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ON THE  
NATURAL HISTORY OF THE  
BAHAMAS**

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# PRELIMINARY STUDIES OF SUCCESSION OF WETLAND PLANT COMMUNITIES IN BAHAMIAN SINKHOLES

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## ABSTRACT

A large number of sinkholes are present on the north end of San Salvador Island, Bahamas in the Line Hole Settlement region. During July 2000, we initiated studies to investigate vegetation composition and replacement of wetland, herbaceous plant assemblages in sinkholes. The vegetation of the Line Hole Settlement region is classified as Blacklands (Coppice). Although this vegetation type is characterized by a diverse assemblage of woody species, no group of woody taxa can be recognized as being dominant. Five sinkhole communities were selected representing different stages of succession. Transect sampling was employed to determine species composition in each sinkhole. A longitudinal transect was run and a second series of measurements were taken across the width of the sinkhole. Importance values (relative coverage + relative density + relative frequency) were calculated for wetland herbaceous species. Based on our results, we noted that classic hydrate succession does not occur in sinkhole communities. Observed wetland communities dominated by *Pluchea carolinensis*, *Paspalum laxum*, and *Eleocharis* (emergent vegetation) were surrounded by *Phyla nodiflora* and *P. stoechadifolia*. If water regresses from the sinkhole, *Phyla stoechadifolia* will completely replace other plant species. Continued sampling of sinkhole communities on the island will provide data necessary for documenting allogenic successional changes driven by rainfall. In particular, it will be valuable to have

a long-term data set so that it can be determined if succession is cyclic. Anthropogenic factors no doubt influenced succession of wetland plant communities in sinkholes. Water withdrawal coupled with agricultural activities and use of sinkholes as livestock watering areas no doubt influenced the water level of these sinkholes and thus plant community composition. In particular, the major factors influencing wetland communities would be the duration and depth of waters. The influence of the width to depth ratio of sinkholes in community succession will also be evaluated.

## INTRODUCTION

Succession has broadly been defined as a change of community structure over time (Smith 1995). Classic definitions of succession (e.g. Clements 1916) often state that the process consists of a unidirectional series of sequential changes ending with a climax community. In regards to aquatic succession, some studies (e.g. Carpenter 1980) describe the process as having three characteristics. First, the body of water is oligotrophic during the initial stage of succession and becomes eutrophic in later stages of succession. Secondly, the amounts of sediments and organic matter within the basin increase with each successional stage. Finally, a procession of communities is typically described starting from pondweeds to emergent vegetation and ending in grassland. This kind of succession, where the plant communities themselves largely bring about changes in community structure, is called autogenic succession. In other cases, aquatic succession

has been documented as a cyclic process driven not only by autogenic changes, but also by allogenic factors such as rainfall (van der Valk 1981).

In the summer of 2000 the authors initiated studies to investigate the patterns of succession exhibited by aquatic-wetland herbaceous plant communities present in the Line Hole area in the north portion of San Salvador Island, Bahamas (Figure 1). Lehnert and colleagues (1997) previously conducted an analysis of vegetation in the region to determine if karst features have influenced the vegetation growth. The results of their study found no significant difference between woody plant communities in karst and non-karst areas. Lehnert and colleagues (1997) also recognized that the complex vegetational composition and disturbance history of the Line Hole area make determination of the original relationship between karst features and plant communities difficult to determine. One of the significant

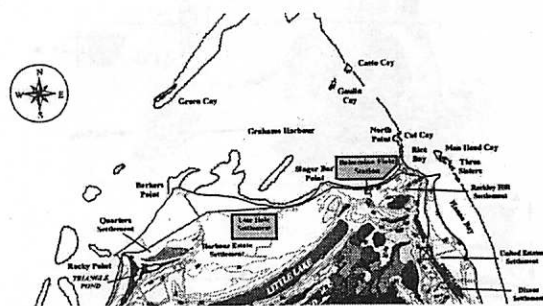
series of plant communities from shallow karst features to aquatic and wetland communities occupying sinkholes. For this preliminary study we selected five communities that appeared to be at different stages of succession. The results will provide a baseline for obtaining temporal data for our continuing studies of freshwater aquatic and wetland communities occupying karst features.

