A FORTY-SEVEN YEAR COMPARISON OF THE VASCULAR FLORA AT THREE ABANDONED RICE FIELDS, GEORGETOWN, SOUTH CAROLINA, U.S.A.

Richard Stalter
Department of Biological Sciences
St. John's University, Jamaica, New York 11439, U.S.A.
stalterr@stjohns.edu

Joseph Rachlin
Department of Biological Sciences
Lehman College, CUNY, 250 Bedford
Park Blvd W, Bronx, New York 10468, U.S.A.

John Baden
U.S. Corp. of Engineers, Retired
2533 Oleander Drive, Wilmington, North Carolina 28403, U.S.A.

ABSTRACT

The vascular flora identified in 1968–1969 in three rice fields of the Winyah Bay Estuary at the Bell W. Baruch Institute for Marine Biology and Coastal Research, Georgetown County, South Carolina, abandoned in 1915, was compared with the vascular flora present in 1987–1991 and 2013–2015. Twenty vascular plant species were identified in 1968–1969 and 22 in 2013–2015 at the most saline marsh, Thousand Acre Rice Field. Forty-seven taxa were reported at Airport Marsh in 1968–1969 and 27 in 2013–2015. Fifty-six taxa were reported at Alderly in 1968–1969 with 41 identified there in 2013–2015. A parsimony algorithm was used to evaluate the distribution and co-occurrence of vascular brackish marsh species in these fields sampled at the three intervals. There was a reduction in flora at the two least saline sites, Alderly and Airport Marsh, from 1968–69 to 1987–91 and 2013–2015. Three factors—rising sea level, an increase in water salinity, and invasion by *Phragmites australis*—may explain this shift. There was also a shift in the flora at Thousand Acre Rice Field from 1967–1969 to 1987–1991 and 2013–2015 after the marsh was savaged by Hurricane Hugo in 1989. Invasion by non-native *Phragmites australis* at all sites and increase in water salinity at all sites best explain the reduction in vascular plant species at Airport Marsh and Alderly over the 47-year collection period.

Key Words: vascular flora, abandoned rice fields, parsimony analysis, Georgetown, South Carolina

RESUMEN

La flora vascular identificada entre 1968–1969 en tres campos de arroz del estuario de la bahía de Winyah en el Instituto Bell W. Baruch de Biología Marina e Investigación Costera, condado de Georgetown, Carolina del Sur, abandonados en 1915, se comparó con la flora vascular presente en 1987–1991 y 2013–2015. Veinte especies de plantas vasculares fueron identificadas en 1968–1969 y 22 en 2013–2015 en el pantano más salino, el Campo de Arroz de Mil Acres. Cuarenta y siete taxones fueron reportados en Airport Marsh en 1968–1969 y veintisiete en 2013–2015. Cincuenta y seis taxones fueron reportados en Alderly en 1968–1969 con 41 identificados en 2013–2015. Se utilizó un algoritmo de parsimonia para evaluar la distribución y co-ocurrencia de especies de marismas salobres vasculares en estos campos muestreados en los tres intervalos. Hubo una reducción en la flora en los dos sitios menos salinos, Alderly y Airport Marsh, de 1968–69 a 1987–91 y 2013–2015. Tres factores—aumento del nivel del mar, aumento en la salinidad del agua, y la invasión de *Phragmites australis*—pueden explicar este cambio. También hubo un cambio en la flora en el Campo de Arroz de Mil Acres de 1967–1969 a 1987–1991 y 2013–2015 después de que el pantano fue salvajemente azotado por el huracán Hugo en 1989. La invasión por *Phragmites australis* no nativo en los sitios estudiados y el aumento de la salinidad del agua explican mejor la reducción de las especies de plantas vasculares en Airport Marsh y Alderly durante el período de recolección de cuarenta y siete años.

INTRODUCTION

Wells (1928) described the plant communities of the coastal plain of North Carolina. Included in his descriptions were the salt marsh community dominated by *Juncus* and *Spartina* and the freshwater marsh community dominated by *Scirpus* and *Typha*. Penfound (1952) described the coastal marsh community as a sedge-rush community where the marsh was inundated by daily tides. Ecological studies of Florida's coastal marshes by Jackson (1952) suggested that salinity was controlled by tidal inundation, rainfall, and evaporation. Hinde (1954) concluded that the vertical distribution of salt marsh taxa along an elevation gradient was related to tide levels. Chapman's (1960) definitive work on salt marshes stressed the importance of salinity, depth and duration of submergence, and interspecific competition as being important factors acting on salt marsh vegetation. Stalter (1968) studied the ecology of salt marsh vegetation on the Baruch Plantation and found that soil and water salinity and depth and duration of flooding were of prime importance affecting zonation of salt marsh

J. Bot. Res. Inst. Texas 15(1): 271–282. 2021
https://doi.org/10.17348/jbrit.v15.i1.1063

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

taxa. His work included transplanting salt marsh vegetation from one marsh zone to another, the first salt marsh taxa transplantation study of its kind (Stalter 1968, 1969). Stalter (1973) examined plant communities of the Cooper River Estuary, South Carolina, along a salinity gradient and noted that vegetation zonation was pronounced in the lower saline portion and indistinct in the slightly brackish and freshwater marshes on the river. Zonation of vegetation was most pronounced at the most saline abandoned rice field marsh at Baruch Plantation, Thousand Acre Rice Field, while there was little difference in zonation among taxa at the less saline Airport Marsh and Alderly (Baden 1971; Baden et al. 1975).

