

**PREDICTING FRESHWATER AND OLIGOHALINE TIDAL MARSH VEGETATION
COMMUNITIES**

Zachariah C. Welch

and

Wiley M. Kitchens

Draft Report Submitted to
U.S. Army Corps of Engineers

Solicitation: W91278-06-T-0012

INTRODUCTION

The productivity and value of tidal freshwater-oligohaline marsh communities to fish and wildlife have been well documented (Odum *et al.* 1984, Latham 1990, Pearlstine *et al.* 1990, Gough and Grace 1998, Mitsch and Gosselink 1993). Despite their importance to downstream fisheries and estuaries, however, their distribution is much reduced from historical levels. A significant portion of the remaining tidal freshwater marshes left in the southeastern U.S. lies within the braided channels of the lower Savannah River deltaic marsh complex. Many studies have focused on the freshwater and brackish marshes of this area since the 1980's (see Kitchens 2003 for compilation), specifically their distribution in response to downstream modifications for shipping industries. Previous studies have focused on documenting community shifts in response to a disturbance, which usually takes several years to accomplish and puts managers in a reactive position, rather than being proactive or adaptive. In the late 1990's, efforts began to provide managers with a predictive tool, capable of assessing impacts to sensitive freshwater and brackish marsh communities in the proposal phase, rather than several years after its inception. This predictive model would eliminate the time lag associated with determining the impacts of a given activity and would help to identify those proposals with potentially serious impacts before being implemented.

The goal of this study was to develop that model by documenting vegetation communities throughout the tidal freshwater and brackish range (roughly 0-7ppt) of the lower Savannah River, identifying the environmental conditions influencing their distribution, and then predicting community distributions based on the underlying gradients. Specifically, the goal was to build a predictive engine based on quantitative, ecologically meaningful measures that would be readily adaptable to GIS applications, and when coupled with predictive hydrologic models could characterize current and future conditions based on climatic or management changes (Kitchens 2003).

One approach in predicting species distributions is to estimate the abundance of a given species and to correlate that to a suite of easily measured habitat variables. The most common methods of estimating abundance are percent cover, frequency, and presence-absence of species within given sample units. While these methods are speedy, non-destructive, repeatable, and allow for a larger sample size due to decreased labor costs, the results can be difficult to interpret ecologically. The presence or absence of a specific stem in a sample has little relevance to the fauna using that area for cover or forage, or to the productivity of that community in terms of litter production, herbivory, nutrient uptake, etc. The percentage of an area a given species covers can vary considerably between observers, habitat structure (canopy vs. sub-canopy), and environmental conditions (high or low water). Rather than using subjective estimates of abundance, a combination of stem density and above-ground biomass collections give representative, quantitative measures of composition, dominance, abundance, etc. While considerably more labor intensive, destructive, and limited in scope due to processing times, these samples represent actual habitat structure and give good inference as to the ecological value of the sampled community.

Furthermore, focusing on individual species and their responses to various conditions ignores competitive effects, mutualisms, and other complex interactions of the community that individual species comprise. The concept of community is absolutely fundamental in plant ecology (Kitchens 2003). The community level is where populations and individuals of plant species can be identified and grouped together and related to environmental variables

characterizing areas ranging from 0.25m² to landscapes (Kent and Coker, 1992). Throughout this paper communities will be defined and discussed, and their compositions and distributions will be simplified to a few species and environmental thresholds for modeling purposes. However, it is important to remember that each of these simplified communities is representative of the complex and diverse habitat structure that comprises the tidal marsh systems.

METHODS

Model Development

Statistical modeling in plant ecology consists of three major components; an ecological model, a data model, and a statistical model (Austin 2002). The ecological model consists of the knowledge of the system under study, in this case, the ecology and functionality of freshwater and brackish tidal marshes. The data model consists of decisions on data collection, i.e. how, when, where and what to collect. The statistical model involves selection of appropriate statistical procedures based on assumptions, error functions, and compatibility with the data collected. The challenge is to combine all three models into one coherent predictive engine. For example, without a thorough knowledge of the ecology of the system, of what the driving factors are in determining species distributions and community compositions, one cannot make sound judgments about the scale of data collection, where to collect data, and what sampling techniques to use. Austin (2002) argues that a limiting factor in using statistical modeling to predict species distributions is ecological knowledge. The biggest discord in ecological literature, however, is between the data model and the statistical model. Often times sampling techniques are not compatible with chosen statistical models or assumptions about data distributions are violated. Most of the data collected in community studies are non-normal, in that species responses to environmental gradients are often skewed, polymodal, and the species optimum often even lies outside the sampled range (McCune and Grace 2002). The techniques designed to deal with the complex nature of these data are few but increasing in popularity and use (Clarke 1993, Vayssières et al. 2000, De'ath 2002).

Many studies have attempted to describe species responses to environmental gradients (Austin 1987, Austin et al. 1990, Austin et al. 1994, Oksanen et al. 1988, Huisman et al. 1993), but the complexity of the problem has defied a general satisfactory solution (McCune and Grace 2002). Most commonly used statistical techniques in community studies have underlying assumptions about linear or unimodal relationships, or use distance measures that are only weakly correlated with ecological distance, but these techniques remain popular (Principle Components Analysis, Correspondence Analysis, Canonical Correspondence Analysis, Discriminate Analysis, Two-Way Indicator Species Analysis (TWINSPAN), etc.). McCune and Grace (2002) describe in great detail the nature of multivariate community data and the incompatibility of many commonly used techniques. All of the analyses used in our model are robust, do not assume multivariate normality, and use appropriate distance measures for multivariate community data when appropriate.

The overall predictive ability of our model depends on the cohesion between our ecological, data, and statistical models. Ecologically, we assumed the primary gradients determining species compositions and distributions in the tidal marshes were salinity and soils characteristics. We also assumed that the soil salinity (interstitial) would be a more direct stressor than river water salinity, and that the salinity gradient of interest was in the freshwater

(<0.5 ppt) to brackish (7.0ppt) range. Our study was designed to sample along the entire gradient of interest, and was stratified within site to account for differences in soils, salinities, flushing rates, elevations, nutrient exchange, etc. between the interior and berm (edge) marsh communities. This design focused our sample efforts on the diverse interior communities (>10m from canals) and avoided the monospecific or even terrestrial berm communities. Our data collection techniques consisted of robust estimates of plant abundance (stem densities and above-ground biomasses), and focused on the peak (June) growing season communities to eliminate seasonal variations. The statistical procedures we selected were all compatible with non-normal data, and the models we chose were favored over other commonly used models (Generalized Linear Models, Generalized Additive Models, Multiple Regressions, etc.) in the ecological literature (Franklin 1998, Vayssieres et al 2000, De'ath 2002, McCune and Grace 2002).

Temporal Scale

Collection efforts for the development of this model began in November of 1999 and ended in June of 2005. This period of study coincided with a watershed drought that lowered river flows to below the 10th percentile for most of 2002. Low river stages began as early as 2000 and continued through 2002, with flows only reaching above the 25th percentile four times during that period. Such low river stages resulted in increasingly saline tides and interstitial salinities peaked at several sample stations during the summer of 2002. The effects of this drought are in manuscript preparation, and it is clear that the community responses varied along the salinity gradient. Our freshest sites did not experience a significant increase in interstitial salinity during the drought and were consequently not affected, while our most saline sites were already dominated by salt-tolerant species and were not significantly affected either. The intermediate areas, however, experienced significant community shifts as those sites had mixed communities of salt-resistant (*Scirpus validus*) and salt-sensitive species (*Eleocharis* spp.) resulting in decreased competition upon salinity increases (Wetzel et al., in prep).

In addition to varied community response, actual salinity changes varied between sites as well, as stations along the Middle River experienced greater salinity changes than those along the Back River, for example. Further, preliminary analyses suggest that community response to increased salinity was very rapid with dramatic changes between consecutive growing seasons at affected sites, while recovery following normal river stages was much slower, even greater than three growing seasons at some locations (Wetzel, et al., in prep). While the marsh communities that exist at any given time are a reflection of both recent and long-term conditions, the purpose of this model was to describe a baseline marsh community from which to predict responses to changing conditions. Such a baseline model would preferably be developed under a prolonged period of average environmental conditions, not during or immediately following historically low river stages. However, the timing of this study gave us an opportunity to describe communities following a period of prolonged low river flows, as well as for a reasonable period of moderate river flows. Therefore, data collection continued for three years after the peak of the drought and for one year beyond the restoration of normal flow. This resulted in a growing season sample representative of drought conditions (June 2002) and of average flow conditions (2005).

