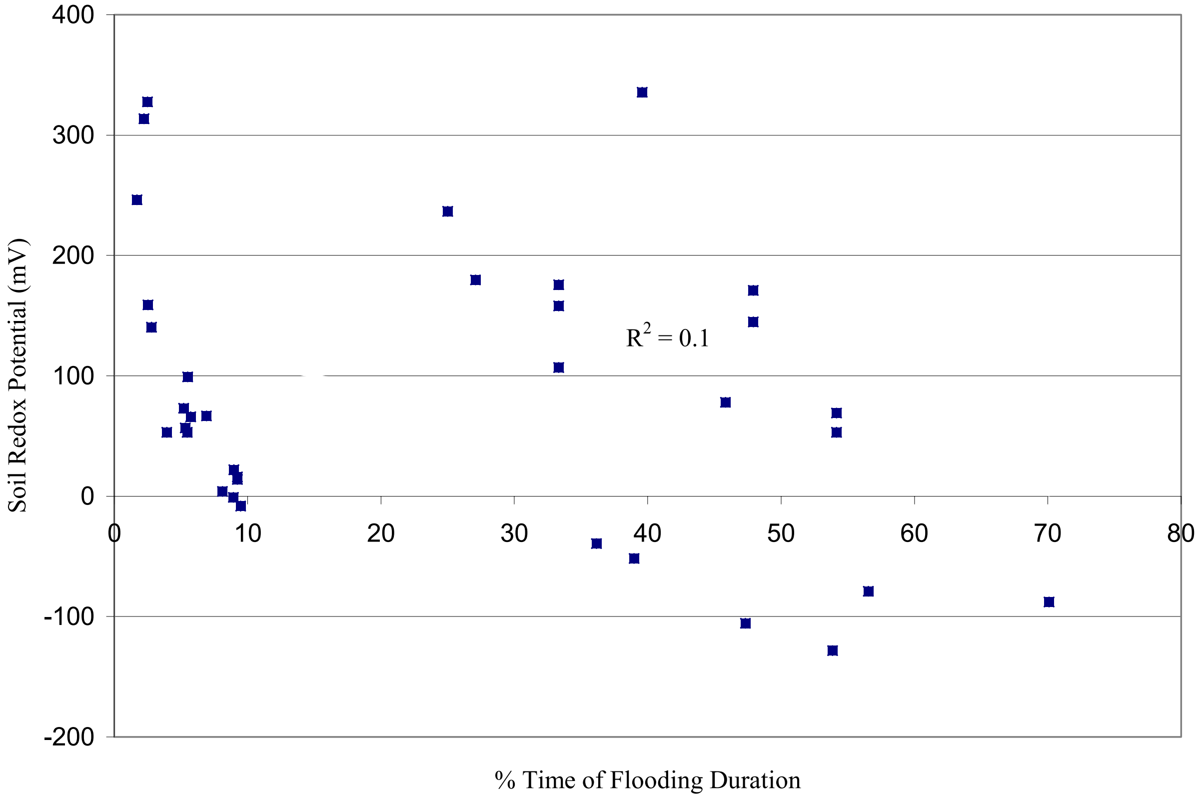


Figure 3.2: Eh values taken at 15 cm below the marsh surface versus % time of flooding duration calculated for the 28 days prior to the May sampling. Combined data set from BC, BL, and LUM. (n =35).

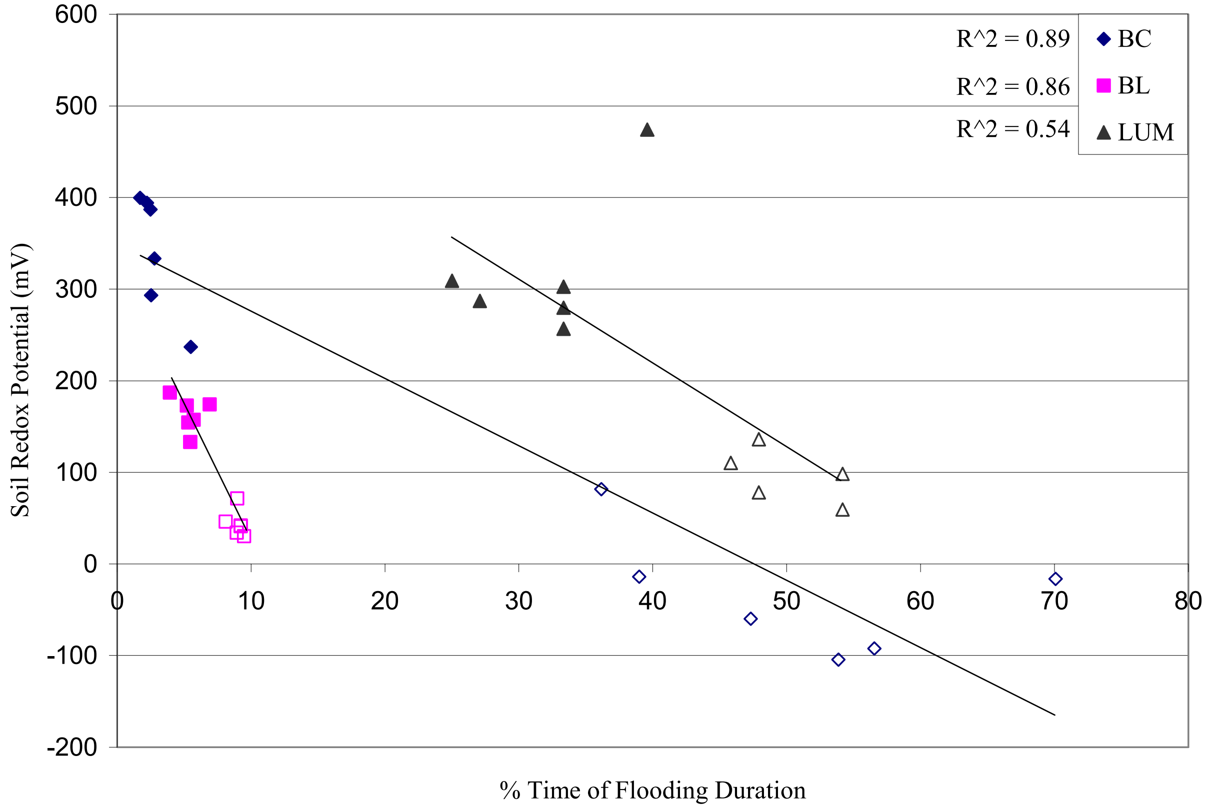


Figure 3.3: Eh values taken at 2 cm below the marsh surface versus % time of flooding duration calculated for the 28 days prior to the May sampling. Sampling sites considered independently from one another. (For BC and BL, n = 12; for LUM, n = 11. Closed symbols refer to data obtained from streamside zones and open symbols refer to data obtained from inner marsh zones).

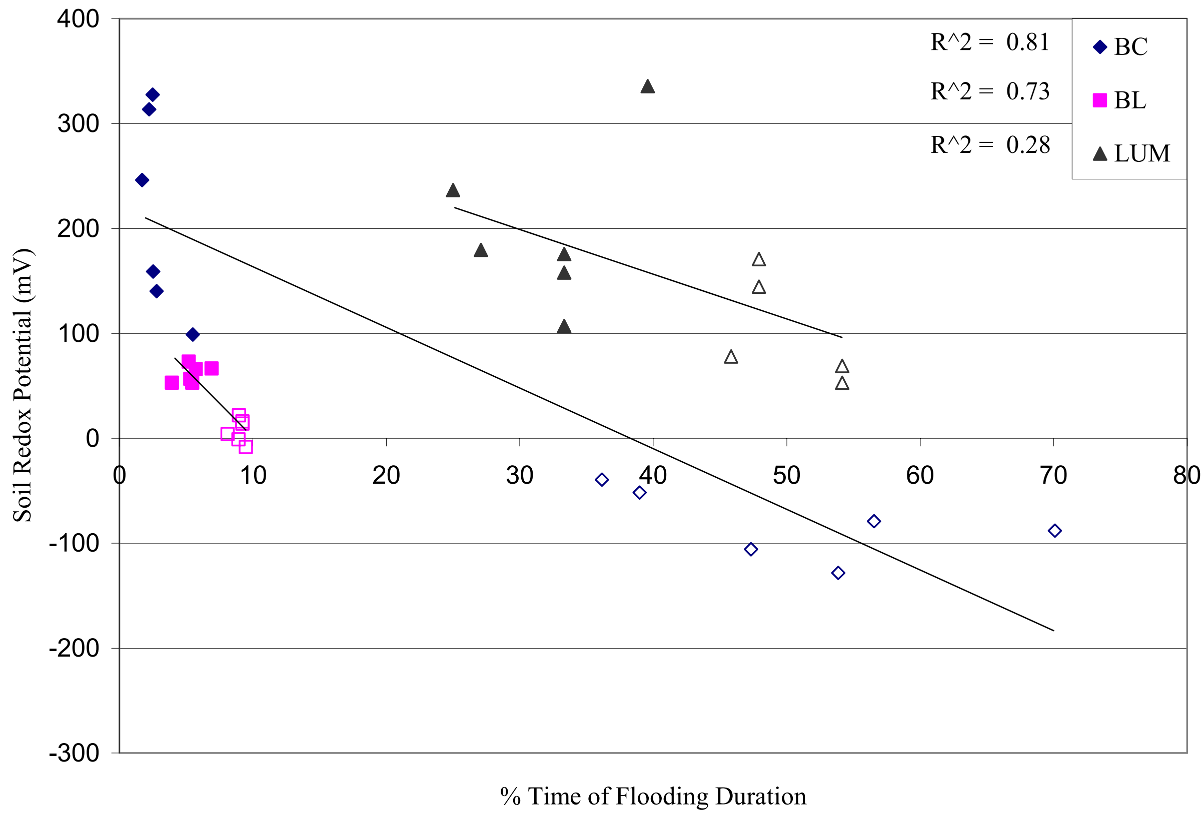


Figure 3.4: Eh values taken at 15 cm below the marsh surface versus % time of flooding duration calculated for the 28 days prior to the May sampling. Sampling sites considered independently from one another. (For BC and BL, n = 12; for LUM, n = 11. Closed symbols refer to data obtained from streamside zones and open symbols refer to data obtained from inner marsh zones).

The observed values for Eh ranged from +474 to -128 mV (as seen in Figures 3.1 through 3.4). This scope of values coincides with Eh levels imposed by Pezeshki et al. (1991; +400 to -100 mV) and Pezeshki et al. (1993; +460 to -110 mV) as they investigated the subsequent impact on the root structure of *Spartina patens*. Mendelssohn and Seneca (1980) noted a similar range of Eh values (+300 to -150 mV) in *Spartina* marshes of North Carolina, as did Howes et al. (1981) in Massachusetts (+350 to -175 mV).

3.1.2 % Time of Flooding Duration and Sulfide Concentration

High levels of flooding duration may result in the accumulation of hydrogen sulfide as alternate electron acceptors, in this case sulfate, are reduced by bacteria during anaerobic metabolic pathways of energy production (Mitsch and Gosselink, 2000). Sulfide accumulation has been observed in soils with Eh values in the upper range of -50 to -125 mV (Harter and

McLean, 1965). The presence of sulfide within soils has been shown to inhibit the uptake of nitrogen, lower root biomass, and suppress the activity of alcohol dehrydogenase (ADH), an enzyme responsible for the final step in anaerobic energy production (Koch et al., 1990; Koch and Mendelssohn, 1989).

Again, % TFD was computed for 28 d, 21 d, 14 d, 7 d, 3d, and 1 d prior to the sampling date. A single sulfide concentration measurement was taken from each plot and compared with the % TFD data. The correlation between sulfide concentration and % TFD was strongest when the % TFD was computed for the 28 days prior to sample collection. Combining the data obtained from BC, BL, and LUM, and performing a linear regression provided an R^2 value of 0.31 (see Figure 3.5). Stronger correlations were found by carrying out the same analysis with samples taken from BC, BL, and LUM being plotted independently of one another. This analysis gave R^2 values ranging from 0.56 to 0.79 (see Figure 3.6). As was noted with the Eh data, site specific characteristics other than % TFD, such as the size of sulfate stocks present in the soil, impart a significant influence on the determination of sulfide concentration. It can also be noted from Figure 3.6 that, within sites, the inner marsh zones always exhibited higher concentrations of sulfide than streamside zones. The data obtained during this study supports the notion that increased % TFD corresponds to increased sulfide concentration.

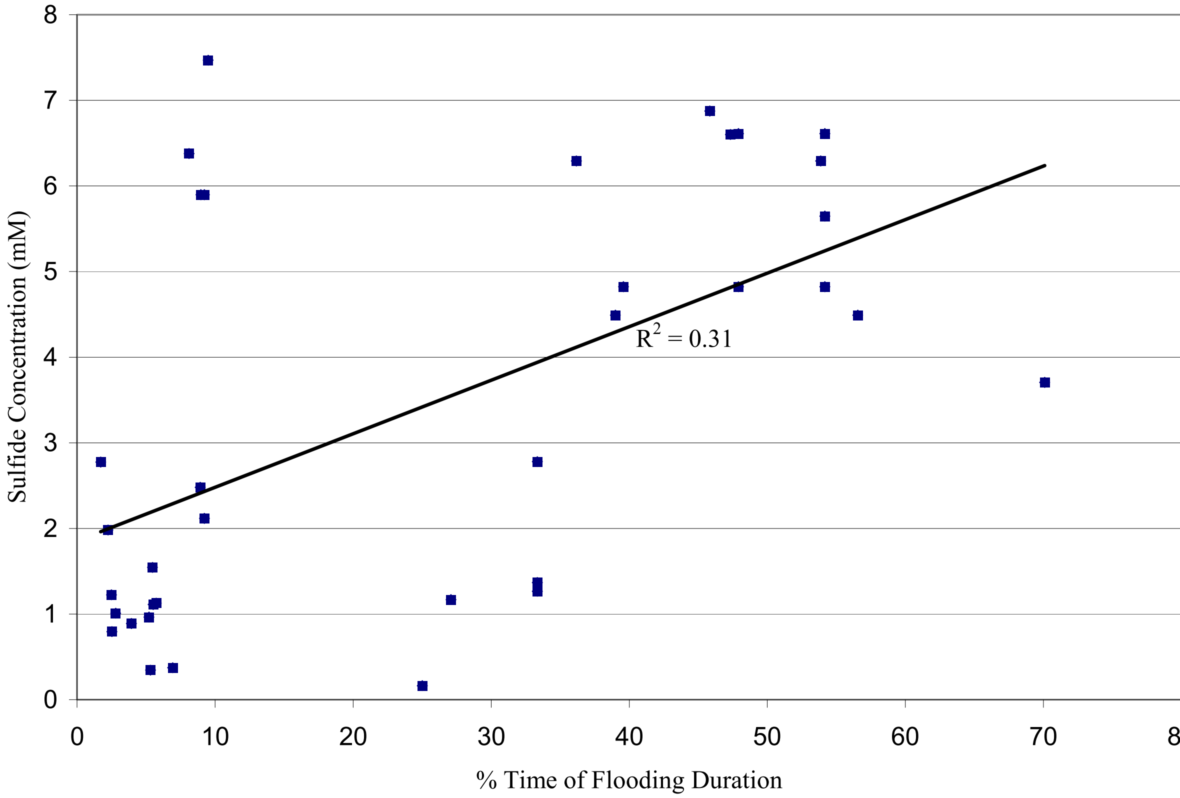


Figure 3.5: Sulfide concentration versus % time of flooding duration calculated for the 28 days prior to the May sampling. Combined data set from BC, BL, and LUM. (n = 36).

