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MUTATIONS FOR CHLOROPHYLL-DEFICIENCY ("ALBINISM") IN THE RED MANGROVES OF SAN SALVADOR ISLAND: MENDEL'S LAW IN BAHAMIAN SWAMPS

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ABSTRACT

Chlorophyll-deficient ("albino") seedlings of the red mangrove (*Rhizophora mangle*) were found in several locations on San Salvador Island, the Bahamas. Red mangroves are self-fertile and produce viviparous seedlings that remain attached to their parent for many months before dropping off and floating to a location where they can root. The greatest portion of the seedling mass (95%) consists of a conspicuous hypocotyl. Mutations such as chlorophyll-deficiency, which occur during development, are easily seen since the seedlings are large and hang from the ends of branches.

We sampled mangrove populations over an extensive portion of shoreline by canoe and on foot; 11.8 km in Pigeon Creek; and 5.5 km in Great Lake. Pigeon Creek is still open to tides and serves as a control population, while Great Lake is a hypersaline lake in the center of the island, cut off from ocean tides and surrounded by Pleistocene dunes. Viviparous albino seedlings were counted while still attached to 26 parent trees; 578 green seedlings and 186 albinos were found on these trees, giving an average ratio of 3.1 green to 1 white seedling per plant. A 3:1 ratio such as this would be expected according to Mendel's laws if both parents are heterozygous for the same allele controlling albinism. One tree sampled had a ratio of 27 green seedlings to 1 white, and thus appears to be a chimera. In Pigeon Creek we counted 4750 seedlings (both green and white) and found albinos on 14 trees. This gives a mutation rate of 0.0074 mutations per haploid genome per generation (26 times that reported for annual plants), while in Great Lake the mutation rate seemed much higher (0.0563), but more data are needed. Additional mutant seedlings were found in Little Lake, Reckley Hill Pond, Oyster Pond, and a roadside swamp near Fernandez bay. A wide spectrum of hypocotyl color were seen in the field ranging from pure white through yellow, to orange, to bright red.

Seedlings brought back to the University of Massachusetts greenhouse were planted and nearly all, both mutant and green, grew successfully for several months. The majority of mutant seedlings began slowly dying after four months, with some lasting as long as twelve, while all green seedlings continued active growth. The chlorophyll-deficient seedlings were apparently living on stored food in their hypocotyls during this period.

INTRODUCTION

Nearly all genetic studies involving plants are done under the controlled conditions of laboratories, greenhouses, and carefully monitored field plots. When inheritance patterns are documented for certain characteristics, the data obtained are usually the result of crossings in which the histories of each parent and subsequent offspring are carefully recorded. Such approaches are usually impossible in the uncontrolled environments of natural ecosystems, where it is indeed rare to find a plant that exhibits an inheritance for a special trait that can actually be measured in the field. However, when a certain trait follows a Mendelian model and can be easily identified in the field, and analysis of inheritance patterns might be accomplished. This is the care with albinism, or other forms of chlorophyll-deficiency, in red mangrove (*Rhizophora mangle*) seedlings which we recently reported for San Salvador Island (Klekowski and Godfrey, 1989). Albino mangrove seedlings were first described from Florida and Puerto Rico by teas, 1982, and Handler and Teas, 1983, but little further mention is made of them in other mangrove literature.

Determining genetic patterns in wild trees poses special problems not encountered in studying the genetics of bacteria, fruit flies, annual plants, and other organisms with short life cycles. Because perennial plants such as trees, shrubs, and rhizomatous herbs produce new tissues from various meristematic regions that persist throughout the life of the individual genet, the probability that errors might occur in the dividing cells becomes greater with the age of the plant. Such changes give rise to somatic mutations that will persist within the plant's meristem through time, and if not lethal will accumulate as the plant ages. (Klekowski *et al.*, 1968). when such changes occur in long-lived plants, such as trees, a prediction can be made that higher mutation rates per generation are likely to occur in such plants than in short-lived species. The accumulation of such mutations within the growing tissues of perennial plants may create a genetic load that increases as the plant ages, and may be an important factor in the evolutionary process (Muller, 1950; Klekowski, 1988; Charlesworth, 1989; Wiens, *et al.*, 1989).

