ENVIRONMENTAL GRADIENTS AND PLANT DISTRIBUTIONS IN CAROLINA BAYS

by

LAURA ELIZABETH BURBAGE

(Under the Direction of Rebecca R. Sharitz)

ABSTRACT

Carolina bays in the southeastern United States harbor a substantial number of rare plant species and are critical amphibian habitat. However, the majority of these wetlands are altered, and many have been considerably damaged. Recent restoration efforts have necessitated the documentation of reference Carolina bays. In addition, there is a need for concrete and detailed information about wetland plants so that restorations may be better planed.

This study investigated four Carolina bays for use as reference systems in restoration projects. Variability of soil characteristics was examined and spatial and elevational gradients of % C, % N, % P, C:N, pH, % sand, % silt, % clay, and available soil water were documented. In addition, environmental variables with relationships to plant distributions were determined. Distribution limits of significant variables were estimated and compared to field distributions for graminoids, floating-leaved species, *Panicum hemitomon* and *Nymphaea odorata.*

INDEX WORDS: Carolina bays, wetland restoration, environmental gradients, *Nymphaea odorata*, *Panicum hemitomon,* South Carolina

ENVIRONMENTAL GRADIENTS AND PLANT DISTRIBUTIONS IN CAROLINA BAYS

by

LAURA ELIZABETH BURBAGE

B.A., Smith College, 1994

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment

of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2004

ENVIRONMENTAL GRADIENTS AND PLANT DISTRIBUTIONS IN CAROLINA BAYS

by

LAURA ELIZABETH BURBAGE

Major Professor: Rebecca Sharitz

Committee: Beverly Collins
Rhett Jackson
Kenneth McLeod

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
December 2004

ACKNOWLEDGEMENTS

I would like to thank Rebecca R. Sharitz, my major professor, for her unwavering support throughout my graduate study. Thanks also to my advisory committee: Beverly Collins, C. Rhett Jackson, and Kenneth McLeod for their thoughtful input. Thanks to Bruce Allen and Paul Stankus for their help with fieldwork, especially to Robert Lide for providing bay hydrologic data. Thanks to Tom Maddox, Dr. Larry West, and Jodi Boyce for laboratory assistance. Finally, I would like to thank my husband Chris and my family for their undying support and patience.

TABLE OF CONTENTS

CHAPTER

LIST OF TABLES

LIST OF TABLES CONTINUED

Page

LIST OF FIGURES

LIST OF FIGURES CONTINUED

Page

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Carolina Bays and Wetland Restoration

Carolina bays are isolated wetlands that are unique geomorphic features in the southeastern U.S. Although the term “Carolina bay” has at times been used ambiguously (Lide 1997), it is generally restricted to wetlands sharing a specific geomorphic structure. Carolina bays are shallow, ovate to elliptical depressions of northwest-southeast orientation, with the deepest portion towards the southeast (Prouty 1952). They vary greatly in size, from 50 m to 8 km along the longest axis (Sharitz and Gibbons 1982). They are surrounded by a sand rim that rises above the surrounding terrain and is usually largest on the southeast side (Prouty 1952, Gamble et al. 1977). Many bays have an impervious clay lens near the underlying soil surface. The lens may be overlain by sands and organic soil or peat (Prouty 1952, Gamble et al. 1977, Sharitz and Gibbons 1982, Bennett and Nelson 1991). It is estimated that 10,000 to 20,000 Carolina bays currently exist (Richardson and Gibbons 1993).

The hydrologic regimes of Carolina bays are driven primarily by precipitation and evapotranspiration. With few exceptions, surface flows in or out of Carolina bays are lacking (Sharitz and Gibbons 1982), and groundwater influence is generally considered to be limited due to the underlying clay hardpan (Lide et al. 1995, Sharitz 2003). However, some bays can exhibit considerable interactions with the water table, such as lateral groundwater discharge from high water tables and vertical recharge during ordinary levels or drought periods (Lide et al. 1995), and a few bays may be spring-fed (Bennett and Nelson 1991). Water levels in individual bays can vary greatly, although ponding usually occurs in the fall and winter, and drying in the spring and summer (Lide et al. 1995). The amount of flooding can vary from nearly continuous to rarely, resulting in a range of wetland types (De Steven and Toner 2004), although many flooded bays can regularly dry completely (Bennett and Nelson 1991, Sharitz 2003). Due to their isolated nature, Carolina bay waters have been found to be ombrotrophic, with low calcium and carbonate concentrations (Schalles and Shure 1989, Newman and Schalles 1990).

The fluctuating hydroperiods of Carolina bays create a constantly shifting environment, which allows for a diverse assemblage of plants and animals. Dominance of the more competitive plants is lessened by the variable hydrologic conditions that create areas where less competitive species find refugia. Differences in hydroperiods between bays due to bay geomorphology and between years due to climatic variation further increase this diversity (Sharitz 2003). Bay ecosystems include various gradations of forest, open pond, pocosin, and depression meadow (Bennett and Nelson 1991, Collins and Battaglia 2001). Strong zonation patterns are often apparent in the vegetation along the water depth gradient (Sharitz and Gibbons 1982, Tyndall et al. 1990, Richardson and Gibbons 1993, Collins and Battaglia 2001). Such zonation patterns are strongly tied to bay morphology and hydrologic regime (Collins and Battaglia 2001).

The ecological importance of hydrologically isolated wetlands has been the focus of recent attention. Isolated wetlands play a crucial role in maintaining regional biodiversity (Semlitsch and Bodie 1998). Naturally occurring ponds are uncommon in South Carolina (Bennett and Nelson 1991). Although Carolina bays are the dominant natural lentic environment in much of the southeast (Richardson and Gibbons 1993), they represent very unusual ecosystems. Many rare and endangered flora and fauna species are known to inhabit Carolina bays (Bennett and Nelson 1991, Sutter and Kral 1994, Edwards and Weakley 2001). Such isolated wetlands with variable hydroperiods are thought to be critical habitats for rare plant and amphibian species, in part as a result of lessened competition or predation (Sutter and Kral 1994, Snodgrass et al. 2000, Gibbons 2003). During droughts or other natural disturbances, rare plants can germinate from the seedbank which is unusually diverse and may contain species not normally reflected in the standing vegetation (Kirkman and Sharitz 1994, Collins and Battaglia 2001).

Many species of waterfowl and non-game wetland birds rely on isolated wetlands for foraging and nesting, with some species also requiring the contiguous uplands (Naugle et al. 2001). Carolina bays provide feeding and nesting habitat for aquatic birds and waterfowl, aquatic reptiles, and upland vertebrates, as well as habitat for many animal species with unique requirements (Richardson and Gibbons 1993). Aquatic predators requiring permanent water are often excluded, creating a sanctuary for many prey species (Sharitz and Gibbons 1982, Richardson and Gibbons 1993), and the role of isolated wetlands as breeding habitat for amphibians has been extensively studied (Semlitsch 1981, Sharitz and Gibbons 1982, Snodgrass et al. 2000, Gibbons 2003). In addition, Carolina bays have an unusually rich community of zooplankton, yielding more species than other temporary water bodies (Mahoney et al. 1990).

In spite of their known ecological benefits, isolated wetlands are offered less regulatory protection than other wetlands, in part due to a lack of recognition of their ecological importance (Kirkman et al. 1999). Recent regulatory decisions regarding the protection of isolated wetlands (Nadeau and Leibowitz 2003), threats to their stability from development (Semlitsch and Bodie 1998, Downing et al. 2003, Whigham and Jordan 2003), and the need for conservation guidance

(Naugle et al. 2001), have prompted efforts to document and understand their ecological processes and environmental functions (Kirkman et al. 1999, Snodgrass et al. 2000, Leibowitz 2003).

Recognition of the value of Carolina bays and their risk of destruction or degradation has resulted in recent studies aimed at encouraging and facilitating bay preservation, conservation, and restoration. The need for the identification of bays has been repeatedly emphasized (Sharitz and Gibbons 1982, Richardson and Gibbons 1993, Sharitz and Gresham 1998). Efforts have been made to catalogue Carolina bays and inventory their flora and fauna, especially in undisturbed bays (Tyndall et al. 1990, Bennett and Nelson 1991). Some studies have begun to quantify the number and distribution of rare plant species in southeastern depression wetlands, as well as investigate traits of these rare plants in terms of life history characteristics, genetic isolation, and the role of the seed bank in their continued existence (Bennett and Nelson 1991, Kirkman and Sharitz 1994, Sutter and Kral 1994, Collins et al. 2001, Edwards and Weakley 2001). In order to facilitate sound management strategies, investigations have begun to decipher the biotic and abiotic interactions of Carolina bays, as well as the effects of natural and anthropogenic disturbances. These studies have documented the important role of the seed bank in concert with fire and soil disturbance in maintaining plant composition and diversity (Kirkman and Sharitz 1994, Collins and Battaglia 2001). Effects of past land use in and around Carolina bays has been found on present-day vegetation (Kirkman et al. 1996), as has current surrounding land use on seed bank composition (Poiani and Dixon 1995).

The Role of Disturbance in Carolina Bays

Natural disturbances are part of the dynamics of Carolina bays and often guide community structure and development (Bennett and Nelson 1991). Fire is a common element in many bays, especially those that are frequently dry (Bennett and Nelson 1991). A variety of community types and rare plant species rely on fire as a part of the habitat (Bennett and Nelson 1991, Sharitz and Gresham 1998), and fire is likely responsible for the suppression of dominant herbs and the prevention of tree establishment (Kirkman and Sharitz 1994). Peat deposits are also reduced by fire (Sharitz and Gibbons 1982). The fluctuating hydrologic regime, characteristic of most Carolina bays, causes frequent restructuring of the plant community and alters recruitment patterns (Kirkman 1992, Collins and Battaglia 2001). Other natural disturbances include windfall of trees (Bennett and Nelson 1991) and rooting by animals during drydown (Kirkman and Sharitz 1994), both of which expose soils, encouraging germination from the seed bank.

Despite the reliance of Carolina bay habitats on natural disturbances, anthropogenic disturbances have caused considerable damage. Few natural Carolina bays remain (Richardson and Gibbons 1993); in South Carolina an estimated 97% of Carolina bays have been disturbed to some extent, with 64% being completely altered in nature (Bennett and Nelson 1991). The common impression of depression wetlands is that they are wastelands (Sharitz and Gibbons 1982). This antipathy towards wetlands, as well as a lack of public appreciation for these habitats (even among ecologists), is partly responsible for the lack of concern regarding the alteration of Carolina bay wetlands (Sharitz and Gibbons 1982, Bennett and Nelson 1991). Small bays of less than 0.75 hectares may represent 32% of all Carolina bays in South Carolina (Bennett and Nelson 1991). Their small size may make them particularly vulnerable to disturbance.

The majority of historic disturbances to Carolina bays were agricultural (Bennett and Nelson 1991), due in part to their ability for providing increased crop yields (Sharitz and

Gresham 1998). Between the 1950s and 1970s, the draining of croplands was encouraged by governmental programs (Sharitz and Gresham 1998). Ditches for draining the bays are extremely common (Sharitz and Gresham 1998), and were observed in almost all bays in a South Carolina study (Bennett and Nelson 1991). The draining of sediments not normally exposed may have increased decomposition rates of the soil organic matter (Richardson and Gibbons 1993). Further preparation of Carolina bays for agriculture has included liming of soils and fertilizing, as well as spraying with herbicides (Sharitz and Gibbons 1982, Sharitz and Gresham 1998). In addition to the draining of bays for row-crops, many were used as pasture, and small wells were sometimes dug as watering holes for cattle in the central portions (Kirkman et al. 1996). Drier bays were often used for pine plantations (Bennett and Nelson 1991, Sharitz and Gresham 1998), and damage from managed forestry practices could be considerable due to the extensive draining and disturbance of the bay soils (Sharitz and Gresham 1998).

The historical suppression of fire may have caused considerable changes in the plant communities in Carolina bays, such as the dominance of more competitive species and the exclusion of rare species that require soil disturbances for establishment (Kirkman and Sharitz 1994). The absence of fire, along with altered hydroperiods, may be responsible for the conversion of some herbaceous bays into forested bays (Kirkman 1992). Soil properties may also be affected by the lack of fire; suppression in bays that would have normally burned likely increases peat deposits (Sharitz and Gibbons 1982). Other past types of disturbances documented in Carolina bays include the presence of roads, especially on the elevated, well-drained sand rims, and occasional sand borrow pits.

Recent disturbances to Carolina bays also include commercial and residential development, which have had severe impacts. Much of this disturbance is unquantifiable due to a lack of records (Richardson and Gibbons 1993). Additionally, a few bays have been used in the treatment of sewage effluent (Richardson and Gibbons 1993, Sharitz and Gresham 1998).

Restoration of Wetland Communities and Knowledge Gaps

During the initial stages of restoration planning, a general understanding of the desired wetland type is necessary. Many studies and reviews have classified and compared plant community types and their associated environmental conditions (Stolt and Rabenhorst 1987, Breen et al. 1988, Brinson 1991, Richardson 1991, Brinson 1993, Zoltai and Vitt 1995, Bedford et al. 1999, Bedford and Godwin 2003). These studies have generally been conducted at the scale of the individual wetland. Such community classifications are helpful when determining feasible restoration goals, as general associations within the biotic community and the abiotic conditions are understood. Current abiotic conditions can be used to determine which wetland communities are likely to succeed, or the desired wetland type may dictate whether environmental conditions must be altered for success. Community-level studies have enabled some fine-tuning of restoration plans. Such studies have compared different plant communities of similar type and have documented subtle differences in their associated abiotic characteristics both between separate wetlands and within contiguous wetlands (Schalles and Shure 1989, van der Valk et al. 1994, Craft et al. 1995, Fisher et al. 1996, Wheeler and Proctor 2000, Girardin et al. 2001, De Steven and Toner 2004). While a good deal is understood about the associations between wetland types, plant community types, and general environmental conditions, there have been few studies of the relationships between specific species and environmental conditions within particular wetlands. Where restoration must include planting or seeding to reach the desired endpoint, detailed information about the requirements of specific species is needed to prevent the installation of species in inappropriate conditions. Such information can be especially important when detailed pre-disturbance assessments are not available. A better understanding of species requirements can also be used to manipulate site conditions to meet desired vegetation patterns, such as the distribution of specific species for wildlife use.

Models of Wetland Community Development

To create assemblages of vegetation for restoration, knowledge about how assemblages are created is needed (Metzker and Mitsch 1997, Lockwood and Pimm 1999). Weiher and Keddy (1995) advocated research towards predicting the assemblage of communities from common species pools by finding the patterns in species assemblages and shared traits as well as determining how these patterns change over space and time. Keddy (1999) proposed that communities are produced by quantifiable relationships between multiple environmental factors and the properties of the communities, and that the factors change through time.

Wisheu and Keddy (1992) proposed that the theory of centrifugal organization could be used to explain the distributions of plants in wetlands and other systems, especially along resource/stress gradients. The main tenet was that there is a core habitat of low disturbance and high fertility in which all species would perform best. Multiple environmental gradients, acting as constraints, sort species by their inclusive niches and competitive hierarchies. The ensuing pattern was postulated to result in large, strongly competitive, leafy dominants in the core habitat and competitive exclusion restricting some species to the peripheral niches.

Illustrations of centrifugal organization theory have been presented as 2-dimensional circles. However, such organization is more likely to be multi-dimensional. The model uses various disturbances and fertilities as gradients, with an example of habitats for each extreme at the outer edges (Wisheu and Keddy 1992). Wetlands include a broad variety of habitats and environmental characteristics, each likely to be an axis. Additionally, centrifugal organization may not explain the distributions of very dissimilar species such as graminoids and floating-leaved plants, or even the distributions of all graminoids. Due to morphological and physiological differences between species, there is not necessarily one ideal niche or core habitat. Some wetland plant species require submergence for survival, yet some require well-drained areas. The abundance of water and flood duration are both stressors and resources. While the vegetation of some wetlands might be arranged into centrifugal or zoned patterns, there may be cases where these patterns are simply coincident rather than causative, and other cases where such arrangement is not possible due to the non-existence of a singular core habitat.

Another model of vegetation assembly was proposed by van der Valk (1981), where succession in wetlands was predicted by species life-history traits. The species in a pool of propagules are filtered by “sieves” of environmental characteristics acting against life-span, propagule longevity, and establishment requirement traits. A key premise of the model was that two environmental characteristics (flooded or drawdown) act as filters or sieves, removing species lacking adaptation mechanisms. For example, annual species with seeds that rely on exposed sediment for germination will be removed from the vegetation in a wetland that becomes flooded. If the seeds of these annuals are short-lived, then the species can be extirpated altogether. However, the model uses environmental characteristics as categories rather than gradients. It assumes that a particular species will survive in either flooded or exposed conditions instead of considering a certain water depth tolerance. It also does not take fluctuating water level conditions into account.

Species Distribution Patterns in Herbaceous Wetlands

The zonation patterns seen in the vegetation of Carolina bays also occur in other wetland types (Spence 1982). It is often thought that such zonation occurs over environmental gradients within the wetland, resulting in gradations of habitat types (Mitsch and Gosselink 1993). Understanding these gradients and their potential effects on vegetation zones can have important implications for wetland restoration, especially if restoration objectives include specified area requirements for the establishment of particular habitat types. In addition, if the restoration plan includes planting and/or seeding of particular species, understanding the environmental constraints on the zonation of different species could improve planting plans, decrease mortality, and increase success rates. Environmental characteristics relating to the depth, duration, and timing of flooding are the most likely to influence the distributions of plants (Holland and Jain 1981, Carter 1986, Moore and Keddy 1988, Shipley et al. 1991, Squires and van der Valk 1992, van der Valk 1994, Casanova and Brock 2000, Lenssen et al. 2000). Other environmental variables include nutrients (Bridgham et al. 1996, Vaithiyanathan and Richardson 1999, Keddy et al. 2000, Svengsouk and Mitsch 2001), soil texture (Keddy 1980, Coops et al. 1991), pH (Glaser et al. 1990, Bridgham et al. 1996), soil water availability, and light (Sharp and Keddy 1985, Breen et al. 1988, Maillette and Keddy 1989). Interspecific competition (Wilson and Keddy 1985, Gaudet and Keddy 1995) may be affected by these environmental variables.

Project Objectives

The purpose of this study was threefold:

1) to thoroughly document soil conditions and plant distributions in Carolina bays to serve as reference systems for restoration projects,
2) to determine environmental characteristics with significant relationships (causal or co-incidental) to the distributions of Carolina bay plants,
3) to determine quantitative values for environmental characteristics that could be used to predict the potential distributions of plants in Carolina bays.

Soil objectives were accomplished by documentation of soil conditions at multiple locations between the basin and the edge of the bay to account for spatial variability in soil characteristics. Plant distribution objectives were accomplished by assessing plant cover at each location to document the plant communities and determine distributions. Quantitative values of significant environmental characteristics were determined that predicted the limits of the species' distributions. Lastly, these predictions were compared to the standing vegetation to determine their usefulness in practical applications, both individually and in concert.

References

Bedford, B. L., and K. S. Godwin. 2003. Fens of the United States: Distribution, characteristics, and scientific connection versus legal isolation. Wetlands **23**:608-629.

Bedford, B. L., M. R. Walbridge, and A. Aldous. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology **80**:2151-2169.

Bennett, S. H., and J. B. Nelson. 1991. Distribution and Status of Carolina Bays in South Carolina. South Carolina Wildlife & Marine Resources Department.

Breen, C. M., K. H. Rogers, and P. J. Ashton. 1988. Vegetation processes in swamps and flooded plains. Pages 223-247 *in* J. J. Symoens, editor. Vegetation of inland waters. Kluwer Academic Publishers, Dordrecht, Netherlands.

Bridgham, S. D., J. Pastor, J. A. Janssens, C. Chapin, and T. J. Malterer. 1996. Multiple limiting gradients in peatlands: A call for a new paradigm. Wetlands **16**:45-65.

Brinson, M. M. 1991. Landscape properties of pocosins and associated wetlands. Wetlands **11**:441-466.

Brinson, M. M. 1993. Changes in the Functioning of Wetlands Along Environmental Gradients. Wetlands **13**:65-74.

Carter, V. 1986. An overview of the hydrologic concerns related to wetlands in the United States. Canadian Journal of Botany-Revue Canadienne De Botanique **64**:364-374.

Casanova, M. T., and M. A. Brock. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? Plant Ecology **147**:237-250.

Collins, B., P. S. White, and D. W. Imm. 2001. Introduction to ecology and management of rare plants of the Southeast. Natural Areas Journal **21**:4-11.

Collins, B. S., and L. L. Battaglia. 2001. Hydrology effects on propagule bank expression and vegetation in six Carolina bays. Community Ecology **2**:21-33.

Coops, H., R. Boeters, and H. Smit. 1991. Direct and indirect effects of wave attack on helophytes. Aquatic Botany **41**:333-352.

Craft, C. B., J. Vymazal, and C. J. Richardson. 1995. Response of Everglades plant communities to nitrogen and phosphorus additions. Wetlands **15**:258-271.

De Steven, D., and M. M. Toner. 2004. Vegetation of Upper Coastal Plain depression wetlands: environmental templates and wetland dynamics within a landscape framework. Wetlands **24**:23-42.

Downing, D. M., C. Winer, and L. D. Wood. 2003. Navigating through Clean Water Act jurisdiction: A legal review. Wetlands **23**:475-493.

Edwards, A. L., and A. S. Weakley. 2001. Population biology and management of rare plants in depression wetlands of the southeastern coastal plain, USA. Natural Areas Journal **21**:12-35.

Fisher, A. S., G. S. Podniesinski, and D. J. Leopold. 1996. Effects of drainage ditches on vegetation patterns in abandoned agricultural peatlands in central New York. Wetlands **16**:397-409.

Gamble, E. E., R. B. Daniels, and W. H. Wheeler. 1977. Primary and secondary rims of Carolina bays. Southeastern Geology **18**:199-212.

Gaudet, C. L., and P. A. Keddy. 1995. Competitive performance and species distribution in shoreline plant communities: a comparative approach. Ecology **76**:280-291.

Gibbons, J. W. 2003. Terrestrial habitat: A vital component for herpetofauna of isolated wetlands. Wetlands **23**:630-635.

Girardin, M. P., J. Tardif, and Y. Bergeron. 2001. Gradient analysis of Larix laricina dominated wetlands in Canada's southeastern boreal forest. Canadian Journal of Botany-Revue Canadienne De Botanique **79**:444-456.

Glaser, P. H., J. A. Janssens, and D. I. Siegel. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River peatland, northern Minnesota. Journal of Ecology **78**:1021-1048.

Holland, R. F., and S. K. Jain. 1981. Insular biogeography of vernal pools in the Central Valley of California. American Naturalist **117**:24-37.

Keddy, P. 1999. Epilogue: from global exploration to community assembly. Pages 393-402 *in* E. Weiher and P. Keddy, editors. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, United Kingdom.

Keddy, P., C. Gaudet, and L. H. Fraser. 2000. Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. Journal of Ecology **88**:413-423.

Keddy, P. A. 1980. Population ecology in an environmental mosaic: *Cakile edentula* on a gravel bar. Canadian Journal of Botany-Revue Canadienne De Botanique **58**:1095-1100.

Kirkman, L. K. 1992. Cyclical vegetation dynamics in Carolina bay wetlands. Ph.D.. Dissertation. The University of Georgia, Athens, GA.

Kirkman, L. K., S. W. Golladay, L. Laclaire, and R. Sutter. 1999. Biodiversity in southeastern, seasonally ponded, isolated wetlands: management and policy perspectives for research and conservation. Journal of the North American Benthological Society **18**:553-562.

Kirkman, L. K., R. F. Lide, G. Wein, and R. R. Sharitz. 1996. Vegetation changes and land-use legacies of depression wetlands of the western coastal plain of South Carolina: 1951-1992. Wetlands **16**:564-576.

Kirkman, L. K., and R. R. Sharitz. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina bays in South Carolina. Ecological Applications **4**:177-188.

Leibowitz, S. G. 2003. Isolated wetlands and their functions: An ecological perspective. Wetlands **23**:517-531.

Lenssen, J. P. M., F. B. J. Menting, W. H. van der Putten, and C. Blom. 2000. Vegetative reproduction by species with different adaptations to shallow-flooded habitats. New Phytologist **145**:61-70.

Lide, R. F. 1997. When is a depression wetland a Carolina bay? Southeastern Geographer **37**:90-98.

Lide, R. F., V. G. Meentemeyer, J. E. Pinder, and L. M. Beatty. 1995. Hydrology of a Carolina bay located on the upper Coastal Plain of western South Carolina. Wetlands **15**:47-57.

Lockwood, J. L., and S. L. Pimm. 1999. When does restoration succeed? Pages 1-20 *in* P. Keddy, editor. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, United Kingdom.

Mahoney, D. L., M. A. Mort, and B. E. Taylor. 1990. Species richness of calanoid copepods, cladocerans and other branchiopods in Carolina bay temporary ponds. American Midland Naturalist **123**:244-258.

Maillette, L., and P. A. Keddy. 1989. Two plants with contrasting architectures: growth responses to light gradients. Canadian Journal of Botany-Revue Canadienne De Botanique **67**:2825-2828.

Metzker, K. D., and W. J. Mitsch. 1997. Modelling self-design of the aquatic community in a newly created freshwater wetland. Ecological Modelling **100**:61-86.

Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands, 2nd edition. John Wiley & Sons Inc., New York.

Moore, D. R. J., and P. A. Keddy. 1988. Effects of a water-depth gradient on the germination of lakeshore plants. Canadian Journal of Botany-Revue Canadienne De Botanique **66**:548-552.

Nadeau, T. L., and S. G. Leibowitz. 2003. Isolated wetlands: An introduction to the special issue. Wetlands **23**:471-474.

Naugle, D. E., R. R. Johnson, M. E. Estey, and K. F. Higgins. 2001. A landscape approach to conserving wetland bird habitat in the prairie pothole region of eastern South Dakota. Wetlands **21**:1-17.

Newman, M. C., and J. F. Schalles. 1990. The water chemistry of Carolina bays: a regional survey. Archiv Fur Hydrobiologie **118**:147-168.

Poiani, K. A., and P. M. Dixon. 1995. Seed banks of Carolina bays: potential contributions from surrounding landscape vegetation. American Midland Naturalist **134**:140-154.

Prouty, W. F. 1952. Carolina bays and their origin. Geological Society of America Bulletin **63**:167-&.

Richardson, C. J. 1991. Pocosins: An ecological perspective. Wetlands **11**:335-354.

Richardson, C. J., and J. W. Gibbons. 1993. Pocosins, Carolina bays, and mountain bogs. Pages 257-310 *in* W. H. Martin, S. G. Boyce, and A. C. Echternacht, editors. Biodiversity of the Southeastern United States. J. Wiley & Sons, New York, NY, USA.

Schalles, J. F., and D. J. Shure. 1989. Hydrology, community structure, and productivity patterns of a dystrophic Carolina bay wetland. Ecological Monographs **59**:365-385.

Semlitsch, R. D. 1981. Terrestrial Activity and Summer Home Range of the Mole Salamander (Ambystoma-Talpoideum). Canadian Journal of Zoology-Revue Canadienne De Zoologie **59**:315-322.

Semlitsch, R. D., and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology **12**:1129-1133.

Sharitz, R. R. 2003. Carolina bay wetlands: Unique habitats of the southeastern United States. Wetlands **23**:550-562.

Sharitz, R. R., and J. W. Gibbons. 1982. The Ecology of Southeastern Shrub Bogs (Pocosins) and Carolina Bays: a Community Profile. FWS/OBS-82/04, U.S. Fish and Wildlife Service, Division of Biological Services, Washington, DC.

Sharitz, R. R., and C. A. Gresham. 1998. Pocosins and Carolina bays. Pages 343-388 *in* M. G. Messina and W. H. Conner, editors. Southern Forested Wetlands Ecology and Management. Lewis Publishers, Boca Raton.

Sharp, M. J., and P. A. Keddy. 1985. Biomass accumulation by *Rhexia virginica* and *Triadenum fraseri a*long two lakeshore gradients: a field experiment. Canadian Journal of Botany-Revue Canadienne De Botanique **63**:1806-1810.

Shipley, B., P. A. Keddy, and L. P. Lefkovitch. 1991. Mechanisms producing plant zonation along a water depth gradient: a comparison with the exposure gradient. Canadian Journal of Botany-Revue Canadienne De Botanique **69**:1420-1424.

Snodgrass, J. W., M. J. Komoroski, A. L. Bryan, and J. Burger. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: Implications for wetland regulations. Conservation Biology **14**:414-419.

Spence, D. H. N. 1982. The zonation of plants in freshwater lakes. Pages 37-125 *in* A. MacFadyen and E. D. Ford, editors. Advances in Ecological Research. Academic Press, New York, NY.

Squires, L., and A. G. van der Valk. 1992. Water-depth tolerances of the dominant emergent macrophytes of the Delta Marsh, Manitoba. Canadian Journal of Botany-Revue Canadienne De Botanique **70**:1860-1867.

Stolt, M. H., and M. C. Rabenhorst. 1987. Carolina Bays on the Eastern Shore of Maryland .1. Soil Characterization and Classification. Soil Science Society of America Journal **51**:394-398.

Sutter, R. D., and R. Kral. 1994. The ecology, status, and conservation of two non-alluvial wetland communities in the South Atlantic and Eastern Gulf Coastal Plain, USA. Biological Conservation **68**:235-243.

Svengsouk, L. J., and W. J. Mitsch. 2001. Dynamics of mixtures of *Typha latifolia* and *Schoenoplectus tabernaemontani* in nutrient-enrichment wetland experiments. American Midland Naturalist **145**:309-324.

Tyndall, R. W., K. A. McCarthy, J. C. Ludwig, and A. Rome. 1990. Vegetation of six Carolina bays in Maryland. Castanea **55**:133-135.

Vaithiyanathan, P., and C. J. Richardson. 1999. Macrophyte species changes in the Everglades: examination along a eutrophication gradient. Journal of Environmental Quality **28**:1347-1358.

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology **62**:688-696.

van der Valk, A. G. 1994. Effects of prolonged flooding on the distribution and biomass of emergent species along a fresh-water wetland coenocline. Vegetatio **110**:185-196.

van der Valk, A. G., L. Squires, and C. H. Welling. 1994. Assessing the impacts of an increase in water-level on wetland vegetation. Ecological Applications **4**:525-534.

Weiher, E., and P. A. Keddy. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos **74**:159-164.

Wheeler, B. D., and M. C. F. Proctor. 2000. Ecological gradients, subdivisions and terminology of north- west European mires. Journal of Ecology **88**:187-203.

Whigham, D. F., and T. E. Jordan. 2003. Isolated wetlands and water quality. Wetlands **23**:541-549.

Wilson, S. D., and P. A. Keddy. 1985. Plant zonation on a shoreline gradient: physiological response curves of component species. Journal of Ecology **73**:851-860.

Wisheu, I. C., and P. A. Keddy. 1992. Competition and centrifugal organization of plant communities: theory and tests. Journal of Vegetation Science **3**:147-156.

Zoltai, S. C., and D. H. Vitt. 1995. Canadian Wetlands - Environmental Gradients and Classification. Vegetatio **118**:131-137.

CHAPTER 2

SPATIAL GRADIENTS OF SOIL CHARACTERISTICS IN CAROLINA BAYS

Introduction

Carolina bays are the most abundant natural lentic system in the Coastal Plains of North Carolina, South Carolina, and parts of Georgia (Newman and Schalles 1990). It is estimated that 10,000 to 20,000 Carolina bays currently exist (Richardson and Gibbons 1993). These bays are elliptical depressions surrounded by sand rims and are often underlain by a clay hardpan covered with a layer of sand and organic soil or peat (Prouty 1952, Gamble et al. 1977, Sharitz and Gibbons 1982, Bennett and Nelson 1991). Most bays are either hydrologically isolated or have limited groundwater interactions; however, wetlands or small ponds formed by precipitation are typically present (Sharitz and Gibbons 1982, Lide et al. 1995). These wetlands are usually ombrotrophic, with low calcium and carbonate concentrations (Schalles and Shure 1989, Newman and Schalles 1990). The amount of flooding can vary from nearly continuous to rare, resulting in a range of wetland types (De Steven and Toner 2004), although many flooded bays periodically dry completely (Bennett and Nelson 1991, Sharitz 2003).

Many rare and endangered flora and fauna are known to inhabit Carolina bays (Bennett and Nelson 1991, Sutter and Kral 1994, Edwards and Weakley 2001). However, few natural undisturbed Carolina bays remain due to damage caused by anthropogenic disturbances (Richardson and Gibbons 1993). Recognition of the ecological value of Carolina bays and a focus on Carolina bay restoration (Federal Register 1998) has driven efforts towards understanding reference bays and the dynamics within them (De Steven and Toner 2004).

Successful wetland restoration requires an understanding of the environmental characteristics and their potential effects on vegetation and community structure (Bledsoe and Shear 2000). The supply of nutrients can affect both the biodiversity and the species contained in a restored wetland (Zedler 2000). Nutrient conditions of the soils can also influence the survivability of transplants (Pezeshki et al. 2000). Habitat-specific information is needed for restoration (Zedler 2000); this is demonstrated by the findings of DeSteven and Toner (2004) that the type of vegetation in Carolina bays is correlated with soil characteristics, as well as other factors. Due to the potential effects of environmental characteristics on both the type of wetland created as well as the distribution of plants within the wetland, quantitative data at the microtopographic scale is needed for planning and hydrologic design of restored wetlands (Bledsoe and Shear 2000).

Spatial variability of soil characteristics in wetlands can be affected by several processes. Variability in particle size distributions can be affected by parent material, elevation, erosion, and deposition (Stolt et al. 2001). Variability in nutrient concentrations can be affected by elevation, flooding, and soil particle size. Aerobic, infrequently flooded soils have high rates of organic matter decomposition, which can result in low carbon (C) and nitrogen (N) concentrations (Stolt et al. 2001). Anoxic, flooded soils have lower rates of decomposition, resulting in higher C concentrations, but can have high rates of denitrification, resulting in lowered N concentrations (Ponnamperuma 1972, Collins and Kuehl 2001, Vepraskas and Faulkner 2001). Phosphorus (P) is soluble in anoxic sediments, and retention can be affected by the exchange capacity (EC) of the soil (Lyon et al. 1952, Vepraskas and Faulkner 2001). Soil

EC can also affect retention of ammonium and nitrate in both aerobic and anaerobic soils (Lyon et al. 1952). Clay particles have a high EC and tend to retain nutrients, whereas sands have a low EC and tend to leach nutrients. Soil nutrients in Carolina bays would therefore be affected by the flooding regime as well as bay geomorphology.

Most studies of Carolina bay soils have relied on few samples per bay and do not account for spatial variability in soil characteristics and chemistry. Some studies have compared the soils of bay rims and depressions (Bliley and Pettry 1979, Pettry et al. 1979); however, information on soil gradients between these points is generally lacking. Reese and Moorhead (1996) systematically sampled transects from the center to the rim of a small bay in South Carolina and found significant gradients of soil clay, pH, organic C, cation EC and base saturation within the A horizon. It is therefore clear that average results of a few soil samples can not represent the soil conditions throughout a bay, and that limited sample numbers may fail to demonstrate gradients or heterogeneity.

Studies of Carolina bay soils have focused primarily on particle size, cations, pH, and organic C (Frey 1950, Bliley and Pettry 1979, Pettry et al. 1979, Schalles et al. 1989, Reese and Moorhead 1996). Limited information is known about soil N or P concentrations (but see De Steven and Toner 2004). To date, spatial variations of soil N, P, and available soil water in bays have not been examined. These soil characteristics, among others, have considerable implications in the development of wetland plant communities (Mitsch and Gosselink 1993). Studies of Carolina bay water chemistry have examined parameters such as dissolved O_2, temperature, pH, alkalinity, conductance, dissolved organic carbon, and cations (Schalles 1989, Newman and Schalles 1990). However, these parameters can often be similar throughout a bay (Schalles et al. 1989) due to mixing of the water column. Water column parameters are likely of less importance in wetland plant ecology than soil parameters, as most wetland and submerged plants absorb nutrients through their roots more efficiently than through stems or leaves (Spence 1982).

Variations in soil characteristics have been shown to have relationships with the distributions of wetland plant species in lake shorelines (Lehmann 1998), herbaceous wetlands (Vaithiyanathan and Richardson 1999), and floodplains (Wikum and Wali 1974, Robertson et al. 1978, Menges 1986). Variations in nutrient availability in the sediments of oligotrophic waters can be especially important in the zonation of wetland and aquatic plants (Spence 1982). Therefore, a comprehensive sampling plan as recommended by Reese and Moorhead (1996) is required in Carolina bays, not just to understand soil and nutrient characteristics, but to understand potential patterns in vegetation distributions as well.

An understanding of spatial variations of soil characteristics and gradients in Carolina bays is necessary to plan restoration projects. The goal of this study was to document the soil characteristics and chemistry in the rooting zone of Carolina bays, especially those characteristics which may affect the distribution of plant species. Specific objectives were to document spatial variability of these characteristics between the depression centers and edges of the bays and to determine whether gradients of these characteristics exist.

Methods

Bay Selection

This study analyzed four Carolina bays on the Department of Energy’s Savannah River Site (SRS) that featured herbaceous plant communities and had hydrologic records available. Certain *a priori* criteria were established for bay selection (Table 2.1). Based on these criteria, the four bays selected were Dry Bay (SRS bay 31; located at 33° 15’ 0.35” N, 81° 44’ 46.89”

W), Ellenton Bay (SRS bay 176; 33° 13’ 18.54” N, 81° 29’ 8.07” W), Flamingo Bay (SRS bay 3; 33° 20’ 12.80” N, 81° 40’ 44.03” W), and Sarracenia Bay (SRS bay 78; 33° 17’ 22.60” N, 81° 29’ 8.07” W) (Figure 2.1). Dry, Ellenton and Flamingo Bays are in Aiken County; Sarracenia Bay is in Barnwell County. Dry and Ellenton Bays are located within the Sunderland Terrace, Flamingo Bay is located within the Aiken Plateau, and Sarracenia Bay is located within the Brandywine Terrace (Davis and Janecek 1997).