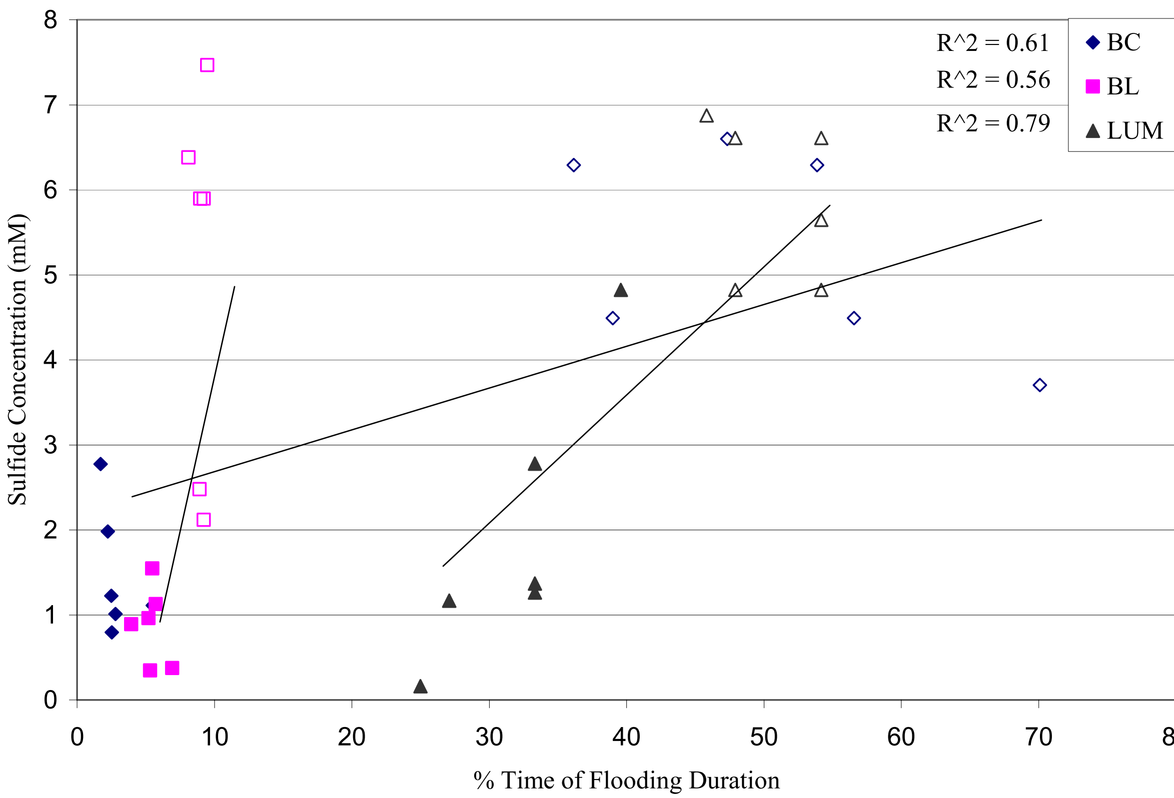


Figure 3.6: Sulfide concentration versus % time of flooding duration calculated for the 28 days prior to the May sampling. Sampling sites considered independently from one another. (n = 12; Closed symbols refer to data obtained from streamside zones and open symbols refer to data obtained from inner marsh zones).

The observed values for sulfide concentration ranged from 0.2 to 7.5 mM (where 1mM is approximately equal to 32.1 ppm). This scope of values is broader than those previously reported. Koretsky et al. (2003) reported a range of 0.0 to 4.5 mM, whereas Mendelssohn and McKee (1988) observed a narrower range of 0.0 to 1.0 mM. The latter is similar to the findings of Mendelssohn and Kuhn (2003) who presented a range of 0.0 to 0.6 mM. High rates of sulfide production at soil depths greater than 15 cm and ensuing diffusion to areas of lower concentration (i.e. soil depths less than 15 cm) could have provided a source of sulfide for the concentrations noted in the data presented here.

3.1.3 Interaction between Environmental Stresses, Aerenchyma Production, and the Specific Gravity of Live Roots

The development of large air spaces within the vascular tissue of roots is a widely recognized adaptation of flood-tolerant species which permits enhanced transportation of atmospheric oxygen and lowers metabolic requirements by reducing the volume of tissue within a root (Aerenovski and Howes, 1992). The degree to which aerenchyma formation took place in the roots of *S. alterniflora* was not directly measured in this study. However, a substantial amount of scientific literature exists establishing a connection between flooding-related stresses and aerenchyma development (see section 1.3.4). At the same time, it is interesting to note that, while advances have been made, the mechanisms linking flood duration and aerenchyma production in the field are yet to be wholly understood. Various lab-scale studies have shown that anoxia, ethylene concentration, the presence of phytotoxins, and the activity of such metabolic enzymes as alcohol dehydrogenase (ADH) all either influence or are influenced by aerenchyma formation (Maricle and Lee, 2002; Koch et al., 1990; Mendelssohn and McKee, 1998; Pezeshki et al., 1991; Pezeshki et al., 1993).

Given that roots respond to increased flooding durations and associated stresses with the formation of air spaces within their tissue, it seems logical that this should correlate to a decrease in specific gravity, a ratio of the density of a substance to the density of water. Nevertheless, performing linear regressions with the specific gravity of *S. alterniflora* roots versus soil Eh, sulfide concentration, and % time of flooding duration provided contrary results.

Combining the data sets from BC, BL, and LUM and performing linear regressions of root specific gravity against Eh, sulfide concentration, and % TFD returned R^2 correlations no greater than 0.18 (see Table 3.1).

The inter-site variations that proved significant for the relationships between soil Eh and % TFD, and sulfide concentration and % TFD were not observed for the root specific gravity data. Examining the data from BC, BL, and LUM independently of each other resulted in limited alterations of R^2 correlations. R^2 only exceeded 0.40 for the relationship between root specific gravity taken at a soil depth of 0-5 cm and sulfide concentration at the BC site. Table 3.2 shows R^2 values for the BC data set, Table 3.3 shows R^2 values for the BL data set, and Table 3.4 shows R^2 values for the LUM data set (The actual plots can be found in the appendix illustrating that non-linear fits are also not present in the data.)

Table 3.1: R^2 values obtained from linear regressions of root specific gravity as a function of either Eh, sulfide concentration, or % TFD. Combined data set from BC, BL, and LUM (May sampling).

Soil Interval Sampled for Root Specific Gravity	Eh: 2 cm (n=35)	Eh: 15 cm (n=35)	Sulfide Concentration (n=36)	% TFD (n=36)
0 – 5	0.01	0.01	0.01	0.02
5 – 10	0.06	0.03	0.10	0.01
10 – 15	0.00	0.01	0.00	0.00
0 – 15	0.07	0.04	0.18	0.11

Table 3.2: May sampling data reported for BC. R^2 values obtained from linear regressions of root specific gravity as a function of either Eh, sulfide concentration, or % TFD.

Soil Interval Sampled for Root Specific Gravity	Eh: 2 cm (n=12)	Eh: 15 cm (n=12)	Sulfide Concentration (n=12)	% TFD (n=12)
0 – 5	0.34	0.29	0.44	0.24
5 – 10	0.02	0.00	0.00	0.00
10 – 15	0.00	0.01	0.03	0.00
0 – 15	0.35	0.28	0.36	0.28

Table 3.3: May sampling data reported for BL. R^2 values obtained from linear regressions of root specific gravity as a function of either Eh, sulfide concentration, or % TFD.

Soil Interval Sampled for Root Specific Gravity	Eh: 2 cm (n=12)	Eh: 15 cm (n=12)	Sulfide Concentration (n=12)	% TFD (n=12)
0 – 5	0.11	0.02	0.01	0.16
5 – 10	0.30	0.32	0.35	0.22
10 – 15	0.26	0.25	0.17	0.25
0 – 15	0.00	0.00	0.12	0.00

Table 3.4: May sampling data reported for LUM. R^2 values obtained from linear regressions of root specific gravity as a function of either Eh, sulfide concentration, or % TFD.

Soil Interval Sampled for Root Specific Gravity	Eh: 2 cm (n=11)	Eh: 15 cm (n=11)	Sulfide Concentration (n=12)	% TFD (n=12)
0 – 5	0.00	0.04	0.00	0.02
5 – 10	0.10	0.10	0.15	0.29
10 – 15	0.09	0.13	0.12	0.02
0 – 15	0.20	0.06	0.21	0.32

The weak R^2 values reported in Tables 3.1, 3.2, 3.3, and 3.4 suggest that interactions between root specific gravity and soil Eh, sulfide concentration, and % TFD were not significant at BC, BL, or LUM. This result is opposite from the proposed hypothesis.

A potential explanation for this contradiction is that the magnitude of stresses observed at BC, BL, and LUM were not great enough to induce root specific gravity modifications. As stated above, however, Eh values coincided with those used in lab-scale studies where specific gravity alterations were reported. Also mentioned above, sulfide concentrations were, if anything, greater than those reported in previous studies. The observed sulfide values indicate that the soils at BC, BL and LUM were indeed stressful in terms of diminished oxygen supply. At the same time, while aerenchyma formation is encouraged by hypoxia it is limited by anoxia as oxygen is required to produce ethylene, a stimulator of aerenchyma development (Buchanan et al., 2000).

The absence of root specific gravity alterations observed here may be attributable, in part, to the fact that soils at BC, BL and LUM may have surpassed hypoxic conditions becoming anoxic.

In regard to its specific affects on *S. alterniflora*, Koch and Mendelssohn found that concentrations of sulfide greater than 1 mM significantly reduced root and total biomass, though determining the impact on root specific gravity was not incorporated into their analysis (1989). Proposed mechanisms for this interaction include inhibited enzyme activity, decreased nutrient uptake, and obstruction of metabolic pathways (Koch and Mendelssohn, 1989 and Koch et al., 1990). The impact of each of these hindrances on the specific gravity of *S. alterniflora* roots remains poorly understood in natural settings. The established interaction between sulfide concentration and root biomass production at the lab-scale coupled with the lack of correlation between sulfide concentration and root specific gravity found in the field-scale data presented here highlights a gap in our understanding of the effect sulfide stress (mediated through various processes) and the specific gravity of roots.

Another possible explanation for the weak correlations observed between root specific gravity values and measured environmental stresses is that pre-existing environmental conditions were such that all sites were already experiencing fairly high flooding stress. This was not expressly observed in the collected data and may, therefore, operate on longer time scales than were recorded during this study. This scenario suggests that aerenchyma development and specific gravity in *S. alterniflora* roots may already have been near optimal levels resulting from air pathway constriction at the stem junction (Aerenovski and Howes, 1992). Maximum aerenchyma formation may be typical for *S. alterniflora* which always grows in the lower intertidal portions of salt marshes. In contrast, root specific gravity may be more variable in a species like *S. patens*, which is found in more diverse stress environments including swales, dunes, and marshes.

Yet another potential explanation for the contradiction between previous lab-scale findings and the field data presented here is that durations of stresses at BC, BL, and LUM were insufficient to stimulate specific gravity alterations in the particular species studied here (i.e., *S. alterniflora)*. % TFD data presented here ranges from 3 to 58 % (± 0.5 to 12.5) for the 28 days prior to sampling. Burdick (1989) subjected *S. patens* to 25 days of continuous flooding (100% of the time). Laan et al. (1989) imposed 3 weeks of continuous flooding in their study of *Rumex* species. Pezeshki et al. (1991 and 1993) induced continuous flooding for 22 and 21 days respectively while studying the subsequent impacts on *S. patens*. While investigating the flooding impact on aerenchyma development in *S. alterniflora* and *S. anglica,* Maricle and Lee (2002) also flooded plants continuously for 3 weeks. Interestingly, Padgett and Brown (1999) instituted a flooding regime that "corresponded with the natural tidal cycle" for swards of *S. alterniflora* used in their lab-scale study. Using a more "natural tidal cycle", Padgett and Brown (1999) found that soil drainage depth had no effect on the accumulation of belowground tissue. Quantifying the specific gravity of this tissue, however, was beyond the scope of their research. In a natural field setting, Burdick and Mendelssohn (1987) observed a significant correlation between soil waterlogging (as indicated by the water content of the soil) and the specific gravity of *S. patens* roots. It is important to note that flooding duration was not determined in their study, which contrasted roots from dune systems, swales, and marshes. The consideration of a more diverse collection of ecosystems by Burdick and Mendelssohn (as compared with this study where all sites were located in salt marshes) may have provided a greater range of stress magnitudes and durations, possibly contributing to the correlation reported between root specific gravity and soil waterlogging.

It seems possible that a threshold of tolerance exists for the combined influence of stress magnitude and duration on root specific gravity. When, for example, the duration of stress exceeds that threshold (as in the lab-scale studies where durations of 100% for several weeks were often used) increased aerenchyma production may take place within the roots. When the threshold is not exceeded (as appears to have been the case for the data presented here at 3-58% flooding durations) no significant increase in aerenchyma development may occur. Further investigation is required to verify the existence of and quantify this stress-tolerance threshold with respect to each of the relevant environmental stresses. This requires extending our understanding of morphological root response with regard to varying magnitudes and durations of individual environmental stresses (e.g., flooding duration) and different combinations of stress magnitude and duration for multiple stressors (e.g., long flooding duration coupled with a short duration of high sulfide concentration).

3.1.4 Modification of the Conceptual Model

The results presented above suggest that the originally proposed conceptual model (see Figure 1.4) requires revision. The data offered here supports the notion that increased flooding duration results in increased environmental stress. The interactions between environmental stress and root specific gravity in a natural setting, however, require further investigation to verify and quantify the proposed stress-tolerance threshold to complete the model. A modified conceptual model incorporating the findings from this research is proposed below. The signs for the arrows simply indicate whether the relationship between boxes is directly or inversely proportional. For example, a negative sign between marsh surface elevation and flooding duration indicates that as surface elevation increases flooding duration decreases and vice versa.