There are a number of long-term coastal vegetation studies including the flora of Sable Island, Canada, from 1899 to 2002 (Stalter & Lamont 2006) and the flora at Orient Beach State Park, New York, 1903 to 1989 (Lamont & Stalter 1991). Stoddart and Fosberg (1981) reported floristic change at the Dry Tortugas, Florida, 1904 to 1977. This paper is valuable since they address the problem of accurately assessing the numbers of taxa reported in various floristic inventories at the Dry Tortugas. They state, "The fact that on all of the islands the total number of native species recorded has increased between 1904 and 1977 we interpret as simply the result of collecting intensity rather than any true increase in the number of native species present." Thus the number of taxa reported at any site may be a reflection on the competence and diligence of the collector, the time spent collecting taxa, seasonality of collecting, and the objective(s) of the study. Stalter and Lamont (2006) reported that when Gussow studied the flora at Sable Island, Nova Scotia, in 1911, he excluded non-native taxa. Stalter and Lamont (2006) reported comparative inventories of the flora of Sable Island; Gussow listed 83 taxa in 1911, Erskine 143 in 1952, Catling et al. 172 in 1981, and Stalter and Lamont 144 in 2002. The comparative studies cited above involved floristic comparisons by two or more different investigators. The present floristic inventory is unique because the flora at the three abandoned rice fields was sampled by the same investigators, Baden and Stalter, over 47 years from 1968 to 2015.

The sites selected for the present study were three abandoned rice fields on the Winyah Bay estuary on the Baruch Plantation in Georgetown County, South Carolina, (now the Belle W. Baruch Institute for Marine Biology and Coastal Research) previously studied by Baden (1971) (Fig. 1) (33.369N, 79.226W). Baden (1971) presented a detailed history of Bernard Baruch's acquisition of rice growing plantations on the Winyah Bay estuary and of rice production on these plantations in his master's thesis. Bernard Baruch purchased rice plantations on Winyah Bay that eventually comprised 17,500 acres (7082.2 ha) in 1905 (Baruch 1957). Commercial rice production ceased at Thousand Acre Rice Field and Alderly by 1905. The last commercial rice was grown in Airport Marsh in 1905 by Harry and Sidney Donaldson (George Chastain, Executive Director, Hobcaw Barony 2019 per. comm.). Baruch continued to use the Airport rice fields for hunting waterfowl (ducks). He deeded his property, Hobcaw, to his daughter, Belle Baruch, whose death preceded his in 1964. Her estate was set up as a Foundation in the State of South Carolina in 1967 with the stipulation that the land be used for biological research (Baden 1971). Research today is conducted on upland sites by scientists at Clemson University while marine science and coastal research are conducted by the University of South Carolina. Factors contributing to the demise of the rice industry in South Carolina were: (1) competition from rice growers in the Gulf States following the War Between the States; (2) labor problems (slave labor was no longer available to work the rice fields at the end of the conflict); (3) depressions of 1873 and 1893; (4) and, most importantly, a series of severe hurricanes, notably a storm-of-a-century in 1893, and additional storms between 1893 and 1911 that destroyed the crops, broke dikes, and ruined fields. Bernard Baruch found rebuilding the rice fields too costly and the fallow rice fields reverted back to natural marsh vegetation (Baruch 1957). While the date of the end of rice growing at Baruch's property is not recorded, it may have occurred as early as 1893, when the site was savaged by the hurricane of 1893, or as late as 1915. The last attempt to grow rice at the sites of the rice fields was in 1915 when portions of the abandoned rice fields were sampled by Alexander (1915).

Alexander (1915) was the first to prepare a floristic inventory of four abandoned rice fields—Strawberry, Friendfield, Marietta, and Bellefield, which are embedded in Airport Marsh. His observations on water salinity as it pertains to the present study are notable, "Except under very unusual conditions the water is entirely fresh."

Some of the fields sampled by Alexander were planted in rice, which was used to bait waterfowl. Alexander