Dry Bay is a somewhat bowl-shaped depressional pond that has standing water covering a portion of the basin at least part of most years (Schalles et al. 1989). It is 45.7 m above sea level and approximately 5 ha in size (Davis and Janecek 1997). The bay’s interior vegetation includes *Panicum hemitomon* and *Nymphaea odorata*, surrounded by bottomland hardwood/swamp forest species on the periphery. Soils within the bay are hydric Ogeechee sandy loam (ponded) and Rembert sandy loam, both poorly drained and slowly or moderately permeable (Davis and Janecek 1997). Pre-1951 history (i.e., prior to the establishment of the SRS) includes agriculture in the area surrounding the bay, and wetland drainage. Prescribed burns in the forested buffer occurred in 1971, 1984, and 1986 (Davis and Janecek 1997).

Ellenton Bay is also a somewhat bowl-shaped depressional pond that has standing water covering a portion of the bay at least part of most years (Schalles et al. 1989). It is 44.2 – 45.7 m above sea level and 11.3 ha in size (Davis and Janecek 1997). Predominant bay vegetation includes *Nymphaea odorata*, *Brassenia schreberi*, and *Panicum* spp., surrounded by pine/mixed hardwood forest uplands and old fields. Soils within the bay consist of ponded Ogeechee sandy loam surrounded by frequently flooded Fluvaquents (poorly drained, moderately permeable soils); the bay rim is Lakeland sand (droughty and excessively drained). Ellenton Bay is bisected by a power line right-of-way and embankment. Its pre-1951 history includes drainage and agriculture. Despite these past and present disturbances, the bay is considered to represent a natural, isolated, relatively undisturbed bay (Davis and Janecek 1997). For the purposes of this study, the larger, southern portion of the bay was used and the power line embankment was not crossed.

Flamingo Bay is a mostly herbaceous wetland with standing water covering a portion of the bay at least part of most years (Schalles et al. 1989). It is located 94.5 m above sea level and is 5.7 ha in size (Davis and Janecek 1997). Flamingo Bay has shallow slopes throughout most of the bay, but has a pond-like deeper area near the northwest side. Vegetation within the bay consists of aquatic and herbaceous species (including *Polygonum* spp., *Nelumbo lutea, and Panicum* spp.), as well as trees and shrubs (including *Nyssa sylvatica* var. *biflora, Acer rubrum, Liquidambar styraciflua*, *Pinus taeda*, and *Cephalantus occidentalis*). The surrounding area supports pine plantations of differing ages. The bay’s soils are Rembert sandy loam and Ocilla loamy sand (both somewhat to poorly-drained, moderately to slowly-permeable soils), with Blanton sand (a somewhat excessively drained, moderately permeable soil) on the rim. The interior of the bay has never been ditched, but the surrounding area was used for livestock prior to 1950 (Davis and Janecek 1997).

Sarracenia Bay is a shallow, pan-shaped depression with gentle slopes that has standing water covering a portion of the bay at least part of most years (Schalles et al. 1989). It is 55.1 m above sea level and 4.0 ha in size (Davis and Janecek 1997). Vegetation was previously described as having two outer zones dominated by *Aristida affinis*/*Andropogon virginicus* and *Rhynchospora traceyi*/*Leerzia hexandra* and two inner zones of *Nymphaea odorata/Eleocharis rabbinsii* and *Nymphaea odorata/Eleocharis equisetoides* (Davis and Janecek 1997). The surrounding upland vegetation is pine/hardwood forest. Soil within the bay is ponded Ogeechee sandy loam, and the surrounding soils include Albany loamy sand and Blanton sand (both somewhat to excessively-well drained soils). Prior to 1950, the areas surrounding the bay were used for crop fields and pastures (Davis and Janecek 1997). Although the SRS boundary runs through the southern portion of the bay, the privately-owned off-site portion is undisturbed.

Sample Locations

Two transects were established from the deepest point of each bay, each radiating toward the rim in one direction only. One transect was established to the edge of the bay along the long axis (i.e., the longest transect possible from the deepest point), and the other was established along the short axis. Water depth and a Spectra-Physics Laserplane leveling system were used to establish elevations along each transect relative to the deepest point of each bay. PVC marking poles were driven into the sediment at every 10 cm change in elevation. Sample plots were located along each transect at 10 cm changes in elevation. If sample points were less than 2 m apart, some sample locations were altered (Figure 3.2). If the distance between sample points was greater than 22 m, an additional sample point was added 20 m from the previous point. Samples were collected from the deepest point of the bay to the estimated edge of the jurisdictional wetland. The actual bay depression might have been larger due to extensive sand rim formation.

Soil Sampling

Samples were collected for chemical and physical analyses from the top 10 cm of soil using a 6.35 cm diameter auger. The roots of wetland plants are often shallow under flooded conditions (Weisner and Strand 1996), and Steinke et al. (1996) demonstrated that the top 10 cm of soil was the expected rooting zone for herbaceous wetland plants. Two sub-samples for chemical analyses were taken from the center of diagonally placed 1 m^2 subplots centered on the sample point (Figure 2.3) and were combined in the field. This process was duplicated to collect a second soil sample (immediately adjacent to the first) for physical analyses.

Soil samples were air dried, crushed, and passed through a 2 mm sieve to remove occasional small stones, roots, or other large organic material. Samples were then stored until further analyses were performed. Additional samples were collected from the top 10 cm of soil adjacent to each sample pole for pH analysis.

Chemical Analyses

Soil pH of fresh samples was measured using a soil slurry as described in Allen et al. (1974). Samples were analyzed the same day as collection, or were stored in a refrigerator overnight before analysis to limit decomposition and any potential impact on pH. Dry samples were prepared for C, N, and P analyses by grinding a 10 ml subsample in an 8000 SPEX CertiPrep mixer/mill using two 1/2 inch steel balls in a hardened steel vial for approximately 4 minutes. Ground subsamples were then placed in scintillation vials and dried at 80 °C for 24 hours. Approximately 25 - 30 mg of soil from each subsample were sealed into tin capsules and analyzed for total C and total N using micro-Dumas combustion analysis in a Carlo Erba NA 1500 CHN Analyzer. In addition, approximately 25 mg of soil from each subsample were used to extract total P using an acid-persulfate digestion procedure (Nelson 1987). Extractions were analyzed using an Alpkem RFA Series Colorimetric Analyzer.

Physical Analyses

Soil water availability and particle size distribution were analyzed because these parameters can have an impact on the amount of water available to plants when soils are not inundated. Soil texture also has been shown to have an impact on wetland plant zonation (Keddy 1982, 1984, Keddy and Constabel 1986). Soil water availability (percent water per gram dried soil) was calculated by determining water retention at 0.1 and 15 bar pressure using a pressure plate apparatus (Klute 1986). Available soil water is best determined using undisturbed cores. However, since undisturbed samples could not be collected from underwater, disturbed (dried, crushed and sieved) samples were used for analysis. Available water was calculated by saturating the samples and subtracting the soil moisture content at 15 bar (the wilting point of most plants, beyond which remaining soil water can not be extracted) from the soil moisture content at 0.1 bar (field capacity) (Dunne and Leopold 1978). Particle size distribution was determined using 10 g of soil in accordance with methods of Kilmer and Alexander (1949). Organic matter was removed using 30% hydrogen peroxide and particles were dispersed using sodium hexametaphosphate and mechanical agitation. Clay fractions were determined using the pipette method, and sand fractions were determined by size sieving. Silt fractions were determined by subtracting the clay and sand fractions.

Statistical Analysis

Soil environmental variables (pH, % C, % N, % P, C:N ratio, N:P ratio, % sand, % silt, % clay, and available soil water) were statistically analyzed using Proc Mixed procedure of SAS (SAS Institute 2001) to determine whether significant spatial gradients exist within the bays (from the center to the rim). Structural auto-correlation in the analyses (e.g. between %sand, % silt, and % clay) was avoided by modeling each variable independently. Instead of a general linear model, the mixed model procedure was used to account for autocorrelation between adjacent plots. To standardize the distances along both transects within each bay, the distance of each sample location along its transect was expressed as the percent of the total transect distance. Since elevation generally varies with distance along the bays' transects, the same environmental variables were also statistically analyzed using the same procedure to determine whether there were significant elevational gradients within each bay. For these analyses, elevation was expressed as relative elevation above the deepest plot in the bay. Correlations between the environmental variables (in all bays combined) were determined using Proc Corr (SAS Institute 2001).

Results

Dry Bay

The long transect in Dry Bay was 150.5 m in length with 18 sample locations, and the short transect was 80.1 m long with 11 sample locations. Changes in elevation along the long and short transects were 110.0 and 100.0 cm, respectively. Analysis of elevation as a function of distance along the transects showed that elevation formed a significant spatial gradient from the deepest point in the bay to the edge (Figure 2.4). Significant negative spatial and elevational gradients were shown for % N, pH, % silt, and available water, for which values were higher in the bay center and lower toward the edge. Positive spatial and elevational gradients were shown for C:N and % sand, which were higher near the bay edge. A significant elevational gradient was shown for % P, but this variable did not show a spatial gradient. Table 2.2 summarizes the significant spatial and elevational gradients found in all bays in this study. Spatial variability of soil characteristics are shown on Figures 2.5 – 2.9 .

Ellenton Bay

The long transect in Ellenton Bay was 202.8 m in length with 26 sample locations and the short transect was 134.5 m long with 22 sample locations. The change in elevation was 150.0 cm along both transects. Analysis of elevation as a function of distance along the transects showed that elevation formed a significant spatial gradient from the deepest point in the bay to the edge. Negative spatial and elevational gradients were shown for % C, % N, % P, pH, % silt, % clay, and available water, and positive gradients were shown for C:N and % sand.

Flamingo Bay

The long transect in Flamingo Bay was 243.3 m long with 25 sample locations, and the short transect was 77.5 m long with 12 sample locations. Changes in elevation along the long and short transects were 100.0 and 110.0 cm. Analysis of elevation as a function of distance along the transects showed that elevation formed a significant spatial gradient from the deepest point in the bay to the edge. Positive spatial and elevational gradients were shown for only C:N and available soil water and a negative gradient was shown for pH.

Sarracenia Bay

The long transect in Sarracenia Bay was 135.2 m with 12 sample locations and the short transect was 49.9 m with 10 sample locations. The change in elevation was 110.0 cm in both transects. Analysis of elevation as a function of distance showed that elevation formed a significant spatial gradient from the deepest point in the bay to the edge. Negative spatial and elevational gradients were shown for % C, % N, % P, % clay, and available water, and a positive gradient was shown for % sand.

Correlations of Environmental Variables

Significant correlations existed between most environmental variables; however, many were weak in nature (Table 2.3). Percent sand was strongly negatively correlated with % clay, % C, % N, and % P and moderately negatively correlated with available soil water. Clay content was strongly positively correlated with % C and % N, but only moderately correlated with % P. Percent C, % N, and % P all showed strong positive correlations with each other, and each was moderately correlated to available soil water.

Discussion

All environmental variables that formed significant spatial gradients in the bays also formed significant elevational gradients, and therefore had relationships with flooding depths. In addition, all variables that formed elevational gradients also formed spatial gradients, with the exception of the P elevational gradient in Dry Bay. The primary variables forming significant gradients were % sand (in three bays), % clay (two bays), % N (three) % C (two) soil pH (three) and available soil water (four). The C:N ratio formed gradients in three bays, but the N:P ratio did not form a significant gradient in any bay. Spatial particle size gradients (sand, silt, or clay) in the bays are likely due to bay geomorphology. Seasonal patterns of wind direction and water level changes may have caused the development of sand rims by the erosion of sands from the centers of the bay and deposition near the edges (Grant et al. 1998). Additionally, rain impact and water erosion may have influenced particle size distributions (Lyon et al. 1952). Soil aggregates on exposed rims can be destroyed during rain events, and clays may have been eroded from the edges and deposited in the centers of the bays.

Particle size gradients found in this study were somewhat similar to those previously found in SRS Bay 93 (Reese and Moorhead 1996). Overall, sand content was higher at the bay edges and clay content was higher in the bay centers. Clay fractions significantly decreased toward the rim in Bay 93, as well as in two of the bays in this study. Sand fractions in three of the four bays in this study significantly increased towards the rim. A similar increase was seen in Bay 93, but it was not significant. While two of the bays in the current study exhibited significant silt gradients, this was not observed in Bay 93.

Significant gradients of % C were found in Ellenton and Sarracenia Bays, with higher concentrations near the bay centers. Accumulation of organic matter is common in wetland soils, where anoxic conditions lower decomposition rates, and soils in depressions often have higher concentrations of organic matter due to their proximity to the water table (Collins and Kuehl 2001). Decomposition rates are likely higher in soils at the edges of the bays, as they are flooded less often and are more likely to be well-drained. Such moist, well-aerated soils create ideal conditions for decomposition by soil organisms (Thompson and Troeh 1957). In addition, windblown organic matter might drift towards the bay center from the exposed, elevated edges. The formation of C gradients in the Carolina bays may be also related to the surrounding landscape, since the amount of C in bay sediments is a function of input and decomposition rates. Percent C did not form significant gradients in Dry and Flamingo Bays. While Ellenton and Sarracenia Bays are surrounded by pine/hardwood forests, Dry Bay is surrounded by bottomland hardwood/swamp forest (Davis and Janecek 1997) that may result in more litter deposition at the edge. Although Flamingo bay also is surrounded by pine/hardwood forest, there is a dense canopy of bottomland hardwood forest species at the bay edges, extending into the bay. In addition, stands of *Nyssa sylvatica* var. *biflora* occur throughout the bay. The lack of a C gradient in this bay may be caused by litterfall from these stands. An organic C gradient was found in the soils of Bay 93 (Reese and Moorhead 1996), which is also surrounded by pine/hardwood forests.

Soils in the bay centers were expected to have lower N concentrations than those near the edges, since N concentrations can often be lower in saturated soils due to denitrification (Ponnamperuma 1972). Conversely, higher N concentrations were expected near the bay edges, where anoxic conditions occur less frequently. In many water bodies, ammonium is transformed to nitrate in a small, oxidized upper layer of the sediments. Nitrate then diffuses into anoxic lower layers of soil, where denitrification occurs (Mitsch and Gosselink 1993). However, significant gradients of % N were found in three bays such that the concentration was higher towards the bay centers. Several processes may be responsible for the unexpected N gradient. Denitrification may be inhibited in the centers of the bays, where bay waters can become stratified. Very low concentrations of dissolved oxygen have been documented in water 40 cm below dense floating-leaved vegetation (Schalles and Shure 1989). Such stratification could effectively eliminate an oxidized sediment layer, which would prevent nitrification of ammonium, thus reducing denitrification rates. This can lead to an accumulation of ammonium-N in the reduced sediments near the centers of the bays (Ponnamperuma 1972, Vepraskas and Faulkner 2001). Additionally, low soil pH in the Carolina bays may inhibit denitrification, as is common in soils where pH is <6 (Vepraskas and Faulkner 2001). Conversely, fluctuations in water depth near the bay edges may increase denitrification rates. Aerobic denitrification of nitrite may occur in alternately wet and dry soils during the conversion of ammonium to nitrate (Ponnamperuma 1972). Alternate wetting and drying can also increase denitrification rates of nitrate. Rather than diffusing into lower anoxic sediments, nitrate in the aerobic top soil layer can be denitrified in place by rising water levels and increased anoxia.

Sandy soil near the edge of the bay would have a low EC, and N can be lost through leaching (Thompson and Troeh 1957). A negative cation EC gradient has been previously documented from the center to the edge of SRS Bay 93 (Reese and Moorhead 1996). It is possible that increased productivity near the bay edge, combined with the potential for nutrient leaching, also results in the removal of N from bay soils. Percent N did not form a gradient in Flamingo Bay. Since % sand did not form a significant gradient in this bay, it is likely that leaching losses are lower there as well.

Significant gradients of % P (total) were found only in Ellenton and Sarracenia Bays, where concentrations were higher toward the bay centers. Phosphorus availability is affected by both soil particle size and pH. Reducing conditions can solublize P, especially in acidic soils (Ponnamperuma 1972, Holford and Patrick 1979). As a result, submerged soils would have lower total P concentrations than exposed, aerobic soils. However, clay can resorb P due to its high EC. This can result in little, if any, P loss in clay soils, while substantially greater amounts of P can be lost from reduced sandy soils (Ponnamperuma 1972). Significant sand gradients in Dry, Ellenton, and Sarracenia Bays likely resulted in P loss from sandy soils along the bay edges. Clay gradients in Ellenton and Sarracenia Bays likely resulted in P retention toward the centers of these bays, and the formation of the P gradients.

Significant C:N gradients were found in Dry, Ellenton, and Flamingo Bays where the ratio is higher near the bay edges. However, presence of a C:N gradient appears to be unrelated to whether C or N gradients exist. If both C and N gradients are present with similar slopes, a C:N gradient would be unlikely to be shown. However, the detection of C, N, and/or C:N gradients may be related to sample size. Gradients with shallow slopes would require a larger sample size to show significance than gradients with steep slopes. This may be the case in Flamingo Bay, where the C gradient was nearly significant ($p = 0.056$). The presence of a significant positive C:N gradient is dependent on the occurrence of either: 1) a larger increase in C concentrations as compared to N; 2) a larger decrease in N concentrations as compared to C; or 3) an increase in C concentrations with a corresponding decrease in N concentrations. However, alterations of these three conditions along the transect could result in a C:N gradient with no net change in C or N concentrations along the transect. The C:N gradient can also be partly the result of the C:N ratio of litter inputs. Tissue C:N is lower in floating-leaved species in the deeper areas of the bays than it is in the surrounding emergent plants (Schalles and Shure 1989).

Although both N and P gradients were found in Ellenton and Sarracenia Bays, as well as a N gradient in Dry Bay, none of the bays studied were found to have a significant N:P gradient. This absence of a N:P gradient may be the result of the very shallow slopes of the N and P gradients.

Significant pH gradients were found in Dry, Ellenton, and Flamingo Bays, where pH was higher near the bay centers. While there were differences in pH among bays, all the bays studied had very acidic soils (pH $\leq$ 5.55). Carolina bays are often ombrotrophic, with low Ca concentrations (Reese and Moorhead 1996), resulting in low buffering capacities. Decomposition rates within the bay vary due to the amount of water in the soil. Organic matter near the edge of the bays would decompose quickly, forming organic acids and lowering the pH (Thompson and Troeh 1957). However, the reduction of submerged soils towards the center of the bays would cause an increase in pH (Ponnamperuma 1972). These combined factors likely create the gradients that were found. Such a gradient is likely absent in Sarracenia Bay as its shallow center would allow the bay to dry more frequently. The oxidation of previously submerged soils can often result in a subsequent decrease in pH (Ponnamperuma 1972). In addition, frequent draining and aeration of these soils could have increased decomposition rates (Thompson and Troeh 1957); as evidenced by the very low pH and C concentrations in this bay.

While three of the bays in this study exhibited soil pH gradients that were higher in the centers and lower towards the edges, the reverse was seen in Bay 93, where soil pH was higher towards the bay edge (Reese and Moorhead 1996). Bay 93 is a predominantly forested bay, with little herbaceous cover. In addition, it has a history of disturbance, where it was drained and rice may have been grown between 1943 and 1951. Water depths in Bay 93 have historically been shallow (Lide Unpublished data). It is possible that the shallow water depths, combined with historical draining, may have allowed oxidation of previously submerged sediments, which could have lowered the pH in the central areas (Ponnamperuma 1972).

Available soil water is related to particle size, organic content, and aggregation (Lyon et al. 1952), where soil water increases with increased clay and/or C, and decreases with increased sand. Both Ellenton and Sarracenia Bays exhibited sand, clay, and C gradients, while only a sand gradient was shown in Dry Bay. It is probable that the transects in Flamingo Bay did not extend to the bay rim. These incomplete transects are the most likely reason for the absence of available soil water, sand, clay and C gradients in this bay.

Although significant correlations existed between most environmental variables, many were weak. Correlations between the soil fractions were not surprising, especially due to the intrinsic relationships among these factors. Positive correlations between % C and % N are expected, as soil C:N ratios generally remain within a small range, with excess C removed as CO_2 or excess N removed through leaching (Lyon et al. 1952). The major source of both C and P in Carolina bays is organic material, due to the ombrotrophic nature of the bays (limiting C concentrations) as well as limited P inputs from the small watershed. The correlations of available soil water with % C, % N, and % P are due to its relationship to organic material. Available soil water correlations with particle sizes are due to their intrinsic causal relationship (Lyon et al. 1952). Although pH can be lowered by the decomposition of organic material, it did not show a significant correlation with % C.

Acknowledgement of the spatial gradients formed by the physical and chemical soil properties in Carolina bays can be very useful for restoration efforts. The gradients seen in this study could affect plant distributions as well as be influenced by them. Soil particle size can have an impact on plant distribution through its effect on the availability of nutrients and available soil water (Lyon et al. 1952). Similarly, nutrient availability can be affected by patterns of organic litter contributions from the bay vegetation (Schalles and Shure 1989). Further study is required to determine the magnitude of the effect of vegetation zones on nutrient gradients. Particle size gradients may be crucial for establishing specific zones of Carolina bay plants and initiating the restoration of disturbed soil chemical properties. The restoration of soil gradients in some cases may require a multi-step plan of soil and vegetation manipulations. In addition, the successful restoration of Carolina bays requires restoration of habitats for aquatic, terrestrial, and soil fauna which may depend in part on soil properties. Thus, restored soil properties could be used both as a medium to facilitate the restoration of vegetation and as a standard with which to judge the success of a restoration.

References

Allen, S. E., H. M. Grimshaw, J. A. Parkinson, and C. Quarmby. 1974. Chemical Analysis of Ecological materials. John Wiley & Sons, New York.

Bennett, S. H., and J. B. Nelson. 1991. Distribution and Status of Carolina Bays in South Carolina. South Carolina Wildlife & Marine Resources Department.

Bledsoe, B. P., and T. H. Shear. 2000. Vegetation along hydrologic and edaphic gradients in a North Carolina coastal plain creek bottom and implications for restoration. Wetlands **20**:126-147.

Bliley, D. J., and D. E. Pettry. 1979. Carolina Bays on the Eastern Shore of Virginia. Soil Science Society of America Journal **43**:558-564.

Collins, M. E., and R. J. Kuehl. 2001. Organic matter accumulation and organic soils. Pages 137-162 *in* J. L. Richardson and M. J. Vepraskas, editors. Wetland Soils: Genesis, Hydrology, Landscapes, and Classification. Lewis Publishers, Boca Raton.

Davis, C. E., and L. L. Janecek. 1997. DOE Research Set-Aside Areas of the Savannah River Site. SRO-NERP-25, The Savannah River Site National Environmental Research Park Program, United States Department of Energy, Aiken, SC.

De Steven, D., and M. M. Toner. 2004. Vegetation of Upper Coastal Plain depression wetlands: environmental templates and wetland dynamics within a landscape framework. Wetlands **24**:23-42.

Dunne, T., and L. B. Leopold. 1978. Water in Environmental Planning. Freeman and Company, New York.

Edwards, A. L., and A. S. Weakley. 2001. Population biology and management of rare plants in depression wetlands of the southeastern coastal plain, USA. Natural Areas Journal **21**:12-35.

Federal Register. 1998. Floodplain and wetlands involvement notification for implementation of the wetland mitigation bank at the Savannah River Site (SRS). Volume 63, Number 72. April 15.

Frey, D. G. 1950. Carolina Bays in Relation to the North Carolina Coastal Plain. Journal of the Elisha Mitchell Science Society **66**:44-52.

Gamble, E. E., R. B. Daniels, and W. H. Wheeler. 1977. Primary and secondary rims of Carolina bays. Southeastern Geology **18**:199-212.

Grant, J. A., M. J. Brooks, and B. E. Taylor. 1998. New constraints on the evolution of Carolina bays from ground- penetrating radar. Geomorphology **22**:325-345.

Holford, I. C. R., and W. H. Patrick, Jr. 1979. Effects of reduction and pH changes on phosphate sorption and mobility in an acid soil. Soil Science Society of America Journal **43**:292-297.

Keddy, P. A. 1982. Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. Aquatic Botany **14**:41-58.

Keddy, P. A. 1984. Quantifying a within-lake gradient of wave energy in Gillfillan Lake, Nova Scotia. Canadian Journal of Botany-Revue Canadienne De Botanique **62**:301-309.

Keddy, P. A., and P. Constabel. 1986. Germination of ten shoreline plants in relation to seed size, soil particle size and water level: an experimental study. Journal of Ecology **74**:133-141.

Kilmer, V. J., and L. T. Alexander. 1949. Methods of Making Mechanical Analyses of Soils. Soil Science **68**:15-24.

Klute, A. 1986. Water retention: laboratory methods. Pages 635-662 *in* A. Klute, editor. Methods of Soil Analysis Part I: Physical and Mineralogical Methods. Soil Science Society of America Inc., Madison.

Lehmann, A. 1998. GIS modeling of submerged macrophyte distribution using Generalized Additive Models. Plant Ecology **139**:113-124.

Lide, R. F. Unpublished data. Savannah River Ecology Laboratory, University of Georgia, Aiken, SC, USA.

Lide, R. F., V. G. Meentemeyer, J. E. Pinder, and L. M. Beatty. 1995. Hydrology of a Carolina bay located on the upper Coastal Plain of western South Carolina. Wetlands **15**:47-57.

Lyon, T. L., H. O. Buckman, and N. C. Brady. 1952. The Nature and Properties of Soils, 5th edition. The Macmillan Company, New York.

Menges, E. S. 1986. Environmental correlates of herb species composition in five southern Wisconsin floodplain forests. American Midland Naturalist **115**:106-117.

Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands, 2nd edition. John Wiley & Sons Inc., New York.

Nelson, N. S. 1987. An acid persulfate digestion procedure for determination of phosphorus in sediments. Communications in Soil Science and Plant Analysis **18**:359-369.

Newman, M. C., and J. F. Schalles. 1990. The water chemistry of Carolina bays: a regional survey. Archiv Fur Hydrobiologie **118**:147-168.

Pettry, D. E., J. H. Scott, Jr., and D. J. Bliley. 1979. Distribution and nature of Carolina Bays on the Eastern Shore of Virginia. The Virginia Journal of Science **30**:3-9.

Pezeshki, S. R., P. H. Anderson, and R. D. DeLaune. 2000. Effects of nursery pre-conditioning on *Panicum hemitomon* and *Sagittaria lancifolia* used for wetland restoration. Restoration Ecology **8**:57-64.

Ponnamperuma, F. N. 1972. The chemistry of submerged soils. Advances in Agronomy **24**:29-96.

Prouty, W. F. 1952. Carolina bays and their origin. Geological Society of America Bulletin **63**:167-&.

Reese, R. E., and K. K. Moorhead. 1996. Spatial characteristics of soil properties along an elevational gradient in a Carolina Bay wetland. Soil Science Society of America Journal **60**:1273-1277.

Richardson, C. J., and J. W. Gibbons. 1993. Pocosins, Carolina bays, and mountain bogs. Pages 257-310 *in* W. H. Martin, S. G. Boyce, and A. C. Echternacht, editors. Biodiversity of the Southeastern United States. J. Wiley & Sons, New York, NY, USA.

Robertson, P. A., G. T. Weaver, and J. A. Cavanaugh. 1978. Vegetation and tree species patterns near the northern terminus of the southern floodplain forest. Ecological Monographs **48**:249-267.

SAS Institute. 2001. SAS/STAT User's Guide Release 8.0, 2nd edition. SAS Institute Inc., Cary, NC.

Schalles, J. F. 1989. Comparative chemical limnology of Carolina bay wetlands on the Upper Coastal Plain of South Carolina. Pages 89-111 *in* R. R. Sharitz and J. W. Gibbons, editors. Freshwater wetlands and wildlife. U.S. Department of Energy, Office of Health and Environmental Research.

Schalles, J. F., R. R. Sharitz, J. W. Gibbons, G. J. Leversee, and J. N. Knox. 1989. Carolina Bays of the Savannah River Plant, Aiken, South Carolina. SRO-NERP-18, Savannah River Plant National Environmental Research Park Program.

Schalles, J. F., and D. J. Shure. 1989. Hydrology, community structure, and productivity patterns of a dystrophic Carolina bay wetland. Ecological Monographs **59**:365-385.

Sharitz, R. R. 2003. Carolina bay wetlands: Unique habitats of the southeastern United States. Wetlands **23**:550-562.

Sharitz, R. R., and J. W. Gibbons. 1982. The Ecology of Southeastern Shrub Bogs (Pocosins) and Carolina Bays: a Community Profile. FWS/OBS-82/04, U.S. Fish and Wildlife Service, Division of Biological Services, Washington, DC.

Spence, D. H. N. 1982. The zonation of plants in freshwater lakes. Pages 37-125 *in* A. MacFadyen and E. D. Ford, editors. Advances in Ecological Research. Academic Press, New York, NY.

Steinke, W., D. J. von Willert, and F. A. Austenfeld. 1996. Root dynamics in a salt marsh over three consecutive years. Plant and Soil **185**:265-269.

Stolt, M. H., M. H. Genthner, W. L. Daniels, and V. A. Groover. 2001. Spatial variability in palustrine wetlands. Soil Science Society of America Journal **65**:527-535.

Sutter, R. D., and R. Kral. 1994. The ecology, status, and conservation of two non-alluvial wetland communities in the South Atlantic and Eastern Gulf Coastal Plain, USA. Biological Conservation **68**:235-243.

Thompson, L. M., and F. R. Troeh. 1957. Soils and Soil Fertility, 3rd edition. McGraw-Hill Book Company, New York.

Vaithiyanathan, P., and C. J. Richardson. 1999. Macrophyte species changes in the Everglades: examination along a eutrophication gradient. Journal of Environmental Quality **28**:1347-1358.

Vepraskas, M. J., and S. P. Faulkner. 2001. Redox chemistry of hydric soils. Pages 85-105 *in* J. L. Richardson and M. J. Vepraskas, editors. Wetland Soils: Genesis, Hydrology, Landscapes, and Classification. Lewis Publishers, Boca Raton.

Weisner, S. E. B., and J. A. Strand. 1996. Rhizome architecture in *Phragmites australis* in relation to water depth: Implications for within-plant oxygen transport distances. Folia Geobotanica & Phytotaxonomica **31**:91-97.

Wikum, D. A., and M. K. Wali. 1974. Analysis of a North Dakota gallery forest: vegetation in relation to topographic and soil gradients. Ecological Monographs **44**:441-464.

Zedler, J. B. 2000. Progress in wetland restoration ecology. Trends in Ecology & Evolution **15**:402-407.

Table 2.1. Criteria and rationale for Carolina bay selection

Criteria	Rationale
Bay must be on the SRS property	• Proximity of bays would reduce differences in geology between bays • Differences in vegetation due to region would be prevented • Ease of access to bays
Bay must be predominantly herbaceous	• Goal of study was to examine response of herbaceous wetland plants to environmental variables
Water depth records must be available through bay hydrologic monitoring program	• Long-term water depth records were needed to determine flooding depths and frequencies
Bay must have some morphological variation	• Variation in morphology may increase variation in multiple environmental characteristics
Bay must not be undergoing a natural or man-made disturbance (e.g. from beaver activity or functioning drainage ditches)	• Plant communities should be as close to equilibrium as possible in response to environmental conditions
Bay must be a functioning wetland and has been since SRS ownership began in 1951	• A natural wetland system is desired for study; recently drained and/or restored wetlands would not be appropriate reference sites

Table 2.2. Soil gradients in Carolina bays. C indicates a gradient where higher values were toward the center of the bay. R indicates a gradient where higher values were toward the rim of the bay. Gradients were determined using a general linear model; $P \leq 0.05$ for all gradients. Independent models were used to avoid structural auto-correlation between variables.

	$p \leq 0.05$	Dry	Ellenton	Flamingo	Sarracenia
Chemical	pH	C	C	C	
	% C (total)		C		C
	% N (total)	C	C		C
	% P (total)		C		C
	C:N	R	R	R	
	N:P				
Physical	% Sand	R	R		R
	% Silt	C	C		
	% Clay		C		C
	Available Soil Water	C	C	R	C

Table 2.3. Pearson correlation coefficients of environmental variables in Carolina bays. N=1632, Prob. > |r| under HO: Rho=0. Values in bold indicate strong correlations.

	pH	**C**	**N**	**P**	**C:N Ratio**	**N:P Ratio**	**Sand**	**Clay**	**Avail. Water**
pH	1.00000	-0.00953 0.7005	0.09577 0.0001	0.21776 <0.0001	-0.43010 <0.0001	-0.28866 <0.0001	-0.16137 <0.0001	-0.00049 <0.0001	0.28904 <0.0001
C		1.00000	**0.96849** **<0.0001**	**0.83332** **<0.0001**	-0.16369 <0.0001	-0.09933 <0.0001	**-0.72895** **<0.0001**	**0.70920** **<0.0001**	0.44998 <0.0001
N			1.00000	**0.87019** **<0.0001**	-0.36249 <0.0001	-0.10342 <0.0001	**-0.79876** **<0.0001**	**0.74352** **<0.0001**	0.56698 <0.0001
P				1.00000	-0.33981 <0.0001	-0.33148 <0.0001	**-0.77025** **<0.0001**	0.69054 <0.0001	0.57196 <0.0001
C:N Ratio					1.00000	0.00279 0.9104	0.52995 <0.0001	-0.34808 <0.0001	-0.49760 <0.0001
N:P Ratio						1.00000	0.08972 0.0003	-0.03694 0.1358	-0.03709 0.1342
Sand							1.00000	**-0.85749** **<0.0001**	-0.65063 <0.0001
Clay								1.00000	0.33475 <0.0001
Avail. Water									1.00000

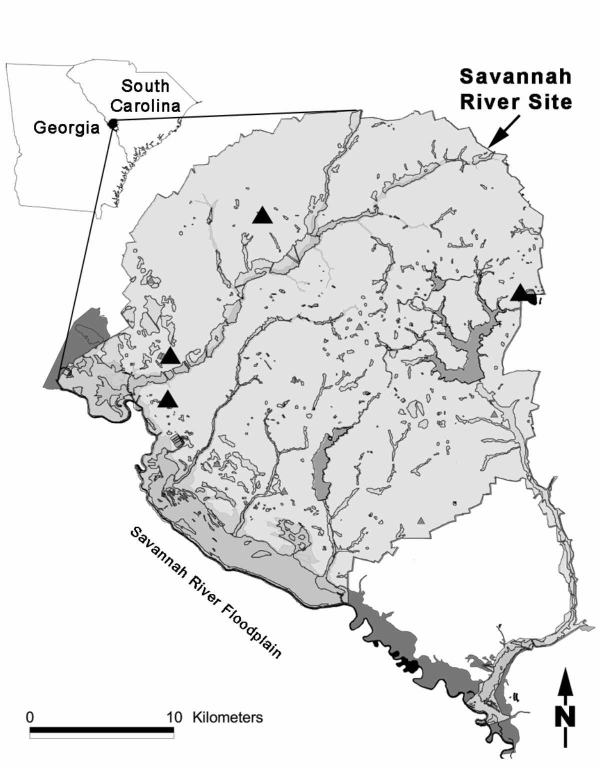


Figure 2.1. Carolina bay locations on the Savannah River Site (SRS), Aiken, South Carolina.

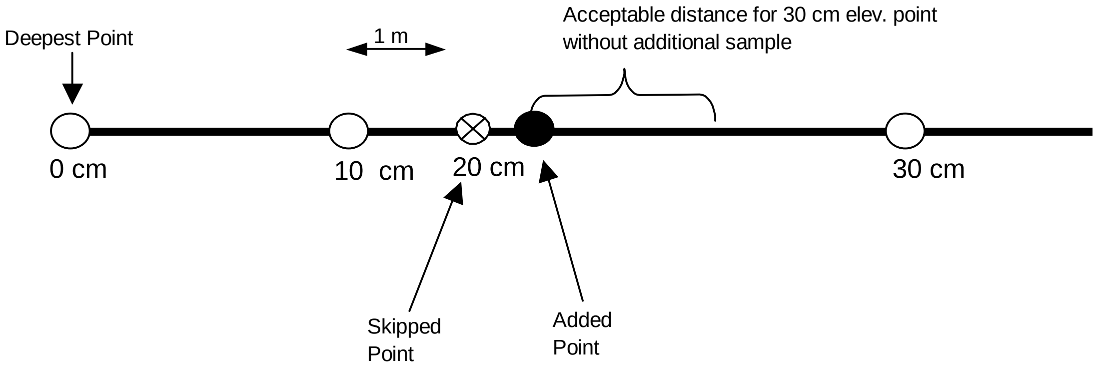


Figure 2.2. Sample location layout strategy. If a sample location on the transect was within 2 m of the previous sample, the location was skipped and a sample point was added 2 m further along the transect.