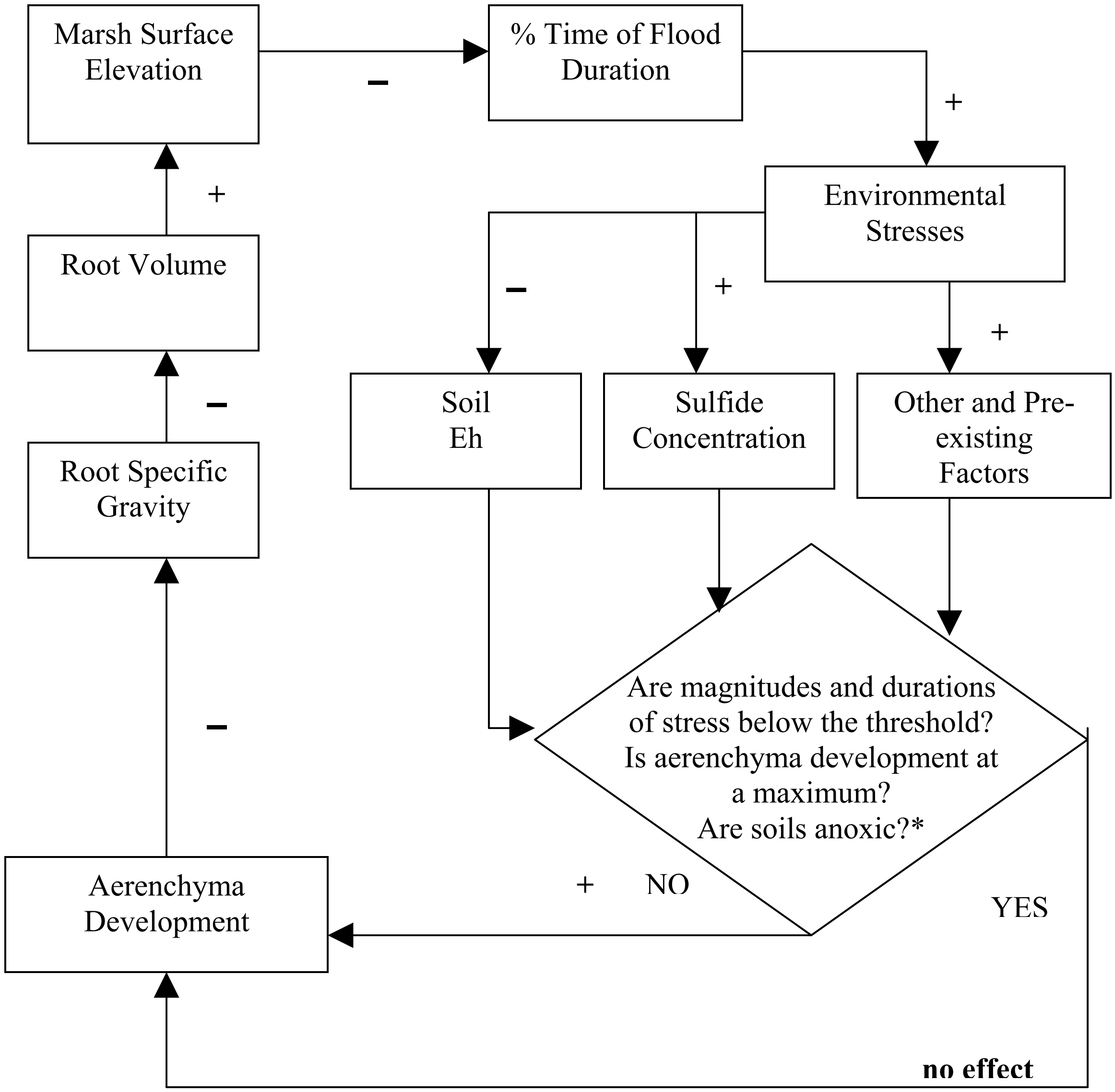


Figure 3.7: Modification of the proposed conceptual model of process interactions assuming constant belowground biomass. (*Further research is required to verify and quantify the proposed stress-tolerance threshold and maximum aerenchyma development in *S. alterniflora*).

3.2 Landscape Interactions: Spatial Changes in Stress

Inspection of the data collected from the three sites across coastal Louisiana highlights the complexity of inter- and intra-site variation with respect to process interactions.

3.2.1 Bayou Chitigue and Blind Lagoon: A Comparison of High RSLR with Low RSLR

Hypothesis 2: Flooding and associated stresses will be greater at BC than at BL correlating to lower root specific gravities for BC.

Trends noted in comparing the stresses at BC with those at BL differ according to the zone sampled. The trends present for the inner marsh coincided with the proposed hypothesis with % TFD and soil Eh stresses at BC exceeding those at BL. The trends noted for the streamside zones were opposite those of the inner marsh with % TFD and soil Eh stresses at BL being greater than those observed at BC. No trend was observed between these two sites for sulfide concentration. Pronounced trends within sites were also observed. At BC and BL, the inner marsh zone experienced higher % TFDs, lower Eh levels, and higher sulfide concentrations.

Differences between mean % TFD values for the 28 days prior to sample collection at BC and BL were highly significant ($P<0.0001$). Within BC and BL, differences between mean % TFD values (again, calculated for the 28 days prior to sampling) for inner marsh and streamside zones were also highly significant ($P=0.0002$ and 0.0009 for BC and BL respectively). Table 3.5 provides mean % TFD data obtained from BC and BL during the May sampling session.

Differences between mean Eh values for BC and BL were significant at 2 cm below the soil surface ($P=0.004$) and 15 cm below the soil surface ($P=0.005$). Within BC and BL, differences between mean Eh values for inner marsh and streamside zones were highly significant at the 2 cm depth ($P=0.0006$ and <0.0001 for BC and BL respectively) and the 15 cm depth ($P=0.001$ and <0.0001 for BC and BL respectively). Table 3.5 also provides mean Eh data obtained from BC and BL during the May sampling session.

Sulfide concentration was not significantly different between BC and BL ($P=0.21$). Variation between zones, however, was significant ($P=0.003$ and 0.005 for BC and BL respectively). Table 3.5 provides mean sulfide concentration data obtained from BC and BL during the May sampling session.

It has been reported that environmental factors, such as sulfide toxicity and anaerobic soil conditions, lead to reduced aboveground growth of *S. alterniflora* (Mendelssohn and McKee, 1988). Aboveground biomass data collected from BC and BL reinforce the trends in relative levels of stress, as noted from interstitial pore water data, observed between these two sites.

Aboveground biomass was significantly different between BC and BL (P=0.004). Variation between zones within a site, however, was not significant at BC or BL (P=0.17 and 0.16 for BC and BL respectively). Still, interstitial pore water data (presented above) indicate that stresses were greater at BC for the inner marsh zone and greater at BL for the streamside zone. The aboveground biomass data collected from these two sites also suggests that stresses were greater at BC for the inner marsh zone and greater at BL for the streamside zone as these were the areas with significantly lower aboveground biomass. Table 3.6 provides mean aboveground biomass data obtained from BC and BL during the May sampling session.

Table 3.5: A comparison of the average values for environmental stresses observed at BC and BL for the May sampling. (Different letters indicate significant difference of means, ANOVA, $\alpha = 0.05$: minimum confidence interval.)

Environmental Variable	Inner Marsh		Streamside	
	BC	BL	BC	BL
% TFD (n=6)	50 ± 12.5^{a}	9 ± 0.5^{b}	3 ± 1.3^{c}	5 ± 1.0^{d}
Eh: 2 cm (mV); (n=5)	-34 ± 68^{a}	$+44 \pm 14^{b}$	$+341 \pm 66^{c}$	$+163 \pm 19^{d}$
Eh: 15 cm (mV); (n=5)	-82 ± 33^{a}	$+8 \pm 11^{b}$	$+214 \pm 95^{c}$	$+61 \pm 8^{d}$
Sulfide Concentration (mM); (n=6)	5.3 ± 1.2^{a}	5.0 ± 2.2^{a}	1.5 ± 0.8^{b}	0.9 ± 0.5^{b}

Table 3.6: Average aboveground biomass (g/m^2) obtained from the inner marsh and streamside zones at BC and BL during the May sampling (Different letters indicate significant difference of means, ANOVA, $\alpha = 0.05$: minimum confidence interval).

Inner Marsh		Streamside	
BC	BL	BC	BL
1638 ± 464^{a}	2471 ± 489^{b}	2265 ± 842^{a}	2018 ± 506^{b}

Mean root specific gravity values were not significantly different between BC and BL. Differences of mean root specific gravity were not significant between inner marsh and streamside zones at both BC and BL for any of the soil intervals sampled. Table 3.7 provides the average specific gravity values of live roots obtained during the May sampling session.

Table 3.7: Average live root specific gravity values obtained from inner marsh and streamside zones at BC and BL during the May sampling.

Soil Depth	Inner Marsh BC	Inner Marsh BL	Streamside BC	Streamside BL
0 – 5 cm (n=6)	0.97 ± 0.07	0.88 ± 0.05	0.89 ± 0.07	0.94 ± 0.23
5 – 10 cm (n=6)	0.89 ± 0.12	0.90 ± 0.07	0.88 ± 0.08	0.85 ± 0.07
10 – 15 cm (n=5 for inner marsh; n=6 for streamside)	0.95 ± 0.08	0.95 ± 0.09	0.86 ± 0.06	0.80 ± 0.10
0 – 15 (n=17 for inner marsh; n=18 for streamside)	0.94 ± 0.09	0.91 ± 0.07	0.88 ± 0.07	0.86 ± 0.16

The mean specific gravity data presented in Table 3.6 varies from 0.80 to 0.97 (± 0.05 to 0.23). These values fall within the upper range of root specific gravities reported by previous studies which range from 0.55 to 1.00 (Burdick and Mendelssohn, 1987; Burdick, 1989; Laan et al. 1989; Maricle and Lee, 2002). The fact that all measured specific gravity values from BC and BL were at the upper end of the reported spectrum reinforces the contention put forward in the discussion of hypothesis 1 that stresses were insufficient (either in magnitude, duration, or both) at BC and BL to induce a significant lowering of root specific gravity.

It was predicted that the macro-scale (or coast-scale, to use the terminology from Figure 1.1) landscape trends would equate to higher stresses for the site located within the region exhibiting higher rates of RSLR (i.e., BC). The deviation from these generalizations at the micro-scale (analogous to the plant- and marsh-scale end of the spectrum in Figure 1.1) highlights the importance of determining the appropriate scale of observation for a study. Given that the relative magnitudes of stresses experienced at BC and BL in the streamside zones were opposite the hypothesis, while the inner marsh zones conformed to the predicted trends, suggests that micro-scale site characteristics play a more important role than macro-scale regional characteristics in determining the environmental conditions and consequent impacts on specific gravity of roots at a particular site. The result is that the proposed hypothesis cannot be accepted in its original form.

A more robust theory would simply state that an area (of size appropriate to the plant- and marsh-scales of observation noted in Figure 1.1) which experiences higher micro-scale stresses (e.g., longer flooding duration or greater concentration of phytotoxins) than another area will have lower root specific gravities. In accordance with the revised conceptual model of Figure 3.7, this relationship will possibly be impacted by the stress-tolerance threshold, soil anoxia/hypoxia, and the potential for further aerenchyma formation (or lack thereof).

Hypothesis 3: The percent organic matter of the soil will be lower at BC than at BL corresponding to lower root specific gravities at BC.

Marsh vegetation located in regions experiencing relatively higher environmental stresses (e.g., increased sulfide concentration) were expected to exhibit diminished belowground biomass production. It was proposed that stresses thought to be associated with a higher rate of RSLR (e.g., increased % TFD) would significantly reduce belowground biomass, and thereby decrease the organic matter content of the soil. Therefore, a region with a higher rate of RSLR (i.e., BC) was expected to be characterized by soils with a lower percentage of organic matter in comparison with a region experiencing a lower rate of RSLR (i.e., BL). The rationale behind hypothesis 2 already linked a region with high RSLR to roots with relatively lower specific gravities. Consequently, soils with lower percentages of organic matter were expected to also contain roots with lower specific gravities.

As was hypothesized, mean soil organic content was significantly lower at BC for all depths sampled (0-5 cm: $P<0.0001$; 5-10 cm: $P=0.003$; 10-15 cm; $P<0.0001$; 0-15 cm: $P<0.0001$). Mean soil organic content was not significantly different between zones at any depth for the BC site. At the BL site, mean soil organic content was significantly greater for the inner marsh plots at soil depths of 10-15 cm and 0-15 cm ($P<0.03$ and $P=0.006$ respectively), but was not significant for the 0-5 cm soil interval. Table 3.8 provides the average soil organic content values obtained during the May sampling.

Table 3.8: A comparison of average soil organic content and average root specific gravity values obtained from BC and BL during the May sampling. (Different letters indicate significant difference of means, ANOVA, α = 0.05: minimum confidence interval)

Soil Organic Content (%)

Soil	Inner Marsh		Streamside	
Depth	BC	BL	BC	BL
0 – 5 cm (n=6)	22.2 ± 3.2[a]	31.5 ± 5.7[b]	20.9 ± 1.7[a]	26.0 ± 1.4[b]
5 – 10 cm (n=6)	21.2 ± 2.3[a]	24.8 ± 4.2[b]	20.8 ± 2.5[a]	21.8 ± 1.9[b]
10 – 15 cm (n=6)	19.5 ± 2.0[a]	31.5 ± 4.9[b]	20.4 ± 1.7[a]	24.3 ± 0.9[c]
0 – 15 (n=18)	20.9 ± 2.6[a]	29.3 ± 5.7[b]	20.7 ± 1.9[a]	24.0 ± 2.2[c]

Root Specific Gravity

Soil	Inner Marsh		Streamside	
Depth	BC	BL	BC	BL
0 – 5 cm (n=6)	0.97 ± 0.07	0.88 ± 0.05	0.89 ± 0.07	0.94 ± 0.23
5 – 10 cm (n=6)	0.89 ± 0.12	0.90 ± 0.07	0.88 ± 0.08	0.85 ± 0.07
10 – 15 cm (n=5 for inner marsh; n=6 for streamside)	0.95 ± 0.08	0.95 ± 0.09	0.86 ± 0.06	0.80 ± 0.10
0 – 15 (n=17 for inner marsh; n=18 for streamside)	0.94 ± 0.09	0.91 ± 0.07	0.88 ± 0.07	0.86 ± 0.16

As expected, significantly higher percentages of organics were found in the soil at BL, the site within the region experiencing a lower rate of RSLR and significantly lower flood-related stresses. At the same time, even though differences in mean soil organic content were significant between BC and BL differences between mean root specific gravity were not (refer to Table 3.8). This suggests that the organic content of soils may not serve as an appropriate indicator of root specific gravity. Performing linear regressions with the root specific gravity and soil organic matter content data reinforces this claim.

Combining the data sets from BC, BL, and LUM and performing linear regressions of root specific gravity against soil organic content for the various soil intervals sampled returned

R^2 values of 0.00 and 0.01 (see Table 3.9). Performing the same analysis with the data from BC, BL, and LUM being considered independently of each other resulted in minor R^2 value changes. The most noteworthy correlation (R^2=0.51) was found at LUM when averages of root specific gravity and soil organic content across the entire soil interval sampled (0-15 cm) were considered. All other R^2 values for LUM, BC and BL, however, were less than 0.31. One notable correlation out of sixteen that is still only able to account for 51% of the variation signifies that the organic content of marsh soils should not be used as a gauge for the specific gravity of roots found within those soils.

Table 3.9: R^2 values obtained from linear regressions of root specific gravity plotted against % organic content of the soil (May sampling).

Soil Depth	BC (n=12)	BL (n=12)	LUM (n=12)	All 3 Sites Combined (n=36)
0 – 5 cm	0.06	0.01	0.19	0.01
5 – 10 cm	0.23	0.00	0.07	0.00
10 – 15 cm	0.01	0.27	0.10	0.00
0 – 15 cm	0.09	0.31	0.51	0.00

3.2.2 Bayou Chitigue and LUMCON: Impact of a Substantial Freshwater Input

Hypothesis 4: Flooding and associated stresses will be greater at BC than at LUM correlating to lower root specific gravities for BC.

Trends observed in comparing the stresses at BC with those at LUM also varied according to the zone sampled. For the inner marsh zones, % TFD and Eh was greater at LUM. For the streamside zones, % TFD was greater at LUM while Eh was greater at BC. No trend was observed between these two sites for sulfide concentration.