### GEOLOGIC, HYDROLOGIC AND KARSTIC FEATURES OF SAN SALVADOR

San Salvador Island is a carbonate platform island approximately 15km by 8 km. The lithology of San Salvador is comprised of Holocene and Pleistocene beachrock, reef rock and cross-bedded eolianite units.

Many studies (Davis and Johnson 1989, Vacher and Bengtsson 1989, Erdman *et al.* 1997) have been undertaken to study the groundwater flow in San Salvador but a true hydrologic model has not yet been fully developed. The high secondary porosity of the limestone karst terrain on San Salvador precludes the existence of flowing surface water even with the estimated 1024 mm of average yearly precipitation (Foos 1994). Another important reason for this is the very high rate of evaporation, calculated at 1428 mm (Foos 1994). The fresh-water lenses on San Salvador are discontinuous and eventually drain by seep conduits into the saline inland lake system (Davis and Johnson 1989). Vacher and Bengtsson (1989) calculated that most of the groundwater residence time on San Salvador to be on the order of less than 10 years with all freshwater passing through in less than 75 years.

Geomorphologically, the land surface on San Salvador exhibits many different types of karstic features. Karst is a terrain underlain by limestones in which the topography is chiefly formed by the dissolution of rock and characterized by karren, dolines, subterranean drainage and caves (Monroe 1970). Many of the surface rocks of San Salvador exhibit deep channels or furrows caused by solution (karren). Dolines or sinkholes are also a dominant feature on the island. A doline (sinkhole is the preferred terminology in the US), as used here, is a basin



**Figure 1.** Map of the northern portion of San Salvador Island, showing location of the study site. (Modified after Robinson, M.C. and Davis, R.L. 1999).

insights provided by this first study was the importance of understanding successional history in accessing the relationship between plant communities and karst features. Aquatic and wetland plants provide an excellent starting point for examining succession in relation to karst features. Unlike woody taxa, the herbaceous taxa occupying sinkholes are less diverse, and water depth and duration will dictate the taxa present. This study focuses on a

or funnel shaped hollow that ranges in size from a few meters to a kilometer in width and a few meters to hundreds of meters in depth (Monroe 1970). Sinkholes can be either a solution or a collapse feature. In the subsurface there exist a large number of caves, conduits and shafts. Mylroie and Carew (1995) have subdivided Bahamian sinkholes into two types; pit caves and banana holes. For Mylroie and Carew (1995) pit caves are vertical shafts with width to depth ratios of  $<1.0$  formed by the dissolution of descending meteoric water from the epikarst, while banana holes are isolated globular chambers that collect organic matter with depth to width ratios  $>1.0$  formed by the collapse of a phreatic cave.

### DESCRIPTION OF STUDY SITES AND METHODS

Sinkholes containing lentic communities were measured using standard pace and compass techniques. The large sinkhole off Line Hole Road (Figure 2) is in a cross-bedded eolianite. It is elongated and the long axis trends N50E with a maximum length of 27 meters. Its width to

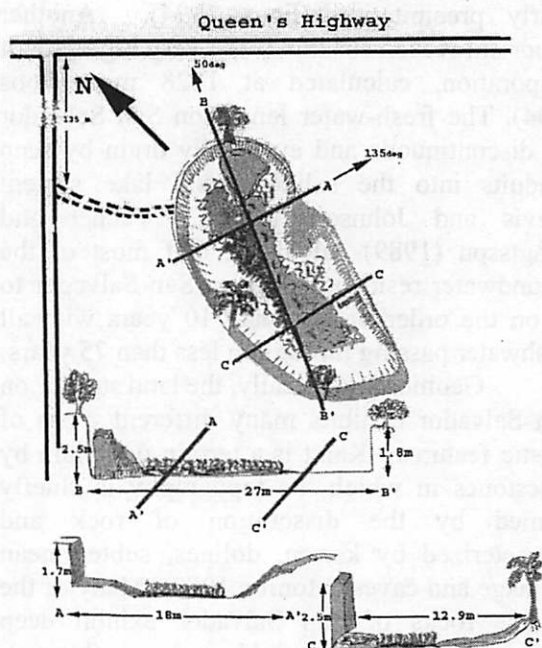


Figure 2. Map of sinkhole off Line Hole Road.