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

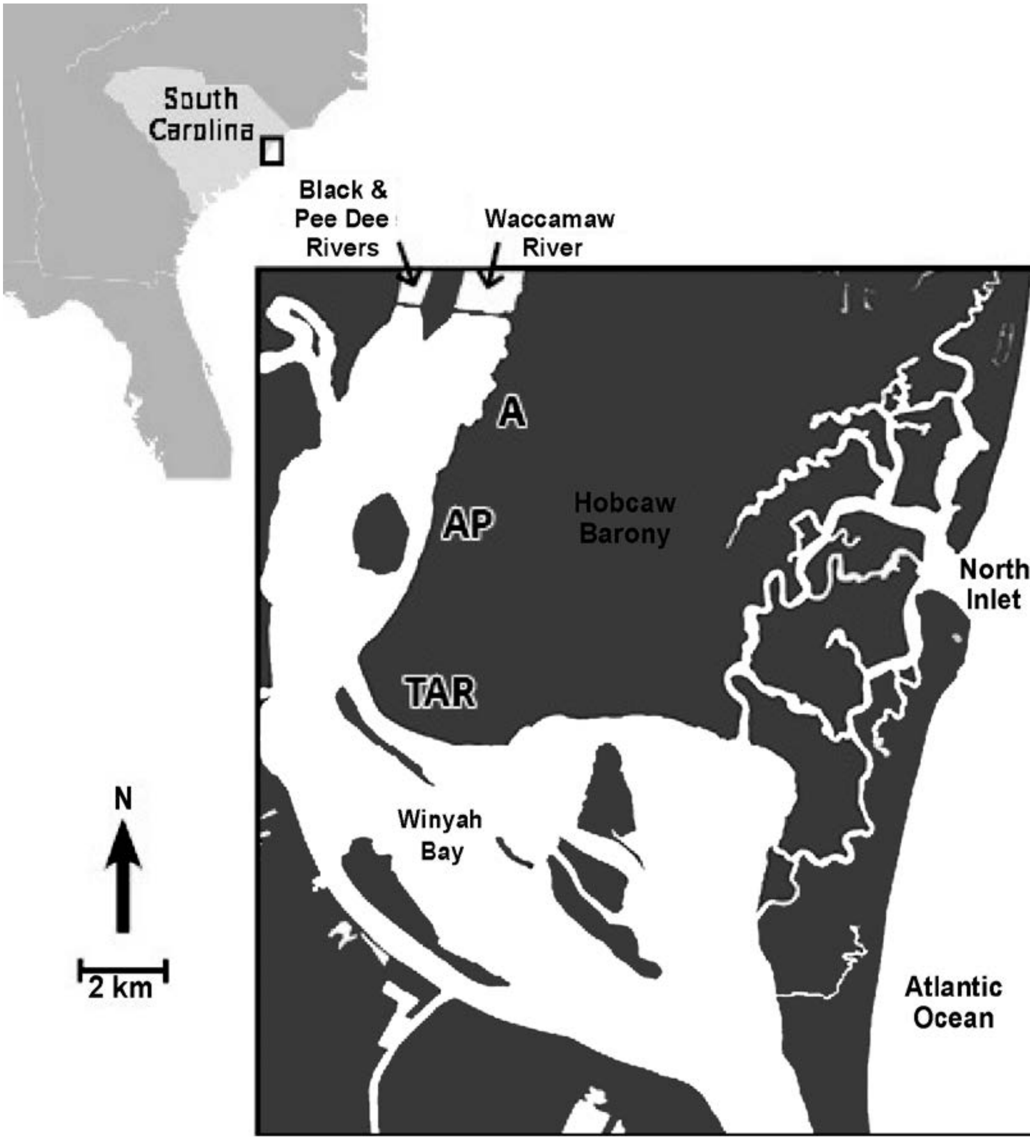

Fig. 1. Map showing the location of the three abandoned rice fields at the Baruch Institute. A = Alderly, AP = Airport Marsh, TAR = Thousand Acre Rice Field. Map prepared by Jennifer Plunket.

(1915) states that the fields at Strawberry were planted in rice in April and May and harvested in August (August 30th in 1915). "The rice is in almost pure stands, with only a little *Echinochloa* intermixed. The heads run 180 to 200 seeds which is a yield of nearly 40 bushels to the acre" (Alexander 1915).

Alexander's Bellefield tract was one of the largest described by him, consisting of eight fields ranging in size from 8.5 to 22 acres. Alexander (1915) states, "They were last planted in rice some 20 years ago," possibly last farmed in 1893, the year the powerful unnamed hurricane savaged the region breaking the dikes necessary for growing rice. The 1893 hurricane was the strongest to strike in the vicinity of Georgetown until powerful Hurricane Hugo, nearly a century later in September 1989.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

Many of the taxa collected by Alexander (1915) are present in the fields today including *Peltandra virginica, Pontederia cordata*, *Scirpus americanus* (*Schoenoplectus pungens*), *Sporobolus cynosuroides* (*Spartina cynosuroides*), *Zizania aquatica*, and *Zizaniopsis miliacea*. Most of these were present when Barry (1968) conducted his studies on the distribution, of taxa at different soil associations at the Baruch Plantation. However, several taxa, notably *Cabomba* sp., *Ceratophyllum* sp., *Najas* sp., *Nelumbo lutea*, *Polygonum carolinensis*, *P. lapathifolium* (*Persicaria lapathifolia*), *P. pensylvanicum* (*Persicaria pensylvanica*), *P. punctatus* (*Persicaria punctata*), *Potamogeton americanus* (*P. nodosus*), and *P. pusillus* were observed exclusively by Alexander (1915).

Hurricanes have had a major impact on rice farming at Baruch Plantation (Baden 1971). Hurricanes could destroy a year's crop, but the longer lasting impact was the destruction of dikes that were necessary for farming rice. Even now, severe hurricane storm surges may inundate the old rice fields with sea water. An additional impact is from the rafts of wrack (dead culms of marsh grasses) that, if left in place for a few months, may smother and kill vegetation. Stalter and Baden (1994) observed huge rafts of vegetation up to one meter thick covering portions of Thousand Acre Rice Field in 1990, a year after storm-of-a-century, Hurricane Hugo. The wrack was colonized by 17 taxa of which nine were those not normally part of the brackish marsh flora. Among these invaders were *Erectites hieraciifolius, Glottidium vesicarium* (*Sesbania vesicaria*), *Panicum amarum,* and *Pinus taeda*. Stalter and Baden (1994) monitored the rafts of wrack at Thousand Acre Rice Field each year following Hugo and noted that the wrack decomposed quickly and within two years was washed away from the marsh by tides. The sites at Thousand Acre Rice Field covered by wrack were repopulated by existing marsh vegetation within five years.

Mean salinity values from Spring 1994 through Fall 2010 at a station at Thousand Acre Rice Field were obtained from http:cdmo.baruch.sc.edu/get/export.cfm. Predictably, lowest salinity values occurred during winters, but not every year. Generally, salinities ranged from 0–5ppt during the winter and 10–15ppt during the fall. Low salinities in the 1990s were correlated with El Nino events during the winters and springs of 1991–2000. Highest salinities occurred during the droughts of 2000–2002 and 2007–2010, peaking at 23 ppt in the summer of 2001 and again during the summer of 2007.

Having previously demonstrated the efficacy of using parsimony analysis as a tool for ecological exploratory analysis (Lambshead & Paterson 1986; Wenzel & Luque 2008; Rachlin et al. 2008, 2017; Rachlin & Warkentine 2012), we applied this technique to evaluate the vascular vegetation community structure at these three abandoned rice fields with varying salinity.

The objective of the present study was to record changes in the vascular flora in three abandoned rice fields on the Belle W. Baruch Institute for Marine Biology and Coastal Research, Georgetown, South Carolina, 33.369N, 79.226W, sampled three times over a 47-year period, 1968–69, 1987–1991, and 2013–15. The vegetation was first sampled by Barry (1968) during the growing seasons of 1967–68. He investigated the distribution of vascular plants at different soil associations at the Baruch Plantation, including at the abandoned rice fields. Common brackish marsh taxa were *Lilaeopsis chinensis, Sagittaria lancifolia, Sporobolus cynosuroides* (*Spartina cynosuroides*)*, Typha angustifolia, Zizania aquatica,* and *Zizaniopsis miliacea.*

Baden's master's thesis, "Factors affecting the distribution of abandoned rice fields, Georgetown County, South Carolina," was a more complete study. He investigated the role of tidal flooding, salinity, pH, soil texture, and organic content on species composition in these marshes. Baden (1971) and Baden et al. (1975) concluded that salinity affected species composition at all three sites and that tidal flooding and salinity affected zonation of vegetation at the most saline marsh sampled, Thousand Acre Rice Field.