Model variables

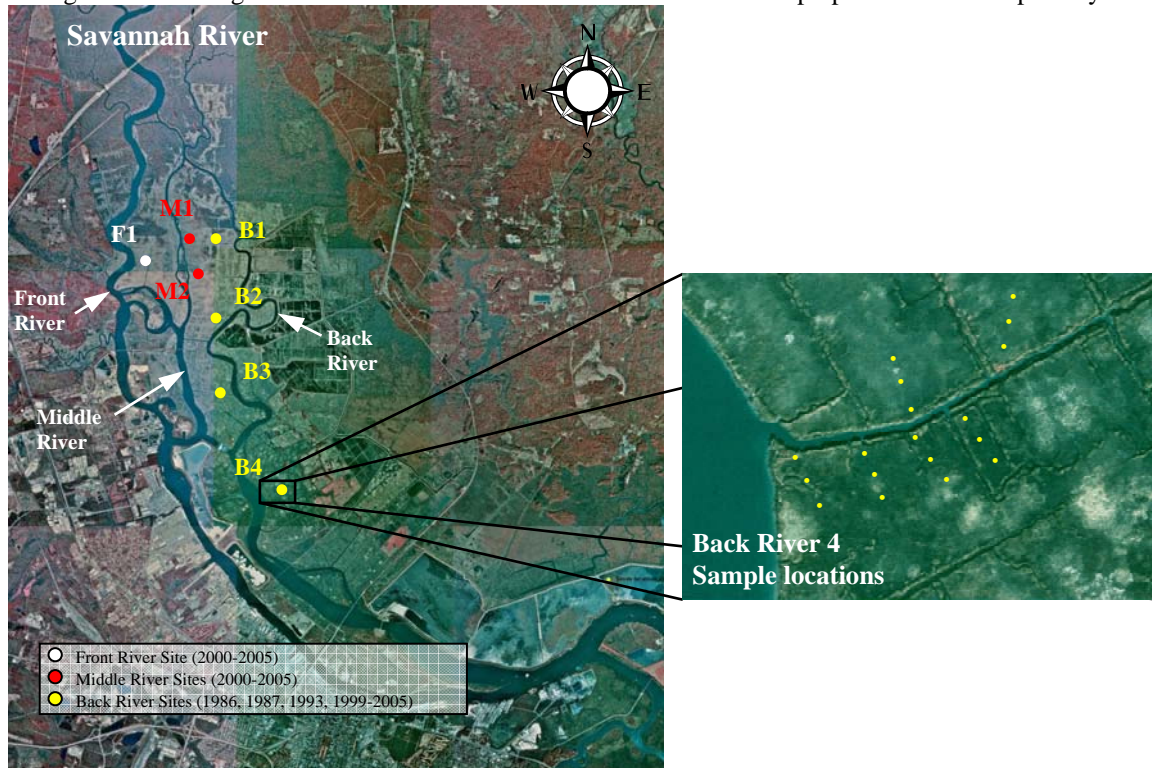
Vegetation

All of the vegetation and soil data collection procedures for this model were described in detail in Kitchens 2003, and will only be briefly touched on here. Seven sites were sampled in June of 2002 and June of 2005, each consisting of six transects oriented roughly parallel to the main river channels and perpendicular to nearest drainage canals (Figure 1). This design produced 126 individual samples stratified across the salinity gradient (inter-site), soils gradient (inter- and intra-site), and from front to back marsh community (inter- and intra-transect). Above-ground vegetation was collected from a randomly placed, 0.25m² quadrat within five meters of each sampling station (126 total), and the stem densities and above-ground, dry biomasses of each species were recorded. Importance values were calculated for each species in each quadrat with the formula:

$$(\text{Relative Biomass} + \text{Relative Density})/2 * 100$$

This produces a value from 0 – 100 that gives a good estimate of species importance within a given quadrat and is not biased towards large, few-stemmed species (e.g., *Typha* spp.) or small, numerous-stemmed species (e.g., *Eleocharis* spp.) (McCune and Grace 2002). This calculation also relativizes the dataset, eliminating the need for transformations typically applied to density or biomass data that can vary by orders of magnitude between species and samples.

Figure 1. Location of sites along the braided channels of the lower Savannah River. Transects within a site were arranged at increasing distances from the river channel and were oriented perpendicular to the primary canal.



Soils

Soil cores were collected from each sampling location in June of 2000 and June of 2001, using cylindrical aluminum corers. These corers measured 7cm in diameter and were used to extract the top 10cm of substrate (Blake and Hartge 1986). After being oven dried to constant weight, bulk densities were determined (Blake and Hartge 1986). Percent of organic content was calculated by loss on ignition of two 1g sub-samples from each core (Chapman and Pratt 1961, Jacobs 1971). We used the average bulk densities and percent organic contents from the 2000 and 2001 samples as soils variables in our models.

Salinities

Interstitial marsh salinities were recorded every 15 minutes using YSI data sondes placed in double-nested PVC wells that were designed to keep surface water out and allow soil water in (Kitchens 2003). One sonde was located at a middle sample station of one transect at each site. While grab salinities from each sample station showed some variability between and within transects, the amount of inter-site variation negated the need for more than one sonde per site. The salinities recorded from each sonde were used for each of the 18 samples at the corresponding site. Salinities from March 1st to October 1st of the year prior to sample event were used to calculate the 90th percentile, mean, and amplitude (max-min) salinities of the previous growing season for each site. For example, the June 2005 sample used the salinity data from March 1st – October 1st of 2004, while the June 2002 sample used data from March 1st – October 1st of 2001. Non-growing season salinities were used in earlier analyses but were less

correlated with community shifts, presumably due to a lower plant response to stresses in the dormant season. Many other salinity variables, including statistics based on 3, 6, 9, 12, 18, and 24 month prior salinities were originally tested for community correlations, and the prior growing-season salinity explained the most variation. Results from the other salinity variables are not included in this report.

Distance to Canal

The entire marsh complex is riddled with the remnants of old, hand-dug drainage canals used to prepare the marshes for rice cultivation prior to the turn of the century. These canals have gradually filled in over the decades and are now only as deep as spring low tides at the intersection of the main river channels. Soils and subsequent vegetation communities tend to differ within a given radius of these canals, due both to their construction and to incoming tides dropping heaviest sediments near the canals. Over time the marshes have leveled at just below high tide elevation, and a general gradient of mineral to organic soils exists as distance from canal increases. To account for this and other potential distance-to-canal correlates (seed dispersal, disturbance) we included a measure of such as a variable in the model.

The distance of each sample point to the nearest drainage creek was determined using ArcGIS software, by overlaying our sample locations onto 1999 Digital Ortho Quarter Quads with 1m resolution and measuring the distance to the closest visually distinct creek in meters.

Analyses

Rare species were removed from the dataset by eliminating those that occurred in less than five percent of the samples. Two transects at the Back River 2 site were also eliminated from our analyses, as aerial photos showed these transects were located in the Middle River watershed and grab salinities showed a poor correlation with the salinity data sonde located on the Back River. The resulting matrices were 120 samples by 31 species for the June 2002 sample, and 30 species for the June 2005 sample.

A hierarchical, agglomerative Cluster Analysis was performed to find groups (or communities) of similar species compositions using the software PCORD 4.20 (McCune and Mefford 1999). Flexible beta (-0.25) linkage and Sorenson distance measures were chosen for their space conserving properties, compatibilities with each other, and their advantages with non-normal data (McCune and Grace 2002). This analysis grouped similar sample units based on species importance values (IV's), using multiple species as a basis for deciding on the fusion of additional groups.

An Indicator Species Analysis was performed for two reasons: 1) to determine the optimum number of clusters for further analysis and 2) to define those clusters in terms of representative species. This analysis uses the proportional IV and frequency of a particular species in a particular cluster relative to its IV and frequency in all other clusters (Dufrene and Legendre 1997). The results are expressed as a percentage, or indicator value, which is a measure of how representative a species is of a particular group. A value of 100 would indicate a perfect representative, a species that was always present in that group and never occurred in any other group. The statistical significance of that value is then evaluated with a Monte Carlo test (1000 permutations), with the null hypothesis being that the value is no larger than expected by chance (McCune and Grace 2002). The corresponding p-values of each species were the

basis for the decision on how many clusters to choose (i.e., the level of clustering that produced the most species with p-values <0.05) (McCune and Grace 2002). The species with low p-values and high indicator values were used as the community descriptors (cluster labels) in future analyses.