depth ratio is 9:1. There is a plantation well on the SSE section that is always filled with water. The sinkhole has steep walls except for the WSW quadrant. It has been extensively modified for agricultural use. The large double-chambered sinkhole (Figure 3) on the road adjacent to Line Hole Road is flat-bottomed and debris filled. The almost circular chambers (9.95m by 10.5 m and 9 m by 8 m) are surrounded by steep vertical walls. This sinkhole has also been modified by agricultural use as shown by the wall enclosure, possibly an animal pen, (J. Winter, pers. comm.) on the SW side.

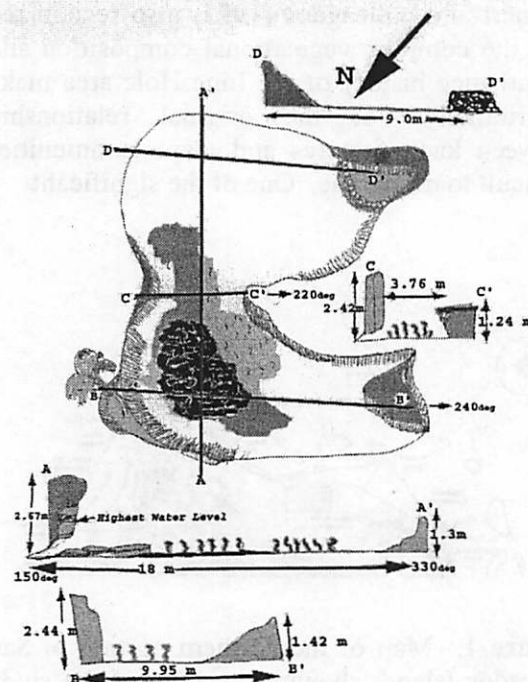


Figure 3. Map of double chambered sinkhole on the road adjacent to Line Hole Road.

This sink shows some of the characteristics that Vacher and Mylroie (1991) indicate for some of the Bermudian-type sinkholes, principally the enlargement of the depression by scarp retreat, vadose processes and cave collapse during glacial low stand of sea level. The numerous solution features, including a  $>1.5$ m long solution channel, would tend to indicate past water table levels.

The line-intercept technique was utilized to determine species composition of three herbaceous plant communities occupying the sinkholes at the main Line Hole and adjacent roads. Measurements were taken at one meter intervals along a transect bisecting the karst feature along its longitudinal axis. The line intercept method is useful in cases where it is difficult to distinguish between individual plants (Becker and Crockett 1973). A number of species present in the sinkhole communities (e.g. both *Phyla* species) reproduce vegetatively and measurements of absolute density cannot be made. The line intercept method enables relative estimates of density to be calculated.