CLIMATE

Climate data for the rice fields is not available; however, the climate is very similar to nearby Georgetown, South Carolina (Anonymous 1996). At Georgetown, the average January temperature is 8.77°C while July temperature averages 27.1°C. Annual rainfall averages 1368 mm. April is the driest month averaging 64.5 mm while July is the wettest month averaging 180 mm. Thirty-four days of 0°C can be expected during an average Georgetown winter. The growing season lasts 243 days.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

METHODS

Collecting trips to the three abandoned rice fields were initiated by Baden in 1968, continued in 1969, and repeated from 1987 to 1991 and from 2013 to 2015, a period of 47 years. Objectives for each trip included collection of voucher specimens and accumulation of information on abundance and site preference for each species. One complete set of vouchers was deposited in the A. C. Moore Herbarium (USCH), University of South Carolina. Duplicates of Cyperaceae were deposited at Eastern Illinois University. Gordon Tucker (EIU) identified the sedges. Grasses were identified by John Nelson (USCH). Eric Lamont provided assistance with the Asteraceae. The checklist is a combination of the results of three separate studies, the first by Baden in 1968–1969, the second in 1987–1991, and the third in 2013–2015. Coordinates for the three abandoned rice fields are in Table 1. Native status and nomenclature at division, class, family, genus, and species follow Weakley (2015). All species names were confirmed using Weakely (2015) and the Integrated Taxonomic Information System (ITIS) http://www.itis.gov.

Using the station codes in Table 1 as a proxy for the abandoned rice field sites, we constructed a data matrix following Rachlin et al. (2008, 2012) and Rachlin and Warkentine (2012) to confine it to our site. In constructing the data matrices, we coded the presence of a plant species at a particular site as “1”, and the absence of a plant species at a particular site as “0” (Table 2). In this coding scheme, we treated each rice field as if it were a “taxon” and the presence/absence of a plant species as a character state of that “taxon” (Lambshead & Paterson 1986; Wenzel & Luque 2008; Rachlin et al. 2008, 2012, 2017; Rachlin & Warkentine 2012). Table 2 shows the data matrices and lists the codes for each of the vascular plant species examined in this study. All species names were confirmed using Weakely. Once the data matrices were generated, we analyzed them as in the past (Wenzel & Luque 2008; Rachlin et al. 2008, 2012, 2017; Rachlin & Warkentine 2012), using WinClada (Nixon 2002) running over NONA (Goloboff 1993) with “slow or Deltran optimization.” A null station consisting of all zeroes was added to the data sets to root the trees generated. The advantage of this method is that it presents an immediate graphic representation of species associations from which community structure can be quickly realized and evaluated. The analysis groups the rice fields on the basis of the presence of species not on their absence.

RESULTS AND DISCUSSION

Soil: pH and Salinity

Soil organic content and soil fraction.—Organic matter was high at all sites, ranging from 19% to 40% (Table 3). Silt was the largest component of the soil and the percentages of sand, silt, and clay were variable in the soil samples taken from each site. We concluded that organic matter and soil texture did not limit species distribution. pH is not a limiting factor because all plants growing in the three marshes were growing within the same pH range (Table 4). Salinity values were highest at Thousand Acre Rice Field and lowest at Alderly. Salinity values varied widely at all sites and they vary from marsh to marsh and with time. In the earliest study we stated that only the highest salinity values should be considered as a limiting factor to vascular plant species distribution (Baden et al. 1975).

THE STUDY AREAS

Thousand Acre Rice Field

Thousand Acre Rice Field, comprising 220 hectares, was the largest and most saline of our study sites (Table 4). *Sporobolus alterniflorus,* the most flood- and salt-tolerant vascular plant species, occupies the lowest zone of this marsh. Salinity values here are variable—0.0 ppt in the spring during heavy rain and 23 ppt during summer drought (Table 4). *Bolboschoenus robustus*, *Cladium jamaicense, Juncus roemerianus*, *Schoenoplectus pungens,* and *Sporobolus cynosuroides* occupy the upper zones of this marsh. *Phragmites australis*, a conspicuous member of the vegetation in 2017, was not present here during the initial study in 1968 (Appendix).

Airport Marsh

Airport Marsh, comprising 167 hectares, is not as saline as Thousand Acre Rice Field (Table 4). Common

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

Table 1. Coordinates for abandoned rice fields listed from the most saline site, Thousand Acre Rice Field, to the least saline site, Alderly, for parsimony analysis of species co-occurrence from which site-specific species data were obtained.

Site Name	Code	Coordinates
Thousand Acre Rice Field	TAR	33° 17'58.10"N 79° 15'30.03"W
Airport Marsh	AP	33° 20'38.28"N 79° 14'23.43"W
Alderly	A	33° 21'32.14"N 79° 14'14.67"W

Table 2. Species codes used in parsimony analysis for all rice fields.

Root
00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Thousand Acre Rice_Field_1968–69
00000001000000010001000000000100010000110000011100001000000000000000000001101011110001010000
Thousand Acre Rice_Field_1987–91
01001101000000010001001000001000101001100000111000010000011000000100010110000111011101000000
Thousand Acre Rice_Field_2013–15
01000001000000010001000000000100010000010000011100001001000101000100000011000011100010100000
Airport_Marsh_1968–69
00111011101000110010011101001110000011111110111000111100001110010001000110101010001101000110
Airport_Marsh_1987–91
00111011110000010010011000101110000010111101001000110111110110000001010110111010001101000100
Airport_Marsh_2013–15
00111011000000001000000000000011000000000000000111000010110001110000001000110001010001101000110
Alderly_1968–69
00110011111111111010011111011111101010110100010101101011000110111000010111110101000111101111
Alderly_1987–91
10110011100000111100001011010110010000101000111110010110101100110110111111011010011111111110
Alderly_2013–15
10110001000000001100010001101111001000000000001010110101100010010100001011110011101011110111

Table 3. Soil physical factors of the three abandoned rice fields: Thousand Acre Rice Field (TAR), Airport Marsh (AP), and Alderly (A).

	Range of Organic Content (%)	Soil Fraction (%)		
Site		Sand	Silt	Clay
TAR	19–33	24	41	35
AP	25–28	18	58	24
A	24–30	25	52	23

Table 4. Water salinity and pH at the three abandoned rice fields: Thousand Acre Rice Field, Airport Marsh and Alderly.