Classification and Regression Tree Model (CART)

A CART model (S-Plus Tree Library, De'ath 2002) was used to predict the communities identified by the cluster analysis using the measured environmental variables alone. These models have been applied most often to classify habitats or vegetation communities based on environmental characteristics, resulting in an overall description of how different the groups are, which variables distinguish the groups and a predictive model that can classify new samples into those groups (Urban 2002). This procedure works by recursively partitioning the multidimensional dataset into subsets that are more homogeneous in terms of the response variable, in this case, cluster or community membership (Vayssieres et al. 2000). The heterogeneity of each subset is measured as an impurity, calculated in our model using the Gini index (Breiman et al. 1984, Crawley 2002, Venables and Ripley 2002). The goal of each split is to maximize the reduction in impurity. The model identifies a single variable (and its threshold value) as the indicator for each branch of the tree, as opposed to groups being distinguished along multivariate axes as in discriminant analysis or logistic regression. This approach allows the inclusion of non-linear species responses and is unaffected by interactions among variables (Vayssieres et al. 2000, McCune and Grace 2002).

Once the largest possible tree has been grown, a process of eliminating superfluous branches begins, called "pruning back to an honest tree" (Breiman et al. 1984). This is done by testing each subtree for its error rate based on data that were not used to grow the largest tree. Using cross validation, which acts as a test sample while extracting information for all the cases of a data set, the final tree is constructed from all of the data, using the best tree size (Vayssieres et al. 2000). The performance of the model is measured by a misclassification rate, while the amount of variation explained by the tree is reported as 1-Relative Error, or more strictly, 1-Cross Validated Error.

The final output is a pruned tree with barplots under each leaf showing the composition of the final groups, as well as the number of samples in that leaf. Threshold values of the variables determining the splits are shown at each node. Several combinations of the variables average growing season salinity, 90th percentile growing season salinity, amplitude of growing season salinity, distance to nearest drainage creek, soil bulk density, and percent organic content of soil were used as continuous predictors in our CART models. The best fit trees for both 2002 and 2005 incorporated average growing season salinity, distance to nearest creek, and percent organic content in the soil.

Multivariate Regression Tree Model (MRT)

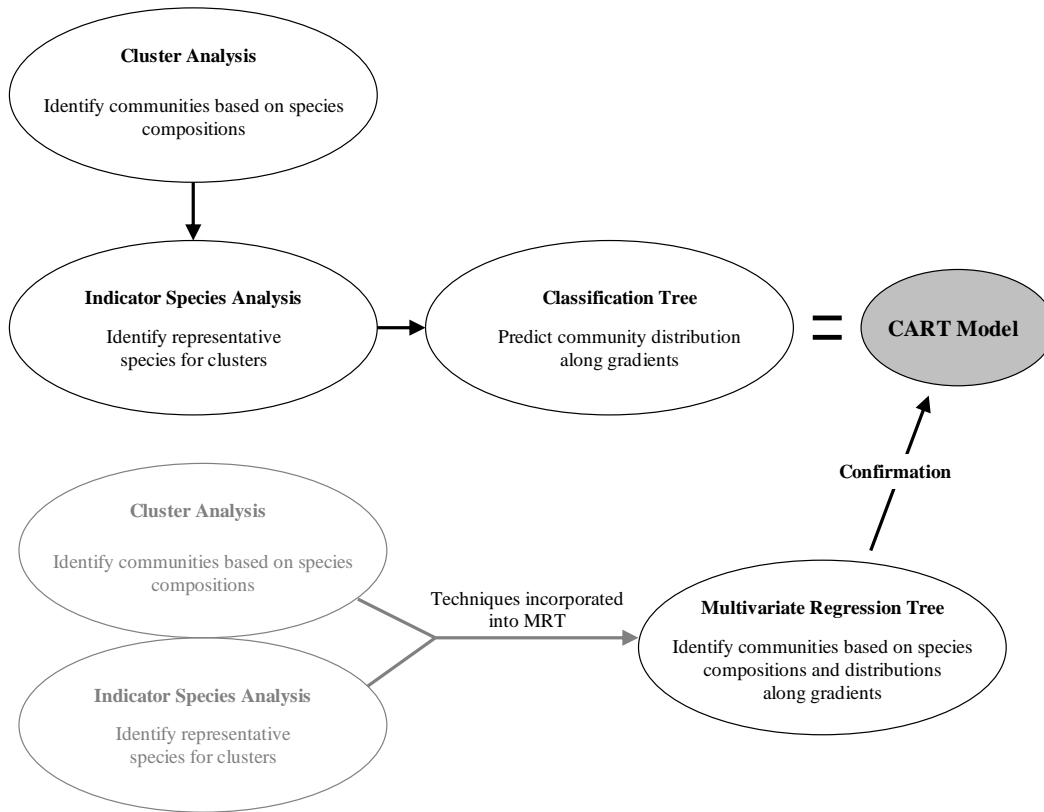
An MRT analysis was conducted to identify communities based on species IV's and where they occurred along environmental gradients, and to compare the resultant communities (leaves of the tree) with those formed in the cluster analysis and CART model. In short, this technique partitions the samples into communities using both species IV's as well as the associated environmental variables, and provides the threshold values for each partitioning

variable. The resultant communities are defined not just by species compositions but where they occurred on the environmental gradients as well, providing a more detailed, inclusive description than those defined by the Cluster Analysis. Essentially, the CART model predicts communities based on pre-defined groups, using only one categorical variable (cluster membership) as a response. The MRT, however, uses all species' importance values to predict communities, using either 31 (June 2002) or 30 (June 2005) continuous response variables. This acts as a confirmatory procedure by comparing the communities produced by the two separate procedures.

The MRT's were performed using the same Tree Library in S-Plus as our CART models. This model uses the sum of squared Euclidian distances about the multivariate mean of samples as an impurity measure of each node, and each split is made to maximize this sum of squares between nodes and to minimize it within nodes (De'ath 2002). Each leaf is then characterized by the multivariate mean of its samples, the number of samples within that leaf and their defining environmental variables. The percent of variation explained by the tree is reported as 1-Relative Error, or more strictly 1-Cross Validated Error. Species variances can also be tabulated to show the contributions of individual species at each split and how well the tree explains their variations, as well as the percent of variation explained by each split.

The use of Euclidian distance measures with non-normal data typical of most ecological, community studies has proven to be less effective than alternatives like Bray-Curtis (Sorenson) or extended dissimilarity (Faith et al. 1987, De'ath 1999). De'ath (2002) and Urban (2002) suggested one alternative method of using a distance-based MRT (db-MRT), which essentially produces a dissimilarity matrix from your original data using the distance measure of choice. The MRT then treats those dissimilarities as distances, and clusters are formed by splitting the data on environmental variables that maximize the sums of squared distances between nodes and minimize it within nodes, just as described earlier. However, because the db-MRT depends solely on the dissimilarities and environmental variables, the species observations themselves are not needed (De'ath 2002). This results in less information being available from the db-MRT than the MRT, like species variance tabulations. For our models we used the Euclidian-based MRT as a confirmatory analysis of the CART model, then produced a db-MRT using Bray Curtis distances as a confirmatory analysis of our MRT model. The db-MRT was performed using the library mvpart (De'ath 2004) in the statistical package R (source). Due to strikingly similar results regardless of distance measure chosen, the db-MRT's were not included in this report. Further, despite the use of Euclidian distance measures, the MRT's are strong candidates for community modeling since 1) unlimited numbers of quantitative and categorical variables can be used as explanatory variables 2) monotonic transformations of explanatory variables are allowed, 3) interactions between explanatory variables are automatically detected 4) they are robust to the collinearity of explanatory variables and 5) they are minimally affected by missing values (De'ath 2002). Figure 2 shows an overall description of each analysis and its purpose.

Figure 2. Flow chart of the CART model development, the MRT model development, and the confirmatory process.



RESULTS

2002 Model

The Cluster and Indicator Species analyses identified four main communities during the drought sample of June 2002 (Table 1). The largest group was the SCIVA community which contained 39% of the samples, and the SPASP_SCIRO community was the smallest with only 12%. The ELEMO community had several secondary indicators, or species with indicator values of between 30-40, including *Cyperus* spp., *Hydrocotyle* spp. and *Saciolepis indica* (Table 2). These species either occurred too infrequently or had too many occurrences in other groups to have high values, but were still weakly associated with the ELEMO community. *Zizaniopsis miliacea* was a strong indicator for the ZIZMI_POLSP community, with *Polygonum* spp. more weakly associated.