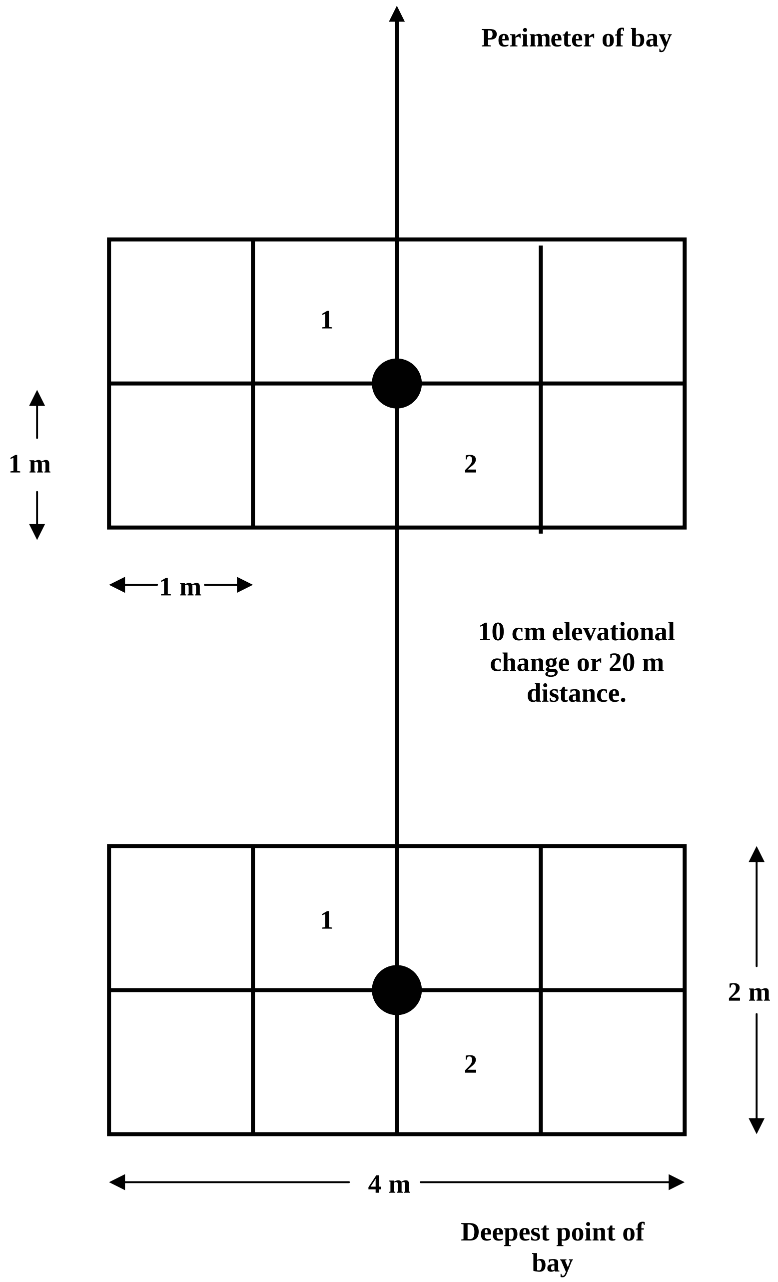


Figure 2.3. Layout of sampling plots used in soil surveys. Samples from subplots 1 and 2 were composited for analysis.

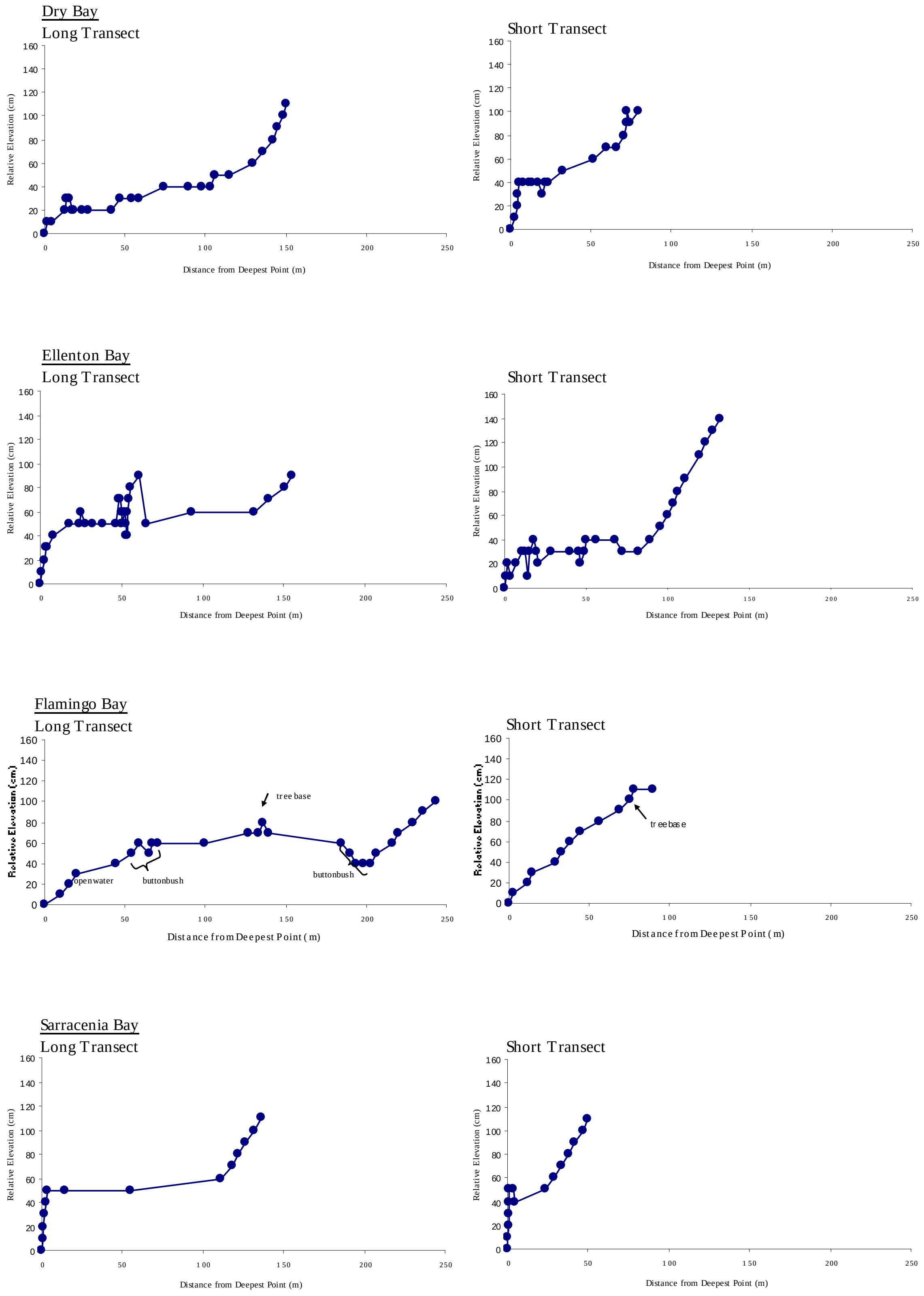
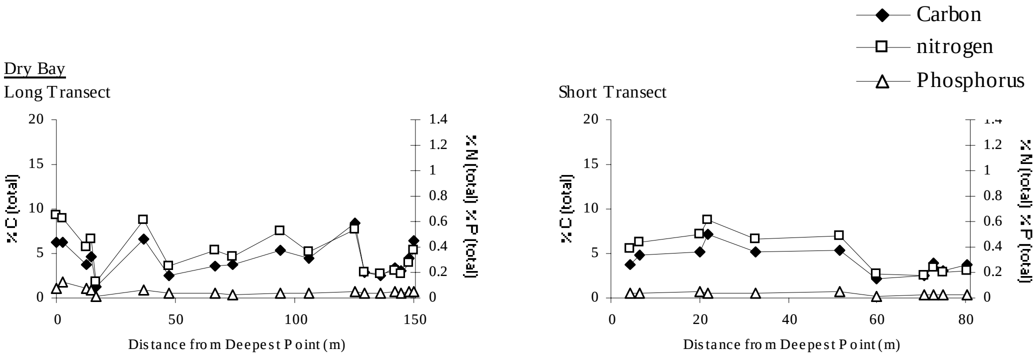


Figure 2.4. Relative elevation profiles of Carolina bays

Dry Bay

Long Transect

Short Transect

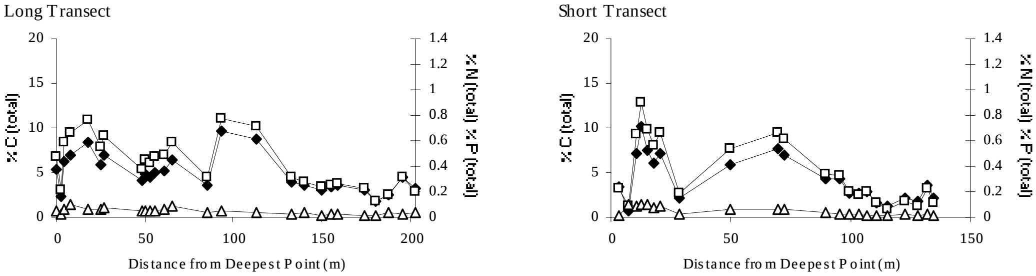


N gradient p = 0.05; P gradient p = 0.046 C gradient is not significant

Ellenton Bay

Long Transect

Short Transect

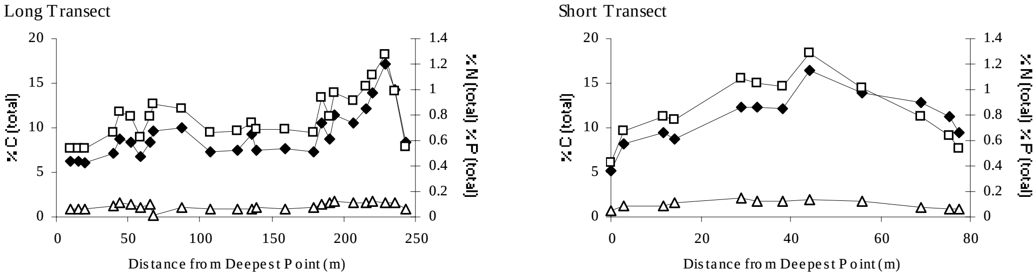


C, N, and P gradients p < 0.01

Flamingo Bay

Long Transect

Short Transect

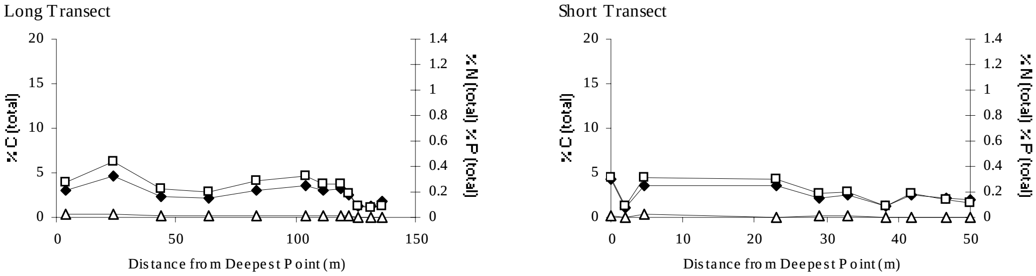


C, N, and P gradients not significant

Sarracenia Bay

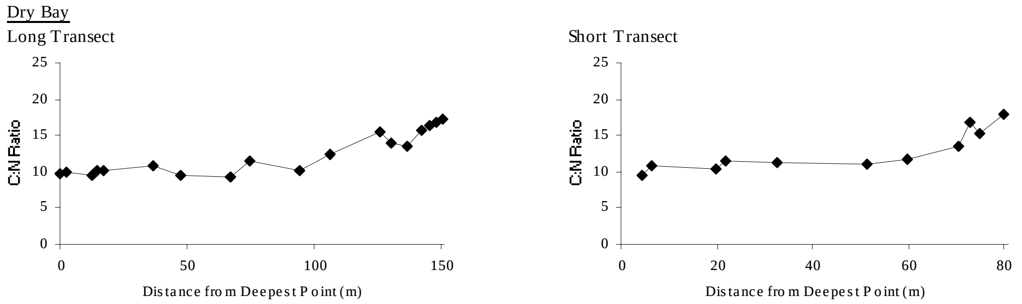
Long Transect

Short Transect



C, N, and P gradients p < 0.01

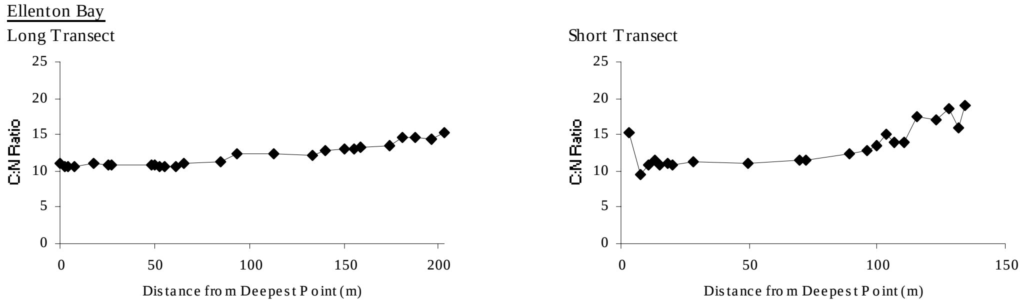
Figure 2.5. Carbon, nitrogen, and phosphorus variability in Carolina bays.


Dry Bay

Long Transect

Short Transect

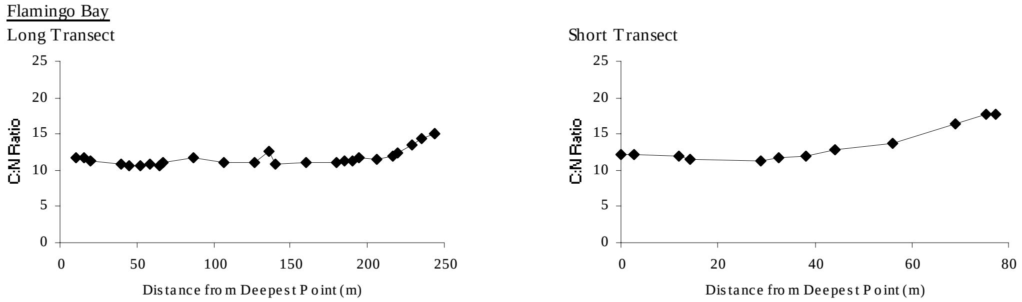
C:N gradient p <0.01


Ellenton Bay

Long Transect

Short Transect

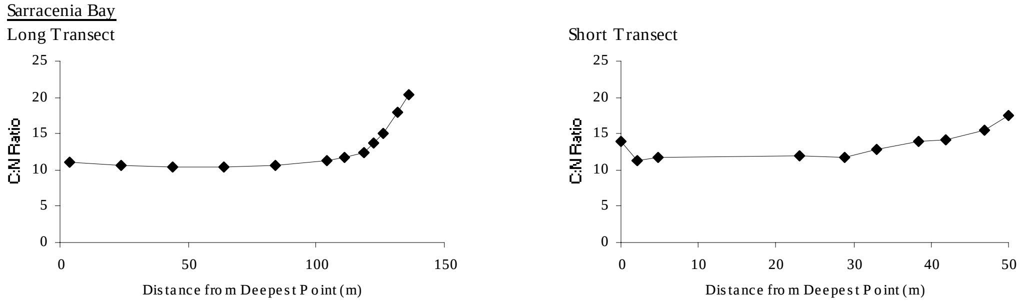
C:N gradient p <0.01


Flamingo Bay

Long Transect

Short Transect

C:N gradient p = 0.027

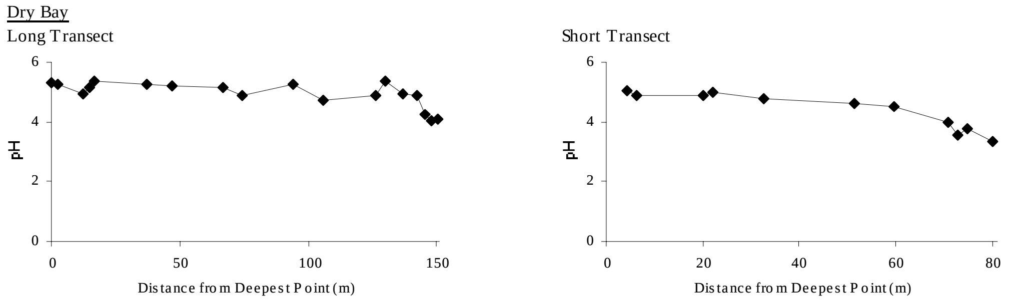

Sarracenia Bay

Long Transect

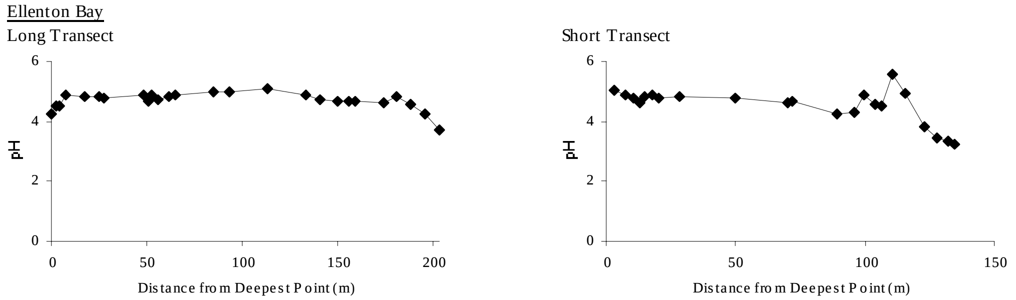
Short Transect

C:N gradient not significant

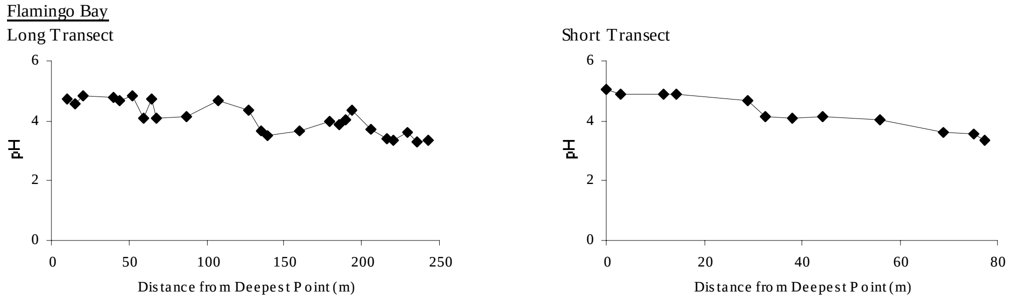
Figure 2.6. C:N variability in Carolina bays.



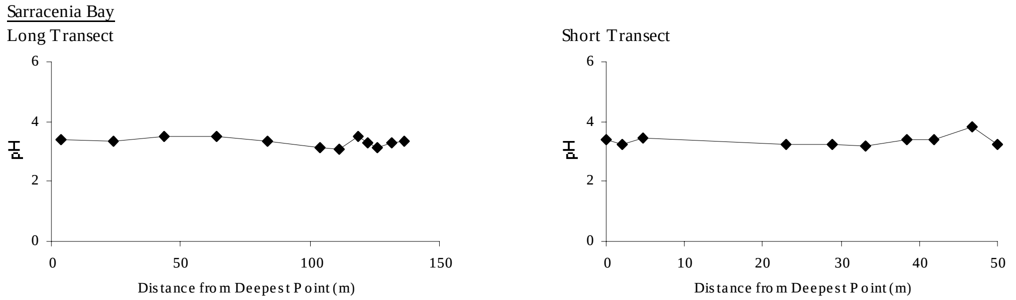
pH gradient p <0.01



pH gradient p = 0.02

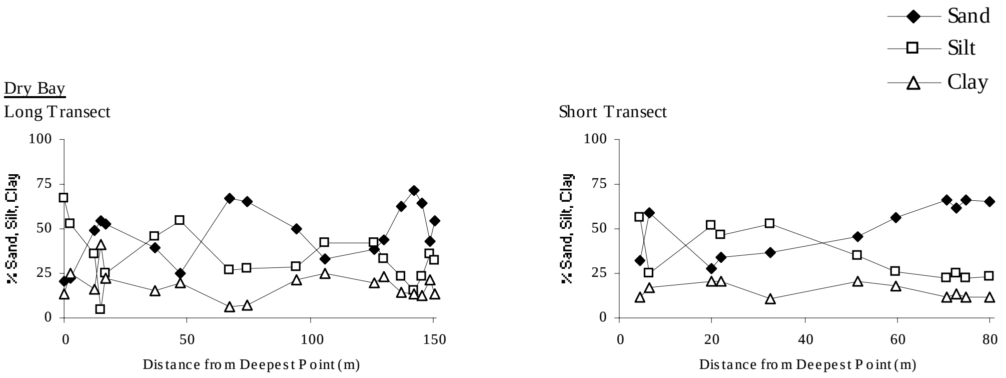


pH gradient p <0.01

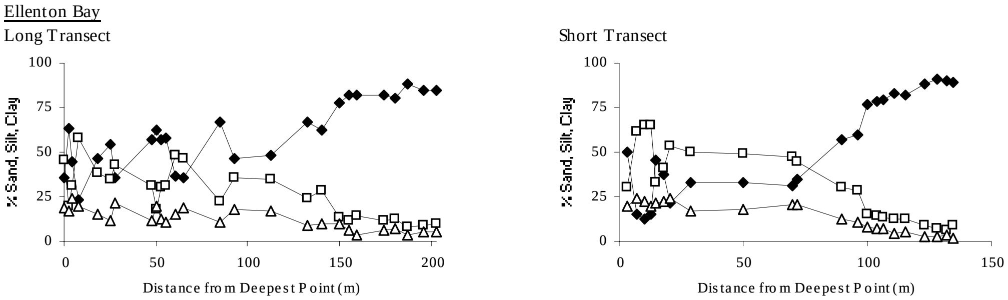


pH gradient not significant

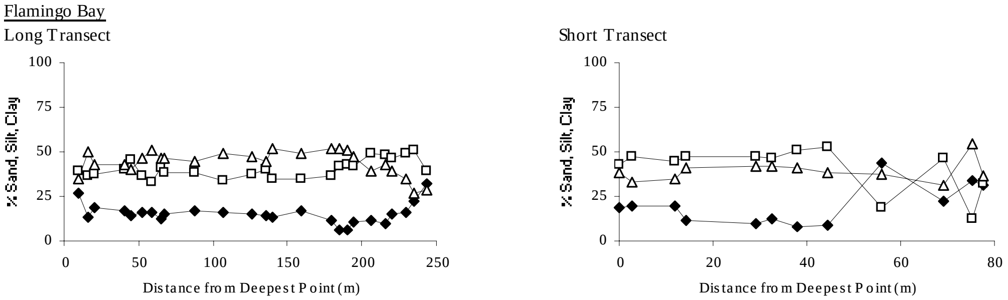
Figure 2.7. pH variability in Carolina bays.



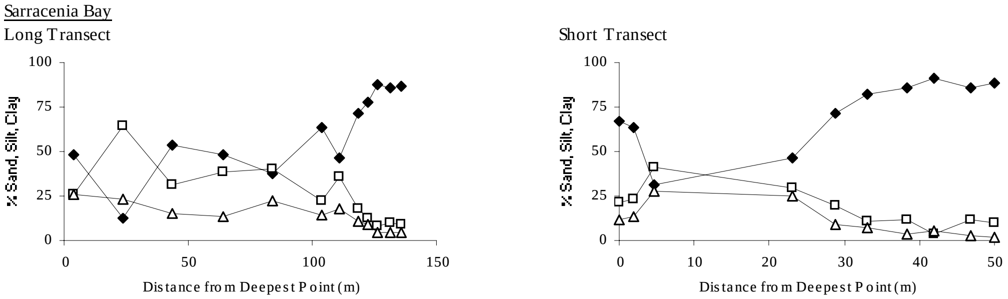
Sand and silt gradients p <0.01. Clay gradient not significant



Sand silt, and clay gradients p <0.01.

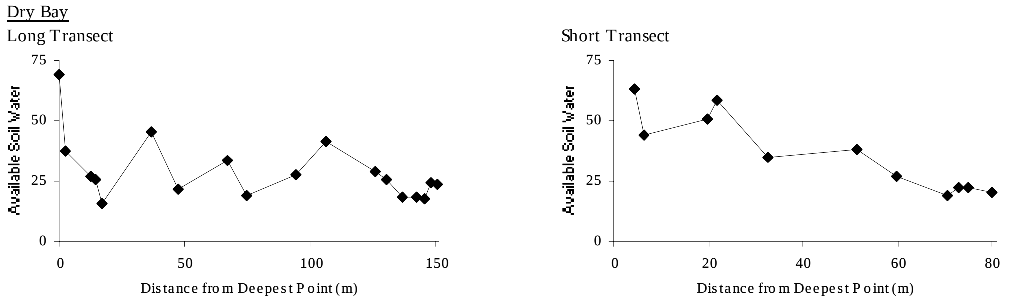


Sand silt, and clay gradients not significant

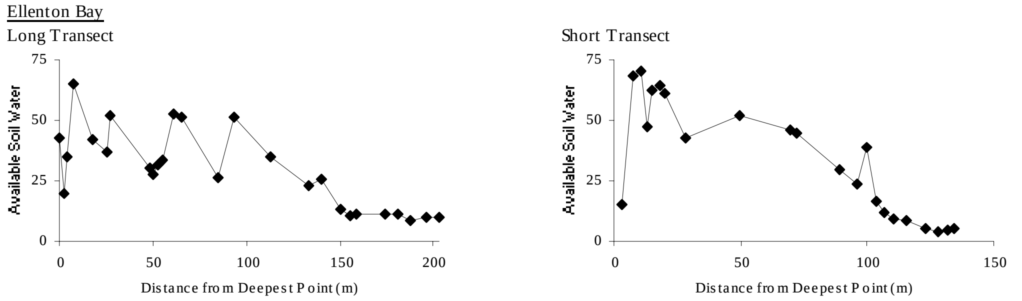


Sand and clay gradients p <0.01. Silt gradient not significant

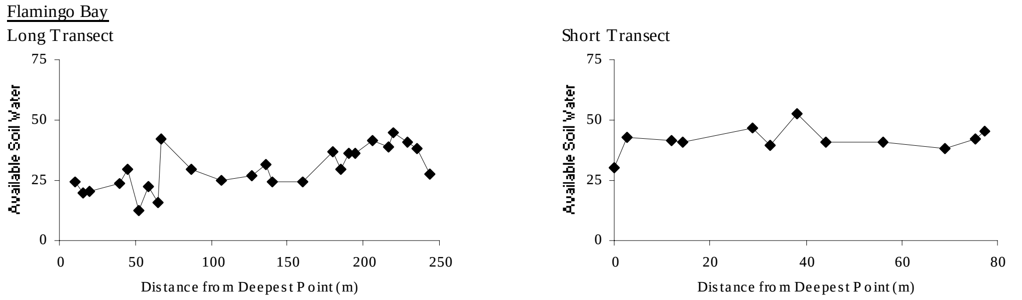
Figure 2.8. Sand, silt, and clay variability in Carolina bays.



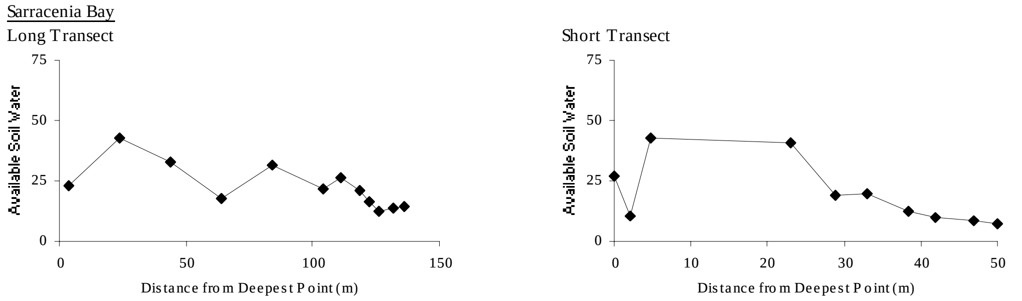
Available soil water gradient $p < 0.01$



Available soil water gradient $p < 0.01$



Available soil water gradient not significant



Available soil water gradient $p < 0.01$

Figure 2.9. Available soil water (g water / 100 g soil) variability in Carolina bays.

CHAPTER 3

RELATIONSHIPS BETWEEN ENVIRONMENTAL GRADIENTS AND PLANT DISTRIBUTIONS IN CAROLINA BAYS

Introduction

Recognition of the value of Carolina bays and their risk of destruction or degradation has resulted in recent works aimed at encouraging and facilitating bay preservation, conservation, and restoration. These isolated depression wetlands display a range of plant communities (De Steven and Toner 2004), and strong zonation patterns are often apparent in the vegetation along the water depth gradient (Sharitz and Gibbons 1982, Tyndall et al. 1990, Richardson and Gibbons 1993, Collins and Battaglia 2001). Many rare and endangered flora and fauna species are known to inhabit Carolina bays (Bennett and Nelson 1991, Sutter and Kral 1994, Edwards and Weakley 2001). An unusually diverse seedbank can contain rare plants that can germinate during droughts or other natural disturbances (Kirkman and Sharitz 1994, Collins and Battaglia 2001).

The need for the identification of bays has been repeatedly emphasized (Sharitz and Gibbons 1982, Richardson and Gibbons 1993, Sharitz and Gresham 1998). Efforts have been made to catalogue Carolina bays and inventory their flora and fauna, especially in undisturbed bays (Tyndall et al. 1990, Bennett and Nelson 1991). In order to facilitate sound management strategies, investigations have begun to decipher the biotic and abiotic interactions of Carolina bays, as well as the effects of natural and anthropogenic disturbances. These studies have documented the important role of the seed bank in concert with fire and soil disturbance in maintaining plant composition and diversity (Kirkman and Sharitz 1994, Collins and Battaglia 2001). Effects of past land use in and around Carolina bays have been found on present-day vegetation (Kirkman et al. 1996), as has current surrounding land use on seed bank composition (Poiani and Dixon 1995). Recent focus on Carolina bay restoration (Federal Register 1998) has driven efforts towards understanding reference bays and the dynamics within them (De Steven and Toner 2004).

In order to restore assemblages of vegetation, a better understanding of how assemblages are created is needed (Metzker and Mitsch 1997, Lockwood and Pimm 1999), as well as how these assemblages change over time. Accurate prediction of community assemblages and plant distributions is necessary for successful wetland restoration. van der Valk (1981) proposed a method of predicting community succession in wetlands by examining the life history characteristics of the available species. This simple model requires knowledge of life history characteristics relating to life span, establishment requirements, and propagule longevity. A key premise of the model is that two environmental characteristics (flooded or drawdown) act as filters or sieves, removing species lacking adaptation mechanisms. The van der Valk model was expanded upon by Keddy (1992) with the proposal of assembly and response rules. It was suggested that communities are assembled by a series of environmental filters which prevent the establishment of species lacking the necessary adaptive traits. It was further proposed that environmental variations change the set of filters over time, removing species without the additional necessary traits. Further establishment from the existing species pool (or possible immigrants) is then regulated by the new set of environmental filters.

While the goal of assembly and response rules was to predict the communities that might occur under specific environmental conditions, centrifugal organization (Wisheu and Keddy

1992) was proposed, in part, to attempt to predict the distributions of organisms. The main tenet of this model was that most wetland species will grow best (largest, fastest, and most fecund) in an environment with high fertility and low disturbance (termed the "core habitat"). It was further suggested that light, water, and mineral nutrients were in greatest supply in the core habitat. For any given species pool, a set of inclusive fundamental niches stemmed from this core habitat, and competitive ability restricted each species to its realized niche. Each resulting community can be found along various environmental vectors extending from the core habitat, with lessening fertility reflected in the intensity of the vector. In this manner, "peripheral habitats" of low fertility and varying disturbances can be arranged about the core habitat.

While the initial phase of any new model must be simple by necessity, the community models proposed by van der Valk (1981), Wisheu and Keddy (1992), and Keddy (1992) present certain problems in their simplicity. The environmental filters in the van der Valk model are binary operators; for example, the state of a wetland can be either flooded or drawn down, and the different life stages of the species are screened by their ability to tolerate or require either state. However, the response of any life stage of a species may be dependent on the intensity of flooding or drawdown, and the potential for a gradient within each environmental category is not considered by this model. In addition, many environmental characteristics that may be required for a plant to complete some part of its life cycle (such as minimum nutrient availability, minimum water depth, or sediment type) are not considered.

Within the centrifugal organization model (Wisheu and Keddy 1992), the assumption of a core habitat at which all species grow best may be flawed. It is quite likely that morphological and physiological differences between species yield distinct ideal niches. Especially important are tolerances to flooding and drydown. Some wetland plant species require submergence for survival, yet some require more well-drained areas; therefore the abundance of water and flood duration can be both stressors and resources. While the vegetation of some wetlands might be arranged into centrifugal patterns, there may be cases when these patterns are simply coincident rather than causative, and other cases where such arrangement is not possible due to the non-existence of a core habitat. Lastly, while the assembly of a trait matrix proposed by Keddy (1992) is a laudable goal, it was admitted that determining the operating environmental filters and the corresponding traits against which they operate would be a large task.

The distributions of wetland plants are mainly influenced by environmental characteristics relating to the depth, duration, and timing of flooding (Holland and Jain 1981, Carter 1986, Moore and Keddy 1988, Shipley et al. 1991, Squires and van der Valk 1992, van der Valk 1994, Casanova and Brock 2000, Lenssen et al. 2000). Other environmental variables that may affect plant growth and/or distribution include nutrients (Bridgham et al. 1996, Vaithiyanathan and Richardson 1999, Keddy et al. 2000, Svengsouk and Mitsch 2001), soil texture (Keddy 1980, 1982, 1984, Keddy and Constabel 1986, Coops et al. 1991), pH (Glaser et al. 1990, Bridgham et al. 1996), soil water availability (Thompson and Troeh 1957), and light (Sharp and Keddy 1985, Breen et al. 1988, Maillette and Keddy 1989). Interspecific competition may be affected by these environmental variables (Wilson and Keddy 1985, Gaudet and Keddy 1995).

The need for sound predictions for the purpose of environmental planning and possible wetland restoration necessitates further work to understand species distributions and assemblages. Weiher and Keddy (1995) advocated research towards predicting the assemblage of communities from common species pools by finding patterns in species assemblages and their shared traits, and determining how these patterns change over space and time. Keddy (1999) has also proposed that plant communities are produced by quantifiable relationships between multiple environmental factors and the properties of the species, and that these factors change through time.

Zonation patterns seen in the vegetation of Carolina bays also occur in other wetland types (Spence 1982). It is often thought that such zonation occurs over environmental gradients within the wetland, resulting in gradations of habitat types (Mitsch and Gosselink 1993). Understanding environmental gradients and their potential effects on vegetation zones can have important implications for wetland restoration, especially if restoration objectives include specified area requirements for the establishment of particular habitat types. In addition, if the restoration plan includes planting and/or seeding of particular species, understanding the environmental constraints on the zonation of different species could improve planting plans, decrease mortality, and increase success rates.

The purpose of this study was to better understand the environmental constraints on the distribution of plants in Carolina bay wetlands. This was done by determining which environmental variables were related to the distributions of individual species or groups of species. A second goal was to relate these variables to restoration uses by determining quantitative values of these variables that may act as filters, outside of which each species would not be expected to occur. Lastly, these values were compared (both individually and in combination) to the standing vegetation in the bays to see if accurate predictions regarding the distributions of the plants could be made.

Methods

Bay Selection

Four Carolina bays on the Department of Energy's Savannah River Site (SRS) were selected that contained herbaceous plant communities and for which hydrologic records were available. To accomplish this, certain *a priori* criteria were established (Table 3.1). Based on these criteria, the four bays were Dry Bay (SRS bay 31; located at 33° 15' 0.35" N, 81° 44' 46.89" W), Ellenton Bay (SRS bay 176; 33° 13' 18.54" N, 81° 29' 8.07" W), Flamingo Bay (SRS bay 3; 33° 20' 12.80" N, 81° 40' 44.03" W), and Sarracenia Bay (SRS bay 78; 33° 17' 22.60" N, 81° 29' 8.07" W) (Figure 3.1). Dry, Ellenton, and Flamingo Bays are in Aiken County; Sarracenia Bays is in Barnwell County. Dry and Ellenton Bays are located within the Sunderland Terrace, Flamingo Bay is located within the Aiken Plateau, and Sarracenia Bay is located within the Brandywine Terrace (Davis and Janecek 1997).

Dry Bay is a somewhat bowl-shaped depressional pond that has standing water covering a portion of the basin at least part of most years (Schalles et al. 1989). It is 45.7 m above sea level and approximately 5 ha in size (Davis and Janecek 1997). The bay's interior vegetation includes *Panicum hemitomon* and *Nymphaea odorata*, surrounded by bottomland hardwood/swamp forest species on the periphery. Pre-1951 history prior to the establishment of the SRS includes agriculture in the area surrounding the bay, and drainage. Prescribed burns in the forested buffer occurred in 1971, 1984, and 1986 (Davis and Janecek 1997).

Ellenton Bay is also a somewhat bowl-shaped depressional pond that has standing water covering a portion of the bay at least part of most years (Schalles et al. 1989). It is 44.2 – 45.7 m above sea level and 11.3 ha in size (Davis and Janecek 1997). Predominant bay vegetation includes *Nymphaea odorata*, *Brasenia schreberi*, and *Panicum* spp., surrounded by pine/mixed hardwood forest uplands and old fields. Ellenton Bay is bisected by a power line right-of-way and embankment. Its pre-1951 history includes drainage and agriculture. Despite these past and present disturbances, the bay is considered to represent a natural, isolated, relatively undisturbed bay (Davis and Janecek 1997). For the purposes of this study, the larger, southern portion of the bay was used and the power line embankment was not crossed.

Flamingo Bay is a mostly herbaceous wetland with standing water covering a portion of the bay at least part of most years (Schalles et al. 1989). It is located 94.5 m above sea level and is 5.7 ha in size (Davis and Janecek 1997). Flamingo Bay has shallow slopes throughout most of the bay, but has a pond-like deeper area near the northwest side. Vegetation within the bay consists of aquatic and herbaceous species (including *Polygonum* spp., *Nelumbo lutea, and Panicum* spp.), as well as trees and shrubs (including *Nyssa sylvatica* var. *biflora, Acer rubrum, Liquidambar styraciflua*, *Pinus taeda*, and *Cephalantus occidentalis*). The surrounding area supports pine plantations of differing ages. The interior of the bay has never been ditched, but the surrounding area was used for livestock prior to 1951 (Davis and Janecek 1997).