Site	pH	Salinity (ppt)
Thousand Acre Rice Field	5.0–5.5	0–23
Airport Marsh	5.0–6.0	0–14
Alderly	5.0–5.5	0–9

vascular plant species here were *Bolboschoenus robustus*, *Cladium jamaicense, Sporobolus cynosuroides,* and *Schoenoplectus pungens*. Also present were *Eleocharis* sp., *Phragmites australis*, *Zizania aquatica* , and *Zizaniopsis miliacea*. *Liliaeopsis chinensis* was common here in 1969 and 1991, but was not observed in our study from 2013–2015. *Phragmites australis* is the most common taxon. Zonation of vegetation is less pronounced than the zonation of vegetation at Thousand Acre Rice Field.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

Alderly

Alderly, comprising 71 hectares, is the smallest, least saline, and most species-rich abandoned rice field (Table 5). Common species here were *Bidens laevis*, *Hibiscus moecheutus*, *Iris virginica*, *Orontium aquaticum*, *Peltandra virginica, Pontederia cordata, Sagittaria lancifolia*, *Schoenoplectus pungens, Sporobolus cynosouroides*, and *Typha angustifolia*. *Liliaopsis chinensis* was not observed at Alderley in 2015–2017. *Phragmites australis* is the most common vascular plant species and is increasing in cover (Fig. 2). *Sporobolus alterniflorus*, a salt marsh associate and recent invader, now occupies the most flood-prone portions of Alderly bordering the Waccamaw River.

Parsimony Analysis

Parsimony analysis generated a single tree for each of the data matrices. The Deltran or slow optimization tends to push character states, rice field species, as far up as possible towards the terminal taxa (the three rice fields). In each of the generated trees (Fig. 3), the code numbers above the circles represent the plant species (Table 2) and the numbers below the circles represent presence (1) or absence (0) of the species at that site. Evaluation of the co-occurrence of plant species at a particular terminal taxon (rice field) is accomplished by reading and recording the coded numbers, representing the plant species, from the terminal taxon back to the origin of the tree, taking note of any zeroes below the species code. In this way we compare the co-occurrence of plant species at a particular rice field in 1968–1969, 1987–1991, and 2013–2015. Open circles on the trees indicate that a plant species occurs in more than one rice field. Filled circles on the trees represent plant species either unique to a particular rice field or supporting a clade of rice fields related to each other by the presence of common plant species.

Data regarding the number of vascular plant species are in Table 5. Thousand Acre Rice Field had the fewest number of taxa at all three collecting dates and showed the least amount of change over 47 years (Table 5). Twenty taxa were observed in 1968–69, 29 in 1987–91, and 22 in 2013–2015. The increase in vascular plant species at the second collecting date may be the result of disturbance including wrack deposition and plant colonization on wrack following Hurricane Hugo (Blood et al. 1991). The site lost two species of *Juncus* but gained the invasive *Phragmites australis* and the "tropical" non-native *Eichhornia crassipes*.

Airport Marsh experienced a decline in the number of taxa from a high of 47 in 1968–1969 to 43 in 1987–1991 to 27 in the last survey, 2013/2015. The most notable change in species composition was the invasion of the aggressive *Phragmites australis,* which is gradually replacing native taxa here. *Phragmites* now occupies roughly 50% of Airport Marsh and has colonized the marsh-upland ecotone where many taxa (e.g., *Eleocharis* and *Juncus* spp.) no longer occur (Appendix). *Phragmites* was first reported in South Carolina at the Baruch Plantation marshes in 1973 by Stalter (1975). Dredging at Baruch Plantation may have created favorable habitat for the establishment of *Phragmites*.

Alderly, the least saline abandoned rice field, supported the greatest number of taxa in 1968/1969, 56 (Table 5). The number of taxa declined slightly to 54 in 1987–1991 and significantly to 41 in the latest study, 2013–2015. *Phragmites* is well established at Alderly. Its presence, plus rising water salinity, may account for the decline of taxa here (Fig. 3). Conspicuous along the water's edge near the L.H. Siau Bridge on Rt. 17 over the Waccamaw River is *Sporobolus alterniflorus* a salt marsh associate not present at Alderly during the surveys of 1968–1969 and 1987–1991.

There have been major changes in species diversity at Airport Marsh and Alderly over the 47 year period, 1968 to 2015. The aggressive *Phragmites australis* is now the dominant taxon at both sites. It forms pure stands and occupies the marsh upland ecotone where *Eleocharis engelmannii, E. quadrangulata, Hydrocotyle* sp , *Juncus biflorus, J. coriaceous*, and others were collected at Airport Marsh in 1968. Absent at Alderly in the present study are *Eleocharis* spp. *Juncus* spp., and many more taxa (Table 5).

Water salinity has increased at all sites in the past 100 years, because Alexander (1915) noted, "the flora was entirely a sweet water one, the brackish element being small or negligible." Salinity plays an important role in species distribution at coastal marshes (Johnson & York 1915; Chapman 1960; Stalter 1968; Stalter 1969; Baden 1971; Baden et al. 1975; Blood et al. 1991; Gardiner et al. 1991; Connor & Inabinette 2005). Sea level rose an average of 3 mm/year at Charleston, South Carolina, during the 20th century. Data from Gardiner et al.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

Fig. 2. Invasive *Phragmites australis* bordering the right side of Alderly Ditch at Alderly in 2013. Photo by Paul Kenny.

(1991) and water salinity data by Clemson University scientists at Marietta Ditch draining Thousand Acre Rice Field to the Waccamaw River indicate a rise in water salinity over 47 years. Moreover, the presence of *Sporobolus alterniflorus*, a salt marsh species at Alderly in the most recent collection period is additional evidence of rising water salinity. Its presence at Alderly may account for the decline in the number of taxa (Table 5). As water salinity increases, vascular plant species diversity declines (Stalter 1973; Baden et al. 1975). A slight rise in sea level and a concomitant elevation in water salinity, plus the invasion of *Phragmites australis* in Airport Marsh and Alderly, may best explain their loss of vascular plant diversity.