Table 1. Cluster indicator species, their associated indicator values and the total number of samples in each cluster.

Community Code	Indicator Species	Ind Value	# of samples
ELEMO	<i>Eleocharis montevidensis</i>	66	33
SCIVA	<i>Scirpus validus</i>	63	47
SPASP_SCIRO	<i>Spartina</i> spp. and <i>Scirpus robustus</i>	99, 87	14
ZIZMI_POLSP	<i>Zizaniopsis miliacea</i> and <i>Polygonum</i> spp.	65, 43	26

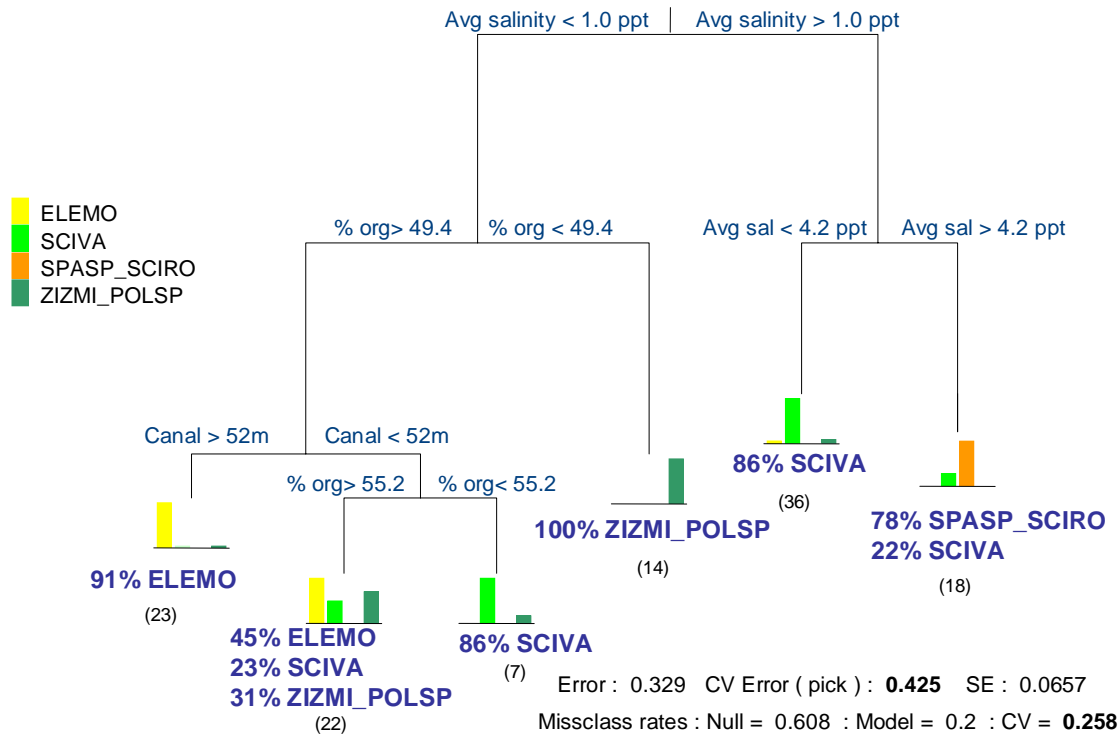
Table 2. Indicator values of all 31 species from the 2002 sample. High indicator values show which species are good representatives for each cluster. Color coding refers to the community each indicator is representative of. Secondary indicators for Cluster 2 are in bold, uncolored text.

P-Value	Species Code	Group ID	Cluster 1	2	3	4	
0.198	AGAPU	1	10	7	0	0	
0.123	ASTEL	1	20	17	4	0	
0.283	CICME	2	8	10	0	0	
0.001	ELEMO	2	14	66	9	0	
0.001	ELEQU	1	26	0	0	0	
0.046	GALTI	2	12	17	0	0	
0.003	HYDUM	2	18	36	1	0	
0.031	IRIHE	2	7	19	1	0	
0.795	LUDSP	3	4	5	6	0	
0.022	MURKE	2	19	24	0	0	
0.001	POLSP	1	43	0	6	0	
0.001	SACIN	2	2	32	0	0	
0.009	LUDAL	1	20	0	1	0	
0.001	ZIZMI	1	65	12	7	0	
0.033	LEESP	2	20	25	0	0	
0.001	BIDMI	2	1	29	0	0	
0.009	JUNMA	2	1	22	4	0	
0.006	SAGLT	2	1	21	0	0	
0.003	CYPSP	2	6	32	0	0	
0.159	CYPHA	2	2	9	0	0	
0.167	POLSA	2	3	9	0	0	
0.006	CARSP	4	1	1	0	17	
0.237	BIDLA	2	2	12	4	0	
0.001	SCIVA	3	4	2	63	19	
0.558	SAGLN	3	1	5	6	0	
0.044	PHYLA	2	5	17	0	0	
0.062	PANSP	1	15	1	0	0	
0.396	TYPSP	2	1	13	10	4	
0.001	SCIRO	4	0	0	0	87	
0.004	ASTTE	4	0	0	7	27	
0.001	SPASP	4	0	0	0	99	

The CART model produced from the 2002 sample resulted in five communities laid out in six leaves, with a relative error of 0.329 and a cross-validated error (CV error) of 0.425 (Figure 3). The node with the largest number of samples was the SCIVA community that occurred between 1.0 and 4.2ppt average growing season salinity, with 30% of the samples. The most accurately classified communities were the ZIZMI_POLSP community occurring in mineral soils at <1.0ppt average salinity, with a 100% classification rate (14 of 14 samples); and the ELEMO community occurring in organic soils at <1.0ppt average salinity and at least 52m from the nearest drainage creek (91% classification rate, or 21/23 samples). The majority of the misclassification and error in the model came from a mixed community of ELEMO, SCIVA and ZIZMI_POLSP groups all occurring at low salinities, <52m from the nearest creek but in soils with >55.2% organic content in soils. This leaf consisted of 18% of the samples and was representative of the highly competitive, variable and diverse marshes that occur in the more

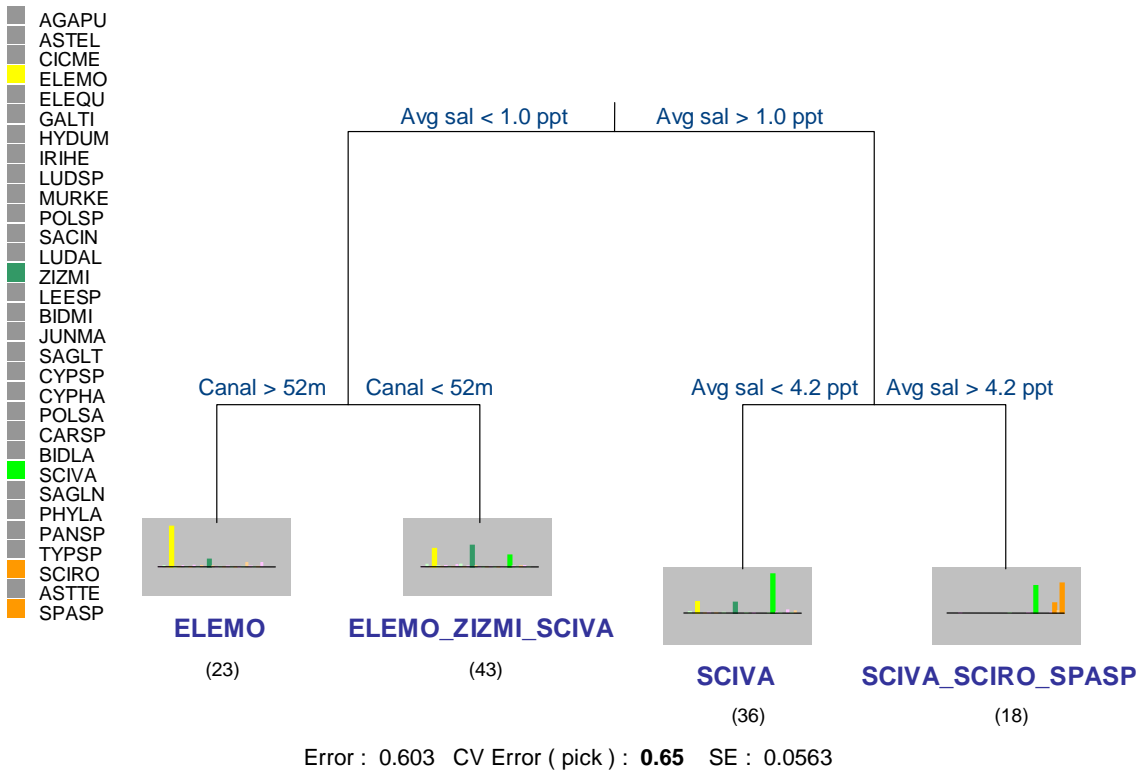
freshwater areas of the Savannah River. As expected, the SPASP_SCIRO community occurred at >4.2ppt average growing season salinity, or in the highest range sampled.