Sarracenia Bay is a shallow, pan-shaped depression with gentle slopes that has standing water covering a portion of the bay at least part of most years (Schalles et al. 1989). It is 55.1 m above sea level and 4.0 ha in size (Davis and Janecek 1997). Vegetation was previously described as having two outer zones dominated by *Aristida affinis*/*Andropogon virginicus* and *Rhynchospora traceyi*/*Leerzia hexandra* and two inner zones of *Nymphaea odorata/Eleocharis rabbinsii* and *Nymphaea odorata/Eleocharis equisetoides* (Davis and Janecek 1997). The surrounding upland vegetation is pine/hardwood forest. Prior to 1951, the areas surrounding the bay were used for crop fields and pastures (Davis and Janecek 1997). Although the SRS boundary runs through the southern portion of the bay, the privately-owned off-site portion is undisturbed.

Sample Locations

Two transects were established from the deepest point of each bay, each radiating toward the rim in one direction only. One transect was established to the edge of the bay along the long axis (i.e., the longest transect possible from the deepest point), and the other was established along the short axis. Sample plots were located along each transect as described in Chapter 2. Samples were collected from the deepest point of the bay to the estimated edge of the jurisdictional wetland. The actual bay depression might have been larger due to extensive sand rim formation.

Vegetation Sampling

Herbaceous vegetation (all vascular non-woody vegetation or woody vegetation that was less than 1 m tall) was sampled between July 20 and September 25, 1999. At each sampling point, vegetation was surveyed in four 1 m^2 sub-plots (Figure 3.2). A modified Braun-Blanquet cover-abundance scale was used to estimate coverage for each species (Table 3.2) (Daubenmire 1968, Mueller-Dombois and Ellenberg 1974). For analysis, values for each species were converted to the midpoint of each coverage class for classes 1 through 6 (e.g., class 6 was converted to 97.5%, class 5 was converted to 85%, and so forth). The midpoint value for each species was then averaged across sub-plots to calculate an estimated cover value for each sampling location (Daubenmire 1968). Classes “+” (few) and “r” (solitary) were not converted to percent cover nor considered in the average calculations as such plants were considered to have negligible cover. Such species were used, however, in determining species richness values.

To assess the amount of direct shade at each sampling point, overhead cover was estimated using a concave spherical densiometer. To assess canopy cover that was most likely to block direct solar radiation, only the central densiometer square was used, minus the northern portion of the central square. Vegetation was identified using Radford et al. (1968), Godfrey and Wooten (1981), and Crow and Hellquist (2000).

Soil Sampling and Analysis

Samples were collected for chemical and physical analyses from the top 10 cm of soil using a 6.35 cm diameter auger. Wetland plants often experience shallow rooting in response to flooding (Weisner and Strand 1996). Steinke et al. (1996) demonstrated that the top 10 cm of soil was the expected rooting zone for most herbaceous wetland plants. Two sub-samples for chemical analyses were taken from the center of diagonally placed 1 m^2 subplots (Figure 3.2) and were combined in the field. This process was duplicated to collect a second soil sample (immediately adjacent to the first) for physical analyses. Additional samples were collected from the top 10 cm of soil adjacent to each sample pole for pH analysis. Samples were prepared and analyzed for pH, C, N, and P, particle size distribution, available soil water as presented in Chapter 2.

Water Level

Water level in each bay was monitored regularly (weekly to monthly) from August 1995 to August 1999 as part of an on-going monitoring program (Lide *unpublished data*). Water level was extrapolated from its point of measurement to each sampling location along the transects using the elevational survey data. The slope of water level change between sampling dates was used to estimate the water level for each day within the three-year period. There were a few cases where a bay dried completely. As piezometer data were not available, negative water depths during the drought period were estimated using the rate of drainage and reinnundation before and after the drydown. To facilitate statistical analysis, the water depths for each sample location were expressed in terms of the number of days per year (August 22 through August 21) or the number of days within the spring growing season (January 1 through June 30) that certain depth conditions were met. Three main types of water variables were calculated. The first represented the total length of time (days) inundated to various depths, for both whole years and spring seasons. The second represented the longest (consecutive) flood duration at various depths, for both whole years and spring seasons. Estimated water depths from August 1996 to August 1999 (3 years) were used to determine these variables. The third water variable type represented median water depths over a period of 1 year or 4 years. Variables calculated for analysis are summarized in Table 3.3

Statistical Analysis

Two subsets of the herbaceous vegetation were analyzed: graminoids (consisting of grasses, rushes, and sedges) and submerged aquatics with floating leaves (consisting of *Brasenia schreberi*, *Nelumbo lutea*, *Nymphaea odorata*, and *Nymphoides cordata*). Each group was statistically analyzed to determine which environmental variables were responsible for significant amounts of variation in plant percent cover. Due to their high cover, additional analyses were performed on *Panicum hemitomon* and *Nymphaea odorata* alone.

To reduce the large number of explanatory environmental variables, water depth variables were analyzed alone (without the other environmental variables) by stepwise multiple regression (Proc. Reg; SAS Institute 2001). Water depth variables were grouped into sets by water year or spring; each set was analyzed separately, both including and excluding the 4-year median. The latest-year (1998-1999) or spring (1999) values of water depth variables showing a trend of significant relationships to plant cover were selected for further analyses with the other environmental variables (% C, % N, % P, C:N, N:P, pH, % sand, % silt, and available soil water) by general linear regressions (Proc. GLM; SAS Institute 2001).

Due to high correlations between the soil concentrations of C, N, and P, the regression for each species or group was performed three times, each with only one of the correlated variables. In addition, due to a high correlation between the 1-year and 4-year median water depths, two sets of these regressions (with C, N, or P) were performed for *P. hemitomon*, each with either the 1-year or 4-year median water depths.

For each species or group, an estimated value for each significant environmental variable was determined that corresponded to the end of the species distribution (the distribution limit) by probit analysis (Proc. Probit; SAS Institute 2001). To eliminate areas where plants might be declining due to changes in environmental conditions, 10% cover was chosen to represent the end of a plant group or species range. Usefulness of the distribution limits were assessed as sole predictors of species distributions by comparing the cover of each group or species to the values of the corresponding environmental variables at each plot. However, some variables likely dominate over others while some could potentially act as modifying agents (increasing or decreasing the chance of occurrence or establishment). To better understand potential interactions between the environmental characteristics identified, the distribution limits were then considered in combination and compared to the actual species and group distributions.

Results

General Vegetation Characteristics

A total of 55 species were found in the herbaceous layer (non-woody and woody plants < 1m tall); 21 with average covers of 1% or higher per bay. Dry Bay had 16 species, with a maximum of 6 per plot. The most common were *Nymphaea odorata* (average cover 17.9%), *Utricularia* spp. (6.5%), *Juncus effusus* (1.8%) and *Panicum hemitomon* (1.6%). This bay was open (no canopy) in the center, while the edges had a woody zone consisting of *Cephalanthus occidentalis, Nyssa sylvatica* var. *biflora, Quercus laurifolia, Liquidambar styraciflua, Taxodium distichum,* and *Acer rubrum*.

Ellenton Bay had 30 species, with a maximum of 8 per plot. The most common were *N. odorata* (average cover 49.8%), *P. hemitomon* (10.6%), *Utricularia* spp. (4.8%), *Decodon verticillatus* (3.9%) and *Panicum verrucosum* (1.1%). The open bay was surrounded by *C. occidentalis*, *N. sylvatica* var. *biflora*, *A. rubrum*, *L. styraciflua*, and *Pinus taeda*.

Flamingo Bay had 25 species, with a maximum of 8 per plot. Most common were *Brasenia schreberi* (average cover 22.0%), *P. hemitomon* (11.1%), *Pontederia cordata* (5.9%), *Leersia hexandra* (2.4%), *Utricularia* spp, (2.4%), *Eleocharis* sp. (2.3%), *Lemna valdiviana* (2.1%), *Sagittaria stagnorum* (1.3%), and *Bacopa caroliniana* (1.1 %). The deepest part of Flamingo Bay is open and fringed with *C. occidentalis*. The long transect in this bay had some areas of dense overhead cover consisting mainly of *C. occidentalis* and *N. sylvatica* var. *biflora*. Cover on the edges of the bay included *N. sylvatica* var. *biflora*, *Diospyros virginiana*, *Q. laurifolia*, *Fraxinus pennsylvanica*, *L. styraciflua*, and *P. taeda*.

Sarracenia Bay had 26 species, with a maximum of 10 per plot. The most common were *N. odorata* (average cover 17.1%), *Panicum spretum* (8.6%), *Scleria reticularis* (7.0%), *P. verrucosum* (4.4 %), *P. hemitomon* (4.1%), *Eleocharis equisetoides* (2.1%), *Centella asiatica* (1.9%), *Viola lanceolata* (1.4 %), and *Lachnanthes caroliniana* (1.0%). Two species listed as species of concern in South Carolina were found: *S. reticularis,* and *Croton eliottii,* (South Carolina Department of Natural Resources 2003), as well as an introduced exotic species, C.

asiatica (Godfrey and Wooten 1981). Sarracenia Bay was open in the center, while the edges had overhead cover from *N. sylvatica* var. *biflora* and *P. taeda*.

When the distributions and cover of graminoids along each transect were compared to those of floating-leaved species, the distinct zonation pattern of these groups was very apparent (Figure 3.3). In many cases, especially along the short transects of Ellenton, Flamingo, and Sarracenia Bays, the transition between zones was relatively abrupt, while in other cases, a localized increase in cover of one group coincided with a decrease in cover of the other. Similar trends appeared when the distributions and cover of *P. hemitomon* and *N. odorata* were compared, albeit to a slightly lesser extent.

Graminoid Species Distributions

Regressions using the water variables (depth and duration of inundation) revealed a significant relationship between graminoid species cover in 1999 and the 4-year median water depth (Table 3.4a). Regressions using this water variable and the other environmental variables showed significant relationships between graminoid species cover and both the 4-year median water depth and the soil C:N ratio. The R^2 values for these three regressions containing %C, %N, and %P were 0.27, 0.28, and 0.27, respectively (Table 3.5).

Probit analysis of the 4-year median water depth predicted 10% cover of graminoid species at 51.3 cm (with 95% fiducial limits [FL] of 39.2 to 69.0) (Table 3.6). Since graminoids generally occurred on the outer edges of the bays, including areas above the water line, 51.3 cm represents the maximum 4-year median depth at which this group is expected to occur. Analysis of the C:N ratio predicted 10% cover of graminoid species at 11.0 (with 95% FL of 1.5 to 13.1). Since the soil C:N ratio formed a significant spatial linear gradient within the bays (except Sarracenia Bay which had a p-value of 0.07), increasing from the center towards the rim, the graminoid species group would not be expected to grow in areas with a C:N ratio of <11.0. Although the calculated 95% FL of the C:N ratio distribution limit on graminoids are very wide (1.5 to 13.3), the observed C:N ratio ranged from 9.4 to 20.3. Therefore, the practical range for the FL for the C:N ratio distribution limit is 9.4 to 13.1. While these values encompass many of the plots sampled, 32% had C:N ratios above the upper FL (thus were well within the expected C:N range for graminoids).

The 4-year median water depth criterion of a maximum of 51.3 cm predicted the presence of graminoid species moderately well (Figure 3.4 and Table 3.7). Graminoid cover was ≥10% in 45% of all the plots with 4-year median water depths less than the predicted maximum, and in only 19% of all the plots exceeding it. Graminoid distribution in Ellenton Bay was particularly well predicted, where 50% of the 20 plots that had water depths less than the predicted maximum for graminoids had ≥10% graminoid cover. Additionally, 89% of the 28 plots with water depths above the maximum had <10% graminoid cover. Graminoid distribution was also well predicted in Flamingo Bay, where 50% of the 16 plots with water depths less than the maximum had ≥10% and 67% of the 21 plots with depths exceeding it had <10% graminoid cover. Sarracenia bay was less well predicted. Although 57% of the 21 plots with depths less than the maximum had ≥10% graminoid cover, there was only one sample in this bay where water depth was too great (<10% graminoid cover was present at this location). However, graminoid cover increased along the water depth gradient from <10% at the edge of the bay (where the four-year median water depth was 20 cm below the soil surface) to a maximum of 134% (at 12.8 cm of flooding), and declined to 10% cover (at 32.8 cm). Graminoid distribution was not well predicted in Dry Bay. Three plots in the bay had graminoid cover above 10%, but these (as well as seven of the eight plots with cover over 5%) had water depths predicted to be too great. Additionally, graminoid cover seems less related to water depth in Dry Bay.

In most bays, the soil C:N ratio was a moderately good predictor of graminoid distribution (Figure 3.5, Table 3.7). Graminoid cover was ≥10% in 39% of all the plots with C:N ratios above the predicted minimum, and in only 15% of all the plots below it. In Sarracenia Bay, 59% of 17 plots that were above the minimum C:N ratio for graminoids had ≥10% cover, while 60% of the 5 plots that were below it had < 10% cover. In the other bays, C:N was less effective as a predictor of graminoid presence. Of the plots that had C:N ratios estimated to be high enough to contain graminoids, ≥10% graminoid cover was found in 45% of 29 plots in Flamingo Bay, 35% of 31 plots in Ellenton Bay, and 12% of 17 plots in Dry Bay. However, the absence of graminoids was well predicted in plots with less than the predicted C:N minimum. In these cases, <10% cover was found in 92% of 12 plots in Dry Bay, 88% of 17 plots in Ellenton Bay, and 75% of 8 plots in Flamingo Bay.

Graminoid distribution patterns were better explained using both of the distribution criteria in combination (Figure 3.6). In Ellenton Bay, these combined distribution criteria were excellent predictors. Plots where the graminoid species group's distribution criteria for both 4-year median water depth and C:N ratio were met were located towards the edges of the bay. Of the 17 plots that met these conditions, 59% had ≥10% graminoid cover. However, graminoids did not occur in areas quite as deep as predicted. Plots where both distribution criteria were met but <10% graminoid cover was present were in deeper areas, having 4-year median water depths from 20.9 to 50.9 cm (with the exception of one plot on the bay edge). In these deeper plots, floating-leaved species were present. Graminoid cover was <10% in 82% of the plots where either the water depth or C:N ratio criteria (or both) were not met. Of the 14 plots where neither criteria were met, two plots, in deeper areas of the bay, had greater than 10% graminoid cover. Graminoids in these locations consisted mainly of floating mats of *P. hemitomon*.

Graminoid distribution was predicted relatively well in Flamingo Bay by using the combined distribution criteria. Of the 14 plots that met both criteria, 50% contained ≥10% graminoid cover. At all of the plots in which both criteria were met but there was <10% graminoid cover, dense canopy (86% or higher) was present. Graminoids occurred in seven plots where the 4-year median water depth was considered too deep (up to 72.5 cm; depth in the bay ranged up to 112.5 cm), but in six of these, the C:N ratio criterion was met. Additionally, concentrations of soil C, N, and P were very high in these plots; C ranged from 10.54 to 12.38% (bay mean was 9.83), N ranged from 0.92 to 1.09% (bay mean was 0.80), and P ranged from 0.10 to 0.15% (bay mean was 0.09). Graminoid cover was <10% in two adjacent plots where the 4-year median water depth was 47.5 cm, and would have been expected based on the criterion of 51.3 cm. One of these locations did not meet the C:N criterion and the other had dense overhead cover (86%). One plot had >10% cover yet did not meet either criteria; soils in this plot had a higher available water value than most other plots along the same transect (although the value was similar to those of the other transect) and much lower P concentrations than elsewhere in the bay.

Graminoid distribution was predicted somewhat poorly in Sarracenia Bay when the distribution criteria were used in combination. Of the 14 plots that met both criteria, 64% contained ≥10% graminoid cover. Five plots met both criteria yet had <10% graminoid cover; three of these were located towards the edge of the bay and had 4-year median water depths below zero, as well as high canopy cover (14, 100, and 100%), and high percent sand. The two other plots without graminoids were not substantially different from other plots in the bays with respect to other environmental variables, and other plant cover was no higher than 50%. Of the 6 plots that did not meet both criteria, four had <10% graminoid cover. Two of the five plots that met the water depth criterion but not the C:N criterion had ≥10% graminoid cover. These two plots had slightly higher %C, lower percent sand, and available soil water values toward the upper end of the range in this bay. The deeper of these two plots contained 96% cover of *Eleocharis equisetoides*, which occurred in only this location in the study. The other plot was in a transition area between the graminoid and floating-leaved species zones and had 38% graminoid cover (consisting of *P. hemitomon*) and 50% *N. odorata* cover. The one plot in Sarracenia Bay that did not meet the water depth criterion had <10% graminoid cover.

Graminoid distribution in Dry Bay was predicted rather poorly by the combined distribution criteria. All of the plots that met the water depth criterion had overhead cover ranging from 24 to 100%; none of these plots had ≥10% graminoid cover. The three plots that had ≥10% graminoid cover were deeper than the predicted maximum. Two of these plots had 4-year median water depths that were close to the criterion for graminoids (7.0 and 9.0 cm too deep) and the other plot contained a floating mat of *P. hemitomon*. Conversely, graminoid absence was predicted well. Of the 12 plots that met neither criteria, 11 had <10% graminoid cover. However, this bay had a low overall cover of graminoids.

<u>*Panicum hemitomon* Distributions</u>

Regressions using the water variables (depth and duration of inundation) showed significant relationships between *P. hemitomon* cover in 1999 and both the 1-year median water depth of multiple previous years and the 4-year annual median water depth (Table 3.4b). Separate regressions using the other environmental variables and either the most recent 1-year median depth or the 4-year median depth showed significant relationships between *P. hemitomon* cover and the 1-year median water depth, the 4-year median water depth, and the C:N ratio in sediments (Table 3.5). The R^2 values for the three regressions containing %C, %N, and %P were 0.23, 0.24, and 0.23, respectively, and were identical whether the 1-year median depth or the 4-year median depth were included in the regression. It should be noted, however, that when the 1-year median water depth was used, the bay variable had a significant relationship with *P. hemitomon* cover. In addition, although nitrogen was not considered to have a significant relationship with *P. hemitomon* cover, it was nearly significant (P= 0.0503).

Probit analysis of the most recent (1998-1999) 1-year median water depth predicted 10% cover of *P. hemitomon* at 30.7 cm (with 95% FL of –9.3 cm to 57.5 cm). Analysis of the 4-year median water depth alone predicted 10% cover at 25.8 cm (with 95% FL of –0.5 to 47.8 cm) (Table 3.6). Since *P. hemitomon* generally occurred on the outer edges of the bays, including areas above the water line, these values represent the maximum 1-year and 4-year median depths at which this species is expected to occur. Analysis of the C:N ratio alone predicted 10% cover of *P. hemitomon* at 14.9 (95% FL could not be calculated, most likely due to the roots of the equation being imaginary); *P. hemitomon* would not be expected to grow in areas with a C:N ratio <14.9. Analysis of N alone was also performed; 10% cover was predicted at 0.80 %N (95% FL again could not be calculated). Since N formed gradients in the bays (except Flamingo Bay) where the concentration was lower towards the edges, this value represents the maximum nitrogen concentration at which this species is expected to occur.

Overall, the 4-year median water depth predicted the distribution of *P. hemitomon* poorly (Figure 3.7, Table 3.8). *Panicum hemitomon* cover was ≥10% in 30% of all the plots below the predicted maximum, and in 15% of all the plots above it. The 1-year median water depth also was not a good predictor; *P. hemitomon* cover was ≥10% in 27% of all the plots below the predicted maximum, and in only 15% of all the plots above it (Figure 3.8, Table 3.8). Both water depth criteria, however, did predict *P. hemitomon* distribution well in Ellenton Bay. Here, the majority of the plots that were below the predicted maximum depth for *P. hemitomon* had ≥10% cover (78% of 9 samples for the 1-year median and 73% of 11 samples for the 4-year median). Conversely, the majority of the plots deeper than either maximum depth criteria had <10% cover (89% of the 39 samples for the 1-year median and 92% of the 37 samples for the 4-year median). *Panicum hemitomon* distribution was somewhat poorly predicted by both water depth variables in Flamingo Bay, where only 18% of the 6 plots below the maximum depth for either criteria had ≥10% cover, although 70% of the 31 plots deeper than either criteria had <10% cover. *Panicum hemitomon* distribution also was rather poorly predicted in Sarracenia Bay, where the 1-year median water depth accurately predicted ≥10% cover in only 12% of 17 plots meeting this criterion (although 100% of the plots with depths above the maximum value had <10% cover). Additionally, *P. hemitomon* cover was ≥10% in only one of 7 plots with water depths below the predicted maximum 4-year median water depth. However, this bay had a large proportion of cover by other graminoid species; *P. hemitomon* contributed only 17% of the graminoid cover. *Panicum hemitomon* distribution was also very poorly predicted in Dry Bay, where no plots with water depths below either predicted maximum had ≥10% cover. However, *P. hemitomon* was observed at ≥10% in only one plot in this bay (as a floating mat), where the mean annual water depth was 101 cm.

The soil C:N ratio did not accurately predict the distribution of *P. hemitomon* (Figure 3.9, Table 3.8). *Panicum hemitomon* cover was ≥10% in only 16% of all the plots with C:N ratios above the predicted minimum (4 plots, all in Ellenton Bay), while cover was ≥10% in 19% of all the plots below it.

The distributions of *P. hemitomon* were better explained using the distribution criteria in combination (Figure 3.10). In Ellenton Bay, this combination predicted the distribution of *P. hemitomon* well. Plots that met all of the distribution criteria for *P. hemitomon* (1-year median water depth, 4-year median water depth and C:N ratio) were located towards the edge of the bay. Of the 5 plots that met all three conditions, 3 had ≥10% *P. hemitomon* cover. The other 2 plots had dense (81%) canopy cover. The 4 plots that met both of the water criteria but not the C:N ratio criterion also had ≥10% *P. hemitomon* cover. Two plots met only one water depth criterion (the 4-year median depth). The C:N ratio criterion was met in 1 of these plots, which had ≥10% *P. hemitomon* cover. The C:N ratio criterion was not met in the other plot, where *P. hemitomon* cover was <10%. Two plots met only the C:N ratio criterion, but these had <10% cover. Of the 35 plots that met none of the criteria, 4 had ≥10% *P. hemitomon* cover, but at least two of these plots contained floating mats of *P. hemitomon*.

When used in combination, the absence of *P. hemitomon in* Flamingo Bay was somewhat well predicted by the distribution criteria; however, *P. hemitomon* was generally not observed where the criteria were met. Only four plots met all the criteria for *P. hemitomon*; six met the criteria for water depth but not C:N ratio. However, only one plot (which met both water criteria) had ≥10% *P. hemitomon* cover; the other plots had very dense overhead cover (from 86 to 95%). *Panicum hemitomon* occurred at ≥10% cover in 9 of the 31 plots where none of the environmental criteria were met. These plots had much higher C, N and P concentrations than elsewhere in Flamingo Bay; C concentrations ranged from 10.59 to 16.44% (bay mean was 9.83), N concentrations ranged from 0.88 to 1.28% (bay mean was 0.84), and P concentrations ranged from 0.12 to 0.15% (bay mean was 0.09). These plots had some of the highest concentrations of these variables in the study.

The combined distribution criteria predicted the absence of *P. hemitomon* in Sarracenia Bay well, but predicted its presence poorly. In this bay, many other graminoid species were also present. Five plots met all of the distribution criteria, eight plots met the criteria for both water depth variables but not C:N ratio, and four plots met only the 1-year median water depth criterion. However, ≥10% cover was seen in only two plots; one of which met both of the water depth criteria, and one of which only met the 1-year median water depth criterion (although it was only 1.0 cm over the maximum 4-year median water depth). Although the mean concentrations of C, N, and P in Sarracenia Bay are quite low (2.59%, 0.23%, and 0.0100%, respectively), both of these plots had higher concentrations than the mean (3.03 and 3.10% C, 0.29 and 0.26% N, and 0.0138 and 0.0135% P). While eight other plots had higher than mean concentrations of C, N, and/or P, only two of these plots met both water depth criteria. In the plots that met all distribution criteria for *P. hemitomon*, 1-year and 4-year median water depths were below the soil surface, and soils consisted of >85% sand with available water values of 7.17 to 14.64 (the mean available water value for Sarracenia Bay soils was 21.43, the lowest of the bays studied). All of the five plots where none of the criteria for *P. hemitomon* were met had <10% *P. hemitomon* cover.

In Dry Bay, the combination of distribution criteria generally predicted *P. hemitomon* absence accurately, but predicted its occurrence poorly. Dry Bay had low overall cover of *P. hemitomon*; ≥10% cover was found in only 1 plot. Dense (50 – 100%) canopy cover was present in the four plots where all the criteria were met, and in the one plot where the 1-year median water depth and C:N ratio criteria were met. Three plots met the criterion for C:N ratio only; these also had <10% *P. hemitomon* cover. Of the 21 plots where none of the criteria for *P. hemitomon* were met, only one had ≥10% cover; which consisted of a floating mat.

Floating-Leaved Species Distributions

Regression of the water variables (depth and duration of inundation) showed a significant relationship between floating-leaved species cover in 1999 and the 4-year median water depth (Table 3.4c). Regressions using this water depth variable and the other environmental variables showed significant relationships between cover and both the 4-year median water depth and soil pH (Table 3.5). The R^2 values for these three regressions containing %C, %N, and %P were 0.55 in each case. In addition, the bay variable was significantly related to the cover of floating-leaved species.

Probit analysis of the 4-year median water depth predicted 10% cover of floating-leaved species at 9.3 cm (with 95% FL of -18.2 to 24.8) (Table 3.6). Since floating-leaved plants generally occurred in the deeper areas of the bays, this limit represents the minimum 4-year median depth at which this group is expected to occur. Analysis of soil pH alone predicted 10% cover at 3.36 (with 95% FL of 2.62 to 3.73). Soil pH formed a significant spatial linear gradient within most bays, where pH decreased from the centers of the bays toward the rims. Therefore, this limit was assumed to be a minimum value for floating-leaved species, which would not be expected to grow in areas with a soil pH of <3.36. Although the lowest soil pH observed was only slightly lower than this (3.08 in Sarracenia Bay), 14% of all plots in the study had soil pH values estimated to be too low for floating-leaved species. In addition, while the FL ranged from 2.62 to 3.73, the practical range for these variables for these bays is 3.08 (the lowest soil pH observed) to 3.73

The 4-year median water depth was a moderately good predictor of the presence of floating-leaved species (Figure 3.11 and Table 3.9). Cover was ≥10% in 70% of plots that had depths greater than the predicted minimum, and in none of the plots below it. Floating-leaved plant distribution was exceptionally well predicted in Ellenton Bay, where 95% of the 40 plots with depths greater than the predicted minimum had ≥10% cover. Additionally, the eight plots with less than this depth had <10% cover. Floating-leaved plant distribution was also well predicted in Sarracenia Bay, where 64% of the 14 plots deeper than the predicted minimum had ≥10% cover. All of the eight sample locations that were too shallow had <10% cover. In Dry Bay, 45% of the 29 sample locations deeper than the predicted minimum had ≥10% cover, but no plots in this bay had water depths below the minimum criterion. Two of these plots with water depths deeper than the predicted minimum lacked floating-leaved cover; these plots had 18 and 21% graminoid cover. Flamingo Bay was poorly predicted by the minimum 4-year median water depth of 9.4 cm, as only 28% of the 36 plots that were deeper had ≥10% floating-leaved plant cover, and only 1 plot (containing <10% floating-leaved plant cover) was too shallow. In many of the plots where floating-leaved species were expected but did not occur, graminoids were present with up to 68% cover. Cover of floating-leaved species did increase dramatically along the water depth gradient in both Flamingo and Dry Bays. In Flamingo Bay it increased from <1% in plots with 4-year median water depths of <45 cm to >90% in plots with 4-year median water depths of >70 cm. In Dry Bay cover increased from <1% in plots with 4-year median water depths of <43 cm to a maximum of 62% in a plot with a 4-year median water depth of 70.3cm. Cover in Dry Bay, however, declined toward the very center of the bay.

Although soil pH had a significant relationship to the cover of floating-leaved species, the minimum criterion of 3.36 was not a good predictor of floating-leaved species distribution (Figure 3.12 and Table 3.9). While floating-leaved species cover was ≥10% in 57% of plots with soil pH above the predicted minimum, and <10% in 11% of plots below it, these values do not represent the distributions on a bay-by-bay basis. The distribution of floating-leaved species was best predicted in Sarracenia Bay, where 60% of the 10 plots with soil pH above the predicted minimum had ≥10% cover and 75% of the 12 plots below it had <10% cover. In Flamingo Bay, only four plots had soil pH below the predicted minimum; all of these plots had <10% cover. Of the 33 plots that were above the predicted minimum, only 30% had ≥10% cover. Very few plots in Dry and Ellenton Bays had soil pH below the predicted minimum (1 plot in Dry Bay and 2 plots in Ellenton Bay); these plots had <10% cover. In Ellenton Bay, 83% of the 46 plots with soil pH above the minimum had ≥10% cover, as was the case for only 46% of the 28 such plots in Dry Bay.

The distributions of floating-leaved species were very well explained using the distribution criteria in combination (Figure 3.13). In general, the water depth criterion served as the primary indicator, while low pH may have limited distribution in some areas. Plots that met only the water depth criterion often had low cover; however, ≥10% was not observed in any plots where pH values were above the predicted minimum but the water depth criterion not was met. In Ellenton Bay, plots where the floating-leaved species group's distribution criteria for both the 4-year median water depth and soil pH were met were located towards the center of the bay. However, the water depth criterion was the main predictor, as these species did not occur below the predicted minimum. *Nymphaea odorata* was the only floating-leaved species in all but one plot (where *B. schreberi* was the only floating-leaved species, at 20% cover). Of the 28 plots that met both criteria, 93% had ≥10% cover; floating-leaved species were expected but not found in two plots. One of these plots was located toward the rim of the bay with graminoid species cover of 75%. The other plot contained part of a tall floating mat of *Decodon verticillatus* (with 52% cover). In other plots near the edge of the bay where floating-leaved species were expected but cover was lower (35, 20, and 29%), graminoid cover was higher (28, 41, and 29%, respectively).

The distribution of floating-leaved species in Dry Bay was somewhat well predicted; however, all the plots met the water depth criterion and only one plot of 29 was below the estimated minimum pH (this plot had <10% cover of floating-leaved species). In many areas where floating-leaved species were expected but not observed, dense overhead cover or, occasionally, graminoids were present. *Nymphaea odorata* was the only floating-leaved species observed in Dry Bay. Of the 28 plots that met both distribution criteria, 46% had ≥10% floating-leaved species cover. Of the 16 plots that met the water depth criterion yet had <10% cover, 81% (13 plots) also had high overhead cover. One plot (without overhead cover) that had <10% cover had slightly lower available soil water (found to be significantly related to *N. odorata* cover) and soil P values than other plots, while the N:P ratio and % sand were slightly higher.

In Sarracenia Bay, the 4-year median water depth distribution criterion was the primary predictor of floating-leaved species distribution, while low pH may have restricted their range. *Nymphaea odorata* was the only floating-leaved species observed. It was not present in any of the eight plots that did not meet the water depth criterion (three of which did meet the pH criterion). Five (83%) of the six plots that met both distribution criteria contained ≥10% cover. Of the eight plots that met the water depth criterion but not soil pH, four plots (50%) had <10% floating-leaved species cover. Three of these four plots had graminoid cover ranging from 39% to 57%. The one plot in Sarracenia Bay that met both criteria yet had <10% floating-leaved species cover had 134% graminoid cover. Of the four plots that had ≥10% floating-leaved species cover but did not meet the pH criterion, three had 4-year water depths that were among the deepest in the bay (30.8 - 32.3 cm). The other plot was less deep (4-year median water depth was 26.8 cm), but had a higher available soil water value than most plots in Sarracenia Bay (31.33 g water/100 g soil as compared to the bay mean of 21.43 g water/100 g soil).

The distribution of floating-leaved plants in Flamingo Bay was poorly predicted by the two distribution criteria. While almost all of the floating-leaved species cover in the other bays consisted of *N. odorata*, this species was rarely observed in Flamingo Bay. Only one plot did not meet either the water depth or the pH criteria and three plots met only the water depth criterion; floating-leaved species were not present. Of the 37 plots, 33 (89%) met both of the distribution criteria; however, only 30% of these plots had ≥10% floating-leaved species cover. Dense canopy cover was generally present in plots where floating-leaved species were expected but that had <10% cover (canopy cover was present in 96% of these plots and ranged from 24 to 100% in 78% of these plots). The one plot having <10% floating-leaved species cover without any canopy cover had high (47%) graminoid cover. These graminoids consisted mostly of species other than *P. hemitomon*, such as *Leersia hexandra* and *Eleocharis* spp. In addition, forbs were present at high cover in this area; notably *Bacopa caroliniana* and *Pontederia cordata*, and N concentrations were slightly lower in this area than elsewhere in the bay.

Nymphaea odorata Distributions

Regressions using the water variables (depth and duration of inundation) revealed significant relationships between *N. odorata* cover in 1999 and 3 water variables during multiple previous years: the 1-year median water depth, the annual longest duration of consecutive spring days (CSD) ≥ 10 cm, and the annual longest duration of CSD ≥ 50 cm (Table 3.4d). Regressions using the most recent (1998-1999) values for these variables along with the other environmental variables showed significant relationships between *N. odorata* cover and all three water variables, as well as available soil water (Table 3.5). The R^2 values for these three regressions containing %C, %N, and %P were 0.73 in each case. The bay variable also had a significant relationship with the cover of *N. odorata*.

Probit analysis of the 1-year median water depth predicted 10% cover of *N. odorata* at 19.8 cm (with 95% FL of –15.1 to 37.5 cm) (Table 3.6). Since *N. odorata* generally occurred in the deeper areas of the bays, this limit represents the minimum 1-year median depth at which this group is expected to occur. Analysis of the estimated longest CSD ≥ 10 cm alone predicted 10% cover at 170 days (95% FL could not be calculated). This length of time encompasses almost the entire spring season of 181 days. Analysis of the longest CSD ≥ 50 cm alone predicted 10% cover at 16 days. Although the 95% FL ranged from –75 to 58 days, the practical range for these values is 0 to 58 days. These CSD distribution criteria represent the minimum duration of flooding required; *N. odorata* would not be expected to grow in areas with fewer than 170 CSD of ≥10 cm water, or fewer than 16 CSD of ≥50 cm water. Analysis of available soil water alone predicted 10% cover at 8.42 g water per 100 g soil. Although the 95% FL ranged from -13.70 to 18.26 g, the practical range for these values is 0.0 g to 18.26 g. Therefore, *N. odorata* would not be expected to grow in areas with available soil water <8.42 g water/100 g soil. Available soil water values for almost all of the plots sampled were greater than this estimated limit; only four plots in Ellenton Bay and one plot in Sarracenia Bay had lower values (4% of all the plots). Even if the actual available soil water distribution criterion were at the upper end of its fiducial range (18.26), the available soil water of 77% of the plots exceeded this value, indicating that *N. odorata* could be expected to occur.

The 1-year median water depth of 30.8 cm predicted the distribution of *N. odorata* extremely well. Cover of *N. odorata* was <10% in all 20 plots where the 1-year median water depth was below the predicted minimum of 19.8 cm. Cover was ≥ 10% in 52% of the 116 plots above this minimum. However, this percentage increases to 75% (of 79 plots) if Flamingo Bay (which contained very little *N. odorata*) is excluded. Distribution in Ellenton Bay was predicted best, where 93% of the 40 plots deeper than the predicted minimum had ≥10% cover, and all of the eight plots that were too shallow had <10% cover (Figure 3.14 and Table 3.10). *Nymphaea odorata* distribution was also very well predicted in Sarracenia Bay, where 67% of the 12 plots deeper than the predicted minimum had ≥10% cover and all of the 10 plots that were too shallow had <10% cover. Dry Bay was somewhat less well predicted, with 46% of the 28 plots deeper than the predicted minimum having ≥10% cover; however, only one plot was predicted to be too shallow (this plot had <10% cover). However, *N. odorata* cover generally increased along a water depth gradient (from <1% in plots with annual median water depths of <43 cm to a maximum of 62% in a plot with an annual median water depth of 71.0 cm). Cover declined in the deeper plots toward the very center of Dry Bay, especially in the short transect. This decline coincided with increased cover from a floating mat of graminoids and the presence of a *Salix nigra* shrub.

The minimum of 170 CSD ≥10 cm predicted the distribution of *N. odorata* extremely well in Dry, Ellenton, and Sarracenia Bays (Figure 3.15 and Table 3.10). In these three bays, *N. odorata* cover was ≥10% in 81% of the 59 plots with flooding durations that met or exceeded the predicted CSD minimum and in none of the 26 plots with less than the predicted CSD minimum; (If Flamingo Bay is included, cover of *N. odorata* was ≥10% in 58% of 104 plots). In plots with flooding durations above the CSD minimum, cover of *N. odorata* was ≥10% in 100% of the nine plots in Sarracenia Bay, 95% of the 39 plots in Ellenton Bay, and 52% of the 25 plots in Dry Bay. In Sarracenia, Ellenton, and Dry bays, plots with shorter flooding durations than the SCD minimum (13, 9, and 4 plots, respectively) had <10% *N. odorata* cover.

The minimum of 16 CSD ≥ 50 cm flooding predicted the distribution of *N. odorata* moderately well in Dry, Ellenton, and Sarracenia Bays (Figure 3.16 and Table 3.10). In these bays, cover was ≥10% in 83% of 51 plots that met or exceeded the CSD minimum (this value decreases to 56% of 93 plots if Flamingo Bay is included) and in 22% of 8 plots with shorter flooding durations. In Ellenton Bay, 97% of the 37 plots that were flooded long enough had ≥10% *N. odorata* cover, and 91% of the 11 plots that were below the minimum duration had <10% cover. In Dry Bay, 57% of the 23 plots that were flooded long enough had ≥10% *N. odorata* cover, and all of the six plots that were below the minimum duration had <10% cover. Distributions in Sarracenia Bay were not well predicted. Only one plot was flooded long enough for *N. odorata* (this plot had ≥10% *N. odorata* cover). However, ≥10% *N. odorata* cover was observed in 38% of the 21 plots with flooding durations below the predicted minimum.