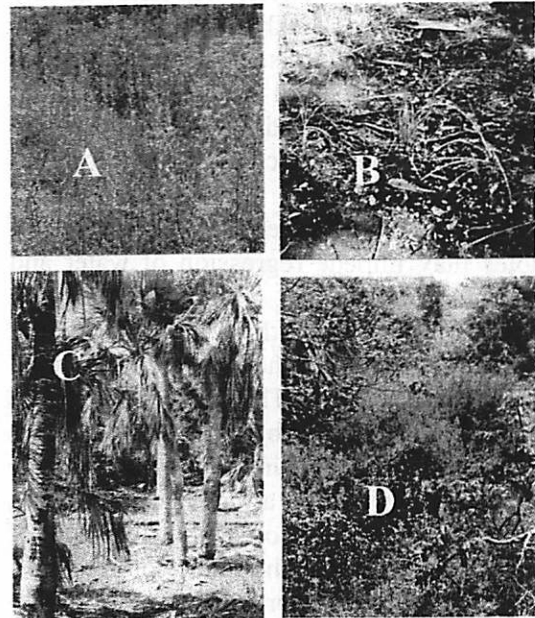
Herbaceous plant communities were sampled 3-13 July 2000. Sampling was not possible during May and June 2001. San Salvador Island experienced an unusual amount of rainfall during May 2001 and the study sites were all flooded.

## RESULTS

Diversity of herbaceous plant species occupying sinkholes is low. A total of ten species were present in the five communities studied. One of these species, *Portulaca oleracea*, was present in the incipient sinkhole (two individuals) but was not represented in the transect sample. *Phyla stoechadifolia* was present at all five sites and had the highest importance value in two of the four sites surveyed. This species is exclusively found on bare limestone outcrops and clearly outcompetes other taxa in sinkholes with little or no standing water. The sinkhole at the end of the road adjacent to Line Hole Rd. contained only *Phyla stoechadifolia* (Figure 4D). Populations of *Pluchea carolinensis* were observed along the edges of standing water within sinkholes (Figure 4A).

Visually, there appears to be differences between herbaceous plant communities in sinkholes with appreciable water and those in dry sinkholes, banana holes and shallow depressions (Figure 4A, B, C, and D). High density species in sinkholes with standing water were *Dichromena colorata*, *Paspalum laxum*, *Phyla stoechadifolia* and *Pluchea carolinensis*

(Table 1). In the absence of water, *P. stoechadifolia* had relative coverage values ranging from 0.25-1.0 (the only species present) and had the highest importance value (0.91-2.3).



**Figure 4.** A- Plant community within Line Hole Road sinkhole dominated by *Paspalum* and *Pluchea*. B-Plant community within double chambered sinkhole. C. Shallow depression located at the end of the road adjacent to Line Hole Road. D. Sinkhole at the end of road adjacent to Line Hole Road containing exclusively *Phyla stoechadifolia*.

Species of *Chamaesyce* tended to increase with decreasing water levels in sinkholes.

Differences also existed between the two sinkholes with lentic systems. The sum total of linear coverage of vegetation (Table 1) is 0.21 for the Line Hole Rd. sinkhole community (Figure 4A) and 0.13 for the second community (Figure 4B). The distribution of plants within the Line Hole Rd. sinkhole is dense, both around and within standing water. In contrast, the second community in the double chambered sinkhole contains plants distributed sparsely within the bottom of the sinkhole. Only one species, *Pluchea carolinensis*, is closely associated with standing water.



Both sinkholes have been impacted by human activity. The Line Hole Rd. sinkhole contains a trough carved into the west wall and a fence just along its northwest perimeter. Livestock have also utilized the pond for water and evidence of their activity was noted in July of 2000. The second sinkhole has been used to dump vehicles and also shows signs of utilization for agricultural purposes. Different sets of disturbances caused by both humans and livestock may be reflected in the present community composition.

Finally, the steep-walled nature of sinkholes may impede regression of water and thus support lentic plant communities longer. The Line Hole Rd. sinkhole has a different profile from that of the double-chambered sinkhole (Figures 2, 3). The double-chambered sinkhole is characterized by steep east and west walls. In contrast, the Line Hole Rd. sinkhole has a steep east wall and a more gently sloping west wall. This may also account for some of the differences between the plant communities. Solution activity is more prevalent in the double-chambered sinkhole than in the Line Hole Rd sinkhole. Differences in canopy cover surrounding sinkholes may retard evapotranspiration and also influence the length of the hydroperiod.