Differences between mean % TFD values (calculated for the 28 days prior to sample collection) at BC and LUM were highly significant ($P<0.0001$). Within BC and LUM, differences between mean % TFD values for inner marsh and streamside zones were also highly significant ($P=0.0002$ and <0.0001 for BC and LUM respectively). Table 3.10 provides % TFD data collected from BC and LUM for the May sampling session.

Differences between mean Eh values at BC and LUM were significant at 2 cm below the soil surface ($P=0.004$) and 15 cm below the soil surface ($P=0.005$). Within BC and LUM, differences in mean Eh values were highly significant between inner marsh and streamside zones at the 2 cm depth (P=0.0006 and <0.0001 for BC and LUM respectively). At the 15 cm soil depth, differences between rows were significant at BC (P=0.001), but were not significant at LUM. Table 3.10 also provides mean Eh data obtained from BC and LUM during the May sampling session.

Sulfide concentration was not significantly different between BC and LUM (P=0.21). Deviation between zones, however, was significant within BC and BL (P=0.003 and 0.008 for BC and LUM respectively). Table 3.10 provides mean sulfide concentration data obtained from BC and BL during the May sampling session.

Aboveground biomass data collected from BC and LUM lend further insight concerning the relative levels of stress, as noted from the interstitial pore water data, observed between these two sites.

Aboveground biomass was significantly different between BC and LUM (P=0.004). Variation between zones was not significant at BC (P=0.17) and was significant at LUM (P=0.03). Interstitial pore water data (presented above) indicate that for the inner marsh zone %TFD stress was greater at LUM while Eh stress was greater at BC. The same data set shows that for the streamside zone stresses were greater at LUM. Aboveground biomass data collected from these two sites suggests that stresses were greater at LUM for both inner marsh and streamside zones as these were the areas with significantly lower aboveground biomass (see Table 3.11). For the inner marsh zone, %TFD and aboveground biomass data coincided as to which site experienced greater stress while Eh data did not. Given that %TFD data was averaged over the four weeks prior to sampling, whereas Eh values were taken only on the day of sampling, and is supported by the aboveground biomass data, it seems that the %TFD data presented here is more representative of the environmental stress at these sites. Table 3.11 provides mean aboveground biomass data obtained from BC and LUM during the May sampling session.

Table 3.10: A comparison of the average values for environmental stresses observed at BC and LUM for the May sampling. (Different letters indicate significant difference of means, ANOVA, α = 0.05: minimum confidence interval)

Environmental Variable	Inner Marsh		Streamside	
	BC	LUM	BC	LUM
% TFD (n=6)	50 ± 12.5^{a}	58 ± 6.7^{b}	3 ± 1.3^{c}	25 ± 6.6^{d}
Eh: 2 cm (mV); (n=5)	-34 ± 68^{a}	$+96 \pm 29^{b}$	$+341 \pm 66^{c}$	$+318 \pm 78^{d}$
Eh: 15 cm (mV); (n=5)	-82 ± 33^{a}	$+103 \pm 52^{b}$	$+214 \pm 95^{c}$	$+199 \pm 79^{b}$
Sulfide Concentration (mM); (n=6)	5.3 ± 1.2^{a}	5.9 ± 0.9^{a}	1.5 ± 0.8^{b}	1.9 ± 1.6^{b}

Table 3.11: Average aboveground biomass (g/m^2) obtained from the inner marsh and streamside zones at BC and LUM during the May sampling (Different letters indicate significant difference of means, ANOVA, α = 0.05: minimum confidence interval).

Inner Marsh		Streamside	
BC	LUM	BC	LUM
1638 ± 464^{a}	844 ± 254^{b}	2265 ± 842^{a}	1160 ± 263^{c}

Mean root specific gravity values were not significantly different between BC and LUM. Differences in mean root specific gravity were not significant between inner marsh and streamside rows at BC or LUM for any of the soil depths sampled. Table 3.12 provides the average specific gravity values of live roots obtained during the May sampling session.

Table 3.12: Average live root specific gravity values obtained from BC and LUM during the May sampling.

Soil Depth	Inner Marsh BC	Inner Marsh LUM	Streamside BC	Streamside LUM
0 – 5 cm (n=6)	0.97 ± 0.07	0.94 ± 0.14	0.89 ± 0.07	0.90 ± 0.11
5 – 10 cm (n=6)	0.89 ± 0.12	0.89 ± 0.18	0.88 ± 0.08	0.78 ± 0.07
10 – 15 cm (n=5 for inner marsh; n=6 for streamside)	0.95 ± 0.08	0.90 ± 0.18	0.86 ± 0.06	0.80 ± 0.08
0 – 15 (n=17 for inner marsh; n=18 for streamside)	0.94 ± 0.09	0.91 ± 0.15	0.88 ± 0.07	0.83 ± 0.10

The mean specific gravity data presented in Table 3.12 ranges from 0.78 to 0.97 (± 0.06 to 0.18). As was the case when specific gravity values were presented for BC and BL, these values also fall in the upper scale of root specific gravity quantities previously reported in the scientific literature which, again, ranges from 0.55 to 1.00 (Burdick and Mendelssohn, 1987; Burdick, 1989; Laan et al. 1989; Maricle and Lee, 2002). This may lend further support to the statements put forward in the discussions of hypotheses 1 and 2 that stresses were insufficient (either in magnitude, duration, or both) at BC and LUM to promote a significant reduction in root specific gravity. At the same time, the theory that root specific gravities were already at optimal values for *S. alterniflora* is also still viable.

It was anticipated that the substantial freshwater input and associated benefits of entrained nutrients and sediments would equate to lower stresses for LUM in comparison with BC. The divergence from these generalizations at the micro-scale further emphasizes the importance of scale of observation. Having established that the relative magnitudes of stresses experienced at BC and LUM were opposite the hypothesis (with the exception of Eh in the inner marsh zones) supports the argument that micro-scale site characteristics provide greater influence than macro-scale regional characteristics in determining the environmental stresses present at a given site. Similar to the findings from hypothesis 2, hypothesis 4 cannot be accepted in its original form.

Adopting the revised language of hypothesis 2 proves apt for this situation as well where an area which experiences higher micro-scale stresses than another area will have lower root specific gravities with the possible impacts of the hypothesized stress-tolerance threshold, soil anoxia/hypoxia, and the potential for further aerenchyma development still being present.

Hypothesis 5: The percent organic matter of the soil will be lower at BC than at LUM corresponding to lower root specific gravities for BC than LUM.

It was hypothesized that environmental factors associated with the absence of a significant freshwater input (e.g., increased salinity) would stress the vegetation located in such marshes. As a result, vegetation in a region that does not receive a significant freshwater contribution was expected to have significantly lower productions of belowground structures and biomass. Therefore, a region lacking a significant freshwater input (i.e., BC) was expected to be characterized by soils with a lower percentage of organic matter in comparison with a region that was influenced by a significant freshwater source (i.e., LUM). The rationale behind hypothesis 4 already linked a region without a freshwater input with roots having relatively lower specific gravities. Consequently, soils with lower percentages of organic matter were expected to also contain roots with lower specific gravities.

Contrary to the hypothesis, mean soil organic content was significantly greater at BC for all depths sampled (0-5 cm: $P<0.0001$; 5-10 cm: $P=0.003$; 10-15 cm; $P<0.0001$; 0-15 cm: $P<0.0001$). Mean soil organic content was not significantly different between zones at any depth for BC or LUM. Table 3.13 provides the average soil organic content values obtained from BC and LUM during the May sampling.

Table 3.13: A comparison of average soil organic content and average root specific gravity values obtained from BC and LUM during the May sampling. (Different letters indicate significant difference of means, ANOVA, α = 0.05: minimum confidence interval)

Soil Organic Content (%)				
Soil Depth	Inner Marsh		Streamside	
	BC	LUM	BC	LUM
0 – 5 cm (n=6)	22.2 ± 3.2[a]	18.9 ± 2.7[b]	20.9 ± 1.7[a]	18.9 ± 1.8[b]
5 – 10 cm (n=6)	21.2 ± 2.3[a]	16.8 ± 1.3[b]	20.8 ± 2.5[a]	19.1 ± 2.8[b]
10 – 15 cm (n=6)	19.5 ± 2.0[a]	14.9 ± 0.7[b]	20.4 ± 1.7[a]	17.7 ± 3.3[b]
Overall (n=18)	20.9 ± 2.6[a]	16.9 ± 2.4[b]	20.7 ± 1.9[a]	18.6 ± 2.6[b]

Root SG				
Soil Depth	Inner Marsh		Streamside	
	BC	LUM	BC	LUM
0 – 5 cm (n=6)	0.97 ± 0.07	0.94 ± 0.14	0.89 ± 0.07	0.90 ± 0.11
5 – 10 cm (n=6)	0.89 ± 0.12	0.89 ± 0.18	0.88 ± 0.08	0.78 ± 0.07
10 – 15 cm (n=5 for inner marsh; n=6 for streamside)	0.95 ± 0.08	0.90 ± 0.18	0.86 ± 0.06	0.80 ± 0.08
Overall (n=17 for inner marsh; n=18 for streamside)	0.94 ± 0.09	0.91 ± 0.15	0.88 ± 0.07	0.83 ± 0.10

Opposite of what was expected, significantly higher percentages of organics were found in the soil at BC, the site lacking a substantial freshwater input. It seems likely that this was observed because increased hydrologic input and exchange, such as the freshwater influx present at LUM, increases the potential for mineral sediment deposition. Greater mineral sediment deposition at a given area would decrease the percentage of organic matter found within the soils of that area, hence the lower soil organic matter contents that were found at LUM. It is also possible that the lack of mineral sediment inputs that would accompany freshwater influxes at BC induced vegetation within these marshes to allocate more biomass to belowground structures in an attempt to maintain rates of accretion that would keep pace with RSLR. This would further contribute to a greater percentage of organic matter within the soils at BC when compared with LUM. In addition, environmental stresses that were expected to be greater at BC were actually greater at LUM. This coincides with the obtained soil organic matter content data.

At the same time, even though differences in mean soil organic content were significant between BC and LUM differences between mean root specific gravity were not significant (refer to Table 3.11) requiring rejection of hypothesis 5. As was put forth in the discussion of hypothesis 3 for sites BC and BL, it appears that the organic content of soils may not serve as an appropriate indicator of root specific gravity. Again, the results of the linear regression analyses (see Table 3.8) established the weak correlation between soil organic content and root specific gravity at BC and LUM indicating that the organic content of marsh soils is not an appropriate indicator of the specific gravity of roots found within those soils. This reinforces the discussion from hypothesis 3 and supports the call for further study of soil organic content responses to environmental drives and plant productivity.

While the results presented for this hypothesis do not establish a link between soil organic content and root specific gravity, they do point to a correlation between soil organic content and hydrologic exchange. The idea that vegetation allocates more biomass belowground in the absence of freshwater inputs, possibly due to the omitted input of associated sediment, is supported by the results presented here. This suggests that soil organic content could serve as an indicator of marsh areas that would benefit from freshwater-derived sediment sources in helping maintain sustainable marsh surface elevations. Further investigation is required to establish the spatial and temporal dynamics of this relationship.

3.3 Landscape Interactions: Temporal Changes in Stress

> **Hypothesis 6**: As a result of the diminished influence of benefits derived from the waning freshwater input at LUM, stresses will increase from the first sample session in May to the third sample session in November. This will correlate to root specific gravities that progressively decrease from May to November.

It was reasoned that the lessening of benefits associated with freshwater inputs during the later months of the growing season would correlate to increased stress and lower root specific gravity values for the November sampling session at LUM. It was proposed that lower specific gravity values, and accompanying greater root volume and marsh surface elevation, would aid in alleviating stresses associated with the absence of the freshwater subsidy.

The data obtained from the LUMCON monitoring station reinforced the assertion that freshwater effects are strongest at LUM during the earlier portions of the year (refer back to Figure 2.2). At the same time, % TFD (calculated for the 28 days prior to each sampling date) decreased significantly from May to November. Differences in mean % TFD were highly significant among the three sample times (P<0.0001) and between inner marsh and streamside zones for each of the three samplings (P<0.0001, =0.0002, and <0.0001 for May, August, and November respectively). Table 3.12 provides the % TFD data observed for the 28 days prior to each of the three sampling sessions.

Table 3.14: Average % time of flooding duration values at LUM for the 28 days prior to each sampling date. (Different letters indicate significant difference of means, ANOVA, α = 0.05: minimum confidence interval)

Inner Marsh			Streamside		
May	August	November	May	August	November
58 ± 6.7^{a}	44 ± 3.6^{b}	34 ± 3.9^{c}	25 ± 6.6^{d}	15 ± 11.8^{e}	9 ± 1.8^{f}

Mean root specific gravity was significantly lowest in May for the streamside zones of all three sampling sessions at soil depths of 5-10 cm (P=0.01) and 0-15 cm (P=0.02). Differences in mean root specific gravity between zones were not significant for any individual sampling session at any of the soil depths sampled. Table 3.15 provides the average specific gravity values of live roots obtained from each discrete soil depth during the three sampling sessions.

Table 3.15: Average live root specific gravity values for the three sampling sessions at LUM. (Different letters indicate significant difference of means, ANOVA, α = 0.05: minimum confidence interval)

Soil Depth (cm)	Inner Marsh			Streamside		
	May	August	November	May	August	November
0 – 5 (n=6)	0.94 ± 0.14	0.97 ± 0.05	0.95 ± 0.12	0.90 ± 0.11	0.92 ± 0.03	0.92 ± 0.06
5 – 10 (n=6)	0.89 ± 0.18	0.93 ± 0.09	0.94 ± 0.06	0.78 ± 0.07[a]	0.90 ± 0.04[b]	0.86 ± 0.03[b]
10 – 15 (n=5 for inner marsh; n=6 for streamside)	0.90 ± 0.18	0.80 ± 0.13	0.94 ± 0.07	0.80 ± 0.08	0.90 ± 0.08	0.87 ± 0.08
0 – 15 (n=17 for inner marsh; n=18 for streamside)	0.91 ± 0.15	0.91 ± 0.11	0.94 ± 0.08	0.83 ± 0.10[a]	0.91 ± 0.05[b]	0.89 ± 0.07[b]

The opposing trends of increasing versus decreasing stresses associated with the magnitude of freshwater influence and % TFD illustrate the complex nature of process interactions through time in a natural setting. The only significant difference in specific gravity values occurred between the streamside rows of the May sampling and the August and November sessions where May values were lower than those observed during the later months. This finding was reverse of what was hypothesized and is possibly attributable to the conflicting trends of stress at LUM.

The results presented do establish the following: the freshwater impact significantly declined at LUM throughout the growing season (as was hypothesized), a subsequent lowering of root specific gravities was not observed (calling for rejection of hypothesis 6), and flooding duration (and presumably related stresses, such as sulfide concentration) significantly decreased at LUM throughout the growing season. The absence of a correlation between magnitude of freshwater input (here a macro-scale factor) and root specific gravity bolsters the argument that micro-scale factors lend more influence toward the determination of root specific gravity.