Although available soil water had a significant relationship to the cover of *N. odorata*, the criterion of 8.42 g water/100 g soil was not a good predictor of *N. odorata* distribution when used alone (Figure 3.17 and Table 3.10). Of a total of 136 sample locations in the study, only five had available soil water values that were below the predicted minimum for *N. odorata* (these five plots did have <10% *N. odorata* cover). In Ellenton Bay, 84% of the 44 plots with available soil water above the predicted minimum had ≥10% cover. However, only 45% of the 29 such plots in Dry Bay and 43% of the 21 such plots in Sarracenia Bay had *N. odorata* cover ≥10%. *Nymphaea odorata* was rarely encountered in Flamingo Bay; only one plot had ≥10% cover (this plot was within the estimated available soil water range for *N. odorata*).

The distributions of *N. odorata* were very well explained using the distribution criteria in combination (Figure 3.18), especially in Ellenton Bay. Of the 47 plots that met all the distribution criteria in this bay, 98% had ≥10% cover. Two plots met all criteria except the CSD

≥50 cm criterion. One of these plots had <10% cover; the available soil water value there was only slightly higher than the distribution limit. Cover was <10% in the one plot where only the 1-year median water depth and available soil water criteria were met, as well as in the four plots where only the available soil water criterion was met. Additionally, cover was <10% where no criteria were met. In one plot, all criteria were met but cover was 0%; this plot was located in a dense floating mat of *D. verticillatus* (yielding 52% cover). In the center of the bay, *N. odorata* cover was ≥10% but lower than in nearby plots; a historical excavation may be present in this location.

The distribution of *N. odorata* was also very well predicted by a combination of the distribution criteria in Sarracenia Bay. In this shallow bay, the CSD ≥50 cm distribution criterion was not met in most locations. However, all of the nine plots where all of the other distribution criteria were met (including two that met the CSD ≥50 cm distribution criterion) contained *N. odorata* cover values ≥10%. Three plots met the 1-year and available soil water criteria but neither the CSD ≥10 cm nor the CSD ≥50 cm criteria; these plots had <10% *N. odorata* cover. All of the 10 plots that met none of the water depth criteria had <10% cover. Only one plot did not meet the criterion for available soil water, which was generally much lower in the plots that did not meet the annual median water depth criterion than it was elsewhere in the bay.

The distribution of *N. odorata* in Dry Bay was exactly the same as for floating-leaved plants, as *N. odorata* comprised all of the floating-leaved vegetation in the sampled plots in this bay. However, the predictions based on a combination of the distribution criteria for *N. odorata* yielded slight improvements over predictions based on floating-leaved species distribution criteria. One or more distribution criteria were not met in six of the plots. Although available soil water was above the distribution limit in these plots, none of them contained *N. odorata*. These six plots as well as five others (meeting all flooding and water depth criteria) located near the edges of the bay had dense canopy cover; <10% *N. odorata* cover was observed in all of these locations. Three plots meeting all the distribution criteria (near the center of the bay) had <10% *N. odorata* cover; two of these had 5 and 62% canopy cover, and one was adjacent to a plot with 14% overhead cover. All of the plots sampled met the available soil water criterion.

Nymphaea odorata was observed in only one plot in Flamingo Bay, although 10 plots contained ≥10% cover of floating-leaved species. Differences were found between the plots in Flamingo Bay with ≥10% *B. schreberi* cover and plots in the other bays with ≥10% *N. odorata* cover with respect to soil particle size and nutrient concentrations. The sand fractions of the plots with *B. schreberi* were much smaller than in the plots with *N. odorata* (mean values were 16.09% and 46.58%, respectively). Plots containing *B. schreberi* also had greater clay fractions (mean value 42.79% as compared to 16.93% in *N. odorata* plots), higher %C (8.38% as compared to 4.84%), and slightly higher %P (0.08 as compared to 0.05%).

Discussion

Plant Distribution and Zonation Patterns

In each bay studied, zonation patterns typical of those previously described in Carolina bays (Sharitz and Gibbons 1982, Schalles and Shure 1989, Tyndall et al. 1990, Sharitz and Gresham 1998) were documented for the graminoid species group, the floating-leaved species group, *P. hemitomon*, and *N. odorata*. These zones generally appeared as concentric circles in Dry, Ellenton, and Sarracenia Bays. However, Flamingo Bay exhibited these concentric traits mostly on the short transect, whereas zones on the long transect were often patchy. *Nymphaea odorata* tended to form a monoculture where it was present, with a relatively distinct boundary;

however, it was not the dominant floating-leaved species in all bays. The dominant floating-leaved species in Flamingo Bay was *B. schreberi*, which formed a near monoculture with little *N. odorata* cover. In most cases, zones of floating-leaved species and graminoids were distinctly segregated (as were zones of *N. odorata* and *P. hemitomon*). However, these groups overlapped in some areas.

Distributions and Environmental Constraints on Graminoids and *P. hemitomon*

While environmental variables were found that related significantly to the cover of graminoids and *P. hemitomon*, they explained relatively little of the variation in cover of these species. Low regression R^2 values indicated that there were clearly other variables related to the distribution of these species. Other environmental variables, as well as inter- and intraspecific competition, could have played a role in determining the species distributions. However, the significant variables that were found do aid in understanding plant distributions in the bays.

Although the graminoid group is dominated by *P. hemitomon*, it can include species that are very different in their requirements. While few graminoid species were found in Dry and Flamingo Bays, many more were found in Ellenton and Sarracenia Bays. This category included grasses, sedges, rushes, and other plants with grass-like growth forms. Thus, the graminoid category is too broad, and different environmental variables may be related to the cover of the different species. Also, when the 1-year median water depth was used as the water variable for *P. hemitomon* regressions, there was a significant bay effect, and bay-specific conditions may have been related to the cover of this species. Such conditions could include surrounding geology, landforms, and land use, as well as bay area and depth.

Similar environmental variables were significantly related to the cover of graminoids and *P. hemitomon*. This is not surprising, as *P. hemitomon* comprised an average of 60% of the graminoid cover. Median water depth was related to cover of both graminoids (4-year median) and *P. hemitomon* (1-year and 4-year medians). However, the maximum 1-year and 4-year median water depths at which *P. hemitomon* was expected to occur (30.1 cm and 25.8 cm, respectively), restrict it to shallower areas than the general graminoid species group (4-year median water depths up to 51.3 cm). Growing in areas deeper than *P. hemitomon* were other graminoid species such as *Eleocharis equisetoides*, *Eleocharis obtusa*, *Panicum spretum* (on newly exposed soils), and *Panicum verrucosum*.

The 95% FL of the 4-year median depth distribution limit of graminoids encompass 29.9 cm. This degree of uncertainty in water depth could potentially cover a large area of the Carolina bay wetland where the elevational gradient is shallow. In Flamingo and Sarracenia Bays, both of which have relatively shallow gradients, a 30 cm elevational change could cover distances of 165 m and 118 m (respectively). The 95% FL of the 4-year median depth distribution limit of *P. hemitomon* also encompass a very wide range, from below the soil surface (-0.49 cm) to well inundated (47.8 cm). The 95% FL for the 1-year median water depth distribution limit are also broad with a total range of 66.8 cm. These elevations encompass large parts of Dry, Ellenton, and Flamingo Bays and almost all of Sarracenia Bay. Such long distances could lead to a very high degree of uncertainty regarding the species distribution, especially within shallower gradient bays.

While the values of the water depth variables may represent the conditions at the deep water end of a species range, they do not account for possible effects at the upland edge of the distribution. For example, biomass of *P. hemitomon* was greater when flooded to 10 cm than to 0 cm (saturated soil) (Willis and Hester 2004). In addition, the values of these variables do not represent the extremes at which a species may survive for shorter periods of time. Kirkman and

Sharitz (1993) found that *P. hemitomon* grew best at a depth of 13 cm in monospecific mesocosm experiments, yet it has been observed surviving temporary water depths up to 1.18 m (Kirkman and Sharitz 1993). This species likely adapts to temporary flooded conditions with rapid shoot elongation which can re-establish leaf contact with air, allowing oxygen transport to the root system (Blom and Voesenek 1996). *Panicum hemitomon* also can form extensive stands as floating mats, consisting mainly of roots and rhizomes with a loosely attached underlying peat layer from the decay of plant material (Swarzenski et al. 1991). In this case, water depth in the wetland may have little to no impact on plant distribution, as the mat floats on the water surface and is not overtopped.

Squires and van der Valk (1992) suggested that the minimum length of time needed to determine the maximum water depth at which a wetland species can grow can be as long as three years, as many species were noted to survive for one to two years in water deeper than their long-term maximums. Such long-term survival under adverse conditions may be difficult to ascertain. For example, it was found that some species of *Scirpus* in Canadian freshwater marshes can survive as tubers for many years in water that is too deep for shoot growth (Squires and van der Valk 1992). It has also been shown that populations of *P. hemitomon* from different locations exhibit intraspecific variation in response to water depth, and that such variation may affect survivability (Lessmann et al. 1997). Due to the clonal nature of *P. hemitomon*, ramets that are more adapted to deep water conditions are more likely to form monogenetic stands at lower elevations. It is therefore possible that different genotypes are present in different bays, and/or at different elevations within one bay, and that their responses to water depth could differ.

Alterations of water depth have been found to affect the distribution of *P. hemitomon* in the Everglades, where it established prior to 1959 due to wetland draining (Loveless 1959).

Since then it became widespread due to its ability to withstand fluctuating water levels and burning. Although it was noted to have a high affinity to dry sites, it also tolerated flooding by growing rapidly during rising water, and remnants were able to survive up to a year in 1 m depth. However, a reduction in *P. hemitomon* later documented by Vaithiyanathan and Richardson (1999) was attributed to a subsequent rise in water levels.

Soil C:N ratio was related to both the graminoid species group and *P. hemitomon* distributions, with a higher minimum distribution criterion for *P. hemitomon* (14.9) than for graminoids (11.0). In most bays, the C:N ratio was a moderately good predictor of graminoid distribution, but this was not the case for *P. hemitomon*, which was present with high cover in many plots below the minimum C:N criterion. In both cases, the C:N ratio predicted the absence of graminoids or *P. hemitomon* better than their presence. Since the C:N ratio is negatively correlated with the 4-year median water depth in the bays, however, it is likely that its relationship to the cover of graminoids and *P. hemitomon* is merely reflective of the relationship to hydrologic condition. The higher predicted minimum C:N ratio of *P. hemitomon* (as compared to graminoids) would therefore be reflective of its distribution in shallower conditions than the graminoid group. The C:N values are minimum ratios, implying that these species' distributions are related to lower N concentrations in relation to C concentrations. Additionally, bacterial processes during decomposition of materials with higher C:N ratios may immobilize mineral-N, resulting in less plant-available N. While a minimum C:N ratio is consistent with the suggestion that a maximum of 0.80 % N may limit *P. hemitomon* distributions, N is commonly perceived as a limiting nutrient. A mean N concentration of 1.5% was found to be limiting *P. hemitomon* growth in a Louisiana coastal freshwater marsh (DeLaune et al. 1986). This is higher than the concentrations observed in the Carolina bays, which would suggest that N limitation may be occurring. Conversely, Daoust and Childers (1999) suggested that high tissue N:P ratios in *P. hemitomon* in the Everglades indicated that this species is P limited.

Use of the median water depth and C:N distribution criteria in combination explained the distributions of the graminoid species group and *P. hemitomon* very well in most cases. Other environmental factors such as canopy cover and localized areas of high or low nutrient concentrations may have positively or negatively affected cover. Additionally, *P. hemitomon* distribution may have been limited by sandy soils and a lack of water near some bay rims. In deeper locations, competition with floating-leaved species may have been a factor where floating-leaved species and graminoid distributions overlapped, and clonal subsidy may have permitted the formation of floating *P. hemitomon* mats (Caraco 1991). Wilson and Keddy (1985) inferred that zonation may be impacted by species interactions in addition to abiotic factors. Water depth and nutrient availability can act together to create zones of many graminoid species (Grace 1988, van den Brink et al. 1991, Weiher and Keddy 1995, Weiher et al. 1996). In some cases, the importance of nutrients in determining plant distribution can override the importance of moisture levels (Shipley and Keddy 1988, Wetzel and van der Valk 1998, Green and Galatowitsch 2001). While not shown in this study, it is possible that the distribution of *P. hemitomon* in the Carolina bays could be influenced by one or more limiting nutrients. Depending on individual site conditions, distribution, survival, and growth of *P. hemitomon* may be affected by limiting N, P, or other nutrients (DeLaune et al. 1986, Daoust and Childers 1999, Pezeshki et al. 2000).

Distributions and Environmental Constraints on Floating-Leaved Species and *N. odorata*

The distribution of *N. odorata* was largely explained by the four water variables found to have significant relationships to cover (regression R^2 values of 0.73). The two variables with significant relationships to the cover of the floating-leaved species group accounted for slightly less variability (regression R^2 values of 0.55). While the floating-leaved species group contained four species, only one species dominated in each bay. Nearly 100% of the floating-leaved species cover in Dry, Ellenton, and Sarracenia Bays consisted of *N. odorata*, but *B. schreberi* dominated in Flamingo Bay, where *N. odorata* accounted for <1% of the floating-leaved species cover. Significant bay effects were found, indicating that some variation may be due to factors that are not equally expressed in the four bays. However, the significant variables have potential application towards understanding floating-leaved species distributions in the bays.

Variables relating to flooding were significant for both the floating-leaved species group and *N. odorata*; however, the manner in which flooding was expressed differed slightly. While depth of flooding was significant for both floating-leaved species and *N. odorata*, the duration of flooding of minimum depths, as well as timing was related to *N. odorata* cover. The minimum 1-year median water depth at which *N. odorata* was expected to occur (19.8 cm) restricts it to slightly deeper areas than the floating-leaved species group (4-year median water depth minimum of 9.4 cm). Two variables relating to the duration of springtime flooding were significantly related to *N. odorata* cover. This species was predicted to be restricted to areas with a minimum duration of 170 CSD ≥10 cm flooding and a minimum duration of 16 CSD ≥50 cm. As the entire spring season is 181 days, the CSD ≥10 cm criterion would require flooding for the majority of the spring, with any dry-down near the beginning or end of the season (early January or late June). Drydown near the beginning of the season may be less likely to restrict *N. odorata*, as it would occur during dormancy or before germination.

The FL of the 4-year median water depth distribution limit on floating-leaved species and the 1-year median water depth distribution limit on *N. odorata* are quite wide. This could lead to high uncertainty regarding the distribution boundaries of these plants within shallow gradient bays. In addition, few plots in the study had 1-year or 4-year median water depths below the lower FL boundaries. The practical FL for the longest CSD ≥ 50 cm were also somewhat wide, and the FL for the longest CSD ≥10 cm water distribution limit on *N. odorata* could not be calculated.

The distribution limit of each significant water variable predicted the distribution of *N. odorata* very well in all bays except Flamingo, where this species was generally absent. In Dry Bay, *N. odorata* was restricted to areas with deeper 4-year median depths than expected. While a minimum of 170 CSD ≥10 cm flooding predicted the distribution of *N. odorata* extremely well in Dry, Ellenton, and Sarracenia Bays, the minimum of 16 CSD ≥50 cm predicted the distribution of *N. odorata* well only in Ellenton and Dry Bays.

The CSD criteria may be minimum durations that must be met for germination or survival of *N. odorata*, while cover or competitive ability may be determined by other variables. In the Carolina bays studied, CSD criteria predicted the presence or absence of *N. odorata* very well, but cover varied greatly in plots where the distribution criteria were met. In addition to the length of flooding, the seasonal timing of flooding can have an effect on plant survival and growth of plants (Klimešová 1994). Springtime water depth variables may be important to *N. odorata* distribution due to particular dormancy breaking and/or establishment requirements. *Nymphaea odorata* becomes dormant during winter months, and floating leaves senesce. After utilizing stored C reserves from the large rhizome, *N. odorata* may require a nearly continuously flooded spring to allow the formation of floating leaves to produce enough carbohydrate for storage. The effect of flooding also depends on the growth stage of the species involved, and whether it is completely submerged (Klimešová 1994). Germinating N. *odorata* seedlings may also require constant inundation to prevent drying of the young rhizome. Seedlings, with smaller rhizomes, may not be able to survive drawdown periods until later in the season.

For some wetland plants, the length of individual flooding events can be more important than combined total inundation time. Inundation/saturation time and soil anaerobiosis can be directly related to species cover and degree of dominance, excluding non-obligate species as the duration of saturation increases (Josselyn et al. 1990). A negative correlation between aquatic and semi-aquatic species richness and the frequency of inundation was documented in areas of the Rhine and Meuse Rivers where an inundation frequency of 20 days or more resulted in a significant decrease in species richness (van den Brink et al. 1991). The length of individual flooding events (rather than total time submerged annually) is likely to be a factor in the distribution of Carolina bay species other than *N. odorata*. Excessive biomass allocation to submerged plants may cause depletion of resources and restrict other species from deeper areas.

Available soil water was related to the cover of *N. odorata* but not the floating-leaved species group. The available soil water criterion, by itself, does not prove useful in predicting the distribution of *N. odorata*, as very few plots in the study had available soil water values below the minimum. However, this does not necessarily negate the potential usefulness of this criterion. The majority of plots with low available soil water values were towards the bay rims. It is likely that available soil water is a factor in *N. odorata* distribution only during periods of drawdown, where the ability of the soil to retain moisture could prevent desiccation of the *N. odorata* rhizome (Thompson and Troeh 1957). Therefore, this variable may only be important in the outer areas of the bays where drawdown is more likely.

Although *N. odorata* was the dominant floating-leaved species in three of the bays, pH was related to the cover of only the floating-leaved species group as a whole. The estimated minimum soil pH criterion of 3.36 had a high degree of certainty, shown by the narrow FL. However, this criterion was not a good predictor when used alone, as very few plots in Dry, Ellenton, and Flamingo Bays were below the minimum and floating-leaved species in these bays were restricted to plots with higher pH values. However, the distribution of this group was relatively well predicted in Sarracenia Bay, where observed pH values were much lower. Since there was a statistically significant bay effect on floating-leaved species cover, it is likely that the very low pH in Sarracenia Bay may have skewed the minimum criterion such that it was too low to adequately represent most bays. Relationships between pH and species composition have often been documented in northern peatland communities, possibly due to the effect of low pH on nutrient availability (Bridgham et al. 1996). Low pH can precipitate soil water nutrients, as well as reduce their adherence to soil particles, thus lowering nutrient availability to plant roots (Thompson and Troeh 1957).

While not shown by this study, dense overhead cover may have reduced the distributions of floating-leaved species in some areas. This may especially be the case in Flamingo Bay, where stands of trees in the center of the bay, as well as around the edges, may be restricting floating-leaved species to a small area. Areas of low or no cover of floating-leaved species in Dry and Ellenton Bays also had corresponding overhead cover from trees or *D. verticillatus*. Competition with other herbaceous species may have resulted in reduced distribution in some areas. This was especially seen in Flamingo and Sarracenia Bays, where many plots with lower floating-leaved species cover than expected had high graminoid cover. If graminoids are able to establish, they may be able to out-compete floating-leaved species for space as the floating leaf requires considerably more area on the water surface. While not significant, low soil P concentrations may also reduce floating-leaved species cover. In one area of Dry Bay where this group was expected but not observed, soil P concentrations were slightly lower than in other plots, and the N:P ratio (as well as % sand) were slightly higher. A similar phenomenon was also seen in Flamingo Bay, where an area of low floating-leaved species cover had lower P concentrations than elsewhere in the bay, as well as higher graminoid and forb cover.

Use of the three flooding criteria in combination explained the distributions of *N. odorata* extremely well, and could be quite useful in predicting distributions for restoration projects. This species was restricted from areas meeting none of the criteria or only the 1-year median depth criterion. Long periods of spring flooding appear to be necessary for *N. odorata* to be present. Plots that were flooded for fewer than 170 CSD ≥10 cm and fewer than 16 CSD ≥50 cm had <10% *N. odorata* cover.

It should be noted that due to the depressional nature of the bays, water levels rise and fall as a plane. Therefore, the significant water depth variables correlate with one another within a single bay. As a result, the water variable criteria met for each plot are auto-correlated, and a hierarchy of criteria was found. All plots that met the CSD ≥50 cm distribution criterion also met the CSD ≥10 cm and 1-year median water depth distribution criterion. Plots that met the CSD ≥10 cm criterion (but not the CSD ≥50 cm criterion) also met the 1-year median water depth criterion.

Potential Effects of Non-Significant Environmental Variables on the Distributions of Plant Species in Carolina Bays

Additional environmental variables may influence plant distributions in Carolina bays. Low observation frequencies of some variables (especially in the ranges necessary to influence distributions) may have prevented statistical significance. Other variables that were not measured may also affect distributions. Phosphorus may have had an effect on the distributions of *P. hemitomon* and the graminoid species group in Flamingo and Sarracenia Bays (where high concentrations may have increased distributions and lower concentrations may have restricted their distributions), and of *N. odorata* and floating-leaved species in Dry and Flamingo Bays (where low concentrations may have restricted their distributions). Phosphorus has been shown to affect the distribution of *P. hemitomon*, as well as other species, in other wetland systems. Vaithiyanathan and Richardson (1999) suggested that changes in macrophyte species composition in the Florida Everglades were strongly related to a coinciding soil and surface water P gradient, which occurred over several kilometers. They also observed that both *P. hemitomon* and *N. odorata* seemed to decline over this gradient (this decline was not statistically significant). *Utricularia purpurea* (found abundantly in the Carolina bays) is a potential indicator of oligotrophic conditions, as it was reduced by the elevated P conditions in the Everglades (Vaithiyanathan and Richardson 1999). Nutrient concentrations in the Carolina bays are much lower than those observed in the Everglades. Maximum concentrations of C, N, and P in the bays were 17.21%, 1.28%, and 0.15%, respectively; values were often much lower. The concentrations of these same nutrients in the Everglades were 25.1%, 1.17%, 0.22%, respectively (Vaithiyanathan and Richardson 1999). Therefore, it is likely that P could have more of a role in species distribution when in higher concentrations.

Although water depth seemed to play a more dominant role than the C:N ratio in predicting the distributions of the graminoid species group and *P. hemitomon*, plant growth has been documented to be affected by substrate organic content and water depth interactions (Lenssen et al. 1999). In addition, substrate organic content may influence germination levels (Moore and Keddy 1988), which could also affect species distributions where establishment from seed is at least a factor contributing to species cover. Field distributions of wetland plants could also be influenced by the redox potential of the soil and N form (rather than nutrient concentrations). van den Brink et al. (1995) found that wetland species distribution predictions based on the effects of sediment type and flooding depth in mesocosms did not completely explain field distributions. They determined that highly reductive conditions in organic sediments in the field resulted in N occurring primarily as ammonium (coinciding with increased biomass allocation to above-ground plant parts), and less reductive conditions resulted in N as nitrate.

Light limitation is well understood to be an important factor in plant productivity, and therefore distribution. While stem elongation can enable some species to escape light-limited conditions caused by neighboring plants (Collins and Wein 2000), shade cast by trees can impact the distribution of herbaceous species (Bouchard and Madsen 1987). The growth form of a species can affect its ability to withstand shade, as shaded ramets of rapidly spreading plants with long internodes can be supported by non-shaded ramets (Lovell and Lovell 1985, Maurer and Zedler 2002). The clonal nature of *P. hemitomon* likely permits it to tolerate some shading in this fashion, while *N. odorata* is likely to be more affected.

Potential Effects of Environmental Characteristics on the Germination and Establishment of Seedlings

Wetland species distributions are not solely functions of the effects of environmental characteristics on adult plants. Vegetation zonation patterns can be caused in part by seedling germination requirements (Keddy and Ellis 1985, Moore and Keddy 1988). Where disturbances are frequent, the soil seed bank can play a major factor in species distribution and zonation. However, plant competitive abilities can override seedbank composition once plants are established. Kirkman (1992) found that Carolina bay seed bank composition did not resemble the standing vegetation in areas dominated by clonal perennials such as *P. hemitomon*. As a result, the conditions for the growth (and resulting distribution) of *P. hemitomon* are not necessarily those that are required for germination. Alternatively, it is possible that the germination requirements for *N. odorata* (and other floating-leaved species) are similar to the requirements for adult growth. Along shorelines where water depth fluctuates frequently, very narrow specialization on particular water levels for germination and seedling establishment might be selected against (Keddy and Ellis 1985, Moore and Keddy 1988).

The conditions required for seedling establishment can be different from those required for germination (Weisner et al. 1993, Lenssen et al. 1998). The boundary between zoned species in Carolina bays may be complicated by these types of effects, as water levels fluctuate depending on rainfall (Lide et al. 1995). Thus, the long-term conditions identified for the distributions of Carolina bay species in this study may not be those needed for initial establishment. Short-term establishment patterns are not necessarily indicative of long-term trends (5 years or more) (Weiher et al. 1996). For example, Budelsky and Galatowitsch (2000) found that optimal first year conditions for *C. lacustris* (rising water levels) were the opposite of optimal third year conditions (falling water levels). Seedbank expression can be affected by depth, duration, and frequency of flooding, but depth may be the least important (Casanova and Brock 2000).

The Value of Understanding Quantitative Environmental Values as they Relate to Species Distributions and Wetland Restoration

This study determined quantitative filters for selected wetland plants. Graminoid distributions were limited by the maximum 4-year median water depth of 51.3cm and the minimum soil C:N ratio of 11.4. *Panicum hemitomon* was limited by the maximum 1-year median water depth of 30.7 cm, the maximum 4-year median water depth of 25.8 cm, and the minimum soil C:N ratio of 14.94. Floating-leaved species distributions were limited by the minimum 4-year median water depth of 9.3 cm and a minimum pH of 3.36, whereas *N. odorata* was limited by the minimum 1-year median water depth of 19.8 cm, the minimum CSD ≥ 10 cm of 170 days, the minimum CSD ≥ 50 cm of 16 days, and a minimum available soil water of 8.42 g water/100 g soil. While environmental filters such as these can influence the distributions of wetland species (van der Valk 1981), many filters may be operating in a system. Subtle differences in the characteristics of different species can result in different responses to environmental conditions. Characteristics such as aerenchyma efficiency, the presence and structure of rhizomes, root metabolic rates and physiology during anoxia, the ability to photosynthesize under water, growth form, and many others can affect the distributions of species. These types of plant characteristics can be used effectively to judge the potential range of a species in a restoration effort, but only if quantitative values are elucidated such that the survival, growth, and reproductive abilities of species can be determined for specific locations. Fluctuating environmental characteristics and the likelihood of interactions between environmental characteristics make this process even more complicated. In addition, care must be taken during the planning of a restoration effort to accommodate any potential changes in conditions required by the desired species. Strict control over environmental conditions may be required if establishment is desired from seed or seedbank, or the installation of adult specimens must be considered.

Although the environmental variables and distribution limits identified here do not necessarily cause the coinciding plant cover and species distributions, their co-incidence can be used in planning a restoration project. Better prediction of individual species distributions can be used to tailor planting schemes to certain environmental conditions, or to assist in determining the conditions required for the desired wetland type. The success rate of wetland restoration efforts can be improved by further determination of quantitative values associated with environmental conditions that affect plant distributions. While knowing which environmental characteristics play roles in growth and/or survival of wetland species is helpful, such quantitative values are needed to guide the restoration practitioner in effectively planning restoration projects.

References

Bennett, S. H., and J. B. Nelson. 1991. Distribution and Status of Carolina Bays in South Carolina. South Carolina Wildlife & Marine Resources Department.

Blom, C. W. P. M., and L. A. C. J. Voesenek. 1996. Flooding: the survival strategies of plants. Tree **11**:290-195.

Bouchard, R., and J. D. Madsen. 1987. The aquatic macrophyte community of Black Earth Creek, Wisconsin. Transactions of the Wisconsin Academy of Science, Arts, and Letters **75**:41-55.

Breen, C. M., K. H. Rogers, and P. J. Ashton. 1988. Vegetation processes in swamps and flooded plains. Pages 223-247 *in* J. J. Symoens, editor. Vegetation of inland waters. Kluwer Academic Publishers, Dordrecht, Netherlands.

Bridgham, S. D., J. Pastor, J. A. Janssens, C. Chapin, and T. J. Malterer. 1996. Multiple limiting gradients in peatlands: A call for a new paradigm. Wetlands **16**:45-65.

Budelsky, R. A., and S. M. Galatowitsch. 2000. Effects of water regime and competition on the establishment of a native sedge in restored wetlands. Journal of Applied Ecology **37**:971-985.

Caraco, T. 1991. On the adaptive value of physiological integration in clonal plants. Ecology **72**:81-93.

Carter, V. 1986. An overview of the hydrologic concerns related to wetlands in the United States. Canadian Journal of Botany-Revue Canadienne De Botanique **64**:364-374.

Casanova, M. T., and M. A. Brock. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? Plant Ecology **147**:237-250.

Collins, B., and G. Wein. 2000. Stem elongation response to neighbour shade in sprawling and upright Polygonum species. Annals of Botany **86**:739-744.

Collins, B. S., and L. L. Battaglia. 2001. Hydrology effects on propagule bank expression and vegetation in six Carolina bays. Community Ecology **2**:21-33.

Coops, H., R. Boeters, and H. Smit. 1991. Direct and indirect effects of wave attack on helophytes. Aquatic Botany **41**:333-352.

Crow, G. E., and C. B. Hellquist. 2000. Aquatic and Wetland Plants of Northeastern North America. The University of Wisconsin Press, Madison.

Daoust, R. J., and D. L. Childers. 1999. Controls on emergent macrophyte composition, abundance, and productivity in freshwater Everglads wetland communities. Wetlands **19**:262-275.

Daubenmire, R. 1968. Plant Communities: a Textbook of Plant Synecology. Harper and Row, New York.

Davis, C. E., and L. L. Janecek. 1997. DOE Research Set-Aside Areas of the Savannah River Site. SRO-NERP-25, The Savannah River Site National Environmental Research Park Program, United States Department of Energy, Aiken, SC.

De Steven, D., and M. M. Toner. 2004. Vegetation of Upper Coastal Plain depression wetlands: environmental templates and wetland dynamics within a landscape framework. Wetlands **24**:23-42.

DeLaune, R. D., C. J. Smith, and M. N. Sarafyan. 1986. Nitrogen cycling in a fresh water marsh of *Panicum hemitomon* on the Deltaic Plain of the Mississippi River. Journal of Ecology **74**:249-256.

Edwards, A. L., and A. S. Weakley. 2001. Population biology and management of rare plants in depression wetlands of the southeastern coastal plain, USA. Natural Areas Journal **21**:12-35.

Federal Register. 1998. Floodplain and wetlands involvement notification for implementation of the wetland mitigation bank at the Savannah River Site (SRS). Volume 63, Number 72. April 15.

Gaudet, C. L., and P. A. Keddy. 1995. Competitive performance and species distribution in shoreline plant communities: a comparative approach. Ecology **76**:280-291.

Glaser, P. H., J. A. Janssens, and D. I. Siegel. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River peatland, northern Minnesota. Journal of Ecology **78**:1021-1048.

Godfrey, R. K., and J. W. Wooten. 1981. Aquatic and Wetland Plants of Southeastern United States. The University of Georgia Press, Athens, GA.

Grace, J. B. 1988. The effects of nutrient additions on mixtures of *Typha latifolia* L. and *Typha domingensis* Pers. along a water-depth gradient. Aquatic Botany **31**:83-92.

Green, E. K., and S. M. Galatowitsch. 2001. Differences in wetland plant community establishment with additions of nitrate-N and invasive species (*Phalaris arundinacea* and *Typha* x *glauca*). Canadian Journal of Botany-Revue Canadienne De Botanique **79**:170-178.

Holland, R. F., and S. K. Jain. 1981. Insular biogeography of vernal pools in the Central Valley of California. American Naturalist **117**:24-37.

Josselyn, M. N., S. P. Faulkner, and W. H. Patrick. 1990. Relationships between seasonally wet soils and occurrence of wetland plants in California. Wetlands **10**:7-26.

Keddy, P. 1999. Epilogue: from global exploration to community assembly. Pages 393-402 *in* E. Weiher and P. Keddy, editors. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, United Kingdom.

Keddy, P., C. Gaudet, and L. H. Fraser. 2000. Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. Journal of Ecology **88**:413-423.

Keddy, P. A. 1980. Population ecology in an environmental mosaic: *Cakile edentula* on a gravel bar. Canadian Journal of Botany-Revue Canadienne De Botanique **58**:1095-1100.

Keddy, P. A. 1982. Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. Aquatic Botany **14**:41-58.

Keddy, P. A. 1984. Quantifying a within-lake gradient of wave energy in Gillfillan Lake, Nova Scotia. Canadian Journal of Botany-Revue Canadienne De Botanique **62**:301-309.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science **3**:157-164.

Keddy, P. A., and P. Constabel. 1986. Germination of ten shoreline plants in relation to seed size, soil particle size and water level: an experimental study. Journal of Ecology **74**:133-141.

Keddy, P. A., and T. H. Ellis. 1985. Seedling recruitment of 11 wetland plant species along a water level gradient: shared or distinct responses? Canadian Journal of Botany-Revue Canadienne De Botanique **63**:1876-1879.

Kirkman, L. K. 1992. Cyclical vegetation dynamics in Carolina bay wetlands. Ph.D.. Dissertation. The University of Georgia, Athens, GA.

Kirkman, L. K., R. F. Lide, G. Wein, and R. R. Sharitz. 1996. Vegetation changes and land-use legacies of depression wetlands of the western coastal plain of South Carolina: 1951-1992. Wetlands **16**:564-576.

Kirkman, L. K., and R. R. Sharitz. 1993. Growth in controlled water regimes of three grasses common in freshwater wetlands of the Southeastern USA. Aquatic Botany **44**:345-359.

Kirkman, L. K., and R. R. Sharitz. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina bays in South Carolina. Ecological Applications **4**:177-188.

Klimešová, J. 1994. The effects of timing and duration of floods on growth of young plants of *Phalaris arundinacea* L. and *Urtica dioica* L.: an experimental study. Aquatic Botany **48**:21-29.

Lenssen, J., F. Menting, W. van der Putten, and K. Blom. 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. Oikos **86**:523-534.

Lenssen, J. P. M., F. B. J. Menting, W. H. van der Putten, and C. Blom. 2000. Vegetative reproduction by species with different adaptations to shallow-flooded habitats. New Phytologist **145**:61-70.

Lenssen, J. P. M., G. E. ten Dolle, and C. Blom. 1998. The effect of flooding on the recruitment of reed marsh and tall forb plant species. Plant Ecology **139**:13-23.

Lessmann, J. M., I. A. Mendelssohn, M. W. Hester, and K. L. McKee. 1997. Population variation in growth response to flooding of three marsh grasses. Ecological Engineering **8**:31-47.

Lide, R. F. Unpublished data. Savannah River Ecology Laboratory, University of Georgia, Aiken, SC, USA.

Lide, R. F., V. G. Meentemeyer, J. E. Pinder, and L. M. Beatty. 1995. Hydrology of a Carolina bay located on the upper Coastal Plain of western South Carolina. Wetlands **15**:47-57.

Lockwood, J. L., and S. L. Pimm. 1999. When does restoration succeed? Pages 1-20 *in* P. Keddy, editor. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, United Kingdom.

Loveless, C. M. 1959. A Study of the Vegetation in the Florida Everglades. Ecology **40**:1-9.

Lovell, P. H., and P. J. Lovell. 1985. The importances of plant form as a determining factor in competition and habitat exploitation. Pages 209-221 *in* J. White, editor. Studies on Plant Demography: a festschrift for John L. Harper. Academic Press, Inc., Orlando, FL.

Maillette, L., and P. A. Keddy. 1989. Two plants with contrasting architectures: growth responses to light gradients. Canadian Journal of Botany-Revue Canadienne De Botanique **67**:2825-2828.

Maurer, D. A., and J. B. Zedler. 2002. Differential invasion of a wetland grass explained by tests of nutrients and light availability on establishment and clonal growth. Oecologia **131**:279-288.

Metzker, K. D., and W. J. Mitsch. 1997. Modelling self-design of the aquatic community in a newly created freshwater wetland. Ecological Modelling **100**:61-86.

Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands, 2nd edition. John Wiley & Sons Inc., New York.

Moore, D. R. J., and P. A. Keddy. 1988. Effects of a water-depth gradient on the germination of lakeshore plants. Canadian Journal of Botany-Revue Canadienne De Botanique **66**:548-552.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York.

Pezeshki, S. R., P. H. Anderson, and R. D. DeLaune. 2000. Effects of nursery pre-conditioning on *Panicum hemitomon* and *Sagittaria lancifolia* used for wetland restoration. Restoration Ecology **8**:57-64.

Poiani, K. A., and P. M. Dixon. 1995. Seed banks of Carolina bays: potential contributions from surrounding landscape vegetation. American Midland Naturalist **134**:140-154.

Radford, A. E., H. E. Ahles, and R. C. Bell. 1968. Manual of the Vascular Flora of the Carolinas. The University of North Carolina Press, Chapel Hill.

Richardson, C. J., and J. W. Gibbons. 1993. Pocosins, Carolina bays, and mountain bogs. Pages 257-310 *in* W. H. Martin, S. G. Boyce, and A. C. Echternacht, editors. Biodiversity of the Southeastern United States. J. Wiley & Sons, New York, NY, USA.

SAS Institute. 2001. SAS/STAT User's Guide Release 8.0, 2nd edition. SAS Institute Inc., Cary, NC.

Schalles, J. F., R. R. Sharitz, J. W. Gibbons, G. J. Leversee, and J. N. Knox. 1989. Carolina Bays of the Savannah River Plant, Aiken, South Carolina. SRO-NERP-18, Savannah River Plant National Environmental Research Park Program.