Figure 3. CART model showing the distribution of the four communities identified by the Cluster and Indicator Species analyses for the 2002 sample. Numbers in parentheses indicate the total number of samples in the leaf and barplots show community membership of those samples. Colors represent communities identified by the Cluster and Indicator Species analyses. Leaves with more than one dominant community have higher misclassification rates. Percentages indicate the number of samples out of the total samples in that leaf that belong to the dominant community.



The MRT model produced very similar communities to those identified by the Cluster, Indicator Species, and CART analyses (Figure 4). The MRT model with the best fit had four leaves, with the first major division occurring again at 1.0ppt average growing season salinity. A SCIVA dominant community was again identified as occurring between 1.0 and 4.2ppt with 30% of the samples occurring in that leaf, while a SPASP_SCIRO community occurred at salinities greater than 4.2ppt. Again, 23/120 samples at <1.0ppt and >52m from the nearest drainage creek were identified as ELEMO dominant, and a mixture of ELEMO, SCIVA and ZIZMI were found at distances <52m. These communities and their distributions along the measured gradients were identical to those produced from the CART model, with the exception of soils characteristics further separating the freshwater mixed community in the CART. The overall fit or variance explained by the MRT was also fairly high (35%) considering the nature of multivariate community data.

Figure 4. MRT model showing the distribution of four communities along salinity, soils, and drainage creek gradients for the 2002 sample. The numbers in parentheses indicate the number of samples in the corresponding leaf and the barplots show the multivariate species mean. Colors represent the communities those species represented in the CART model.



The contribution of individual species to each split and how well each species is explained by the splits can be shown by tabulating the species variance. The variance of SCIVA comprised 34.5% of the total species variance, of which 13.78% was explained by the tree, with 12.34% explained by the first split (Table 3). ELEMO also contributed to the first split, with 6.35% of its variance explained. ZIZMI had little of its variance explained by the tree (4.25%) but did contribute to the first and second splits. As expected, SPASP was largely responsible for the third split, with SCIVA contributing minimally.

Table 3. Amount of variation explained by each species at each split for the 2002 MRT model. Indicator species contributing to splits are color coded to match CART model communities. The last column shows the percent of total species variance each species contributed, and the Tree Total column shows the percentage of that variation explained by the tree.

Species	Salinity <1.01ppt	Canal >52m	Salinity <4.15ppt	Tree Total	Species Total
AGAPU	0	0	0	0	0.04
ASTEL	0.08	0.01	0	0.09	1.41
CICME	0	0	0	0	0.01
ELEMO	6.35	4.67	0.86	11.87	22.61
ELEQU	0	0.01	0	0.01	0.14
GALTI	0	0	0	0	0.05
HYDUM	0.04	0	0	0.04	0.72
IRIHE	0	0	0	0	0.01
LUDSP	0	0	0	0	0.06
MURKE	0.11	0	0	0.12	1.4
POLSP	0.06	0.08	0	0.14	0.82
SACIN	0.01	0.02	0	0.03	0.23
LUDAL	0	0	0	0.01	0.23
ZIZMI	1.67	1.79	0.78	4.25	18.04
LEESP	0.03	0	0	0.03	0.39
BIDMI	0	0	0	0	0
JUNMA	0	0	0	0	0.01
SAGLT	0	0	0	0	0.02
CYPSP	0	0	0	0	0.07
CYPHA	0	0	0	0	0
POLSA	0	0	0	0	0
CARSP	0	0	0	0	0
BIDLA	0	0	0	0	0.06
SCIVA	12.34	0.39	1.05	13.78	34.5
SAGLN	0	0	0.01	0.01	0.41
PHYLA	0	0	0	0	0.01
PANSP	0.01	0	0	0.01	0.36
TYPSP	0	0.07	0.04	0.12	3.89
SCIRO	0.19	0	0.64	0.83	1.95
ASTTE	0.11	0	0	0.11	1.28
SPASP	1.77	0	6.42	8.19	11.26
Total	22.78	7.06	9.82	39.67	100.00

2005 Model

The Cluster and Indicator Species analyses identified four main communities for the 2005 sample, which took place following 1-2 years of normal flow conditions (Table 4). The most dominant community was again SCIVA with 35% of the samples belonging to that group, followed by the ZIZMI_POLSP community (32%) and the ELEMO community (20%). GALTI and SAGLT were added as additional indicators for the flood year model to the ELEMO community, while ASTTE was added as an indicator to the SPASP_SCIRO community. The strength of each species' representation of these communities is tabulated in Table 5 by their indicator values.

Table 4. Cluster indicator species, their associated indicator values and the total number of samples in each cluster for the 2005 sample.

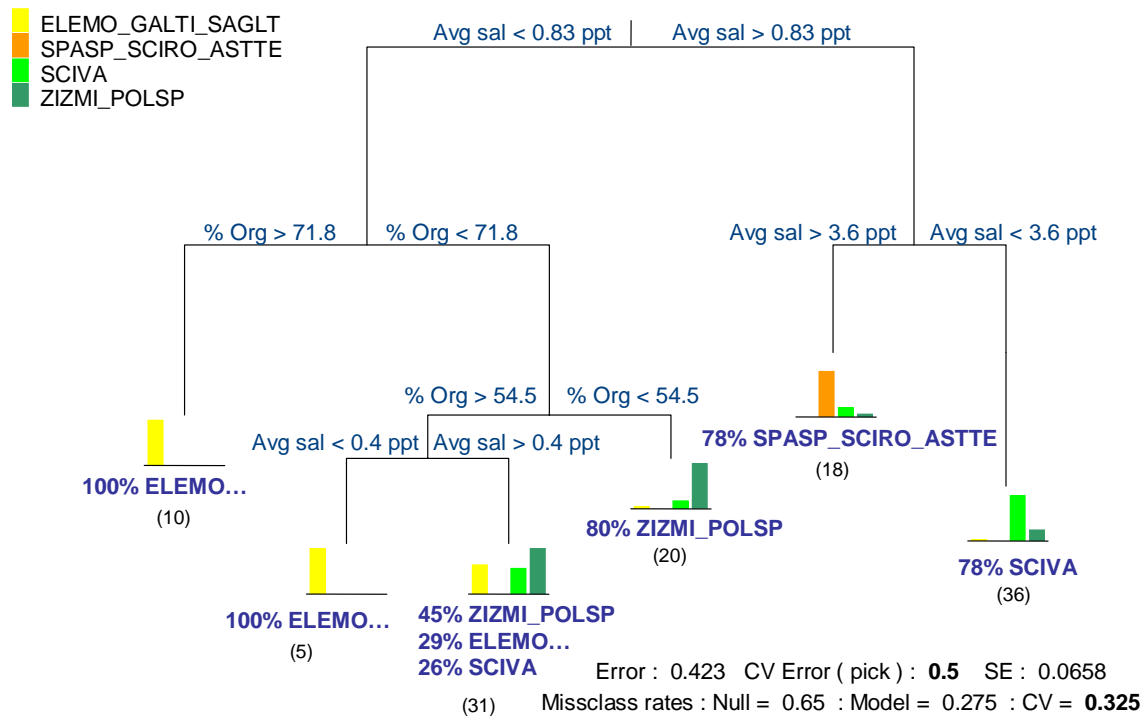
Community Code	Indicator Species	Ind Value	# of samples
ELEMO_GALTI_SAGLT	<i>Eleocharis montevidensis</i> , <i>Galium tinctorum</i> and <i>Sagittaria latifolia</i>	67, 43, 46	26
SCIVA	<i>Scirpus validus</i>	55	42
SPASP_SCIRO_ASTE	<i>Spartina</i> spp., <i>Scirpus robustus</i> and <i>Aster tenuifolius</i>	100, 70, 57	14
ZIZMI_POLSP	<i>Zizaniopsis miliacea</i> and <i>Polygonum</i> spp.	75, 40	38

Table 5. Indicator values of all 30 species from the 2005 sample. High indicator values show which species are good representatives for each cluster. Species are color coded according to which cluster or community they are representative of.