Chapter Four: Summary and Conclusions

A recurring theme in the preceding discussion is the relative importance of micro- versus macro-scale factors in determining the specific gravity of roots within salt marshes. Hypotheses 2 through 6, dealing with landscape interactions, were developed according to macro-scale characteristics (e.g., RSLR) of the sampling sites. Deviations from these trends at the micro-scale (e.g., microtopographic variation), however, proved significant. This ultimately led to the rejection of the hypotheses dealing with landscape interactions, and established that micro-scale factors impart a greater influence than macro-scale factors on root specific gravity modifications.

The idea of a stress-tolerance threshold, which once exceeded calls for root specific gravity alterations, was put forth in the discussion of the hypothesis dealing with process interactions. The possibility that maximum aerenchyma formation within roots may have already occurred as a result of pre-existing environmental conditions was also discussed.

A conceptual model (Figure 3.7) was proposed incorporating the findings of previous research efforts, which link increased environmental stress to increased aerenchyma production and decreased root specific gravity, with those of this study, which highlight the importance of micro-scale factors (e.g., soil chemistry and flooding regime) and propose a threshold of stress tolerance regulating whether vegetation is capable of modifying root specific gravity.

The following conclusions can be made from the data presented:

- Micro-scale factors have a greater impact than macro-scale landscape features on the environmental stresses affecting live root specific gravity.
- A threshold of flood-induced stress tolerance may exist beyond which vegetation will attempt to compensate for these stresses with advantageous alterations in live root specific gravity. Alternatively, aerenchyma formation in roots may already be near maximum in *S. alterniflora* because of constriction in the air pathway at the stem junction (Aerenovski and Howes, 1992).
- The organic content of marsh soils may serve as an indicator of areas where improving natural hydrologic exchange can have a beneficial impact on salt marsh sustainability by increasing throughput and delivering sediments.

Areas of further research that would contribute to the results of this study include:

- Further investigation into the relationships among root specific gravity and the mechanisms of aerenchyma formation including, but not limited to, soil Eh, the concentration of phytotoxins, ethylene concentration, metabolic enzyme activity, and nutrient uptake ability as they operate in a natural field setting. Such data may be used to verify the existence of and quantify a potential stress-tolerance threshold proposed by this study.
- Responses of soil organic matter content to threshold-level stresses and subsequent impact on the relationship between soil organic matter content and root specific gravity.
- Extension of the understanding of variations in root specific gravity and marsh surface elevation through time with respect to nearby tidal creeks for this and other species.

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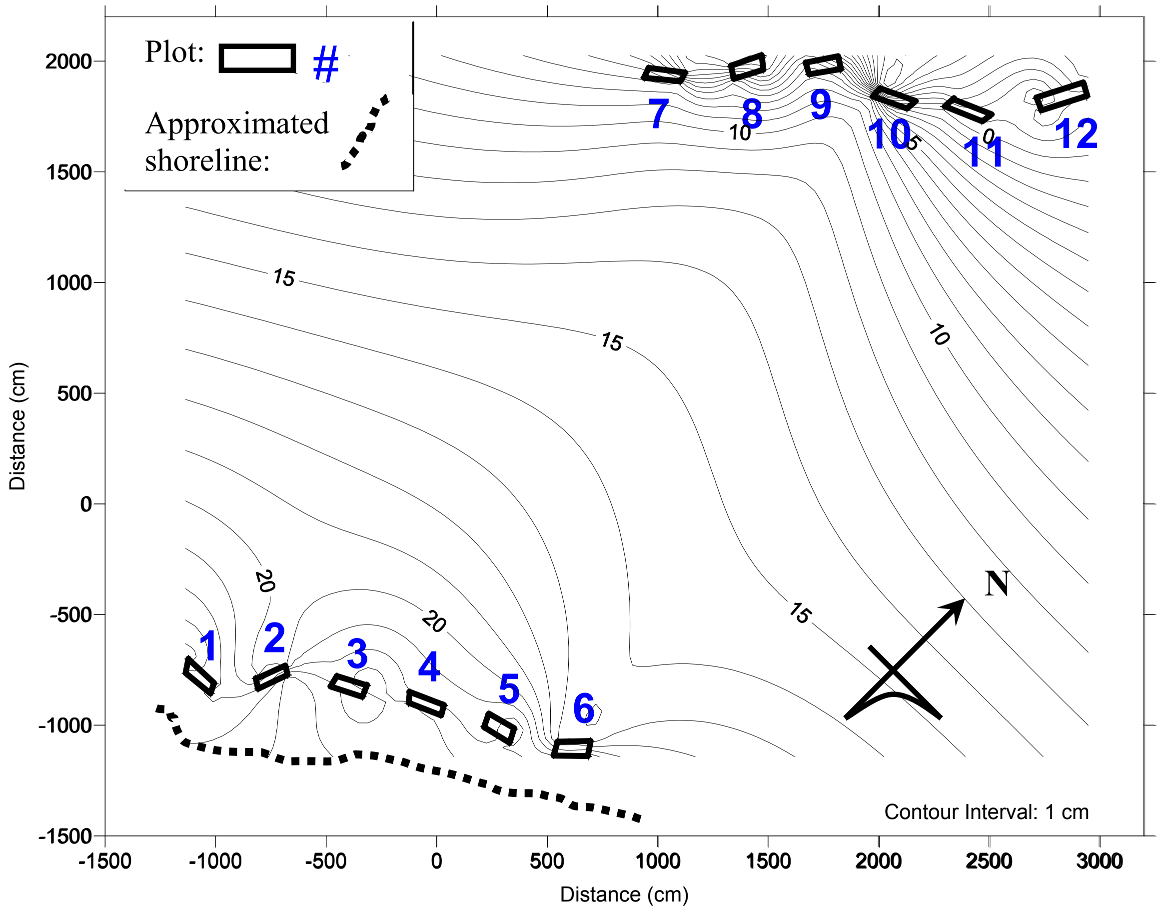
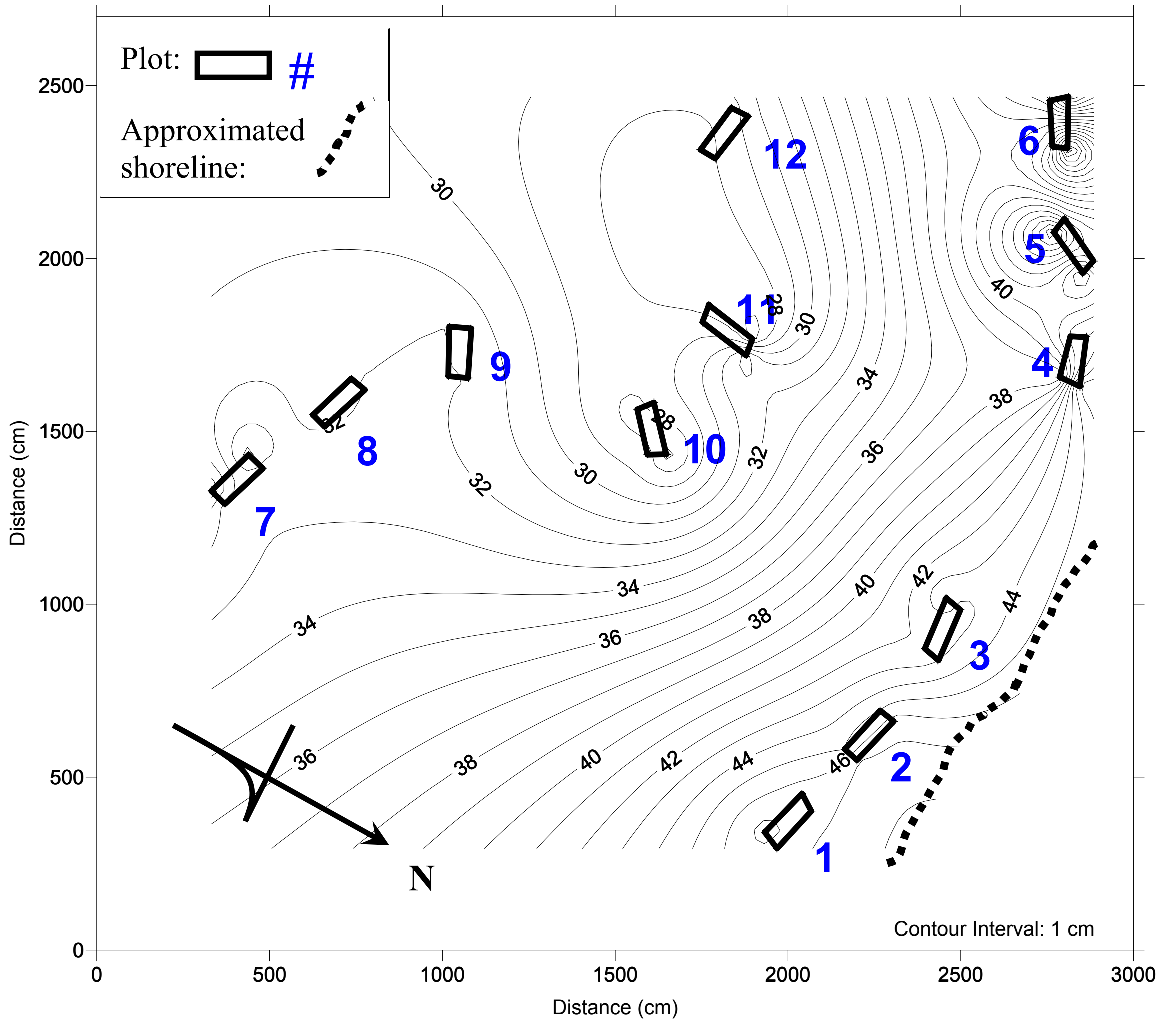
Appendices



Surfer 8 plot of map view of BC plot layout using surveyed elevation of respective water level sensor as a local datum.



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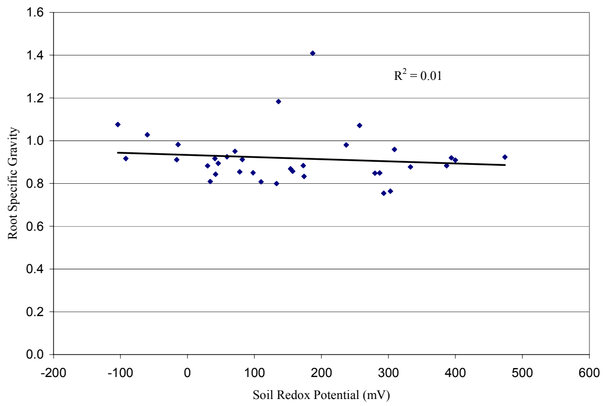
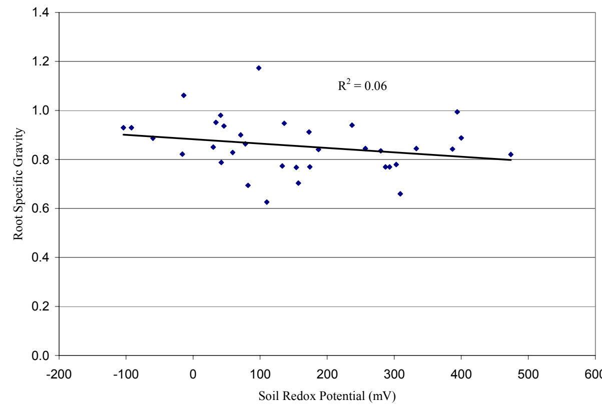
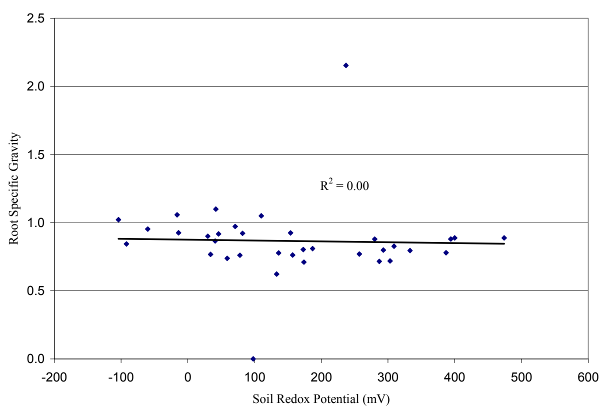
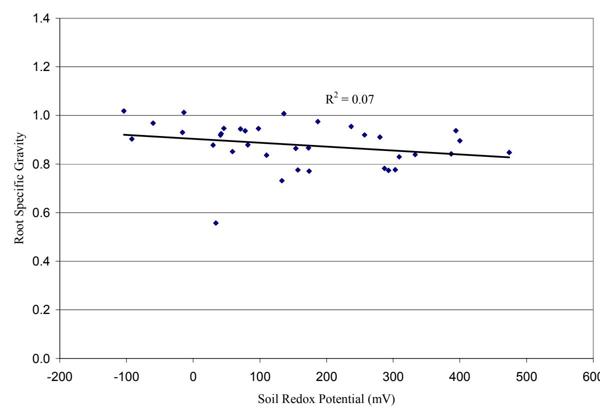


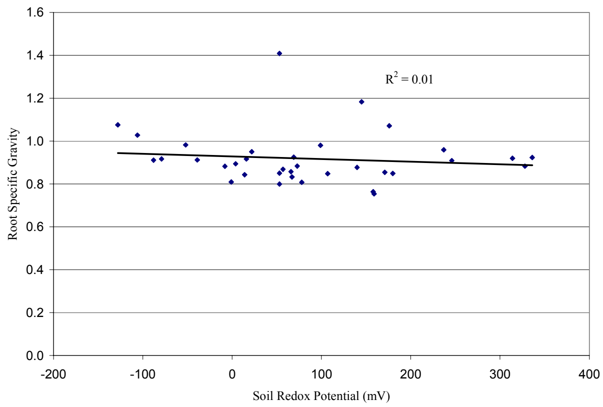


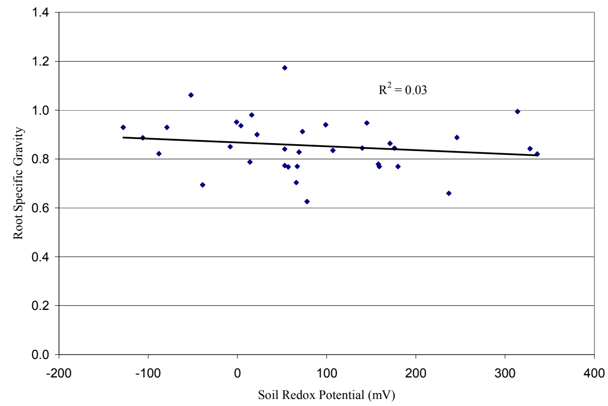
Root specific gravity versus soil redox potential taken at 2 cm below the soil surface taken during the May sampling. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; Combined data set from BC, BL, and LUM (n=35).