Schalles, J. F., and D. J. Shure. 1989. Hydrology, community structure, and productivity patterns of a dystrophic Carolina bay wetland. Ecological Monographs **59**:365-385.

Sharitz, R. R., and J. W. Gibbons. 1982. The Ecology of Southeastern Shrub Bogs (Pocosins) and Carolina Bays: a Community Profile. FWS/OBS-82/04, U.S. Fish and Wildlife Service, Division of Biological Services, Washington, DC.

Sharitz, R. R., and C. A. Gresham. 1998. Pocosins and Carolina bays. Pages 343-388 *in* M. G. Messina and W. H. Conner, editors. Southern Forested Wetlands Ecology and Management. Lewis Publishers, Boca Raton.

Sharp, M. J., and P. A. Keddy. 1985. Biomass accumulation by *Rhexia virginica* and *Triadenum fraseri a*long two lakeshore gradients: a field experiment. Canadian Journal of Botany-Revue Canadienne De Botanique **63**:1806-1810.

Shipley, B., and P. A. Keddy. 1988. The relationship between relative growth rate and sensitivity to nutrient stress in twenty-eight species of emergent macrophytes. Journal of Ecology **76**:1101-1110.

Shipley, B., P. A. Keddy, and L. P. Lefkovitch. 1991. Mechanisms producing plant zonation along a water depth gradient: a comparison with the exposure gradient. Canadian Journal of Botany-Revue Canadienne De Botanique **69**:1420-1424.

South Carolina Department of Natural Resources. 2003. South Carolina Rare, Threatened, & Endangered Species Inventory. http://www.dnr.state.sc.us/pls/heritage/county_species.list?pcounty=all updated June 9, 2003. South Carolina Department of Natural Resources, Columbia, SC.

Spence, D. H. N. 1982. The zonation of plants in freshwater lakes. Pages 37-125 *in* A. MacFadyen and E. D. Ford, editors. Advances in Ecological Research. Academic Press, New York, NY.

Squires, L., and A. G. van der Valk. 1992. Water-depth tolerances of the dominant emergent macrophytes of the Delta Marsh, Manitoba. Canadian Journal of Botany-Revue Canadienne De Botanique **70**:1860-1867.

Steinke, W., D. J. von Willert, and F. A. Austenfeld. 1996. Root dynamics in a salt marsh over three consecutive years. Plant and Soil **185**:265-269.

Sutter, R. D., and R. Kral. 1994. The ecology, status, and conservation of two non-alluvial wetland communities in the South Atlantic and Eastern Gulf Coastal Plain, USA. Biological Conservation **68**:235-243.

Svengsouk, L. J., and W. J. Mitsch. 2001. Dynamics of mixtures of *Typha latifolia* and *Schoenoplectus tabernaemontani* in nutrient-enrichment wetland experiments. American Midland Naturalist **145**:309-324.

Swarzenski, C. M., E. M. Swenson, C. E. Sasser, and J. G. Gosselink. 1991. Marsh mat flotation in the Louisiana Delta Plain. Journal of Ecology **79**:999-1011.

Thompson, L. M., and F. R. Troeh. 1957. Soils and Soil Fertility, 3rd edition. McGraw-Hill Book Company, New York.

Tyndall, R. W., K. A. McCarthy, J. C. Ludwig, and A. Rome. 1990. Vegetation of six Carolina bays in Maryland. Castanea **55**:133-135.

Vaithiyanathan, P., and C. J. Richardson. 1999. Macrophyte species changes in the Everglades: examination along a eutrophication gradient. Journal of Environmental Quality **28**:1347-1358.

van den Brink, F. W. B., M. M. J. Maenen, G. Van der Velde, and A. bij de Vaate. 1991. The (semi-)aquatic vegetation of still waters within the floodplains of the rivers Rhine and Meuse in The Netherlands: historical changes and the role of inundation. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie **24**:2693-2699.

van den Brink, F. W. B., G. van der Velde, W. W. Bosman, and H. Coops. 1995. Effects of substrate parameters on growth-responses of 8 helophyte species in relation to flooding. Aquatic Botany **50**:79-97.

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology **62**:688-696.

van der Valk, A. G. 1994. Effects of prolonged flooding on the distribution and biomass of emergent species along a fresh-water wetland coenocline. Vegetatio **110**:185-196.

Weiher, E., and P. A. Keddy. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos **74**:159-164.

Weiher, E., I. C. Wisheu, P. A. Keddy, and D. R. J. Moore. 1996. Establishment, persistence, and management implications of experimental wetland plant communities. Wetlands **16**:208-218.

Weisner, S. E. B., W. Graneli, and B. Ekstam. 1993. Influence of submergence on growth of seedlings of *Scirpus lacustris* and *Phragmites australis*. Freshwater Biology **29**:371-375.

Weisner, S. E. B., and J. A. Strand. 1996. Rhizome architecture in *Phragmites australis* in relation to water depth: Implications for within-plant oxygen transport distances. Folia Geobotanica & Phytotaxonomica **31**:91-97.

Wetzel, P. R., and A. G. van der Valk. 1998. Effects of nutrient and soil moisture on competition between *Carex stricta*, *Phalaris arundinacea*, and *Typha latifolia*. Plant Ecology **138**:179-190.

Willis, J. M., and M. W. Hester. 2004. Interactive effects of salinity, flooding, and soil type on Panicum hemitomon. Wetlands **24**:43-50.

Wilson, S. D., and P. A. Keddy. 1985. Plant zonation on a shoreline gradient: physiological response curves of component species. Journal of Ecology **73**:851-860.

Wisheu, I. C., and P. A. Keddy. 1992. Competition and centrifugal organization of plant communities: theory and tests. Journal of Vegetation Science **3**:147-156.

Table 3.1. Criteria and rationale for Carolina bay selection

Criteria	Rationale
Bay must be on the SRS property	• Proximity of bays would reduce differences in geology between bays • Differences in vegetation due to region would be prevented • Ease of access to bays
Bay must be predominantly herbaceous	• Goal of study was to examine response of herbaceous wetland plants to environmental variables
Water depth records must be available through bay hydrologic monitoring program	• Long-term water depth records were needed to determine flooding depths and frequencies
Bay must have some morphological variation	• Variation in morphology may increase variation in multiple environmental characteristics
Bay must not be undergoing a natural or man-made disturbance (e.g. from beaver activity or functioning drainage ditches)	• Plant communities should be as close to equilibrium as possible in response to environmental conditions
Bay must be a functioning wetland and has been since SRS ownership began in 1951	• A natural wetland system is desired for study; recently drained and/or restored wetlands would not be appropriate reference sites

Table 3.2. Cover-abundance scale used for herbaceous vegetation sampling

Cover-Abundance Scale*	Percent Cover	Abundance	Midpoint (used for calculations)
6	95-100	any	97.5 %
5	75-95	any	85 %
4	50-75	any	62.5 %
3	25-50	any	37.5 %
2	5-25	any	15 %
1	< 5	numerous	2.5 %
+	small	few	0 %
r	small	solitary	0 %

* a modified Braun-Blanquet scale was used (Daubenmire 1968, Mueller-Dombois and Ellenberg 1974)

Table 3.3. Expressions of water depth and/or duration used for statistical analysis

Duration and timing of flooding

Total number of days per year	Maximum number of consecutive days per year	Total number of days per spring season	Maximum number of consecutive days per spring season
≤ 0 cm (dry)	≤ 0 cm (dry)	≤ 0 cm (dry)	≤ 0 cm (dry)
≥ 10 cm	≥ 10 cm	≥ 10 cm	≥ 10 cm
≥ 20 cm	≥ 20 cm	≥ 20 cm	≥ 20 cm
≥ 30 cm	≥ 30 cm	≥ 30 cm	≥ 40 cm
≥ 100 cm	≥ 40 cm	≥ 100 cm	≥ 50 cm
	≥ 50 cm		

Depth of flooding

1-year median water depth
4-year median water depth

Table 3.4a. Water variables with significant effects on graminoid cover for each year or season. Analysis performed by stepwise multiple regression; all variables shown are significant at the 0.05 level. Variables showing a trend of significance (shaded) were selected for further analysis.

Period	Without 4-year Median Depth	With 4-year Median Depth
1998-1999	1-year median depth	4-year median depth
1997-1998	maximum consecutive days ≥ 50 cm 1-year median depth	4-year median depth
1996-1997	maximum consecutive days ≤ 0 cm	4-year median depth
Spring 1999	maximum consecutive days ≤ 0 cm maximum consecutive days ≥ 20 cm	maximum consecutive days ≤ 0 cm maximum consecutive days ≥ 20 cm
Spring 1998	maximum consecutive days ≥ 10 cm maximum consecutive days ≥ 40 cm 1-year median depth	4-year median depth
Spring 1997	maximum consecutive days ≤ 0 cm	4-year median depth
Variable chosen:	4-year median depth	

Table 3.4b. Water variables with significant effects on *Panicum hemitomon* cover for each year or season. Analysis performed by stepwise multiple regression; all variables shown are significant at the 0.05 level. Variables showing a trend of significance (shaded) were selected for further analysis.

Period	Without 4-year Median Depth	With 4-year Median Depth
1998-1999	1-year median depth	4-year median depth
1997-1998	maximum consecutive days ≥ 50 cm 1-year median depth	maximum consecutive days ≥ 50 cm 1-year median depth 4-year median depth
1996-1997	1-year median depth	1-year median depth
Spring 1999	1-year median depth	1-year median depth 4-year median depth
Spring 1998	maximum consecutive days ≤ 0 cm	maximum consecutive days ≤ 0 cm
Spring 1997	maximum consecutive days ≥ 20 cm 1-year median depth	maximum consecutive days ≥ 20 cm 1-year median depth
Variables chosen:	1-year median depth 4-year median depth	

Table 3.4c. Water variables with significant effects on floating leaved species cover for each year or season. Analysis performed by stepwise multiple regression; all variables shown are significant at the 0.05 level. Variables showing a trend of significance (shaded) were selected for further analysis.

Period	Without 4-year Median Depth	With 4-year Median Depth
1998-1999	maximum consecutive days ≥ 10 cm	maximum consecutive days ≥ 10 cm
	maximum consecutive days ≥ 50 cm	maximum consecutive days ≥ 50 cm
1997-1998	maximum consecutive days ≥ 10 cm	maximum consecutive days ≥ 10 cm
	1-year median depth	4-year median depth
1996-1997	1-year median depth	1-year median depth
		4-year median depth
Spring 1999	1-year median depth	1-year median depth
Spring 1998	1-year median depth	1-year median depth
		4-year median depth
Spring 1997	maximum consecutive days ≥ 20 cm	maximum consecutive days ≥ 20 cm
	1-year median depth	1-year median depth
		4-year median depth
Variable chosen:	4-year median depth	

Table 3.4d. Water variables with significant effects on *Nymphaea odorata* cover for each year or season. Analysis performed by stepwise multiple regression; all variables shown are significant at the 0.05 level. Variables showing a trend of significance (shaded) selected for further analysis.

Period	Without 4-year Median Depth	With 4-year Median Depth
1998-1999	maximum consecutive days ≥ 30 cm	maximum consecutive days ≥ 30 cm
1997-1998	maximum consecutive days ≥ 20 cm	maximum consecutive days ≥ 20 cm
	1-year median depth	1-year median depth
1996-1997	maximum consecutive days ≥ 10 cm	maximum consecutive days ≥ 20 cm
	maximum consecutive days ≥ 50 cm	maximum consecutive days ≥ 50 cm
	1-year median depth	4-year median depth
Spring 1999	maximum consecutive days ≥ 20 cm	maximum consecutive days ≥ 20 cm
	maximum consecutive days ≥ 50 cm	maximum consecutive days ≥ 50 cm
Spring 1998	maximum consecutive days ≥ 10 cm	maximum consecutive days ≥ 10 cm
	1-year median depth	1-year median depth
Spring 1997	maximum consecutive days ≥ 20 cm	maximum consecutive days ≥ 10 cm
	maximum consecutive days ≥ 50 cm	maximum consecutive days ≥ 50 cm
	1-year median depth	4-year median depth
Variables chosen:	springtime maximum consecutive days ≥ 10 cm springtime maximum consecutive days ≥ 50 cm 1-year median depth	

Table 3.5. Environmental variables shown to have significant relationships to the cover of Carolina bay plants. Significance was determined by a general linear model. Three regressions were performed for each group or species due to the high correlation between C, N, or P. For each, one of these variables plus the other environmental variables were analyzed. In addition, two sets of regressions were performed for *Panicum hemitomon*, as the 1-year median water depth and the 4-year median water depth are highly correlated. Only significant ($P \leq 0.05$) variables are listed.

	First Regression (with Carbon) Pr > f	Second Regression (with Nitrogen) Pr > f	Third Regression (with Phosphorus) Pr > f
Graminoid species			
4-year water depth median	0.0005	0.0006	0.0005
C:N	0.0158	0.0390	0.0265
regression R^2 value	0.27	0.28	0.27
Panicum hemitomon			
(using 1-year median water variable)			
Bay	0.0297	0.0420	0.0203
1-year water depth median	0.0007	0.0008	0.0006
C:N	0.0327	n.s.	n.s.
N		0.0503*	
regression R^2 value	0.23	0.24	0.23
(using 4-year median water variable)			
4-year water depth median	0.0007	0.0008	0.0006
C:N	0.0327	n.s.	n.s.
N		0.0503*	
regression R^2 value	0.23	0.24	0.23
Floating-leaved species			
Bay	<0.0001	<0.0001	<0.0001
4-year water depth median	0.0027	0.0030	0.0026
pH	0.0087	0.0079	0.0059
regression R^2 value	0.55	0.55	0.55
Nymphaea odorata			
Bay	<0.0001	<0.0001	<0.0001
1-year water depth median	0.0043	0.0030	0.0028
Maximum consecutive spring days $\geq$ 10 cm water	<0.0001	<0.0001	<0.0001
Maximum consecutive spring days $\geq$ 50 cm water	0.0001	0.0001	<0.0001
Available Soil Water	0.0330	0.0147	0.0116
regression R^2 value	0.73	0.73	0.73

* N variable is included for *P. hemitomon* due to its near significance.

Table 3.6. Estimated distribution limits for Carolina bay species. Values represent the condition at which 10% cover is expected as determined by probit analysis. Fiducial limits indicated with "nc" were not able to be calculated.

			95% Fiducial Limits	
	Value	Units	Low	High
Graminoids				
4-year water depth median	51.3	cm	39.18	69.04
C:N ratio	11.04		1.46	13.12
Panicum hemitomon				
1-year median water depth	30.7	cm	-9.32	57.51
C:N ratio	14.94		nc	nc
N	0.80	percent	nc	nc
4-year water depth median	25.8	cm	-0.49	47.777
Floating-leaved species				
4-year water depth median	9.3	cm	-18.16	24.77
pH	3.36		2.615	3.729
Nymphaea odorata				
1-year median water depth	19.8	cm	-15.10	37.51
Maximum consecutive spring days ≥ 10 cm water	170	days	nc	nc
Maximum consecutive spring days ≥ 50 cm water	16	days	-74.97	58.35
Available Soil Water	8.42	g water / 100 g soil	-13.40	18.26

Table 3.7. Comparison of graminoid species field distributions to predicted distributions.

4-Year Median Water Depth

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	0.00	100.00	5	15.38	84.62	13
Short Transect	0.00	100.00	5	16.67	83.33	6
Total	0.00	100.00	10	15.79	84.21	19
Ellenton Bay						
Long Transect	41.67	58.33	12	14.29	85.71	14
Short Transect	62.50	37.50	8	7.14	92.86	14
Total	50.00	50.00	20	10.71	89.29	28
Flamingo Bay						
Long Transect	54.55	45.45	11	28.57	71.43	14
Short Transect	40.00	60.00	5	42.86	57.14	7
Total	50.00	50.00	16	33.33	66.67	21
Sarracenia Bay						
Long Transect	58.33	41.67	12	-	-	0
Short Transect	55.56	44.44	9	0.00	100.00	1
Total	57.14	42.86	21	0.00	100.00	1

C:N Ratio

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	22.22	77.78	9	0.00	100.00	9
Short Transect	0.00	100.00	8	33.33	66.67	3
Total	11.76	88.24	17	8.33	91.67	12
Ellenton Bay						
Long Transect	42.86	57.14	14	8.33	91.67	12
Short Transect	29.41	70.59	17	20.00	80.00	5
Total	35.48	64.52	31	11.76	88.24	17
Flamingo Bay						
Long Transect	47.06	52.94	17	25.00	75.00	8
Short Transect	41.67	58.33	12	-	-	0
Total	44.83	55.17	29	25.00	75.00	8
Sarracenia Bay						
Long Transect	71.43	28.57	7	40.00	60.00	5
Short Transect	50.00	50.00	10	-	-	0
Total	58.82	41.18	17	40.00	60.00	5

Table 3.8. Comparison of *Panicum hemitomon* field distributions to predicted distributions.

1-Year Median Water Depth

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	0.00	100.00	2	0.00	100.00	16
Short Transect	0.00	100.00	3	12.50	87.50	8
Total	0.00	100.00	5	4.17	95.83	24
Ellenton Bay						
Long Transect	100.00	0.00	5	9.52	90.48	21
Short Transect	50.00	50.00	4	11.11	88.89	18
Total	77.78	22.22	9	10.26	89.74	39
Flamingo Bay						
Long Transect	33.33	66.67	3	18.18	81.82	22
Short Transect	0.00	100.00	3	55.56	44.44	9
Total	16.67	83.33	6	29.03	70.97	31
Sarracenia Bay						
Long Transect	18.18	81.82	11	0.00	100.00	1
Short Transect	0.00	100.00	6	0.00	100.00	4
Total	11.76	88.24	17	0.00	100.00	5

4-Year Median Water Depth

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	0.00	100.00	2	0.00	100.00	16
Short Transect	0.00	100.00	3	12.50	87.50	8
Total	0.00	100.00	5	4.17	95.83	24
Ellenton Bay						
Long Transect	83.33	16.67	6	5.00	95.00	20
Short Transect	60.00	40.00	5	11.76	88.24	17
Total	72.73	27.27	11	8.11	91.89	37
Flamingo Bay						
Long Transect	33.33	66.67	3	18.18	81.82	22
Short Transect	0.00	100.00	3	55.56	44.44	9
Total	16.67	83.33	6	29.03	70.97	31
Sarracenia Bay						
Long Transect	14.29	85.71	7	20.00	80.00	5
Short Transect	0.00	100.00	6	0.00	100.00	4
Total	7.69	92.31	13	11.11	88.89	9

Table 3.8. (continued)

C:N Ratio

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	0.00	100.00	5	0.00	100.00	13
Short Transect	0.00	100.00	3	12.50	87.50	8
Total	0.00	100.00	8	4.76	95.24	21
Ellenton Bay						
Long Transect	100.00	0.00	1	24.00	76.00	25
Short Transect	42.86	57.14	7	13.33	86.67	15
Total	50.00	50.00	8	20.00	80.00	40
Flamingo Bay						
Long Transect	0.00	100.00	1	20.83	79.17	24
Short Transect	0.00	100.00	3	55.56	44.44	9
Total	0.00	100.00	4	30.30	69.70	33
Sarracenia Bay						
Long Transect	0.00	100.00	3	22.22	77.78	9
Short Transect	0.00	100.00	2	0.00	100.00	8
Total	0.00	100.00	5	11.76	88.24	17

Table 3.9. Comparison of floating-leaved species field distributions to predicted distributions.

4-Year Median Water Depth

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	38.89	61.11	18	-	-	0
Short Transect	54.55	45.45	11	-	-	0
Total	44.83	55.17	29	-	-	0
Ellenton Bay						
Long Transect	95.45	4.55	22	0.00	100.00	4
Short Transect	94.44	5.56	18	0.00	100.00	4
Total	95.00	5.00	40	0.00	100.00	8
Flamingo Bay						
Long Transect	16.00	84.00	25	-	-	0
Short Transect	54.55	45.45	11	0.00	100.00	1
Total	27.78	72.22	36	0.00	100.00	1
Sarracenia Bay						
Long Transect	62.50	37.50	8	0.00	100.00	4
Short Transect	66.67	33.33	6	0.00	100.00	4
Total	64.29	35.71	14	0.00	100.00	8

pH

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	38.89	61.11	18	-	-	0
Short Transect	60.00	40.00	10	0.00	100.00	1
Total	46.43	53.57	28	0.00	100.00	1
Ellenton Bay						
Long Transect	80.77	19.23	26	-	-	0
Short Transect	85.00	15.00	20	0.00	100.00	2
Total	82.61	17.39	46	0.00	100.00	2
Flamingo Bay						
Long Transect	18.18	81.82	22	0.00	100.00	3
Short Transect	54.55	45.45	11	0.00	100.00	1
Total	30.30	69.70	33	0.00	100.00	4
Sarracenia Bay						
Long Transect	80.00	20.00	5	14.29	85.71	7
Short Transect	40.00	60.00	5	40.00	60.00	5
Total	60.00	40.00	10	25.00	75.00	12

Table 3.10. Comparison of *Nymphaea odorata* field distributions to predicted distributions.

1-Year Median Water Depth

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	41.18	58.82	17	0.00	100.00	1
Short Transect	54.55	45.45	11	-	-	0
Total	46.43	53.57	28	0.00	100.00	1
Ellenton Bay						
Long Transect	90.91	9.09	22	0.00	100.00	4
Short Transect	94.44	5.56	18	0.00	100.00	4
Total	92.50	7.50	40	0.00	100.00	8
Flamingo Bay						
Long Transect	0.00	100.00	25	-	-	0
Short Transect	9.09	90.91	11	0.00	100.00	1
Total	2.78	97.22	36	0.00	100.00	1
Sarracenia Bay						
Long Transect	71.43	28.57	7	0.00	100.00	5
Short Transect	60.00	40.00	5	0.00	100.00	5
Total	66.67	33.33	12	0.00	100.00	10

Minimum of 170 Consecutive Spring Days with 10 cm or More Flooding

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	43.75	56.25	16	0.00	100.00	2
Short Transect	66.67	33.33	9	0.00	100.00	2
Total	52.00	48.00	25	0.00	100.00	4
Ellenton Bay						
Long Transect	95.24	4.76	21	0.00	100.00	5
Short Transect	94.44	5.56	18	0.00	100.00	4
Total	94.87	5.13	39	0.00	100.00	9
Flamingo Bay						
Long Transect	0.00	100.00	22	0.00	100.00	3
Short Transect	11.11	88.89	9	0.00	100.00	3
Total	3.23	96.77	31	0.00	100.00	6
Sarracenia Bay						
Long Transect	100.00	0.00	5	0.00	100.00	7
Short Transect	100.00	0.00	4	0.00	100.00	6
Total	100.00	0.00	9	0.00	100.00	13

Table 3.10. (continued)

Minimum of 16 Consecutive Spring Days with 50 cm or More Flooding

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	46.67	53.33	15	0.00	100.00	3
Short Transect	75.00	25.00	8	0.00	100.00	3
Total	56.52	43.48	23	0.00	100.00	6
Ellenton Bay						
Long Transect	95.00	5.00	20	16.67	83.33	6
Short Transect	100.00	0.00	17	0.00	100.00	5
Total	97.30	2.70	37	9.09	90.91	11
Flamingo Bay						
Long Transect	0.00	100.00	20	0.00	100.00	5
Short Transect	12.50	87.50	8	0.00	100.00	4
Total	3.57	96.43	28	0.00	100.00	9
Sarracenia Bay						
Long Transect	-	-	0	41.67	58.33	12
Short Transect	100.00	0.00	1	33.33	66.67	9
Total	100.00	0.00	1	38.10	61.90	21

Available Soil Water

	Percent of Sample Locations					
	Within Expected Range			Outside Expected Range		
	≥ 10% cover	< 10% cover	Total	≥ 10% cover	< 10% cover	Total
Dry Bay						
Long Transect	38.89	61.11	18	-	-	0
Short Transect	54.55	45.45	11	-	-	0
Total	44.83	55.17	29	-	-	0
Ellenton Bay						
Long Transect	76.92	23.08	26	-	-	0
Short Transect	94.44	5.56	18	0.00	100.00	4
Total	84.09	15.91	44	0.00	100.00	4
Flamingo Bay						
Long Transect	0.00	100.00	25	-	-	0
Short Transect	8.33	91.67	12	-	-	0
Total	2.70	97.30	37	-	-	0
Sarracenia Bay						
Long Transect	41.67	58.33	12	-	-	0
Short Transect	44.44	55.56	9	0.00	100.00	1
Total	42.86	57.14	21	0.00	100.00	1

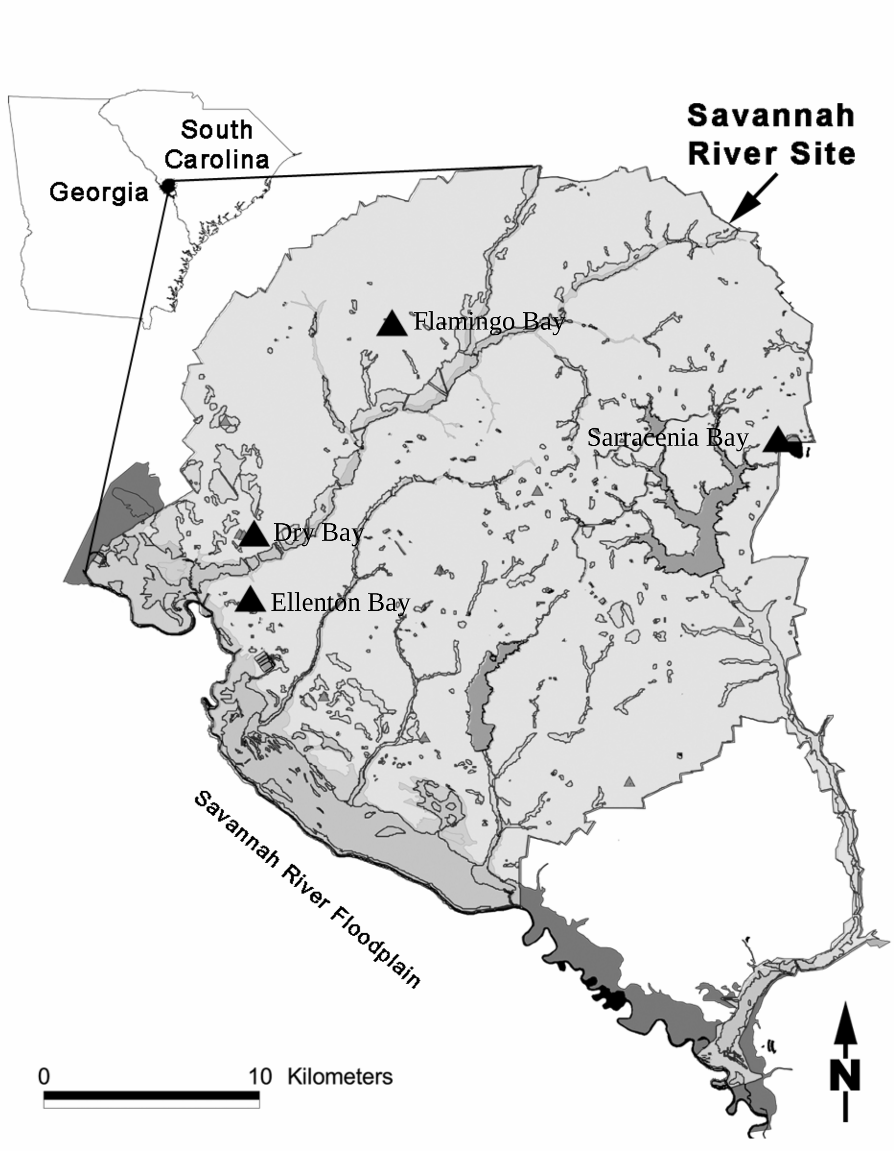


Figure 3.1. Carolina bay locations on the Savannah River Site (SRS), Aiken, South Carolina.

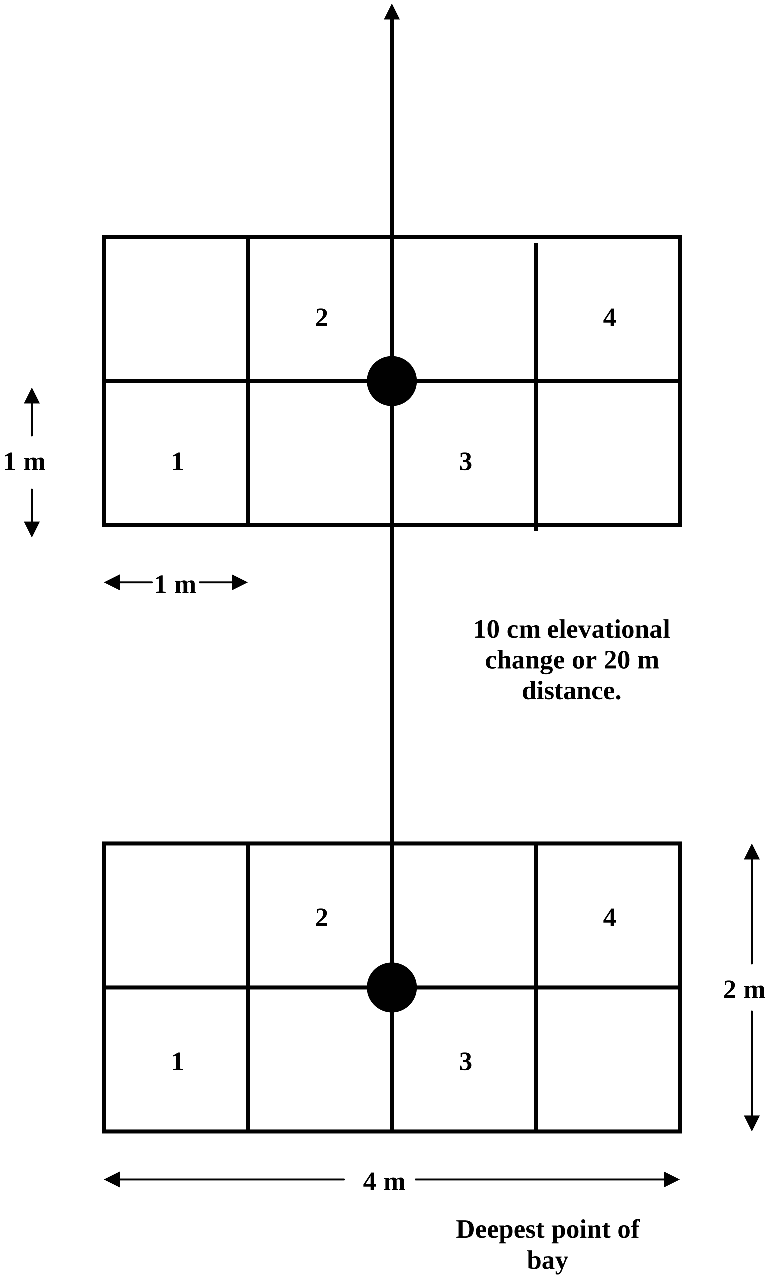


Figure 3.2. Layout of sampling plots used in vegetation and soil surveys. Subplots 1, 2, 3, and 4 were used for vegetation sampling. Subplots 2 and 3 were used for soil sampling.

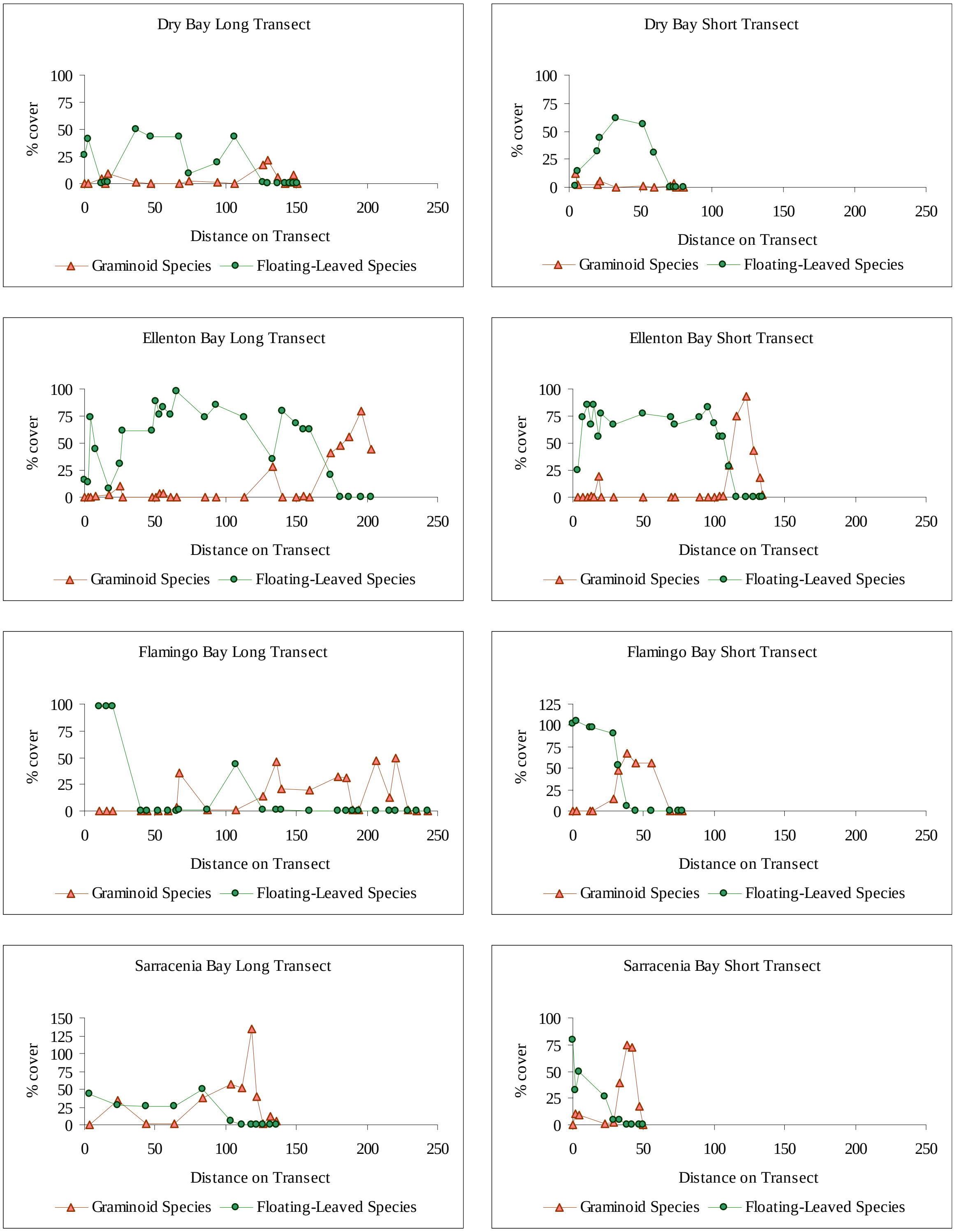


Figure 3.3. Cover of graminoids and floating-leaved species in Carolina bays.

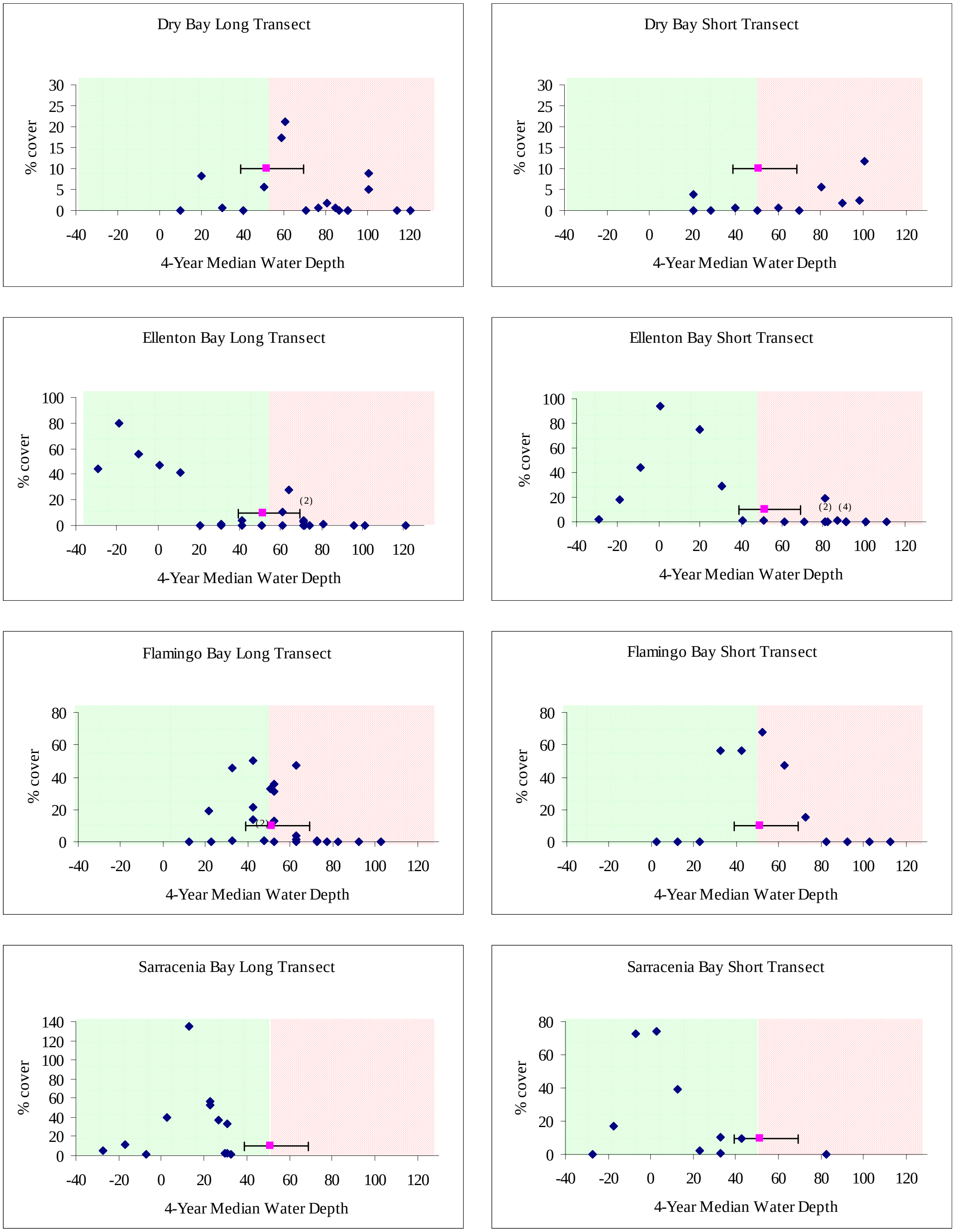


Figure 3.4. Relationship between graminoid species cover and the 4-year median water depth. Plant presence is expected in the green area and not expected in the red. The estimated distribution limit is shown with fiduciary limits.