The advantage of using parsimony analysis to evaluate ecological data is that it permits a graphical visualization of the precise nature of that structure by treating the study sites as if they were taxa and the presence of vascular plants as character states of those taxa (Fig. 3). This visual representation permits a direct reading from the terminal branches of the generated trees back to the base of the tree, all of the rice field plant species present at the terminal site that allows us to see which rice field plant species are unique to a site, which are not, and which grouping of sites share plants. Thus, the community structure of the vascular rice field vegetation is readily discernible and comparisons among rice fields are easily made.

Parsimony analysis has been previously applied to ecological data by Lambshead and Paterson (1986), Rachlin et al. (2008, 2012, 2017), Rachlin and Warkentine 2012), and Wenzel and Luque (2008). In this study, its application is an appropriate, and valid approach to understanding the fine detail of the community structure of vascular rice field vegetation and helps elucidate changes in this structure possibly brought about by rising sea level and a concomitant increase in water salinity. Occurrence of species follows their greater or

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

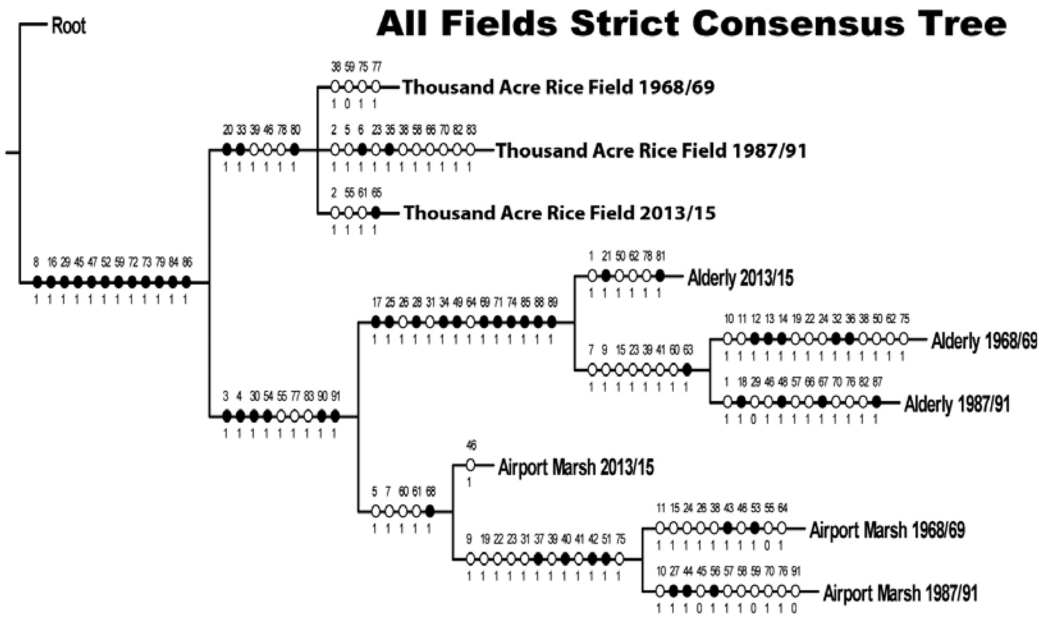

Fig. 3. Trees generated by parsimony analysis. Site codes per Table 2. Closed black circles represent species either unique to a site or uniquely supporting a clade of sites. Open circles represent species not unique to a site or clade. The number above the circles represents the species codes per Table 2. The number 1 or 0 below the circles, indicate the presence (1) of that species or the absence (0) of that species at a particular site.

Table 5. Number of vascular plant species present at Thousand Acre Rice Field, Airport Marsh, and Alderly abandoned rice fields when sampled in 1968–69, 1989–1991, and 2013–2015.

Site Name	Years Sampled		
	1968–1969	1989–1991	2013–2015
Thousand Acre Rice Field	20	29	22
Airport Marsh	47	43	27
Alderly	56	54	41

lesser tolerance to such environmental parameters as annual rainfall, tidal influence, water salinity, soil types, and other edaphic conditions that vary from rice field to rice field over a span of 47 years.

In the Strict Consensus Tree (Fig. 3) there is a clear break between all three abandoned rice fields. The most saline site, Thousand Acre Rice Field, is separated from the two lesser saline sites, Airport Marsh and Alderly. The break (branching) at the most saline site between 1968–1969 and the later studies in 1987–1991 and 2013–2105 is best explained by the impact of Hurricane Hugo. Hugo deposited wrack up to one meter thick on portions of Thousand Acre Rice Field. The wrack was populated by ephemeral vegetation which persisted for a couple of years and then disappeared. However, the vegetation post-Hugo was different than that present prior to the storm.

At Airport Marsh there was a change in vegetation at the site in 2013–2015 as compared to the vegetation present in the two earlier studies. An increase in water salinity, invasion of *Phragmites australis*, and a gradual increase in the water column probably account for a reduction in the number of taxa and changes in species composition. The changes in vegetation were similar at Alderly. Invasion of *Phragmites* and an increase in water salinity brought a reduction in species diversity at this site (Table 5).

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

CONCLUSIONS

There have been major changes in water salinity at the three abandoned rice fields over the past 100 years. When Alexander (1915) conducted his vegetation inventory 100 years ago, "the flora was entirely a sweet (fresh) water one, the brackish, small or negligible." In the past century, a gradual rise in sea level with concomitant rise in water salinity has shifted the flora from primarily freshwater to primarily brackish water species.

There were major variations in vascular plant species composition at Thousand Acre Rice Field, Airport Marsh and Alderly since both Alexander's study 100 years ago and the present study over 47 years (Table 5). These variations consisted in the loss of some species and the gain of others. Each abandoned rice field had its special component of marsh taxa with the most saline, Thousand Acre Rice Field, the least species-rich plant community. There was a shift in species composition in the two least saline rice fields, Alderly and Airport Marsh from 1967–1968 to 1987–1991 to 2013–2015. The presence of the salt marsh taxon *Sporobolus alterniflorus* at the least saline marsh, Alderly in 2013/2015 indicates a rise in water salinity at this site over 47 years. With a predicted sea level rise during this century, further impacts on these rice field vegetation communities is anticipated.