P-value	Species Code	Group ID	Cluster 1	2	3	4
0.002	AGAPU	2	3	28	0	0
0.092	BIDLA	21	8	2	18	0
0.001	BIDMI	2	1	32	0	0
0.001	ELEMO	2	13	67	8	0
0.003	FUIBR	2	2	32	0	0
0.001	GALTI	2	1	43	0	0
0.076	HYDUM	1	24	21	2	0
0.001	IRIHE	2	1	37	0	0
0.003	JUNMA	2	2	32	4	0
0.059	LUDSP	1	23	4	3	0
0.014	MURKE	1	30	25	0	0
0.277	PHYLA	2	7	12	1	0
0.003	POLSP	1	40	2	4	0
0.052	PTICA	2	8	18	0	0
0.001	SCIVA	21	10	3	55	18
0.001	ZIZMI	1	75	6	5	0
0.583	ELEQU	2	4	6	2	0
0.015	LEESP	2	13	29	1	0
0.15	LOBSP	2	1	9	1	0
0.006	SAGLN	2	2	24	1	0
0.001	SAGLT	2	0	46	0	0
0.066	SAUCE	1	12	1	0	0
0.024	TYPSP	21	1	6	23	0
0.043	ASTEL	2	12	25	3	0
0.008	CICME	2	1	20	0	0
0.002	ARTHI	2	1	26	0	0
0.004	PANSP	2	1	20	0	0
0.001	SCIRO	49	0	0	1	70
0.001	SPASP	49	0	0	0	100
0.001	ASTE	49	0	0	1	57

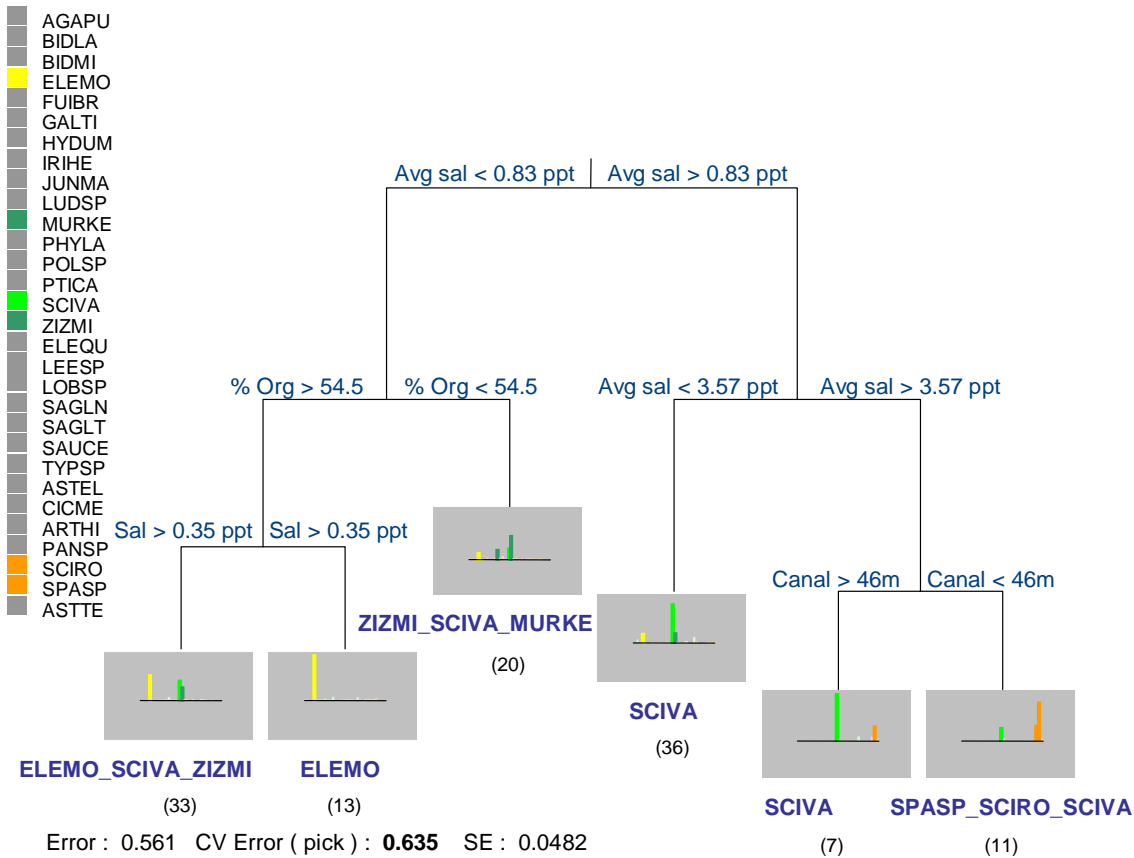
The CART model for the 2005 sample was strikingly similar to the 2002 drought model, with five communities again predicted on six leaves, including a mixture of ELEM0, ZIZMI and SCIVA occurring in highly organic soils at low salinity levels (Figure 5). Very strong classification rates of 100% occurred for the ELEM0 community at low salinities and >72% organic content of soils, and again at >55% organic content at even lower salinity levels. Once again the SCIVA and SPASP communities dominated at sites >0.83ppt average salinity, while no such SCIVA community occurred at lower salinities. The ZIZMI community was more prominent in the 2005 model, occupying sites with more mineral soils at lower salinity levels.

Figure 5. CART model showing distribution of the four 2005 communities identified by the Cluster and Indicator Species analyses. Numbers in parentheses indicate the total number of samples in the leaf and barplots show community membership of those samples. Colors represent communities identified by the Cluster and Indicator Species analyses. Leaves with more than one dominant community have higher misclassification rates. Percentages indicate the number of samples out of the total samples in that leaf that belong to the dominant community.



The MRT model produced from the 2005 sample predicted very similar communities as those found by the CART model (Figure 6). Again, the first major break was at 0.83ppt average prior growing season salinity, with ELEMO or a mixture of ELEMO, SCIVA and ZIZMI occurring at the lower salinities, depending on soil organic content. An additional species was identified in more mineral soils at low salinity levels, *Murdania kesiak* (MURKE). This is an invasive exotic species, and has shown an increasing dominance in areas closer to drainage creeks in less saline sites. SCIVA and SPASP communities were again dominant at higher salinities, though in the MRT an additional SCIVA community was identified in the interior marsh at >3.57ppt salinities. Again, the amount of variation explained by this model (36.5%) was fairly high given the nature of multivariate community data.

Figure 6. MRT model showing the distribution of five communities along salinity, soils, and drainage creek gradients for the 2005 sample. The numbers in parentheses indicate the number of samples in the corresponding leaf and the barplots show the multivariate species mean. Colors represent the communities those species represented in the CART model.



The species variances for the MRT show that ELEMΟ and SCIVA were primarily responsible for the first split, while ZIZMI and SPASP explained less of the variation in the tree (Table 6). The fact that SCIVA contributed to every split suggests it was found at nearly all locations in the marsh, but with varying dominance determined by salinity, soils characteristics and distance to nearest drainage creek. Though MURKE and SCIRO did not contribute much to

the overall variation explained by the tree, they were identified in terminal branches with MURKE occurring as a subdominant in mineral soils at lower salinity levels, and SCIRO occurring nearer drainage canals at high salinity levels.

Table 6. Amount of variation explained by each species at each split for the 2005 MRT model. Indicator species contributing to splits are highlighted according to community membership. The last column shows the percent of total species variance each species contributed, and the Tree Total column shows the percentage of that variation explained by the tree.