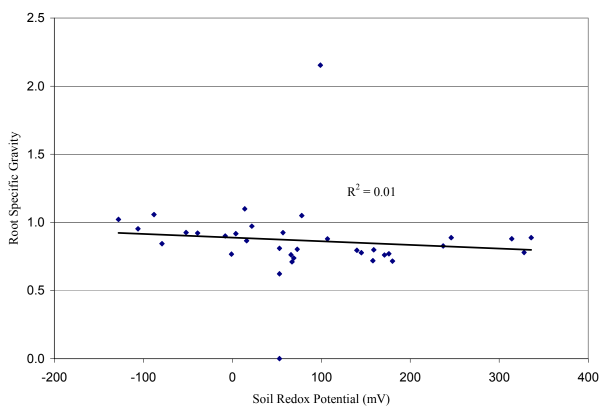


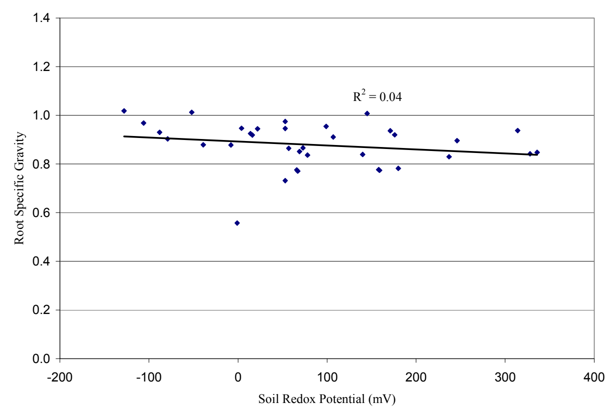
Root specific gravity versus soil redox potential taken at 2 cm below the soil surface taken during the May sampling. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; Combined data set from BC, BL, and LUM (n=35).



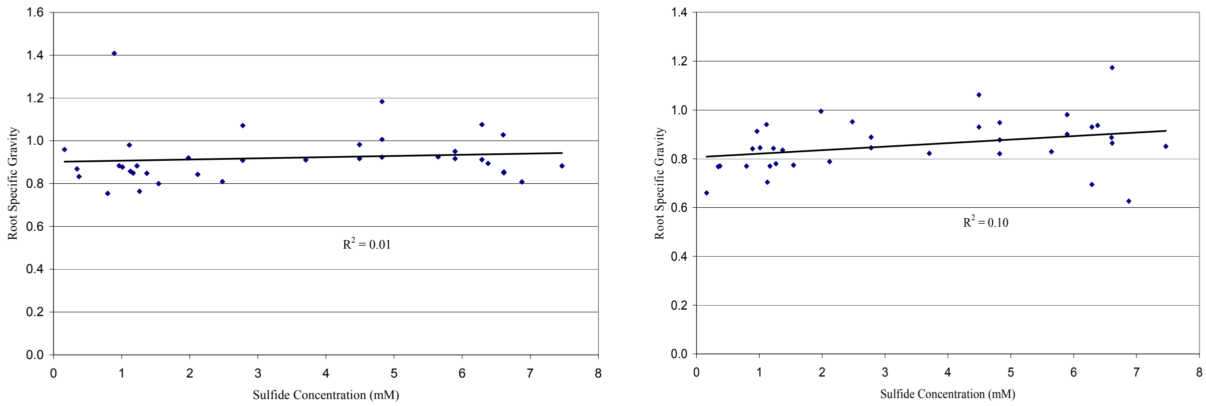


Root specific gravity versus soil redox potential taken at 15 cm below the soil surface taken during the May sampling. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; Combined data set from BC, BL, and LUM (n=35).

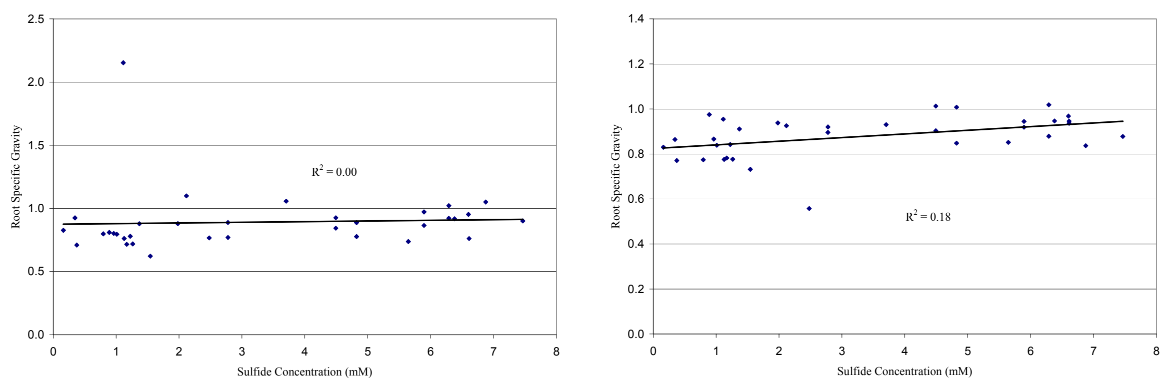




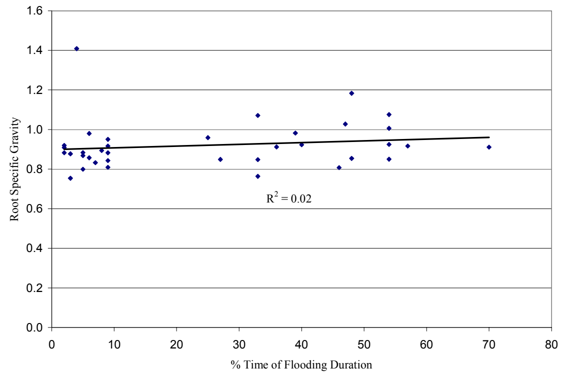
Root specific gravity versus soil redox potential taken at 15 cm below the soil surface taken during the May sampling. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; Combined data set from BC, BL, and LUM (n=35).

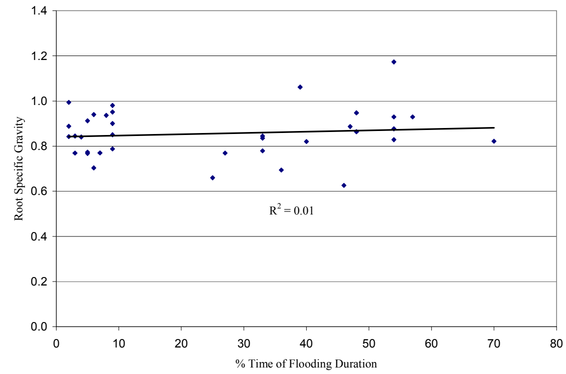


Root specific gravity versus sulfide concentration taken during the May sampling. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; Combined data set from BC, BL, and LUM (n=36).

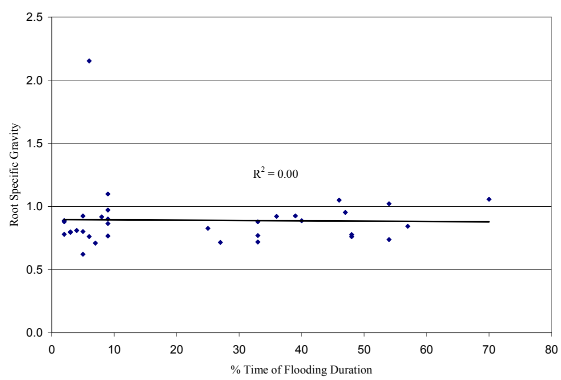


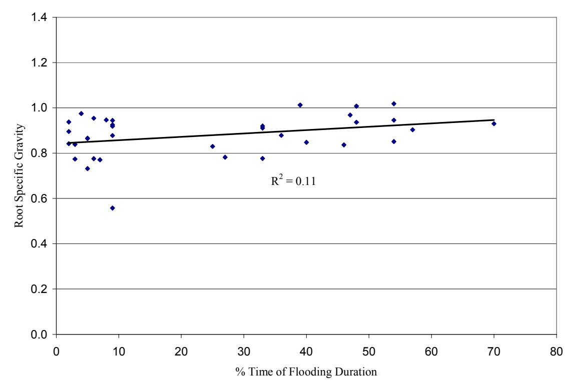
Root specific gravity versus sulfide concentration taken during the May sampling. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; Combined data set from BC, BL, and LUM (n=36).



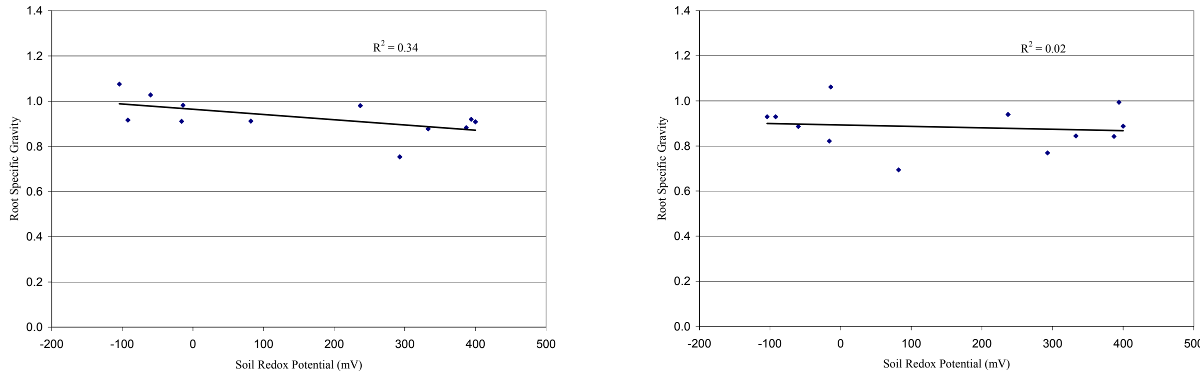


Root specific gravity versus % TFD (averaged over the 28 days prior to sample collection) taken during the May sampling. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; Combined data set from BC, BL, and LUM (n=36).

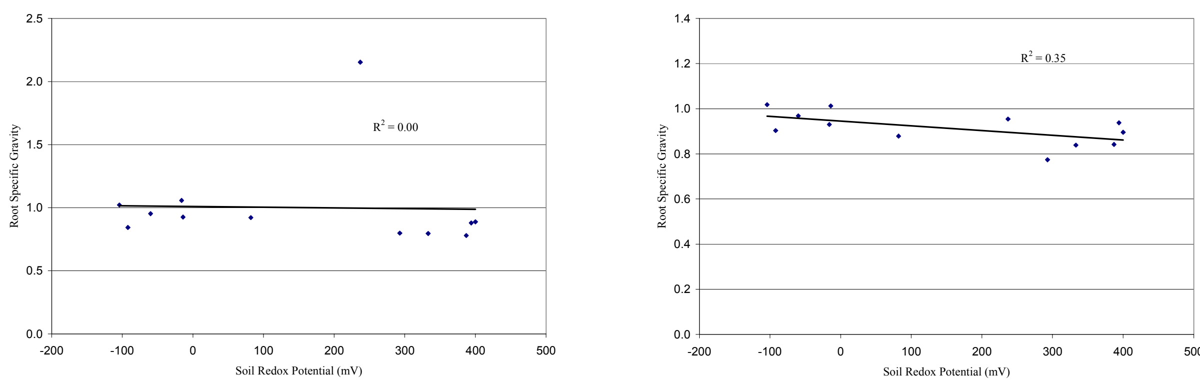




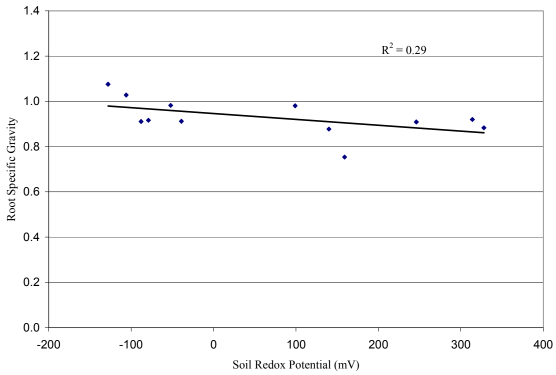
Root specific gravity versus % TFD (averaged over the 28 days prior to sample collection) taken during the May sampling. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; Combined data set from BC, BL, and LUM (n=36).

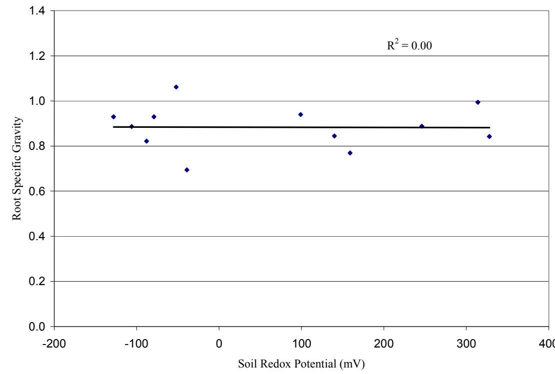


Root specific gravity versus soil redox potential taken at 2 cm below the soil surface. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; BC data set for the May sampling session (n=12).

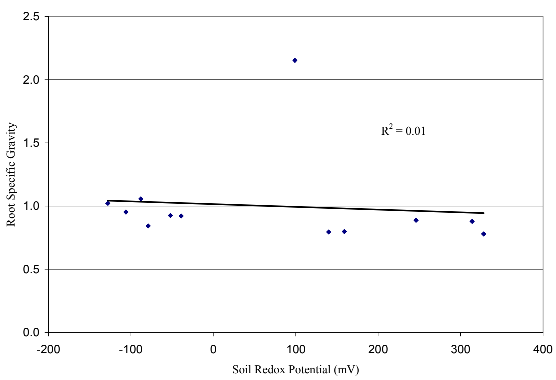


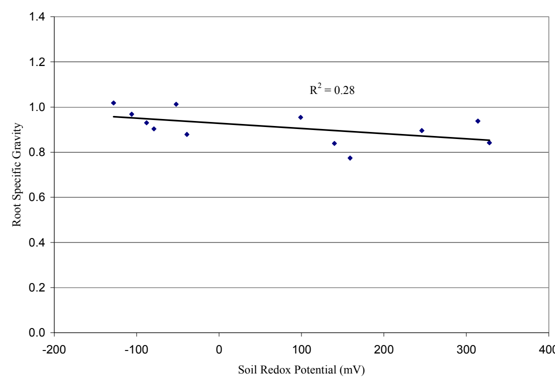
Root specific gravity versus soil redox potential taken at 2 cm below the soil surface. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; BC data set for the May sampling session (n=12).



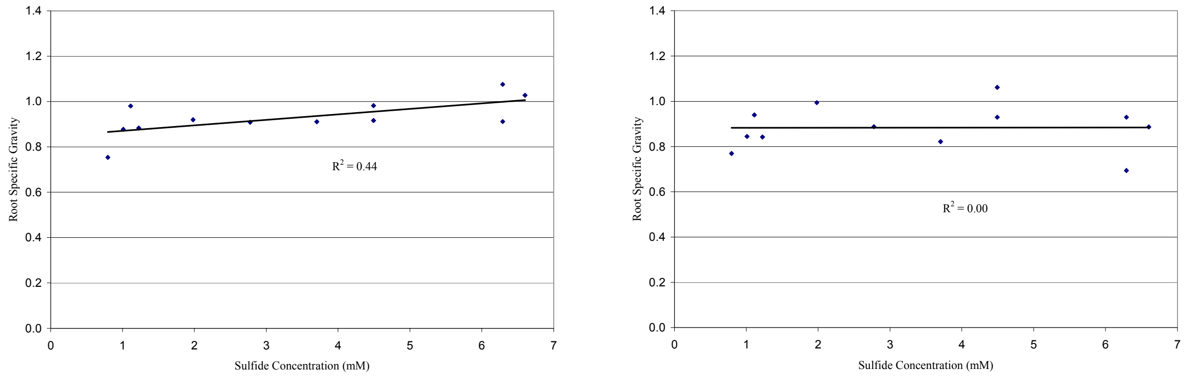


Root specific gravity versus soil redox potential taken at 15 cm below the soil surface. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; BC data set for the May sampling session (n=12).