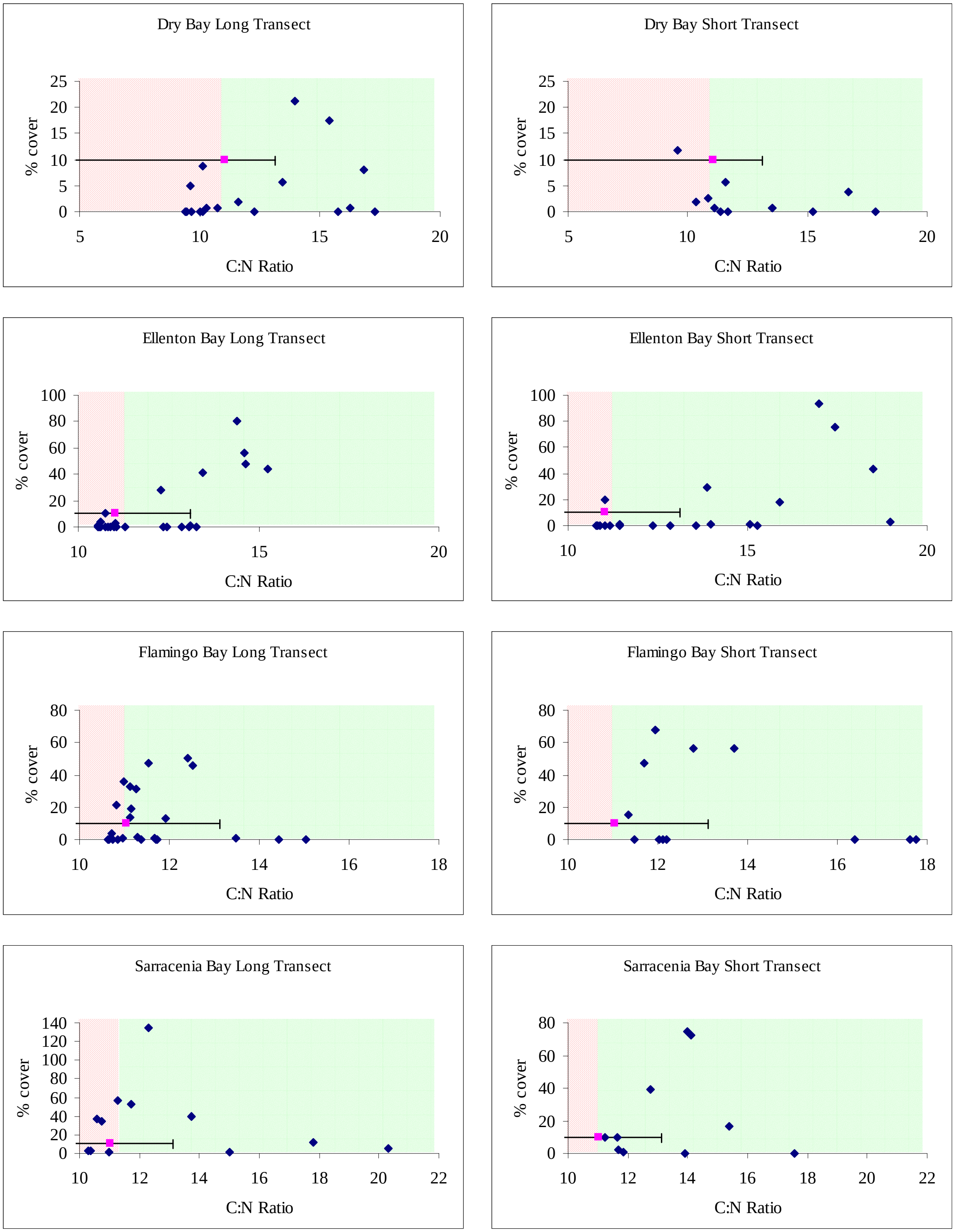


Figure 3.5. Relationship between graminoid species cover and the soil C:N ratio. Plant presence is expected in the green area and not expected in the red. The estimated distribution limit is shown with fiduciary limits.

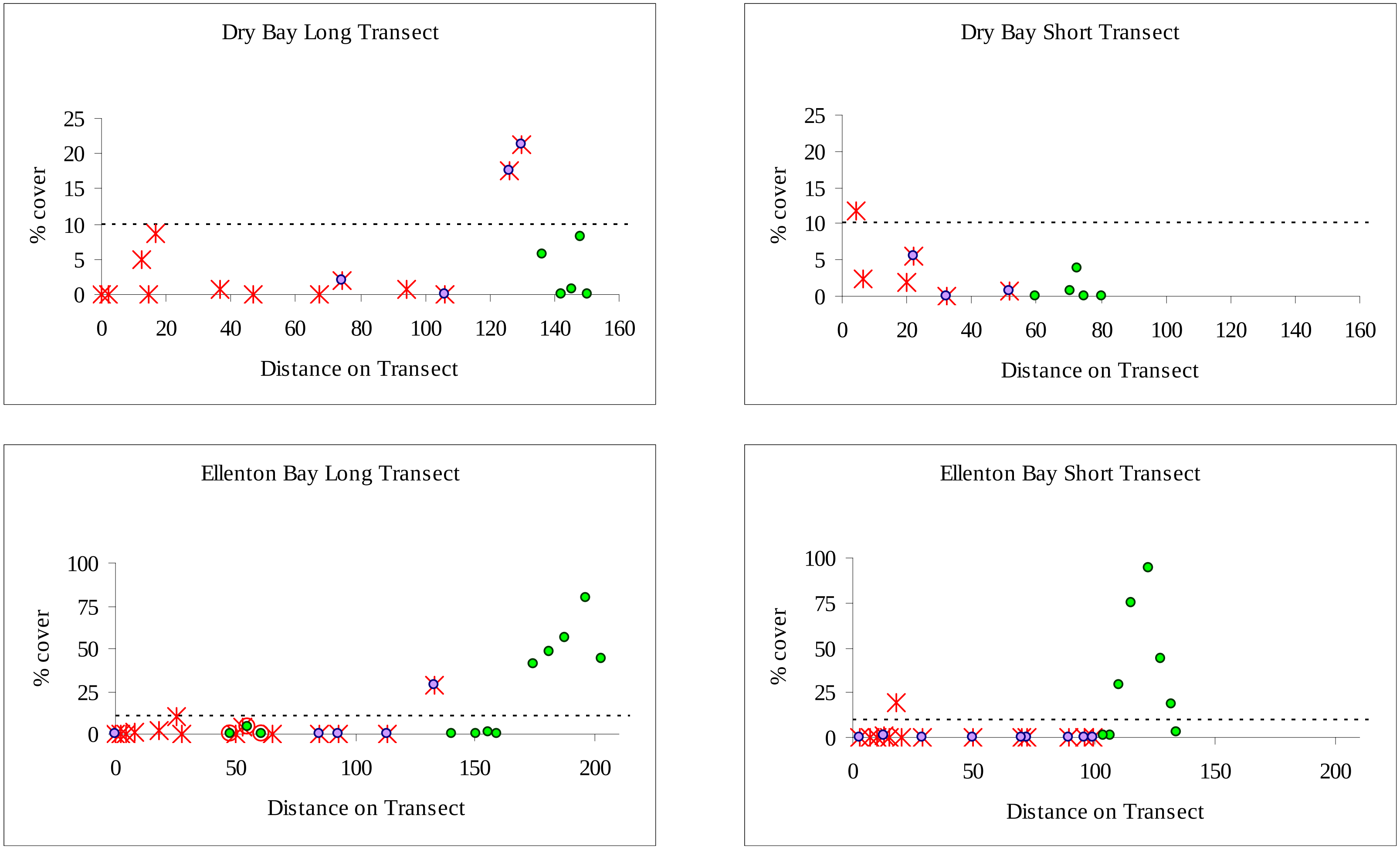


Figure 3.6. Prediction of graminoid species distribution based on distribution limit combination. Green circles show plots where the 4-year median water depth and the C:N criteria were both met. Green circles with red rings show plots where only the 4-year median water depth was met. Red stars with purple circles show plots were only the C:N ratio was met. Red Stars show plots were no criteria were met.

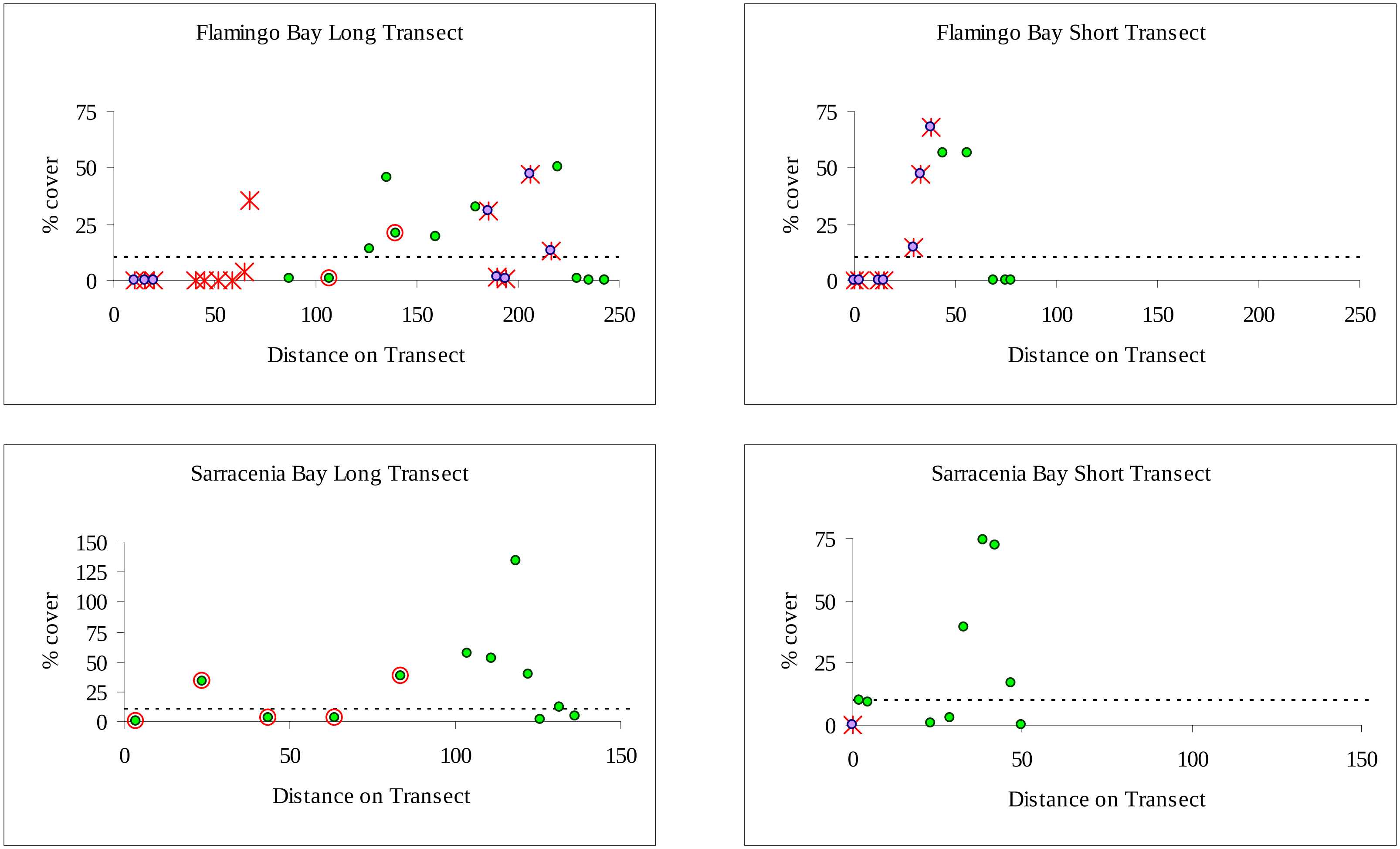


Figure 3.6. (continued)

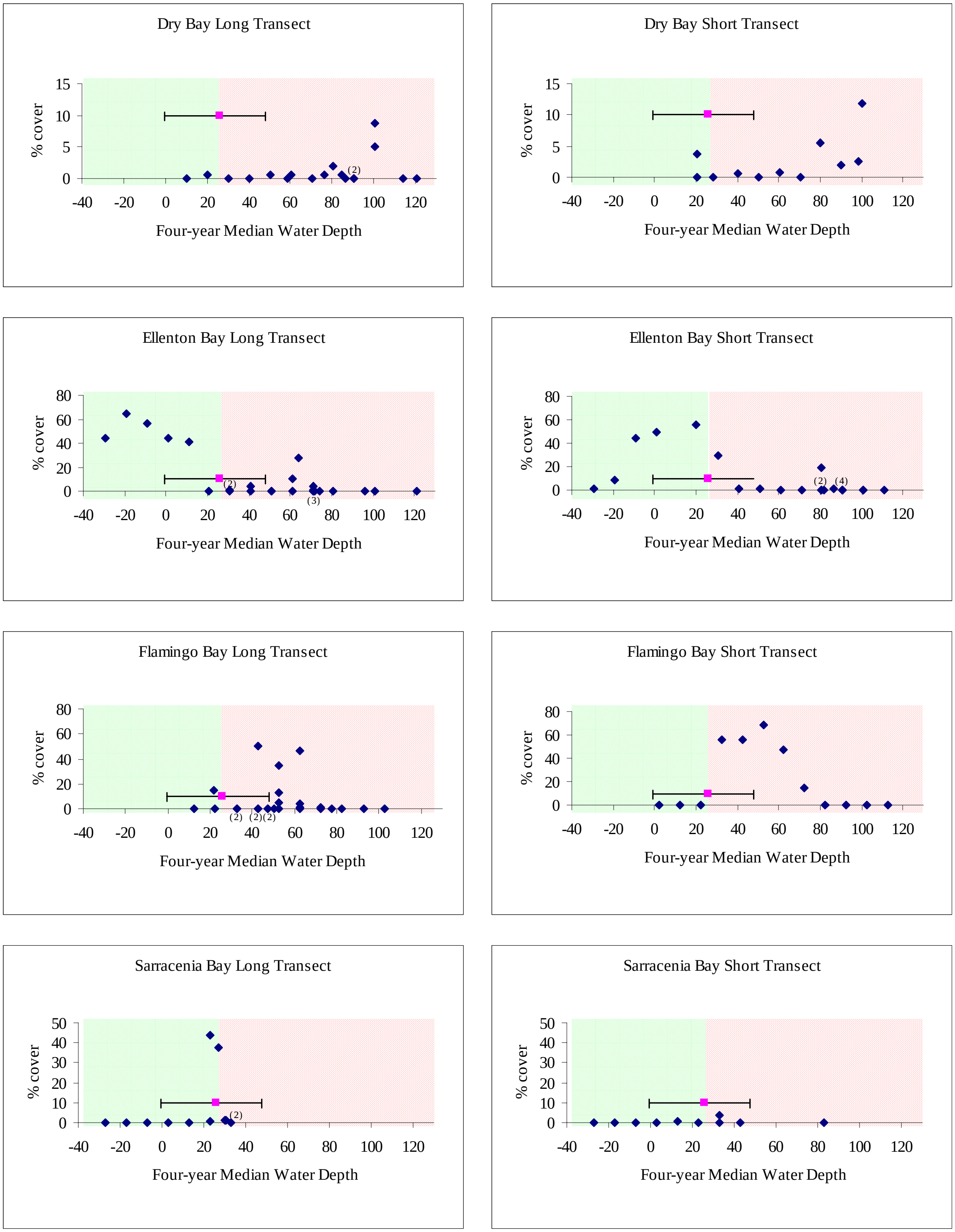


Figure 3.7. Relationship between *Panicum hemitomon* cover and the 4-year median water depth. Plant presence is expected in the green area and not expected in the red. The estimated distribution limit is shown with fiduciary limits.

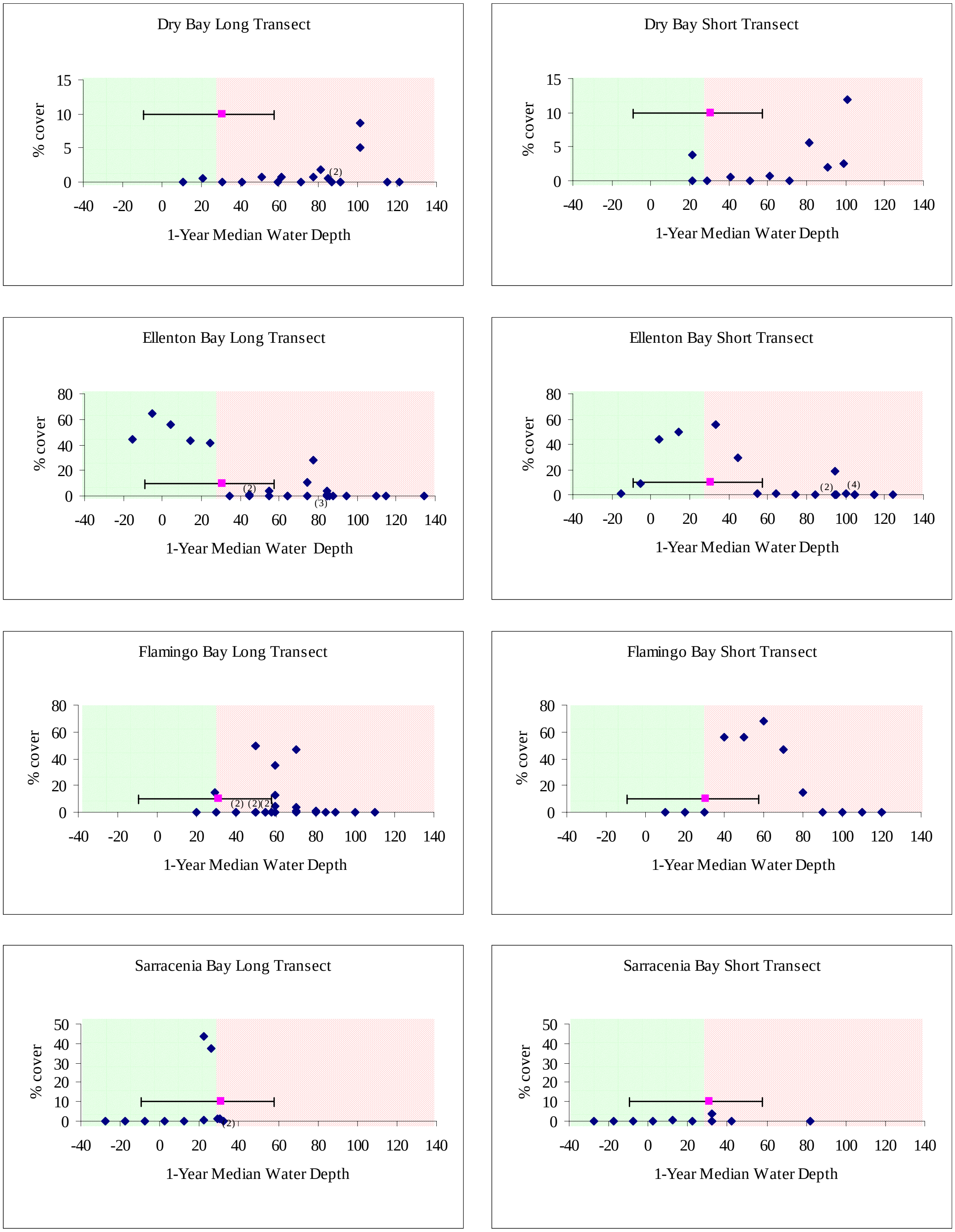


Figure 3.8. Relationship between *Panicum hemitomon* cover and the 1-year median water depth. Plant presence is expected in the green area and not expected in the red. The estimated distribution limit is shown with fiduciary limits.

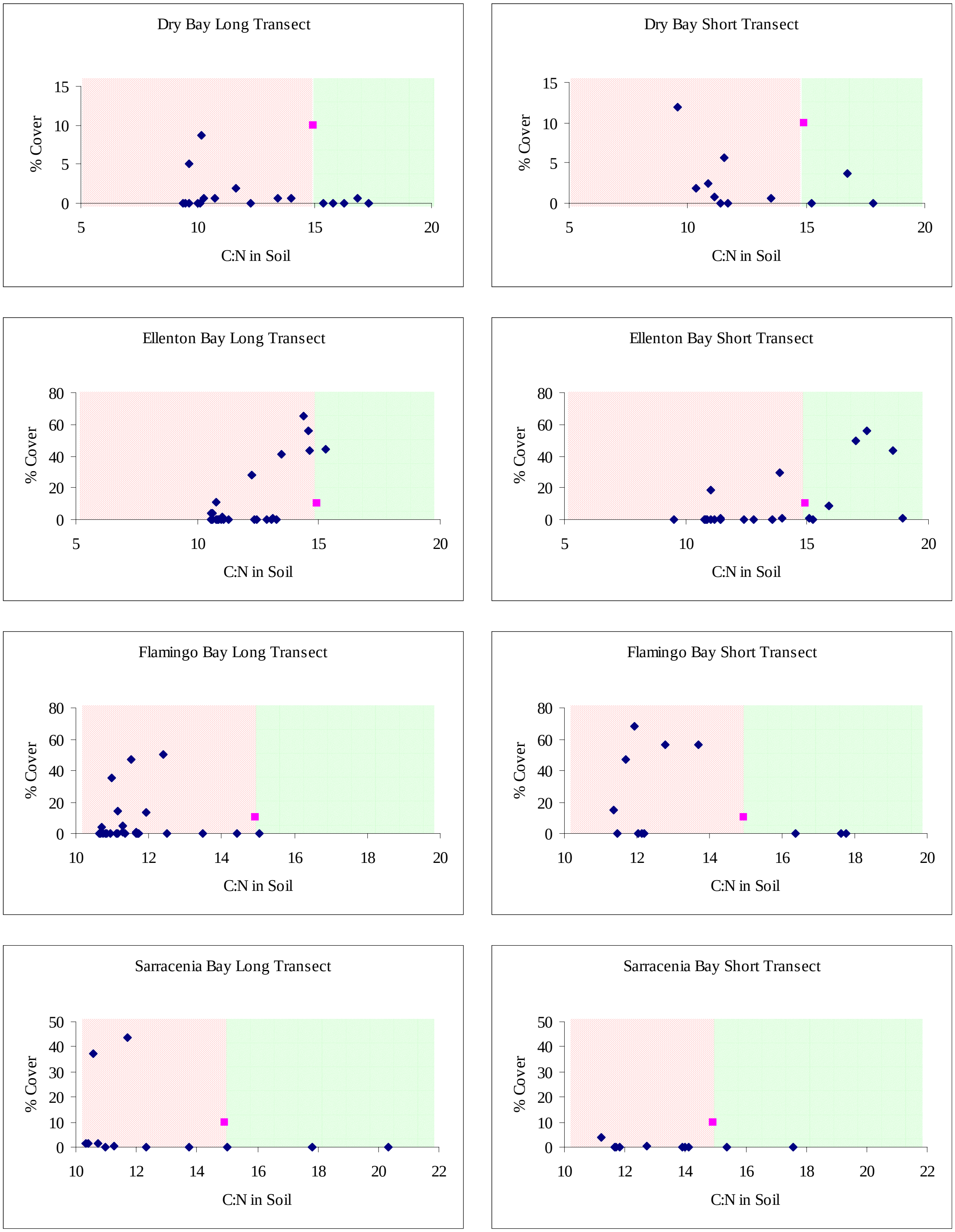


Figure 3.9. Relationship between *Panicum hemitomon* cover and the C:N ratio. The estimated distribution limit is shown; fiduciary limits are not able to be calculated.

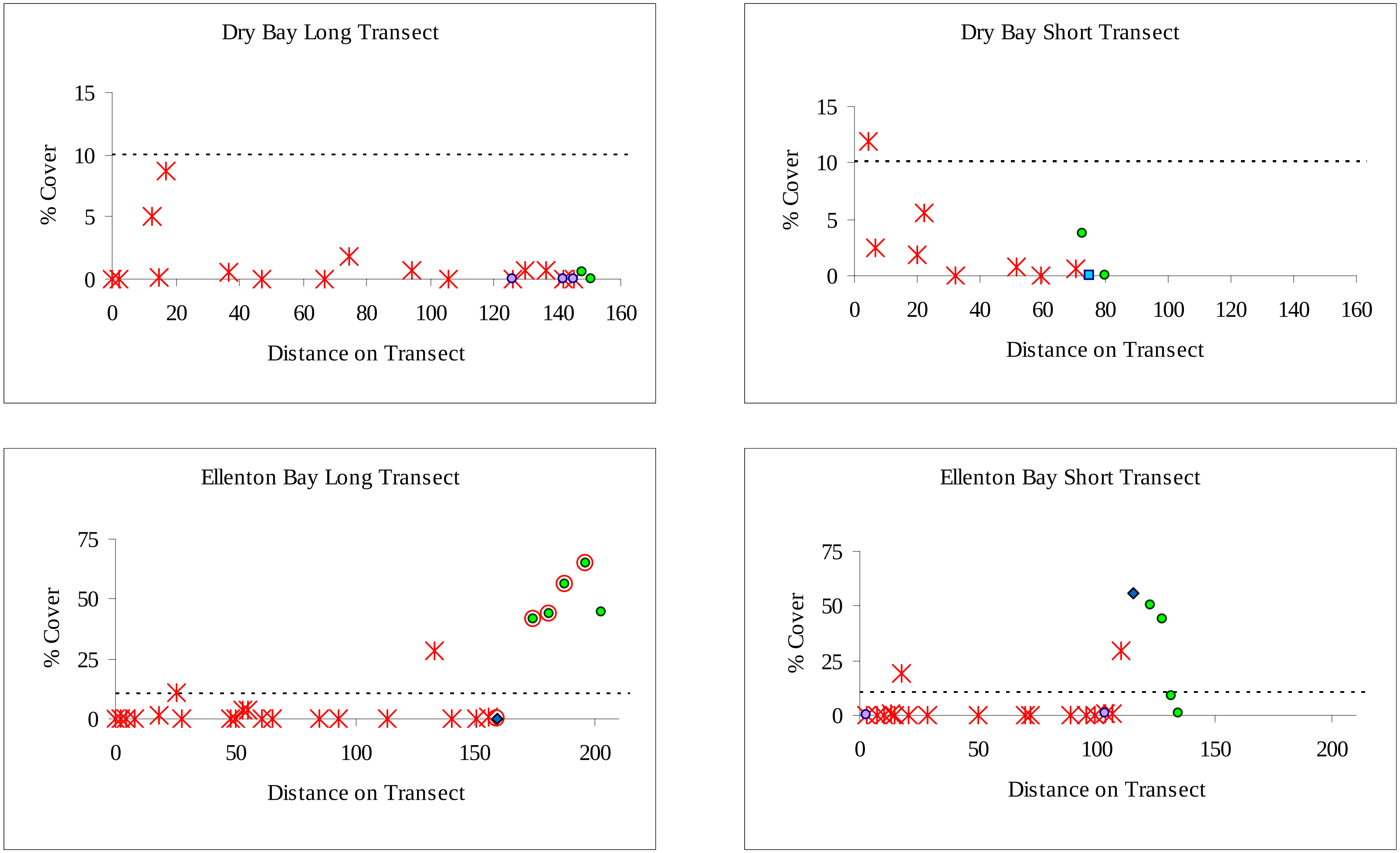


Figure 3.10. Prediction of *Panicum hemitomon* distribution based on distribution limit combination. Green circles show plots where all criteria were met. Green circles with red rings show plots where only the water depth criteria were met. Blue squares show plots where the 1-year median water depth and C:N ratio criteria were met. Blue squares with red rings show plots where only the 1-year median water depth criterion was met. Dark blue diamonds show plots where the 4-year median water depth and C:N ratio criteria were met. Dark blue diamonds with red circles show plots where only the 4-year median water depth criterion was met. Red stars with purple circles show plots where only the C:N criterion was met. Red stars show plots where no criteria were met.

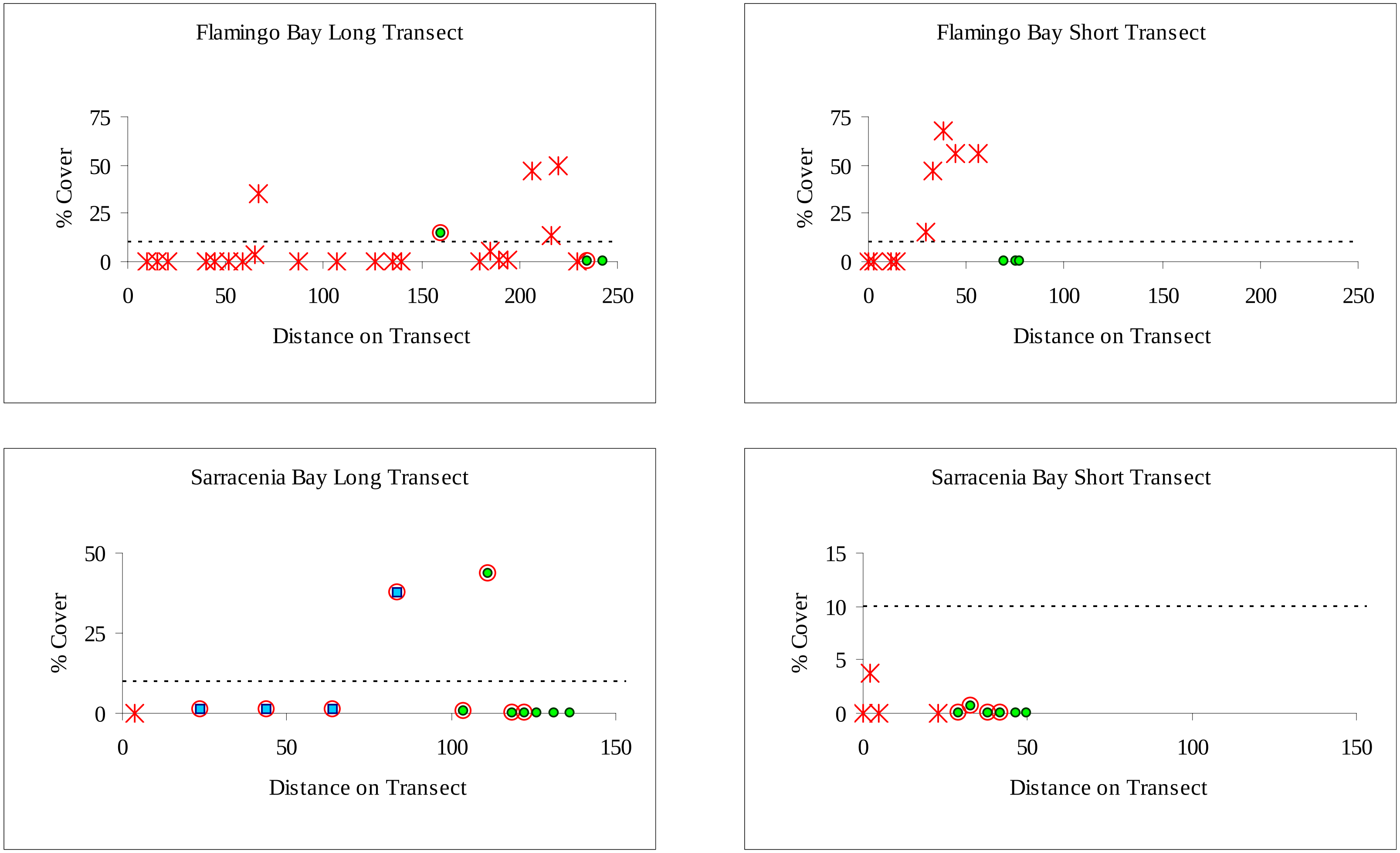


Figure 3.10. (continued)

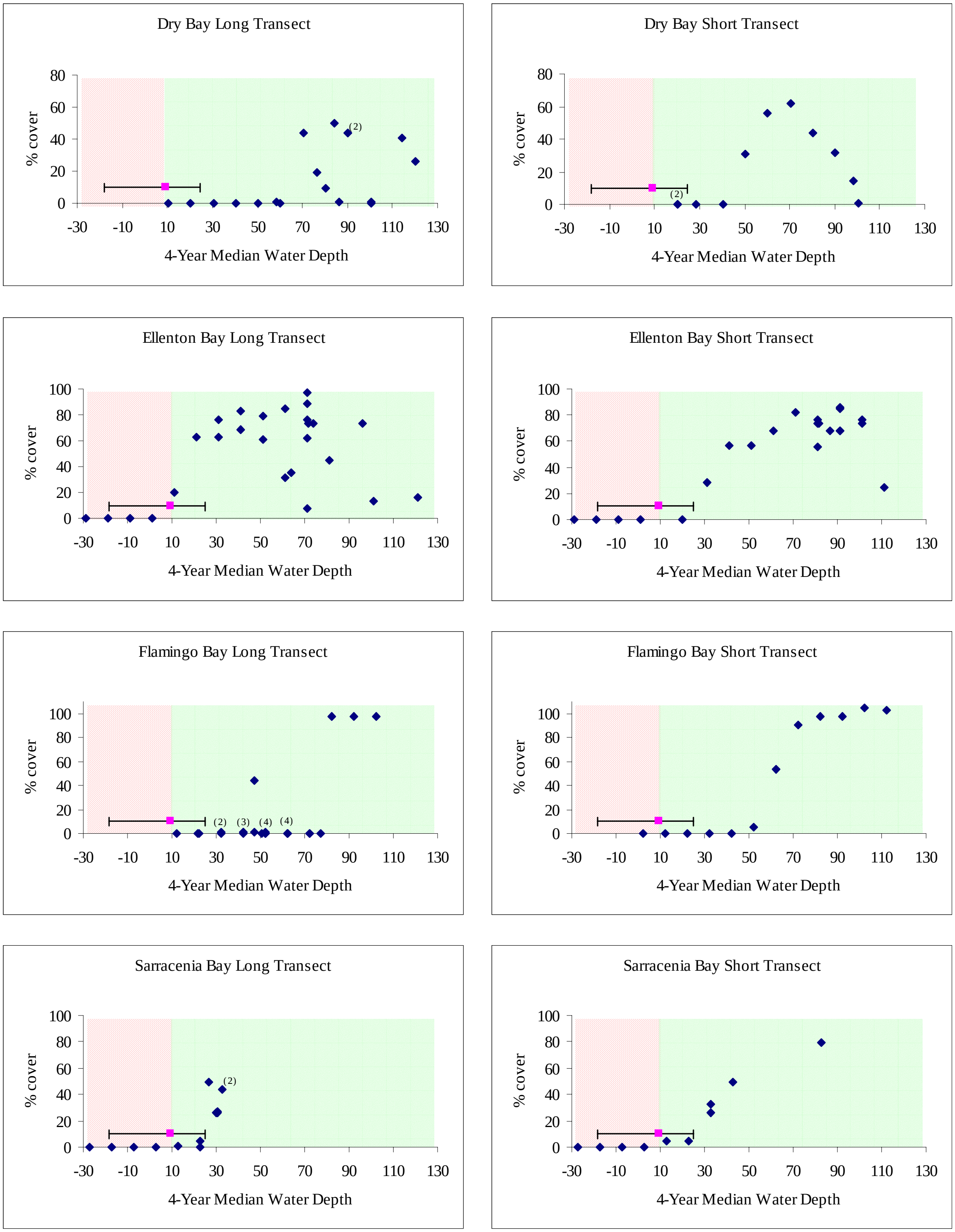


Figure 3.11. Relationship between floating-leaved species cover and the 4-year median water depth. Plant presence is expected in the green area and not expected in the red. The estimated distribution limit is shown with fiduciary limits.