Species	Salinity <0.83ppt	Percent org <54.5	Salinity <3.57ppt	Salinity <0.35ppt	Canal <46m	Tree Total	Species Total
AGAPU	0.05	0.05	0.00	0.02	0.00	0.12	0.25
BIDLA	0.29	0.06	0.22	0.01	0.00	0.58	1.12
BIDMI	0.01	0.01	0.00	0.01	0.00	0.04	0.09
ELEMO	3.73	3.11	0.61	2.17	0.00	9.63	21.13
FUIBR	0.03	0.03	0.00	0.02	0.00	0.08	0.17
GALTI	0.04	0.04	0.00	0.03	0.00	0.10	0.22
HYDUM	0.20	0.18	0.02	0.08	0.00	0.47	0.96
IRIHE	0.08	0.07	0.01	0.05	0.00	0.20	0.43
JUNMA	0.06	0.05	0.01	0.03	0.00	0.15	0.32
LUDSP	0.16	0.13	0.02	0.04	0.00	0.35	0.66
MURKE	0.72	0.73	0.00	0.26	0.00	1.71	3.39
PHYLA	0.12	0.11	0.01	0.03	0.00	0.27	0.51
POLSP	0.27	0.16	0.10	0.02	0.00	0.56	1.03
PTICA	0.03	0.03	0.00	0.02	0.00	0.08	0.17
SCIVA	5.49	1.84	3.47	1.03	1.76	13.58	31.03
ZIZMI	2.59	1.85	0.72	0.69	0.13	5.97	12.11
ELEQU	0.09	0.07	0.02	0.03	0.00	0.21	0.44
LEESP	0.19	0.19	0.00	0.08	0.00	0.45	0.92
LOBSP	0.01	0.01	0.00	0.00	0.00	0.02	0.05
SAGLN	0.25	0.18	0.07	0.10	0.00	0.59	1.24
SAGLT	0.04	0.04	0.00	0.03	0.00	0.11	0.26
SAUCE	0.04	0.04	0.00	0.00	0.00	0.08	0.13
TYPSP	0.64	0.17	0.44	0.10	0.12	1.48	3.20
ASTEL	0.31	0.21	0.10	0.13	0.00	0.75	1.59
CICME	0.04	0.04	0.00	0.02	0.00	0.09	0.19
ARTHI	0.02	0.02	0.00	0.01	0.00	0.06	0.13
PANSP	0.11	0.12	0.00	0.06	0.00	0.29	0.60
SCIRO	0.43	0.00	0.40	0.00	0.74	1.57	4.63
SPASP	1.03	0.00	0.98	0.00	1.95	3.96	11.89
ASTTE	0.11	0.00	0.11	0.00	0.18	0.40	1.15
Total	17.17	9.52	7.31	5.07	4.87	43.94	100.00

DISCUSSION

Interpretation

All four of the models described above produced very similar results, with only minor changes in community compositions and their environmental thresholds. Regardless of

technique or sample event, every model described four basic communities dominated by the same five species. The distribution of these four communities remained fairly constant as well: *Eleocharis montevidensis* dominated the interior marshes in areas <1.0ppt, while *Zizaniopsis miliacea* dominated areas closer to the berms at <1.0ppt. *Scirpus robustus* and *Spartina* spp. dominated areas with roughly >3.5ppt average salinity, while *Scirpus validus* occurred between 1.0ppt and 3.5ppt. These results were very consistent with what Kitchens (2003) found, as that report identified three basic marsh types according to salinities: freshwater (<0.05ppt), intermediate (0.05-3.0ppt), and brackish (3.0-7.0ppt). Our model essentially describes the freshwater community as *Eleocharis* and *Zizaniopsis*, the brackish community as *Spartina* and *Scirpus robustus*, and the intermediate, transitional community as *Scirpus validus*.

The main changes we saw between the 2002 (drought) and 2005 (average conditions) models was decreased diversity in the ELEM community in 2002, as *Eleocharis montevidensis* was the only strong indicator for that group, and a stronger presence of the SCIVA community at lower salinity levels in 2002. The 2005 model showed *Galium tinctorum* and *Sagittaria latifolia* as additional indicators of the ELEM community, and the SCIVA community began to appear in the interior marshes at >3.5ppt that were dominated by the SPASP_SCIRO during the drought. These results were expected since increases in salinity have been shown to lower diversities (Kitchens 2003) and since *Eleocharis* and *Scirpus validus* have been shown to competitively exclude one another at different salinities (Wetzel et al. 2004).

Scirpus validus is essentially omnipresent in the salinity range our sites focus on and its distribution is probably the most completely sampled of any species we encountered. Most of the freshwater species, like *Eleocharis montevidensis* and a host of sub-dominants, likely occur well up-river of the freshwater extreme of our sites, while *Spartina* spp. and *Scirpus robustus* likely occur at much higher salinities (down-river) than the areas we sampled. These models have no inference to the areas beyond our sampled gradient. However, our site locations and the intensive sampling methods used enabled us to track subtle changes in community structures within the most sensitive, responsive marshes along this gradient (freshwater-brackish). Despite the fact *Scirpus validus* is present throughout our study area, differences in abundance in relation to other stem densities and biomasses showed up-stream shifts in the dense, *Scirpus*-dominated community in response to salinity increases during the drought. Conversely, the ELEM community lost salt-sensitive subdominants like *Galium* and *Sagittaria latifolia* during the drought. The fact that the ELEM community did not have any other significant indicator species in the 2002 CART model suggests a substantial difference between the 2002 and 2005 freshwater communities, essentially a much lower diversity in terms of dominant species. Although the distribution of the ELEM community did not change between models, the structure and composition of that community changed significantly.

Other communities showed compositional changes following the drought as well. The ZIZMI_POLSP community that occurred in areas <1.0ppt in the 2002 model had another significant indicator species in 2005, *Murdania kesiak*. This is an invasive exotic species, and while present as early as our 1999 November sample, the distribution and abundance of this species has increased significantly since the end of the drought. Perhaps the removal of other salt-sensitive species during prolonged increases in salinity allowed *Murdania* to occupy more areas, or perhaps it was able to rapidly colonize those areas after salinities decreased. This species seems to have increased its presence at our Middle River 1 site most substantially, possibly coincident with the highest salinity intrusion occurring along the Middle River during the drought.

An additional indicator species was also identified in the most saline community in the 2005 model, *Aster tenuifolius*. Though present at our two furthest down-river sites throughout our period of study, its abundance and frequency has increased following average river flow conditions. This suggests that mildly salt-tolerant species are beginning to recolonize areas down-stream that were too saline during the drought. Again, the addition of a sub-dominant to a community description suggests a substantial compositional shift and represents an important change in habitat structure.

Overall, the environmental thresholds or defining gradients for the communities were consistent regardless of year or model (CART vs. MRT). During 2002 the major splits in community distributions occurred at 1.0ppt and then again at 4.2ppt (Figure 3). In 2005 these thresholds were 0.83ppt and 3.6ppt (Figure 5). This suggests that the core of the *Spartina*, *Scirpus validus*, and *Eleocharis* communities did not change distribution between 2002 and 2005, but the conditions at those communities changed by <1.0ppt. Most of the differences in the models occurred at lower splits on the trees, representing the subtle compositional shifts at the edges of distinctive communities.

Model Performance

The MRT models produced as confirmatory analyses closely resemble the results of the Cluster, Indicator Species, and CART analyses. The wholly separate approach allows for direct comparison of resultant communities and in this case, confirms the results. Regardless of technique, threshold values were similar or exactly the same between the CART and MRT models, and often the leaves of the tree contained the same number of samples. When there were dissimilarities between the two types of models it usually had to do with the criteria involved in pruning the tree, or deciding on the final number of leaves. For example, in the 2002 sample the CART model produced four leaves on the left side of the tree, while the MRT produced two. The CART model did a better job of isolating the ZIZMI_POLSP community in areas of less organic soil content, and even isolated a small SCIVA community nearer canals. However, 22 samples on the left side of the tree were combined into a grouping of three community types, showing a poor correlation of those samples to our measured environmental variables. The MRT showed a relatively small amount of information gained by further splitting the ELEMOMO_ZIZMI_SCIVA group, and left them together as a scattered, less predictable community occurring mainly nearer canals. This slight disagreement in the freshest areas of the marsh is to be expected, as under less stressful conditions autogenic factors (e.g. interspecific competition) tend to play a greater role in influencing species compositions than allogenic factors (e.g. salinity).

There was slightly more disagreement between the models for the 2005 sample, but the primary splits and communities were similar. The CART model showed a secondary split in the fresh areas at >72% organic soils, then isolated the ZIZMI community to areas of low organic soil content, as the 2002 model did. There was also considerable confusion at intermediate levels of organic content between 0.4ppt and 0.8ppt. Again, misclassification at these levels is due to a weaker correlation of species compositions to environmental gradients, since competition is undoubtedly a major factor in these systems. The MRT had similar results at <0.8ppt and essentially found mixes of ELEMOMO, SCIVA and ZIZMI in the majority of the fresh samples. It also isolated a ZIZMI_SCIVA_MURKE community as occurring in more mineral soils conditions.