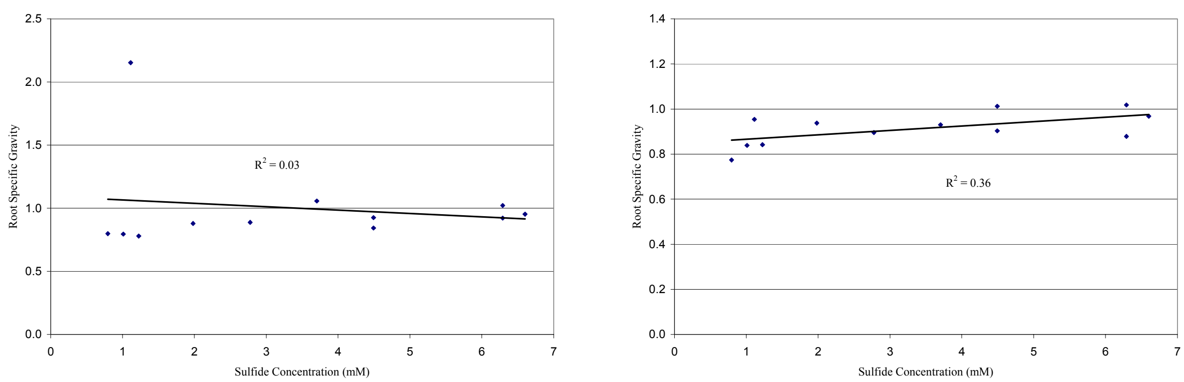




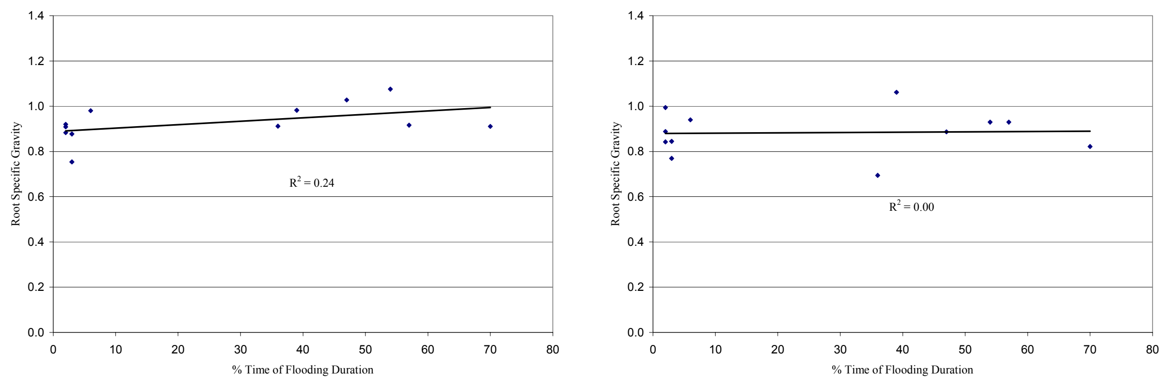
Root specific gravity versus soil redox potential taken at 15 cm below the soil surface. Left: root specific gravity taken at 10-5 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; BC data set for the May sampling session (n=12).



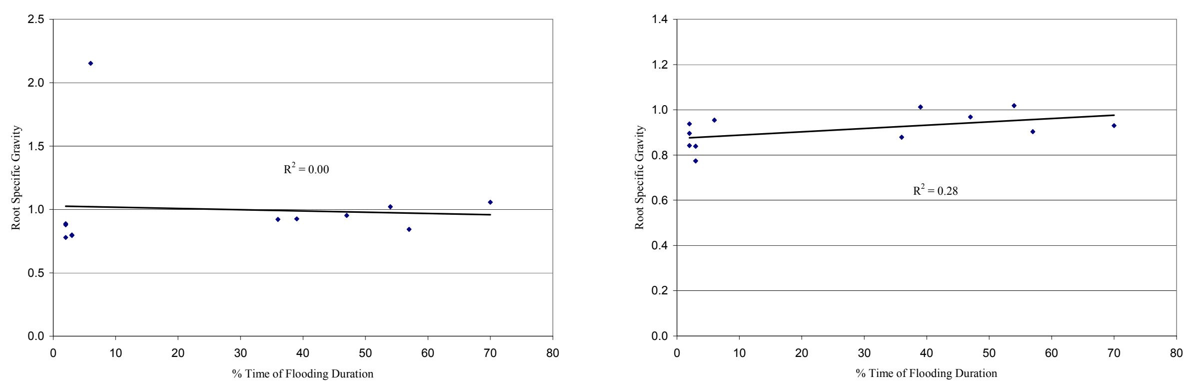
Root specific gravity versus sulfide concentration. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; BC data set for the May sampling session (n=12).



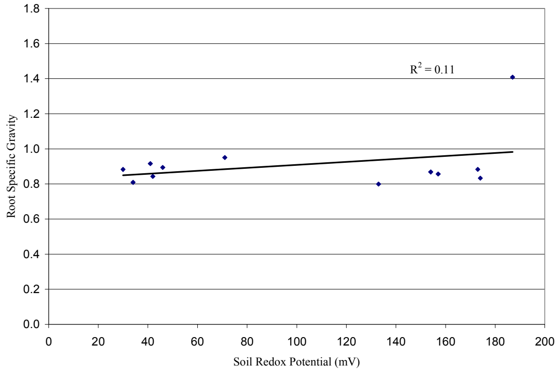
Root specific gravity versus sulfide concentration. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; BC data set for the May sampling session (n=12).

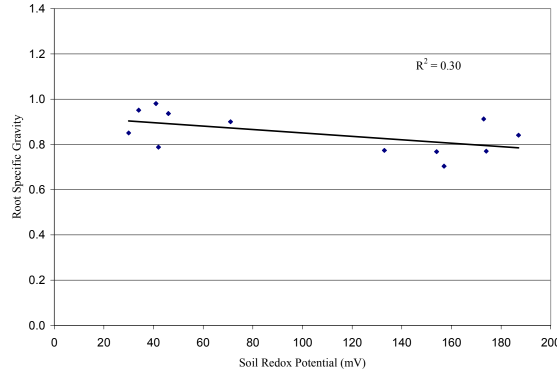


Root specific gravity versus % TFD (averaged over the 28 days prior to sample collection). Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; BC data set for the May sampling (n=12).

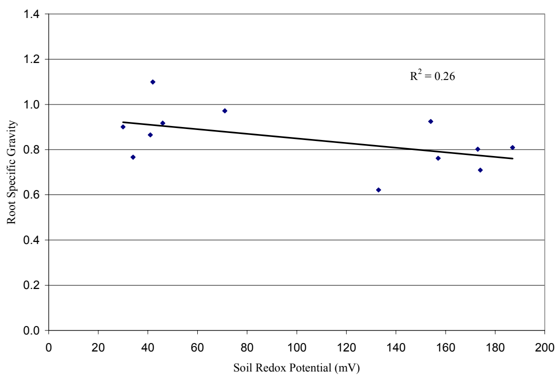


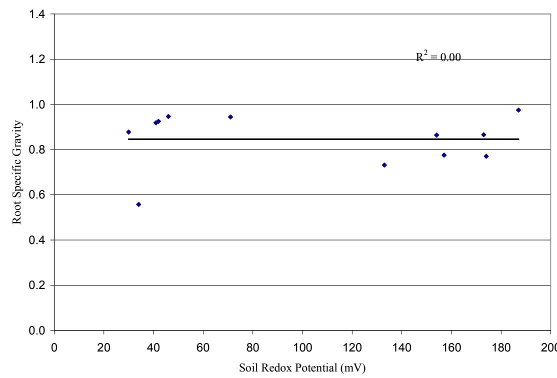
Root specific gravity versus % TFD (averaged over the 28 days prior to sample collection). Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; BC data set for the May sampling (n=12).



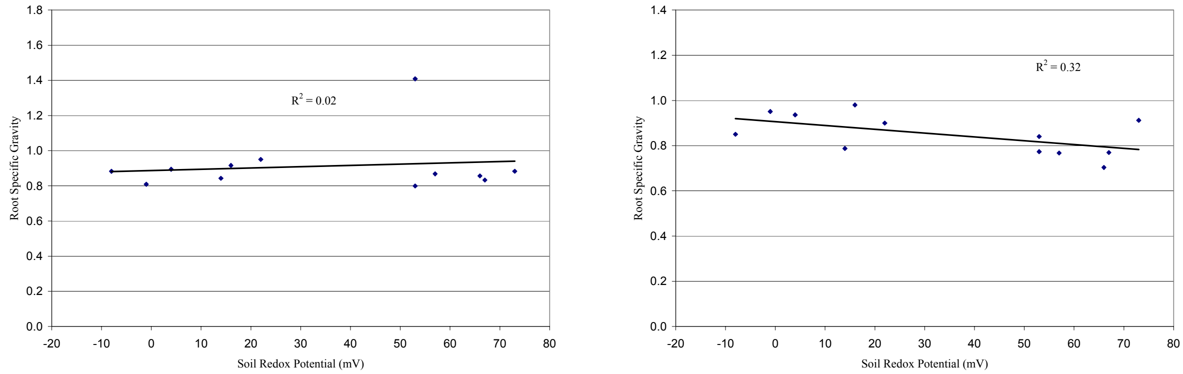


Root specific gravity versus soil redox potential taken at 2 cm below the soil surface. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; BL data set for the May sampling session (n=12).

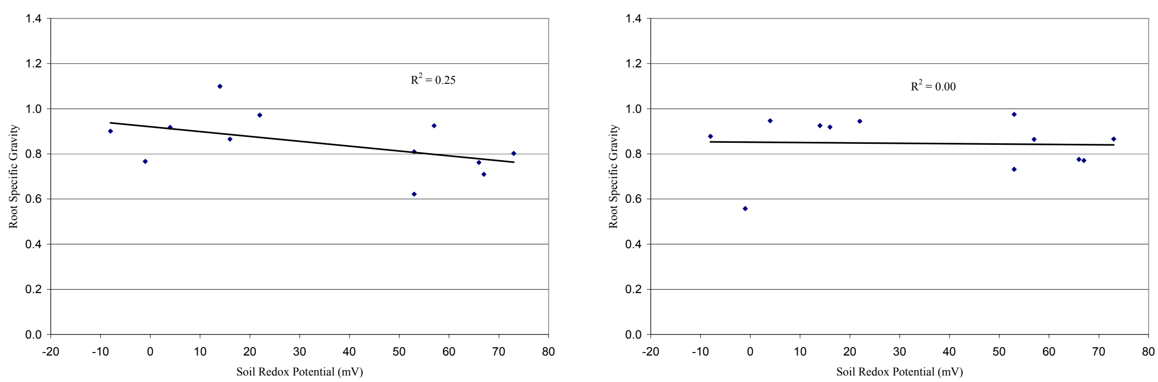




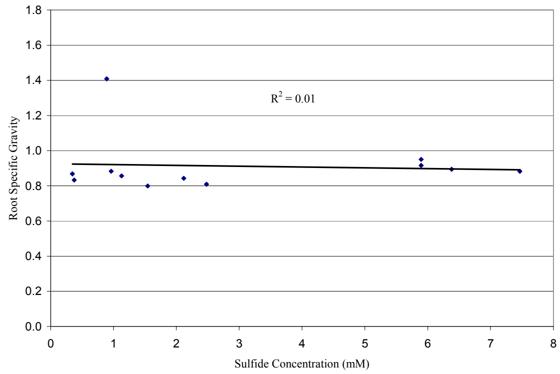
Root specific gravity versus soil redox potential taken at 2 cm below the soil surface. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; BL data set for the May sampling session (n=12).

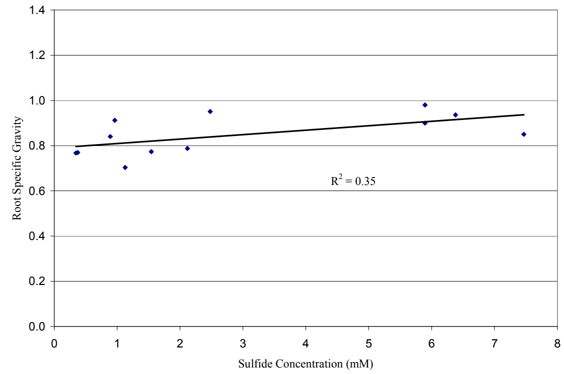


Root specific gravity versus soil redox potential taken at 15 cm below the soil surface. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; BL data set for the May sampling session (n=12).

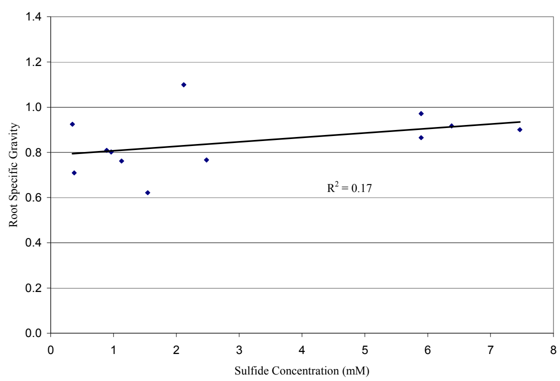


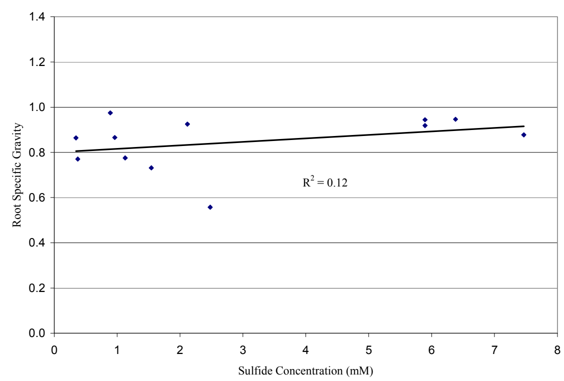
Root specific gravity versus soil redox potential taken at 15 cm below the soil surface. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; BL data set for the May sampling session (n=12).



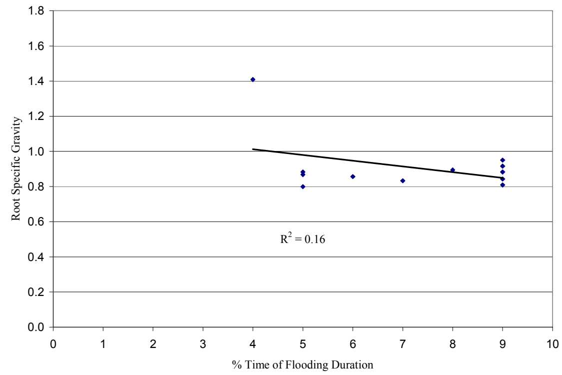


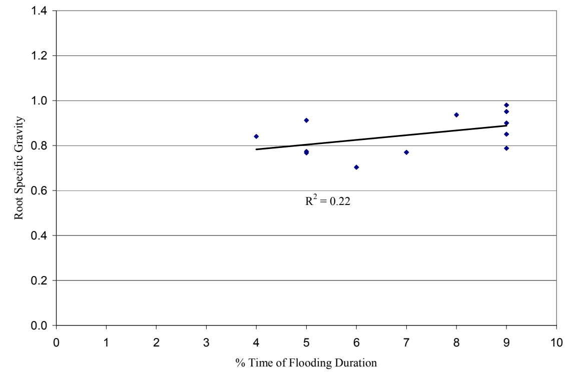
Root specific gravity versus sulfide concentration. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; BL data set for the May sampling session (n=12).