## DISCUSSION

Succession is not a unidirectional process on San Salvador Island. The concept of classic, autogenic succession in lentic communities in temperate regions (e.g. Carpenter 1980) is not a sufficient model for aquatic succession in sinkhole communities. First, lentic systems undergoing autogenic succession fill in with both organic debris and sediment. A true soil with well defined horizons would be present at the final stage of autogenic succession. Plant communities at this successional stage would contain woody species. Although woody taxa surround the rims of sinkholes, no woody taxa occupy the floor of karst features within the study area.

Although there is an abundant supply of detrital material, consisting largely of senescent leaves of *Sabal*, there is no inflow of sediment

particles. Soil formation is not possible without both weathered rock materials and organic matter. Limestone, which would be the parent material for soils on San Salvador, is removed by dissolution and not broken down by physical processes that would contribute the clastic grains needed for true soil formation. The typical terra rossa soil found on limestones is very thin. On a larger scale, the continued dissolution of the doline could prevent a sufficient accumulation of debris to shift a community to the next stage of succession.

Succession of aquatic and wetland communities within sinkholes will only be understood with long term studies integrating climatologic, hydrologic and vegetative data. Smith (1993) observed taxa that are clearly indicative of a more open water habitat (e.g. *Najas*, *Potamogeton*) than those observed during our study. It is not possible to survey all stages of succession during the course of a single field season because succession is driven by changes in water level within sinkholes. In turn, water levels are directly related to precipitation patterns. San Salvador Island has a brief rainy season in September and October (Shaklee 1996). However, isolated months of unusually high precipitation (e.g. May 2001) clearly can increase the water level within sinkholes and return lentic communities to an open water successional stage. Unlike communities in temperate regions, succession of wetland plant assemblages probably follows a cyclic series of successional stages.

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Table 1. Table showing standard vegetation parameters for four sites sampled using transect method.

Double Chambered Sinkhole

Species	Relative Density	Relative Frequency	Linear Coverage	Relative Coverage	Importance Value
<i>Dichromena colorata</i>	0.33	0.30	0.038	0.29	0.92
<i>Pluchea carolinensis</i>	0.22	0.23	0.043	0.32	0.77
<i>Chamaesyce blodgettii</i>	0.25	0.23	0.037	0.27	0.75
<i>Phyla nodiflora</i>	0.14	0.12	0.013	0.099	0.36
<i>Phyla stoechadifolia</i>	0.056	0.12	0.0035	0.026	0.20

Line Hole Road Sinkhole

Species	Relative Density	Relative Frequency	Linear Coverage	Relative Coverage	Importance Value
<i>Paspallum laxum</i>	0.67	0.30	0.036	0.13	1.1
<i>Phyla stoechadifolia</i>	0.150	0.27	0.043	0.36	0.78
<i>Pluchea carolinensis</i>	0.077	0.21	0.11	0.41	0.70
<i>Phyla nodiflora</i>	0.044	0.12	0.023	0.085	0.25
<i>Eleocharis bahamensis</i>	0.056	0.091	0.0038	0.014	0.16

Shallow Karst Depression

Species	Relative Density	Relative Frequency	Linear Coverage	Relative Coverage	Importance Value
<i>Phyla stoechadifolia</i>	0.25	0.23	0.072	0.43	0.91
<i>Phyla nodiflora</i>	0.23	0.30	0.040	0.24	0.77
<i>Polygonum densiflorum</i>	0.33	0.23	0.013	0.074	0.63
<i>Dichromena colorata</i>	0.15	0.12	0.030	0.18	0.45
<i>Chamaesyce blodgettii</i>	0.050	0.12	0.013	0.074	0.20

Banana Hole

Species	Relative Density	Relative Frequency	Linear Coverage	Relative Coverage	Importance Value
<i>Phyla stoechadifolia</i>	0.87	0.61	0.25	0.87	2.3
<i>Chamaesyce hypericifolia</i>	0.070	0.22	0.014	0.048	0.34
<i>Euphorbia blodgettii</i>	0.058	0.17	0.023	0.80	0.30