APPENDIX
Annotated Checklist of Species

The vascular plant taxa found at three abandoned rice fields have been arranged according to the following categories: Pteridophytes, gymnosperms, angiosperms (dicots and monocots). Within each category, families and lower taxa are arranged alphabetically. Nomenclature primarily follows Weakly (2015). Numbers following each species indicate abandoned rice field. 1=Thousand Acre Rice Field, 2=Airport Marsh, 3=Alderly. Each entry includes the following information sequence: scientific name, pertinent synonyms enclosed in brackets, asterisk for non-native species.

PTERIDOPHYTA

Osmundaceae
Osmunda spectabilis Willd., –2

PINOPHYTA

Taxodiaceae
Taxodium distichum L.C. Rich., –1,2,3

MAGNOLIOPHYTA-MAGNOLIOPSIDA

Amaranthaceae
Alternanthera philoxeroides (Mart.) Griesb., –3*
Amaranthus cannabinus J.D. Sauer, –2,3

Araliaceae
Hydrocotyle umbellata L., –3

Apiaceae
Eryngium aquaticum L., –2,3
Hydrocotyle verticillata L., –2
Lilaeopsis chinensis (L.) Kuntze, –1,2,3
Ptilimnium capillaceum (Michx.) Raf., –2
Sium suave (L.) Walter, –3

Asteraceae
Baccharis halimifolia L., –1,2
Bidens laevis (L.) Britton, Sterns, & Poggenb., – 2,3
Eupatorium album L., –2
Eupatorium pilosum Walter, –3
Iva frutescens L., –1
Mikania scandens (L.) Willd., –3
Pluchea camphorata (L.) DC., – 2,3,
Pluchea foetida (L.) DC., –1,2
Solidago sempervirens L. subsp. mexicana (L.) Semple var. mexicana (L.) Fernald [S. sempervirens L. var. mexicana], –1,2,3
Symphyotrichum subulatum (Michx.) G.L. Nesom, –1,3
Symphyotrichum tenuifolium (L.) G.L. Nesom [Aster tenuifolius L.], –1,2,3
Verbesina occidentalis (L.) Walter, –3

Chenopodiaceae
Chenopodium album L., –3

Convolvulaceae
Ipomoea sagittata Poir., –1

Cuscutaceae
Cuscuta campestris Yunck., –3

Fabaceae
Chamaecrista fasciculata (Michx.) Greene, –2.3

Gentianaceae
Sabatia calycina (L.) Heller, –1,3
Sabatia stellaris Pursh, –3

Lamiaceae
Amorpha fruticosa L., –1,2

Lythraceae
Lythrum lineare L., –1,2

Malvaceae
Hibiscus moscheutos L., –2,3

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

Nymphaeaceae
Nuphar sagittifolia Walter (Pursh), –3

Plantaginaceae
Bacopa monnieri (L.) Wettst., –3

Polygonaceae
Persicaria hydropiperoides (Michx.) Small, –2
Rumex verticillatus L., –2

Pontederiaceae
Eichhornia crassipes (Mart.) Solms., –3*
Pontederia cordata L., –2,3

Primulaceae
Samolus parviflorus L., –1

Rubiaceae
Cephalanthus occidentalis L., –2,3

Saururaceae
Saururus cernuus L., –1,3

Verbenaceae
Phyla lanceolata (Michx.) Greene, –2

MAGNOLIOPHYTA (MONOCOTS)

Alismataceae
Sagittaria lancifolia L., –3
Sagittaria sp., –2

Amaryllidaceae
Crinum americanum L. var. americanum, –3
Hymenocallis crassifolia Herb., –3

Araceae
Orontium aquaticum L., –3
Peltandra virginica L., –2,3

Arecaceae
Sabal minor (Jacq.) Pers., –1

Cyperaceae
Carex spp., –2,3
Bolboschoenus robustus (Pursh) Soják [Scirpus robustus Pursh], 1,2,3
Cladium jamaicense Crantz, –1,2,3
Cyperus spp., –2,3
Eleocharis engelmannii Steud., –1,2
Eleocharis quadrangulata (Michx.) Roem. & Schult., –2,
Fimbristylis castanea (Michx.) Vahl, –1,2,3
Rhynchospora colorata (L.) H. Pfeiff., –3
Rhynchospora sp., –3
Schoenoplectus pungens (Vahl) Palla, –1,2,3
Scirpus cyperinus L., –3

Iridaceae
Iris virginica L., –3

Juncaeae
Juncus acuminatus Michx., –3
Juncus articulatus L., –2
Juncus biflorus Elliott, –1,2,3
Juncus coriaceus Mack., –1,2,3
Juncus dichotomus Elliott, –2
Juncus effusus L., –2,3
Juncus marginatus Rostk., –2
Juncus megacephalus M.A. Curtis, –2
Juncus nodosus L., –2
Juncus roemerianus Scheele, –1,2,3

Orchidaceae
Spiranthes odorata (Nutt.) Lindl., –3

Poaceae
Arundo donax L., –2,3*
Chasmanthium latifolium (Michx.) Yates, –3
Chasmanthium laxum (L.) Yates, –3
Cinna arundinacea L., –2
Distichlis spicata (L.) Greene, –1
Echinochloa crusgalli (L.) P. Beauv., –2,3*
Erianthus giganteus (Walter) P. Beauv., –3
Panicum virgatum L., –1,2,3
Paspalum distichum L., –2
Phragmites australis (Cav.) Trin. ex Steud., –1,2,3
Setaria magna Griseb., –1,2,3
Sporobolus alterniflorus (Loisel.) P.M. Peterson & Saarela [Spartina alterniflora Loisel.], –1,3
Sporobolus cynosuroides L. [Spartina cynosuroides (L.) Roth], –1,2,3
Sporobolus pumilus (Roth) P.M. Peterson & Saarela [Spartina patens (Aiton) Muhl.], –1
Tripsacum dactyloides L., –3
Zizania aquatica L., –2,3
Zizaniopsis miliacea (Michx.) Dõll & Asch., –2,3

Typhaceae
Typha angustifolia L., –1,2,3
Typha domingensis Pers., –3
Typha latifolia L., –3

ACKNOWLEDGMENTS

We wish to thank Dennis Allen, Assistant Director, Belle W. Baruch Institute for Marine Science and Coastal Research, for granting collecting permits, for providing us with general information on water salinity, and providing a vehicle and a boat, which were used in collecting forays at the Institute; Paul Kenny, Baruch Institute, who provided us with boat transportation; the late Steve Hutchinson, Baruch Institute, who provided us with salinity data for the Winyah Bay Estuary; Eric Lamont for identifying the Asteraceae; the late Steve Clemants, Brooklyn Botanical Garden, for identifying *Juncus*; Robert Nazci, New York Botanical Garden, and John Nelson, USC Herbarium, for identifying several taxa; Gordon Tucker (EIU) for identifying Cyperaceae; Georgia Angelopoulos, Eleni Franxhi, Meryem Toppa, Sabrina Truc, and Kimarie Yap, undergraduate research students at St. John's University, and St. John's University for purchasing herbarium supplies.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

REFERENCES

Alexander, C.P. 1915. Report #8 on the aquatic flora of South Carolina in relation to the food of water fowl. Unpublished report.