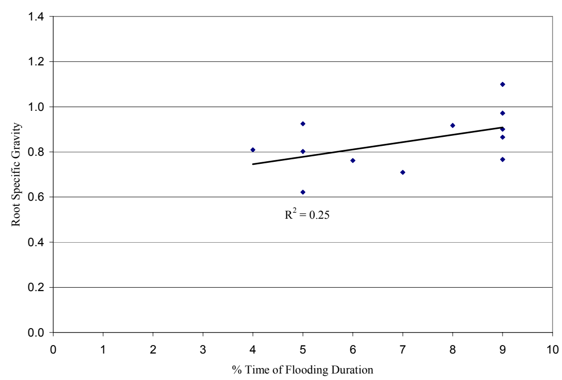


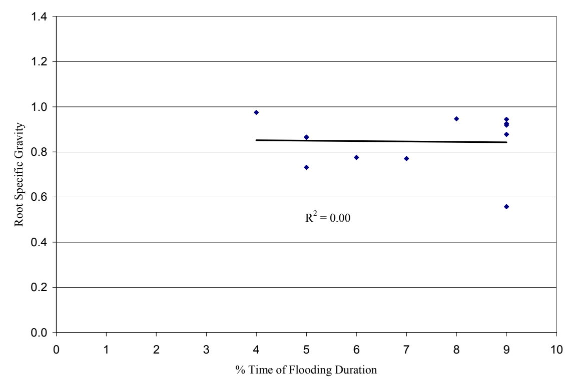
Root specific gravity versus sulfide concentration. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; BL data set for the May sampling session (n=12).



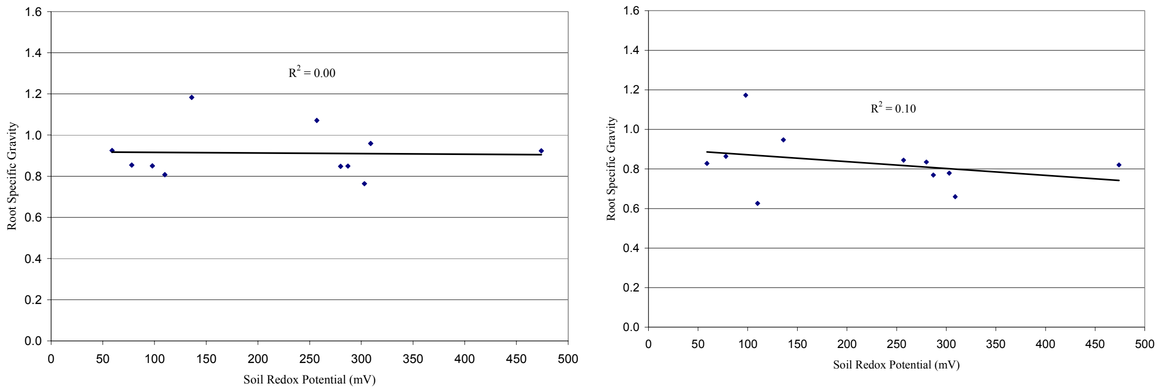


Root specific gravity versus % TFD (averaged over the 28 days prior to sample collection). Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; BL data set for the May sampling (n=12).

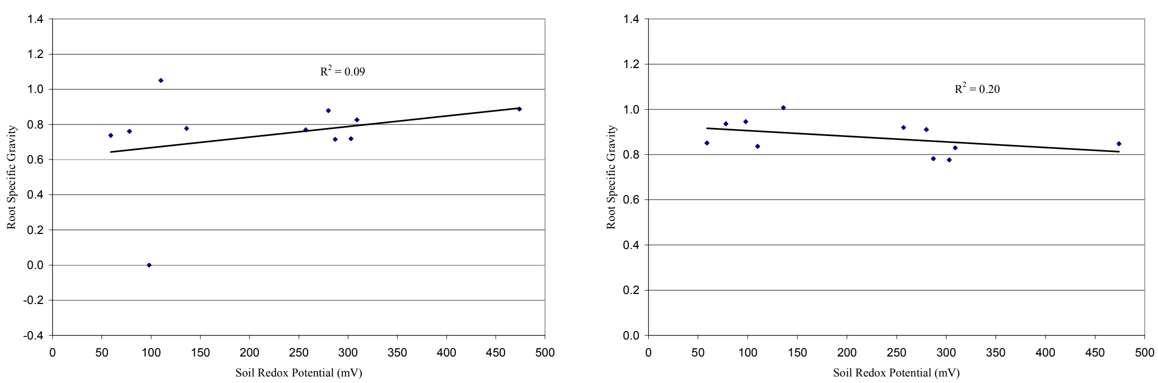




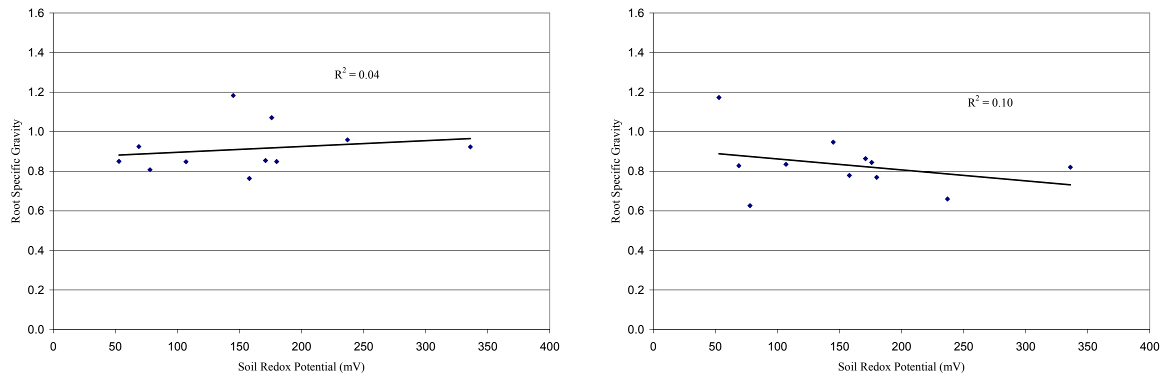
Root specific gravity versus % TFD (averaged over the 28 days prior to sample collection). Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; BL data set for the May sampling (n=12).



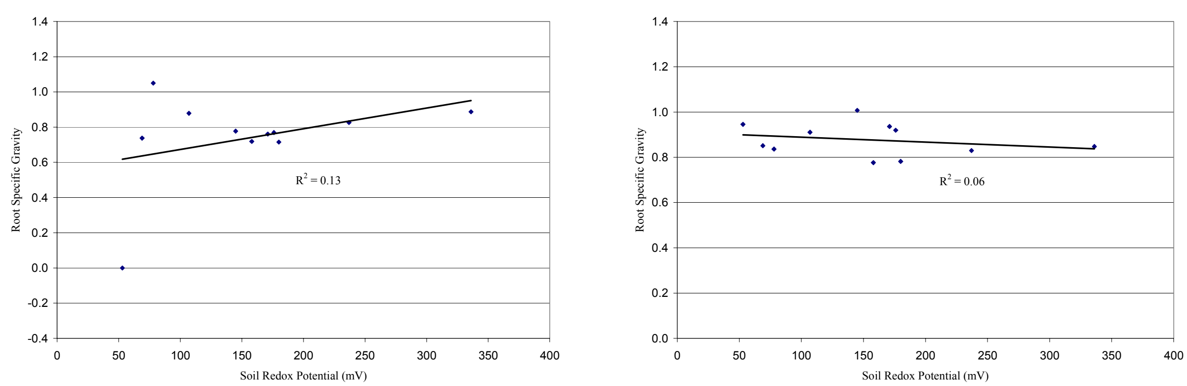
Root specific gravity versus soil redox potential taken at 2 cm below the soil surface. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; LUM data set for the May sampling session (n=11).



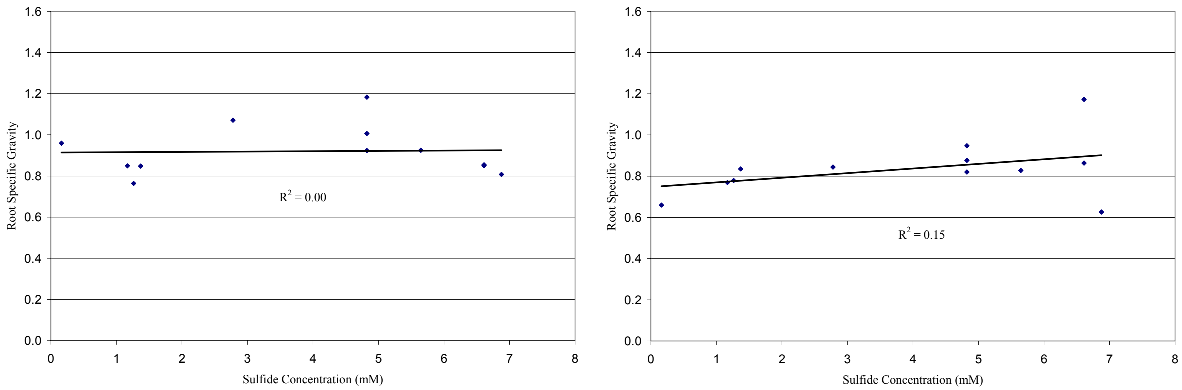
Root specific gravity versus soil redox potential taken at 2 cm below the soil surface. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; LUM data set for the May sampling session (n=11).



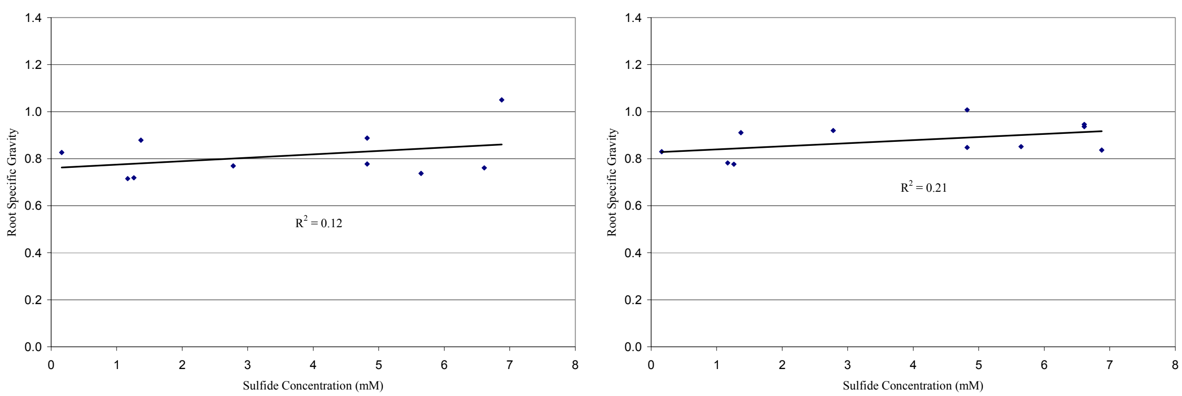
Root specific gravity versus soil redox potential taken at 15 cm below the soil surface. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; LUM data set for the May sampling session (n=11).



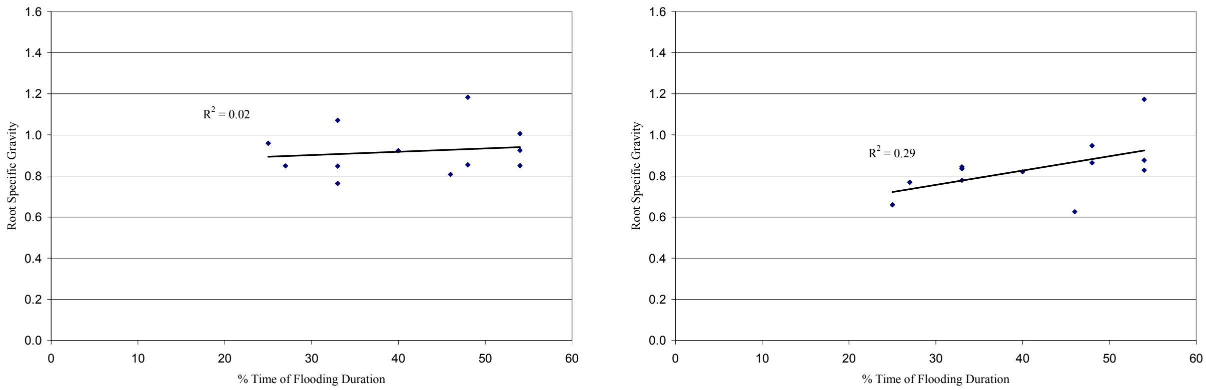
Root specific gravity versus soil redox potential taken at 15 cm below the soil surface. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; LUM data set for the May sampling session (n=11).



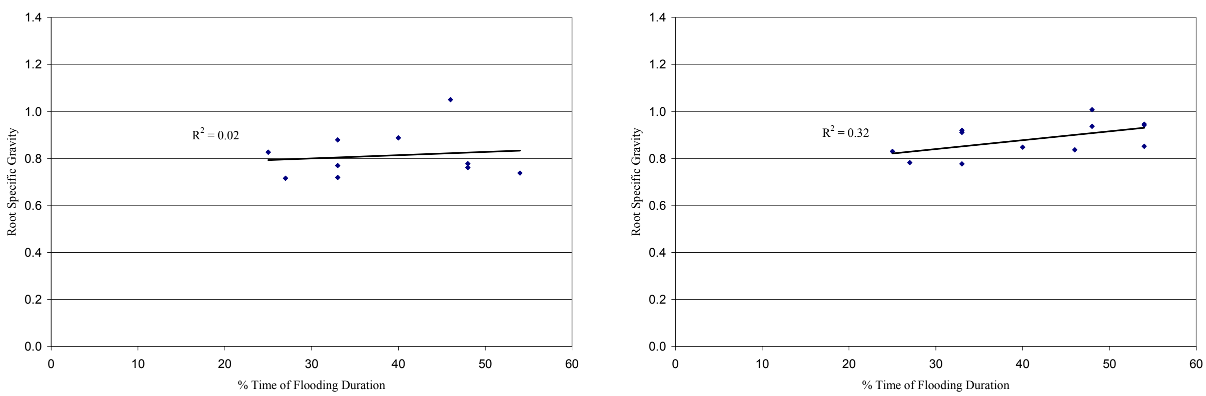
Root specific gravity versus sulfide concentration. Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; LUM data set for the May sampling session (n=12).



Root specific gravity versus sulfide concentration. Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; LUM data set for the May sampling session (n=12).



Root specific gravity versus % TFD (averaged over the 28 days prior to sample collection). Left: root specific gravity taken at 0-5 cm soil depth; Right: root specific gravity taken at 5-10 cm soil depth; LUM data set for the May sampling (n=12).



Root specific gravity versus % TFD (averaged over the 28 days prior to sample collection). Left: root specific gravity taken at 10-15 cm soil depth; Right: root specific gravity taken at 0-15 cm soil depth; LUM data set for the May sampling (n=12).

Vita

Daniel Gill was raised in Mentor, Ohio. He received his B.S. in Biological Engineering from The Ohio State University.