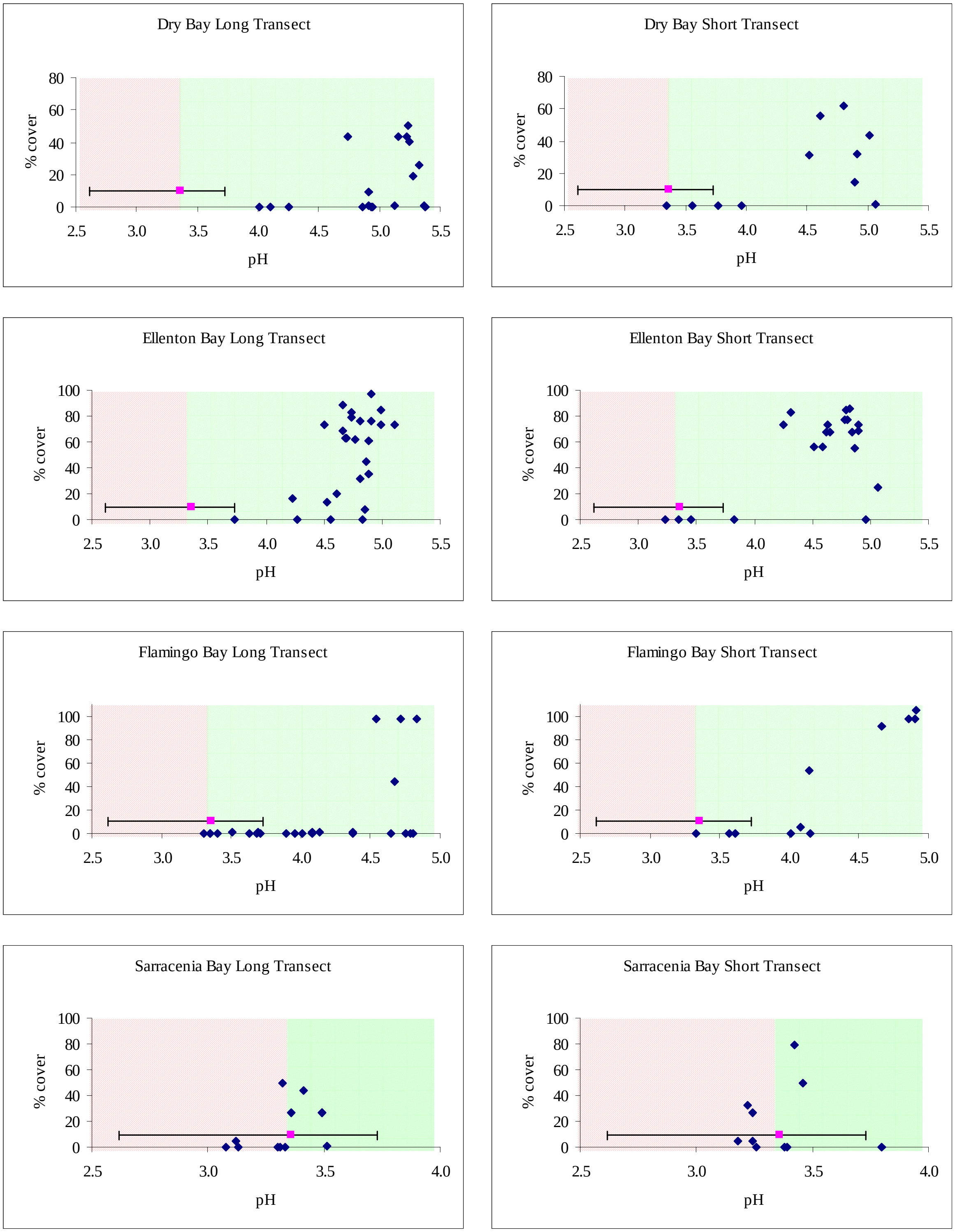


Figure 3.12. Relationship between floating-leaved species cover and soil pH. The estimated distribution limit is shown with fiduciary limits.

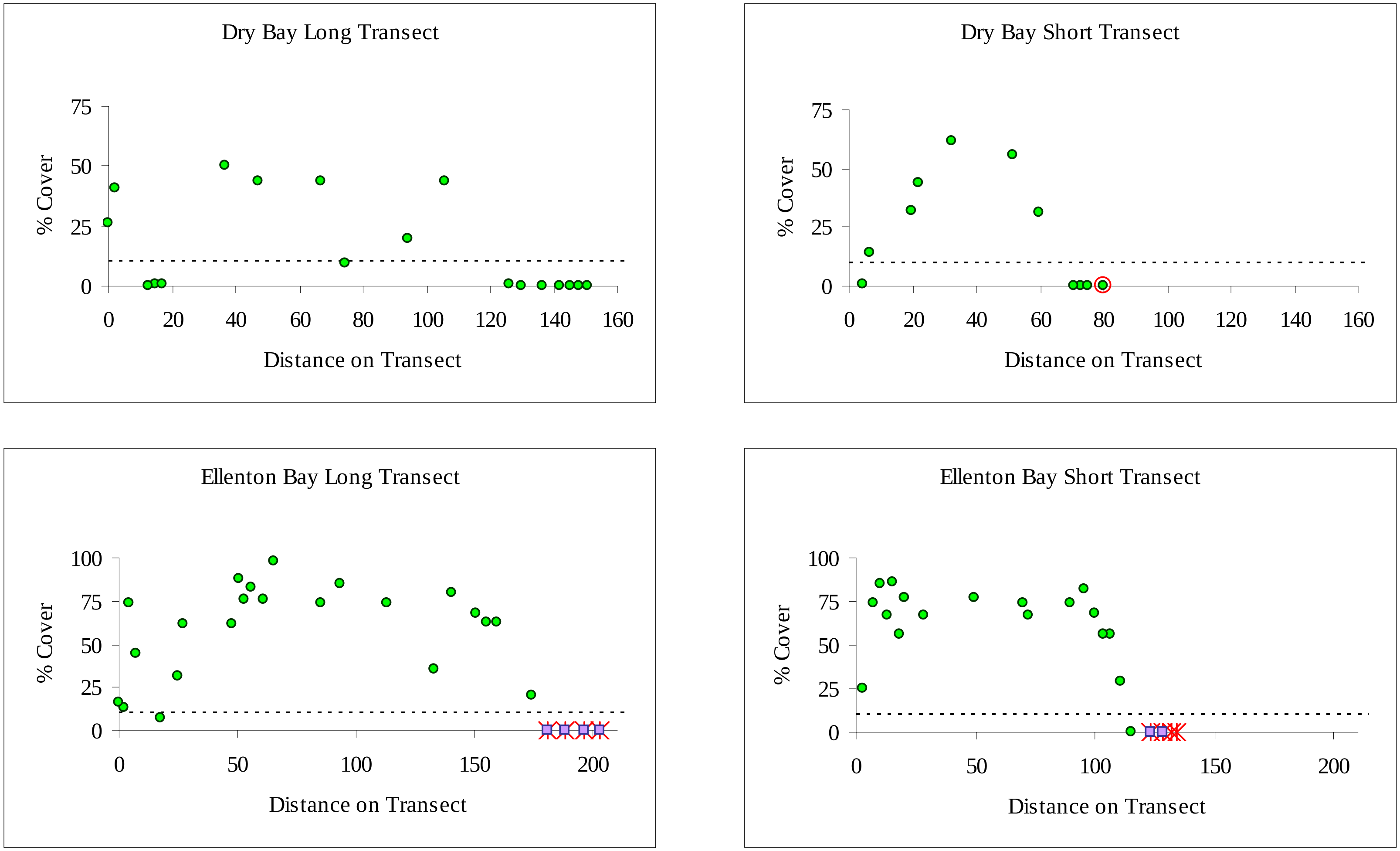


Figure 3.13. Prediction of floating-leaved species distribution based on distribution limit combination. Green circles show plots where both the 4-year median water depth and the pH criteria were met. Green circles with red rings show plots where only the 4-year median water depth criterion was met. Red stars with purple squares show plots where only the pH criterion was met. Red stars show plots where neither criteria was met.

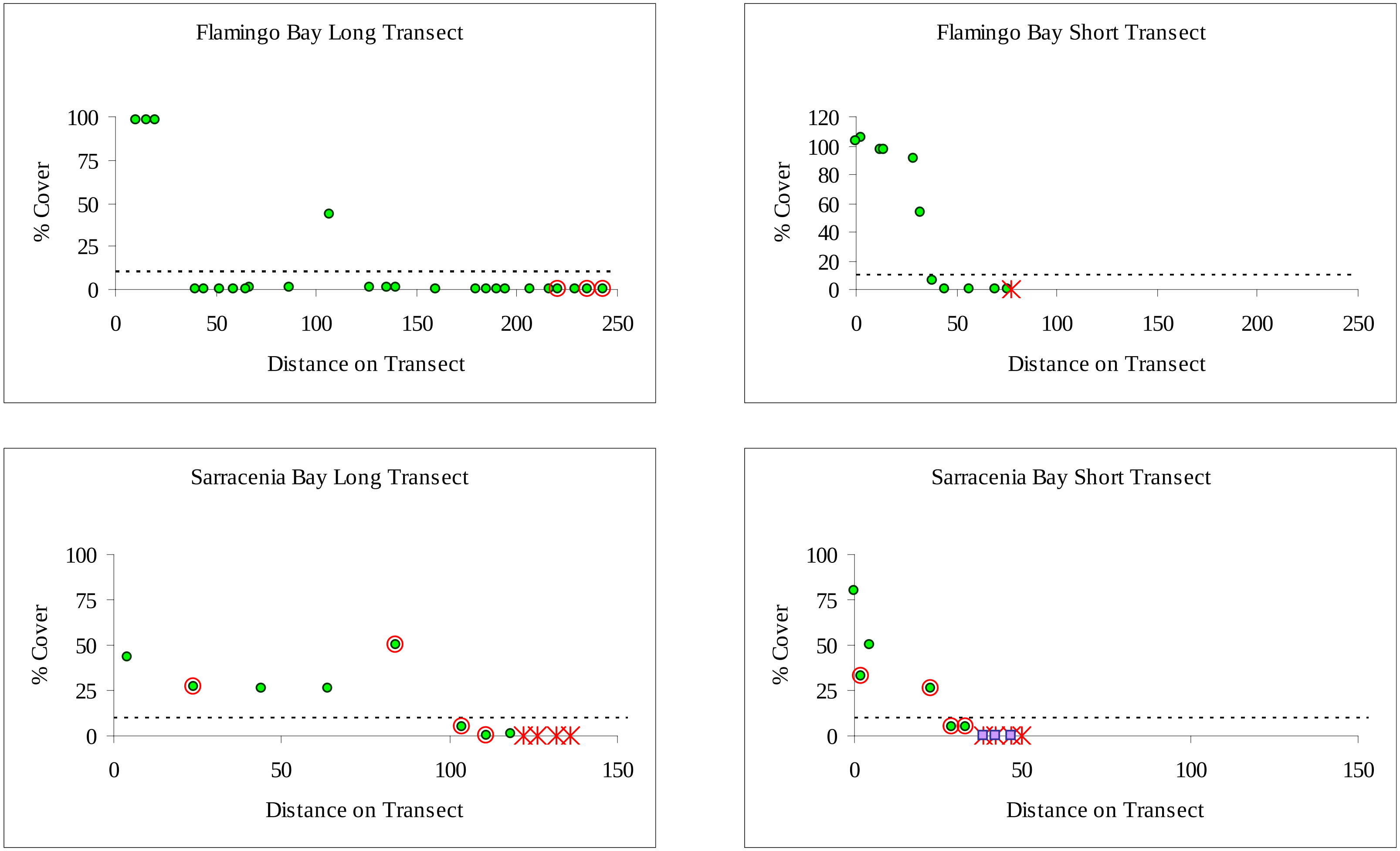


Figure 3.13. (continued)

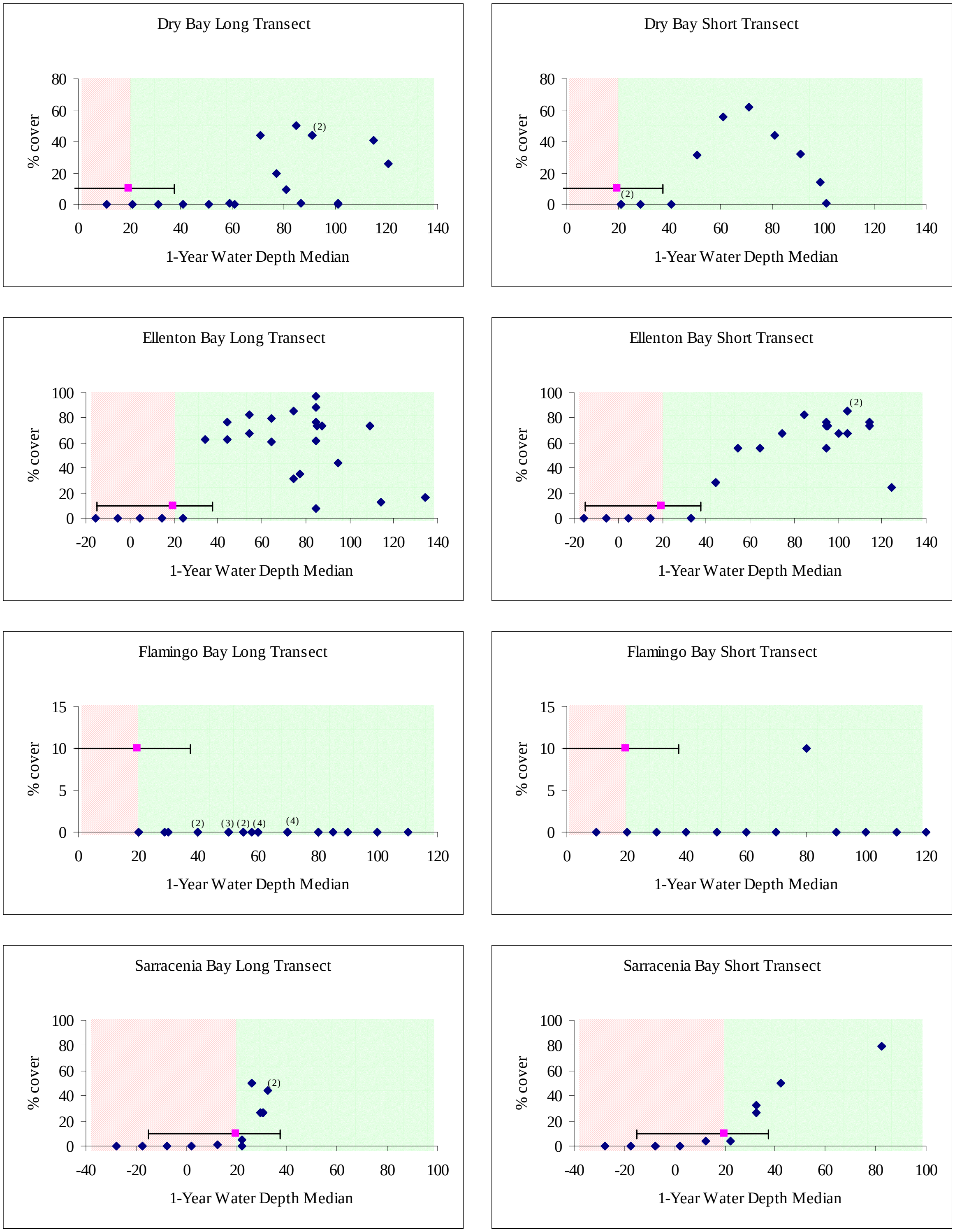


Figure 3.14. Relationship between *Nymphaea odorata* cover and the 1-year median water depth. The estimated distribution limit is shown with fiduciary limits.

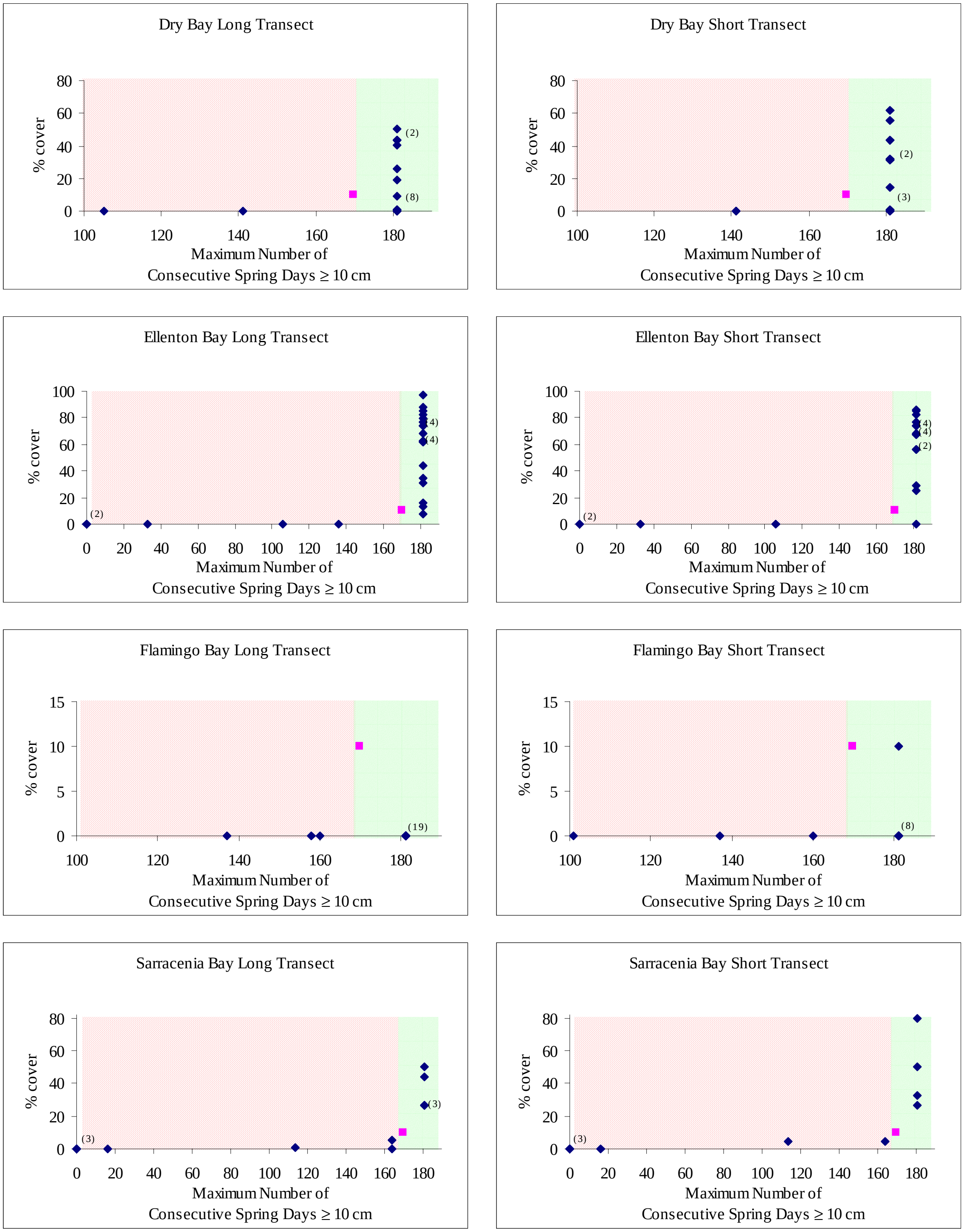


Figure 3.15. Relationship between *Nymphaea odorata* cover and the minimum of 170 consecutive number of spring days with 10 cm or more flooding. The estimated distribution limit is shown; fiduciary limits were not able to be calculated.

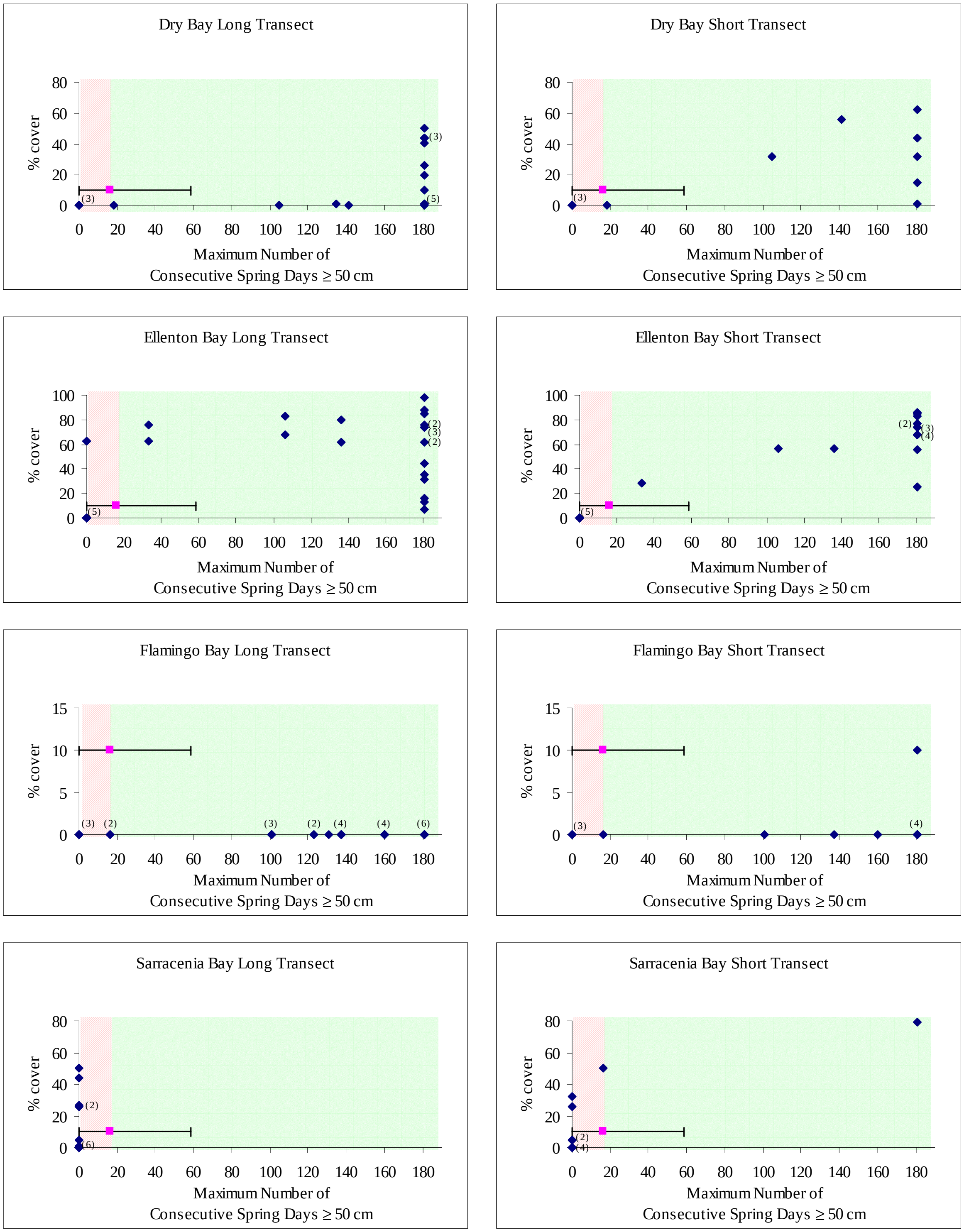


Figure 3.16. Relationship between *Nymphaea odorata* cover and the minimum of 16 consecutive number of spring days with 50 cm or more flooding. The estimated distribution limit is shown with fiduciary limits.

Figure 3.17. Relationship between *Nymphaea odorata* cover and available soil water. The estimated distribution limit is shown with fiduciary limits.

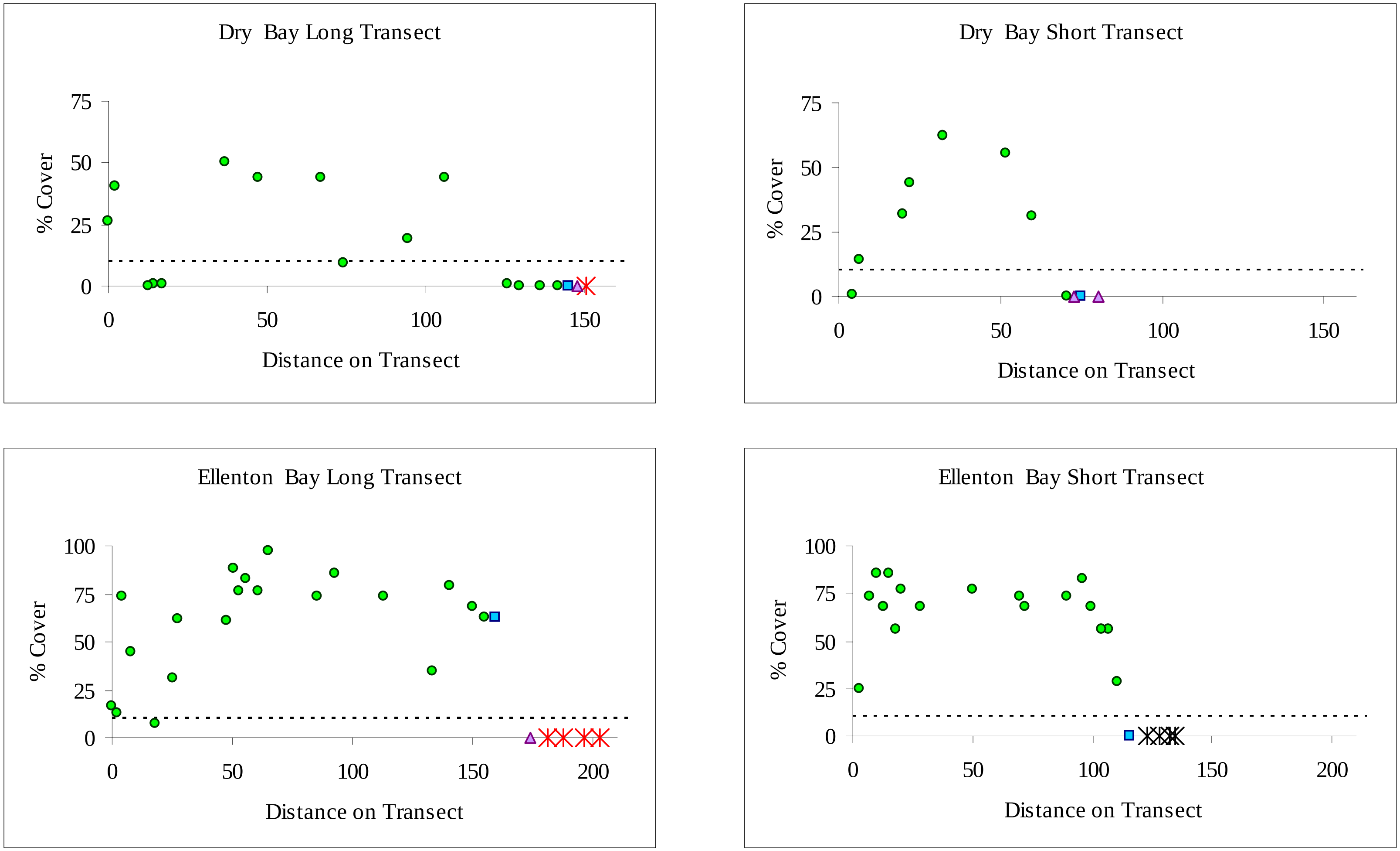


Figure 3.18. Prediction of *Nymphaea odorata* distribution based on distribution limit combination. Green circles met all water criteria. Blue squares met criteria based on the annual median water depth and the maximum number of consecutive number of days with 10 cm or more water. Purple triangles met the 1-year water depth criterion. Red stars and black stars met no water depth criteria. All plots met the available soil water criterion except black stars.

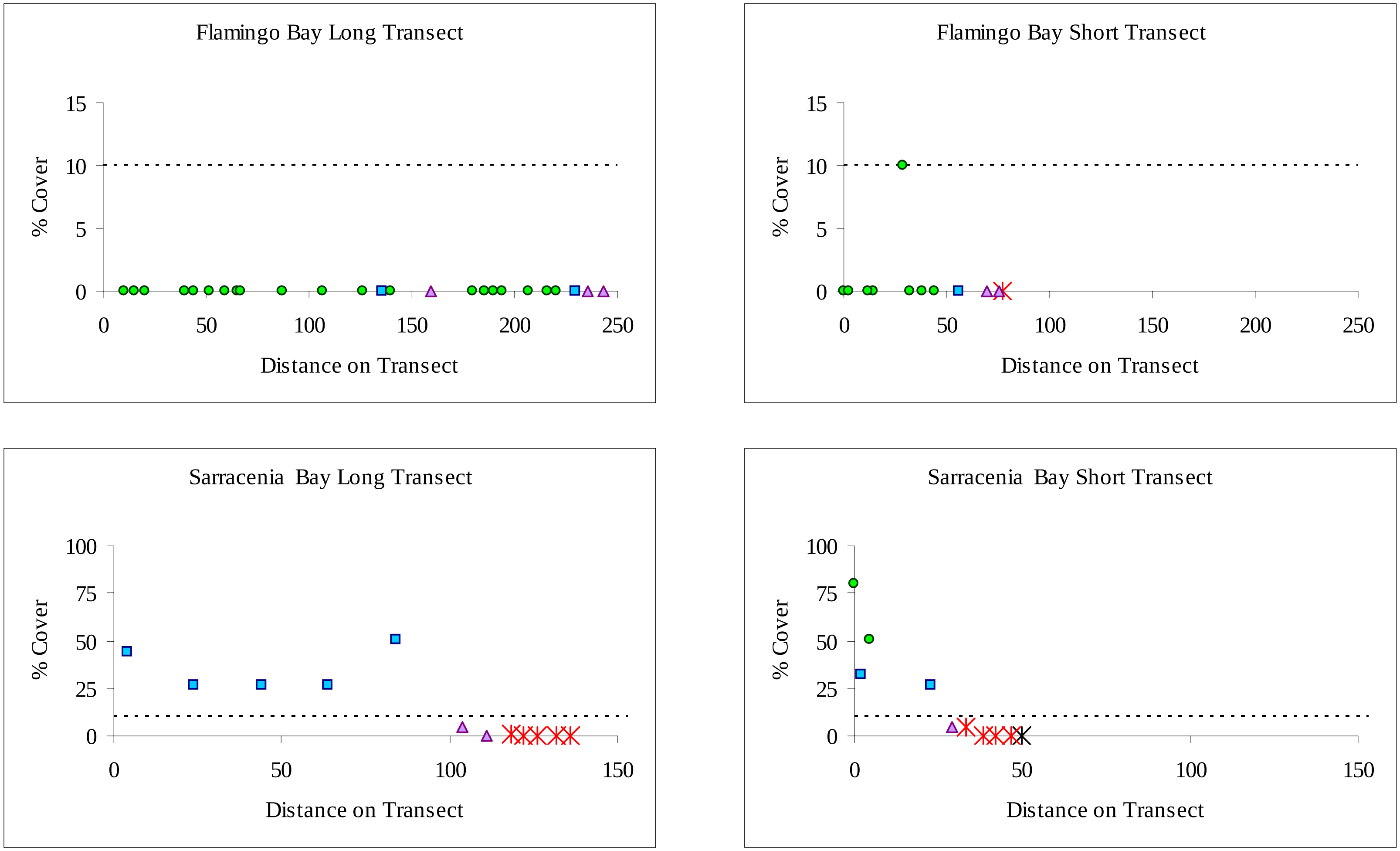


Figure 3.18. (continued)

CHAPTER 4

CONCLUSIONS

Carolina bay wetlands are unique systems, valuable as both natural and cultural resources. They are not only unusual features, cryptic as to their origins, but if better appreciated could be a cherished symbol of southeastern natural heritage due to their endemism to the area as well as their role as a haven for rare species and unique wildlife. The considerable amount of historic damage and destruction of these bays, coupled with ever-increasing development pressures, creates an urgent need for their protection and restoration. Unlike other wetland systems where creation might be attempted, Carolina bays are irreplaceable due to their unique geomorphology.

The recent trend in attempting to understand the processes that create assemblages of species will certainly assist in the protection of bays by enabling the management and/or restoration of bays so that they might recover from past damages. However, more detailed knowledge of the specific species that inhabit these systems is needed in order to guide restoration projects along specific trajectories. The goal of this study was to provide information on reference Carolina bays for use in restoration projects. Specific objectives were to 1) document soil characteristics in Carolina bays and determine if these characteristics form spatial gradients within bays, 2) determine specific, quantifiable, environmental variables that could be used to predict the distributions of wetland plants, and 3) determine specific values of these variables that could be used as indicators of the limits of plant distributions.

Significant soil gradients of % carbon (C), % nitrogen (N), % phosphorus (P), pH, % silt, % clay, and available soil water were found such that values were higher towards the bay centers. Gradients of C:N ratio and % sand were found with values that were higher towards the bay rims. These gradients can potentially affect and/or be caused by bay hydrologic condition as well as plant distributions and organic matter inputs. Successful restoration of Carolina bays must take these soil gradients and potential gradient-forming processes into account.

Several environmental characteristics were found to be significantly related to the distributions of graminoid species, floating-leaved species, and the dominants *Panicum hemitomon* and *Nymphaea odorata*. Not surprisingly, variables associated with the depth, duration, and/or timing of flooding were found to be related to the distributions of these groups and species. In addition, the C:N ratio, soil pH, and soil water availability were found to relate to plant presence in some cases. The distributions of floating-leaved species and *N. odorata* could to be explained to a considerable extent, in part due to strong relationships with the water variables. Even when isolated from interaction effects, specific values of these variables were estimated that predicted the distributions of these types of plants quite well, especially when considered in concert with each other. Due to the complex nature of the effects and interactions of biotic and abiotic influences on plant communities, only a relatively small amount of the distribution of graminoids and *P. hemitomon* could be explained and further exploration is necessary for these species.

Continued investigation into quantifiable distribution limits associated with a variety of environmental characteristics could be used to model plant distributions effectively and improve the outcome of restoration projects. Where restoration goals include the creation of areas of specific habitat types, distribution limits could guide the manipulation of the environmental characteristics for these areas. Similar use of distribution limits could aid in designing or protecting areas for endangered species. The use of such quantifiable values will greatly improve the planning of restoration projects and enhance the likelihood of success.

APPENDIX

Appendix: Species occurrences and cover ranges in Carolina bays

Dry Bay

	Average Cover	Max Cover	# plots observed
Herbaceous Species			
Nymphaea odorata	17.87	61.88	18
Utricularia (*purpurea, fibrosa*)	6.47	28.75	20
Juncus effusus	1.77	20.63	6
Panicum hemitomon	1.59	11.88	19
Lemna valdiviana	0.41	9.45	8
Smilax rotudifolia	0.34	8.13	3
Sagittaria stagnorum	0.13	3.75	1
Ampelopsis arborea	0.07	0.65	3
Bidens discoidea	0.02	0.63	2
Woody Species			
Cephalanthus occidentalis	0.43	4.38	8
Taxodium distichum	0.11	1.25	3
Nyssa sylvatica var. *biflora*	0.06	1.25	2
Quercus phellos	0.04	0.63	2
Acer rubrum	0.04	0.63	2
Liquidambar styraciflua	<0.01	0.03	1
Unknown	0.21	3.75	1

Appendix (continued)

Ellenton Bay

	Average Cover	Max Cover	# plots observed
Herbaceous Species			
Nymphaea odorata	49.80	97.50	38
Panicum hemitomon	10.58	65.00	24
Utricularia (*purpurea*, *fibrosa*)	4.79	31.88	34
Panicum verrucosum	1.13	43.75	3
Leersia hexandra	0.47	18.80	3
Brasenia schreberi	0.42	20.00	1
Rhexia mariana var. *mariana*	0.25	10.00	3
Eupatorium capellifolium	0.18	2.50	7
Hydrocotyle ranunculoides	0.12	4.38	2
Hydrocotyle verticillata	0.09	3.75	2
Juncus effusus	0.09	3.75	2
Triadenum walteri	0.05	1.88	4
Polygonum hirsutum	0.03	0.63	2
Carex albolutescens	0.01	0.63	1
Fuirena pumila	0.01	0.63	1
Habenaria repens	0.01	0.63	1
Juncus acuminatus	0.01	0.63	1
Solidago fistulosa	0.01	0.63	1
Fuirena breviseta	<0.01	0.05	1
Galium tinctorium var. *tinctorium*	<0.01	0.03	1
Woody Species			
Decodon verticillatus	3.88	51.88	11
Pinus taeda	0.05	1.25	2
Acer rubrum	0.03	1.25	3
Diospyros virginiana	0.01	0.63	1
Unknowns (6)	0.34	11.25	6

Appendix (continued)

Flamingo Bay

	Average Cover	Max Cover	# plots observed
Herbaceous Species			
Brasenia schreberi	22.97	97.50	12
Panicum hemitomon	11.13	68.13	16
Pontederia cordata	5.88	64.38	10
Leersia hexandra	2.42	32.50	9
Utricularia (*purpurea, fibrosa*)	2.40	19.38	9
Eleocharis sp.	2.28	41.25	2
Lemna valdiviana	2.05	31.88	10
Sagittaria stagnorum	1.30	17.50	9
Bacopa caroliniana	1.13	29.38	6
Bidens discoidea	0.81	8.13	12
Smilax rotudifolia	0.78	20.00	3
Nelumbo lutea	0.47	7.50	5
Nymphoides cordata	0.42	11.88	5
Rotala ramosoir	0.34	5.00	6
Nymphaea odorata	0.27	10.00	1
Hibiscus moscheutos	0.25	3.75	4
Eupatorium capellifolium	0.02	0.65	1
Myriophyllum sp.	<0.01	0.03	1
Polygonum hydropiperoides	<0.01	0.03	1
Woody Species			
Cephalanthus occidentalis	0.07	0.63	4
Pinus taeda	0.02	0.65	1
Nyssa sylvatica var. *biflora*	0.02	0.63	1
Unknowns (3)	0.05	0.68	3

Appendix (continued)

Sarracenia Bay

	Average Cover	Max Cover	# plots observed
Herbaceous Species			
Nymphaea odorata	17.07	79.38	13
Panicum spretum	8.55	50.00	8
Scleria reticularis	7.05	79.38	7
Panicum verrucosum	4.37	56.25	12
Panicum hemitomon	4.10	43.75	10
Eleocharis equisetoides	2.05	32.50	6
Centella asiatica	1.88	37.50	2
Viola lanceolata	1.42	20.63	5
Lachnanthes caroliniana	1.02	13.75	7
Drosera rotundifolia	0.40	5.00	3
Utricularia (*purpurea, fibrosa*)	0.31	5.00	3
Leersia hexandra	0.29	3.78	4
Eleocharis obtusa	0.23	5.00	1
Panicum virgatum	0.07	0.65	1
Eriocaulon compressum	0.06	0.63	2
Rhynchospora decurrans	0.06	0.63	2
Rhexia virginica	0.03	0.65	1
Smilax rotudifolia	0.03	0.63	1
Croton elliottii	<0.01	0.05	1
Woody Species			
Pinus taeda	0.14	1.88	3
Diospyros virginiana	0.09	0.63	3
Nyssa sylvatica var. *biflora*	0.03	0.63	1
Unknowns (4)	2.14	26.25	9