Anonymous. 1996. Weather America. Toucan Valley Publications, Inc., Millpita, California, U.S.A.

Baden, J. 1971. Tidal marsh vegetation on abandoned rice fields, Winyah Bay, Georgetown, South Carolina. M.S. thesis. University of South Carolina, Columbia, U.S.A.

Baden, J., W.T. Batson, & R. Stalter.1975. Factors affecting the distribution of vegetation of abandoned rice fields, Georgetown County, South Carolina. Castanea 40:171–184.

Barry, J.M. 1968. A survey of the native vascular plants of the Baruch Plantation. Georgetown, South Carolina. M.S. thesis. University of South Carolina, Columbia, U.S.A.

Baruch, B.M. 1957. Baruch: My own story. Henry Holt and Co., New York, New York, U.S.A.

Blood, E.R., P. Anderson, P.A. Smith, C. Nybro, & K.A. Ginsberg. 1991. Effects of Hurricane Hugo on coastal soil solution chemistry in South Carolina. Biotropica 23:348–355.

Chapman, V.J. 1960. Salt marshes and salt deserts of the world. The University Press, Aberdeen, Scotland.

Conner, W.H. & L.W. Inabinette. 2005. Identification of salt tolerant baldcypress (*Taxodium distichum* (L.) Rich. for planting in coastal areas. New Forests 29:305–312.

Gardner, L.R., E.R. Michener, T.M. Blood, D.J. Williams, M.E. Llosco, & W. Jefferson. 1991. Ecological Impact of Hurricane Hugo-salinization of a coastal forest. J. Coastal Res. Spec. Issue 8:8301–8317.

Goloboff, P.A. 1993. NONA, Version 2, Published by the author. Tucuman, Argentina. Integrated taxonomic information system (ITIS) http://www.itis.gov. Accessed 15 June 2015.

Hinde, H.P. 1954. The vertical distribution of salt marsh phanerogams in relation to tide level. Ecol. Monogr. 24:209–225.

Jackson C.R. 1952. Some topographic and edaphic factors affecting plant distribution in a tidal marsh. Quart. J. Florida Acad. Sci. 15:137–145.

Johnson, M.S. & H.H. York. 1915. Relation of plants to tide levels. Carnegie Institution of Washington, Publication No. 206. Washington, D.C., U.S.A.

Lambshead, P.J.D. & G.L.J. Paterson. 1986. Ecological cladistics: An investigation of numerical cladistics as a method for analyzing ecological data. J. Nat. Hist. 20:895–909.

Lamont, E.E. & R. Stalter. 1991. The vascular flora of Orient Beach State Park, Long Island, New York. Bull. Torrey Bot. Club 118:459–468.

Nixon, K.C. 2002. WinClada, Version 1.00.08. Published by the author, Ithaca, New York, U.S.A.

Penfound, W.T. 1952. Southern swamps and marshes. Bot. Rev. (Lancaster) 18:413–446.

Rachlin, J.W., R. Stalter, D. Kincaid, & B.E. Warkentine. 2012. Parsimony analysis of east coast salt marsh plant distributions. N. E. Naturalist. 19:279–296.

Rachlin, J.W., R. Stalter, D. Kincaid, & B.E. Warkentine. 2017. The effect of Superstorm Sandy on salt marsh vascular flora in the New York Bight. J. Torrey Bot. Soc. 144:40–46.

Rachlin, J.W. & B.E. Warkentine. 2012. An evaluation of fish assemblages of the Saw Mill River, New York: An urban stream. N. E. Naturalist. 19:129–142.

Rachlin, J.W., B.E. Warkentine, & T. Pappantoniou. 2008. Use of a parsimony algorithm as a method for evaluating ichthyofaunal distribution and co-occurrence in an urban stream. J. Freshwater Ecol. 23:1–11.

Stalter R. 1968. An ecological study of a South Carolina salt marsh. Ph. D. dissertation. University of South Carolina. Columbia , U.S.A.

Stalter, R. 1969. Transplantation of salt marsh vegetation, Georgetown County, South Carolina. Ecology 50:1087–1089.

Stalter, R. 1973. Factors influencing the distribution of vegetation of the Cooper River Estuary. Castanea 38:18–24.

Stalter, R. 1975. *Phragmites communis* in South Carolina. Rhodora 77:159.

Stalter, R. & J. Baden 1994.A twenty year comparison of vegetation of three abandoned Rice Fields, Georgetown County, South Carolina. Castanea 59:69–77.

Stalter, R. & E.E. Lamont. 2006. The historical and extant flora of Sable Island, Canada. J. Torrey Bot. Soc. 133:362–374.

Stoddart, D. & F.R. Fosberg. 1981. Topographic and floristic change, Dry Tortugas, Florida, 1904–1977. Atoll Res. Bull. No. 253:1–55.

Weakley, A.S. 2015. Flora of the southern and mid-Atlantic States. www.herbarium.unc.edu/FloraArchives/WeakleyFlora 2015-05-29.pdf. Accessed 18 December 2017.

Wells, B.W. 1928. Plant communities of the coastal plain of North Carolina and their successional relations. Ecology 9:230–242.

Wenzel, J.W. & G.M. Luque. 2008. Parsimony analysis of ecological succession, a powerful tool for interpreting changes in community structure. Cladistics 24:746–757.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.