Of interest was the addition of another SCIVA dominant community at >3.6ppt in the MRT model of 2005, which did not appear in any other model. As mentioned earlier, this suggests a downstream encroachment of a community that was isolated further upstream during the drought. The disagreement between the CART and MRT models in this respect was again due to the criteria involved in deciding the ultimate number of leaves for the tree.

The amount of variation explained by the models, their subsequent errors, and misclassification rates were all very good considering the nature of multivariate community data (McCune and Grace 2002). The cross-validated error is a much more stringent measure of model fit and both CART models had CV errors of 50% or less. The cross-validated misclassification rates were a phenomenal 26% and 33% for the 2002 and 2005 models, respectively. The CART models inherently have lower error rates than the MRT models due to the fact they use categorical response variables instead of quantitative variables. Essentially, the CART models classified 120 samples into four pre-defined communities as identified by the Cluster Analysis, while the MRT model defined the ideal communities based on the abundances of 30 or more species in 120 samples, as well as those sample's corresponding environmental variables. Considering that daunting task, error rates of 65% and 63% for the 2002 and 2005 MRT models were very reasonable.

Application and Constraints

The intent of these models is to provide users of the M2M_Model (Connecting the Water Level and Specific Conductance Response of Tidal Wetlands to the Savannah River) with a predictive engine that will determine marsh communities based on salinity outputs from user-specified hydrologic scenarios. Incorporation of our algorithms into GIS layers was performed by USACE specialists and will not be detailed herein. Users should choose between the 2002 and 2005 models based on the severity of alterations to channel salinities. If users predict large, prolonged increases in upstream salinities as a result of some disturbance or modification, the 2002 model would be more appropriate. Additionally, if users want to predict community response to some modification during a severe, prolonged drought versus average river stages, they should also choose 2002. The two models merely provide baseline communities based on either environmental conditions or the severity of alteration desired or predicted. It is recommended that for each scenario the user runs the CART and MRT models in order to see possible discrepancies in terms of marsh surface area. While the CART models have better fits and high classification rates, we feel they should be confirmed with the separate MRT approach.

These and all other models have constraints that should be stated before application. Firstly, predictions cannot be made beyond the gradients that we sampled, as no data exists for those areas. For example, the SPASP_SCIRO community was found to occur at salinities at >4.0ppt in 2002 but the highest average growing season salinities recorded for any of our sites was roughly 7.0ppt. Therefore, our models make no predictions for communities occurring above 7.0ppt average prior growing season salinity. If the M2M_Model outputs suggest a huge displacement of brackish marsh with salinities of 10.0ppt, for example, no predictions can be made for those communities.

Secondly, there were 120 sample stations located throughout the marsh, but these were predominantly stratified along the Back River to document tide gate disruptions in the 1980's. Though three new sites were added in the freshest areas of the Front and Middle Rivers in 2000,

estimates of community compositions and distributions along the more saline sections of the Middle and Front Rivers will likely have less predictive value.

Lastly, these models are based on snapshots of an extremely dynamic system that does not respond linearly to disturbance or fluctuation. Grace and Guntenspergen (1999) showed that the distribution of salt marsh communities was largely affected by extreme historical disturbances, in addition to current salinities. Most statistical models are based on an assumption that vegetation is in equilibrium with the environment, or where change is at least slow relative to the lifespan of the biota. The overall success of these models depends on the degree to which history and disturbance are important to the system (Austin 2002). Certainly there are channel modifications or disturbances that would produce effects beyond the predictive range of these models. There must be thresholds that once passed would affect distributions for many years after returning to normal conditions. However, given the many constraints of these models, we feel they perform very well for such a dynamic and complex biome and have tremendous predictive power within the sampled range and system. Our succession engine when combined with associated hydrologic models will provide much needed insight to managers and stakeholders regarding future changes to the lower Savannah River.

Literature Cited

- Austin, M. P. 1987. Models for the analysis of species response to environmental gradients. *Vegetatio* **69**:35-45.
- Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990. Measurement of the realized quantitative niche: environmental niches of five *Eucalyptus* species. *Ecological Monographs* **60**:161-177.
- Austin, M. P., A. O. Nicholls, M. D. Doherty, and J. A. Meyers. 1994. Determining species response functions to an environmental gradient by means of a beta-function. *Journal of Vegetation Science* **5**:215-228.
- Blake, G. R., and K. H. Hartge. 1986. Bulk density. *In* A. Klute, editor. *Methods of soil analysis: part 1. Physical and mineralogical methods*. American Society of Agronomy, Madison, WI.
- Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. *Classification and regression trees*. The Wadsworth Statistics/Probability Series, Chapman & Hall, New York, NY.
- Chapman, H. D., and P. F. Pratt. 1961. *Methods of analysis for soils, plants and waters*. University of California, Riverside, CA.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**:117-143.
- Crawley, M. J. 2002. *Tree models*. *In* *Statistical computing: an introduction to data analysis using S-Plus*. John Wiley & Sons, West Sussex, England.

- De'ath, G. 2004. Multivariate Partitioning, mvpart R package Version 1.1-1. Modified *from* Recursive Partitioning and Regression Trees, rpart R package. Therneau, T.M., B. Atkinson, B. Ripley, and J. Oksanen,.
- De'ath, G. 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology* **83**:1105-1117.
- De'ath, G. 1999. Extended dissimilarity: a method of robust estimation of ecological distances from high beta diversity data. *Plant Ecology* **144**(2):191-199.
- Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**:345-366.
- Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**:57-68.
- Franklin, J. 1995. Predictive vegetation mapping: geographic modeling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography* **19**:474-499.
- Gough, L., and J. B. Grace. 1998. Effects of flooding, salinity, and herbivory on coastal plant communities, Louisiana, United States. *Oecologia* **117**:527-535.
- Grace, J. B. and G. R. Guntenspergen. 1999. [The effects of landscape position on plant species density: Evidence of past environmental effects in a coastal wetland](#). *Ecoscience* **6**(3): 381-391.
- Huisman, J., H. Olff, and L. F. M. Fresco. 1993. A hierarchical set of models for species response analysis. *Journal of Vegetation Science* **4**:37-46.
- Jacobs, H. S. 1971. Soils laboratory exercise source book. American Society of Agronomy, Madison, WI.
- Kent, M., and P. Coker. 1992. Vegetation description and analysis: a practical approach. CRC Press, Boca Raton, FL.
- Kitchens, W. M. 2003. Tidal wetland resource utilization studies. Progress Report. United States Army Corps of Engineers.
- Latham, P. J., 1990. Plant distributions and competitive interactions along a gradient of tidal freshwater and brackish marshes. PhD. Dissertation. University of Florida, Gainesville, FL, USA.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.
- McCune, B., and M. J. Mefford. 1999. Multivariate analysis of ecological data, version 4.20. MjM Software Design, Gleneden Beach, OR.

- Mitsch, W. J., and J. G. Gosselink. 1993. *Wetlands*. Second edition. John Wiley & Sons, New York, NY.
- Odum, W. E., T. J. Smith, J. K. Hoover, and C. C. McIvor. 1984. The ecology of tidal freshwater marshes of the United States East Coast: A community profile. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC, USA. FWS/OBS-83-17.
- Oksanen, J., E. Laara, P. Huttunen, and J. Merilainen. 1988. Estimation of pH optima and tolerances of diatoms in lake sediments by the methods of weighted averaging, least squares and maximum likelihood, and their use for the prediction of lake acidity. *Journal of Paleolimnology* **1**:39-49.
- Pearlstine, L. P., Latham, W. Kitchens, and R. Bartleson. 1990. Development and application of a habitat succession model for the wetland complex of the Savannah National Wildlife Refuge. Vol II. FL Coop. Fish and Wildl. Res. Unit. Gainesville, FL, USA.
- Urban, D. L. 2002. Classification and regression trees. *In* B. McCune, and J. B. Grace, editors. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR.
- Vayssières, M. P., R. E. Plant, and B. H. Allen-Diaz. 2000. Classification trees: an alternative non-parametric approach for predicting species distributions. *Journal of Vegetation Science* **11**:679-694.
- Venables, W. N., and B. D. Ripley. 2002. *Statistics and computing: modern applied statistics with S*. Fourth edition. J. Chambers, W. Eddy, W. Hardle, S. Sheather and L. Tierney, series editors. Springer-Verlag, New York, NY.
- Wetzel, P. R., W. M. Kitchens, J. M. Brush, M. L. Dusek. 2004. Use of a reciprocal transplant study to measure the rate of plant community change in a tidal marsh along a salinity gradient. *Wetlands* **24**(4):879-890.