The reproductive system of *Rhizophora mangle* is unusual in that seedlings germinate while still within the fruit on the tree, a pattern shared by several other mangroves. this habit of vivipary ensures that young seedlings will obtain food subsidies from the parent plant for up to several months before being released into the environment (Sussex 1975, Tomlinson 1986). (See figures in the paper by Kass and Stephens, this publication.)

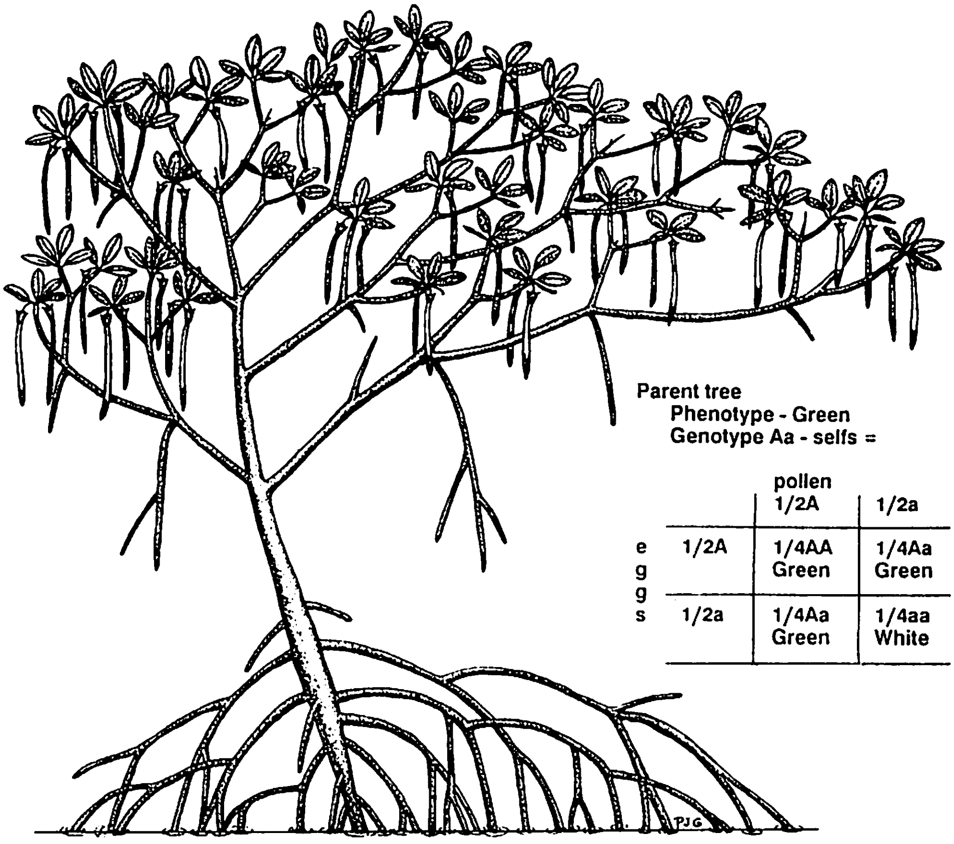
Red mangrove flowers are relatively inconspicuous, with four petals and four sepals. they have been shown to be hermaphroditic, their anthers opening in the bud stage. Soon after opening, the petals are lost. It has been suggested that *Rhizophora mangle* is self-fertilized and also wind-pollinated (Primack and Tomlinson 1980). Our data (Klekowski and Godfrey 1989) support the premise that red mangrove is self-fertile. Insects have been seen within and visiting the flowers of red mangrove, but what role they may have in pollination is unknown at present (our own observations, as well as those of R. Lowenfeld). Since this species is considered self-compatible, it is likely to be much more inbred than other tropical trees. Each flower contains two carpels with two ovules each, only one of which usually grows. As a result, one seedling will emerge from the fruit and grow for six or more months, while still attached to its parent. On occasion, twin seedlings may be produced from one fruit (see Klekowski and Godfrey, 1989, Fig. 1). Flower production and germination are most common during the winter in the Caribbean, and by mid to late summer, seedlings 10 to 25 cm long will be hanging form the trees. By late summer and fall, most seedlings have dropped. However, some flowers and attached seedlings can be found all year in any given location.

Because these unusually large seedlings remain attached to the parent for so long, some classes of mutants will survive and be visible in the field. This is quite unlike the behavior of most other species whose seedlings are small and dependent on stored food within their usually minute seeds for initial growth. Without chlorophyll, albino seedlings will die very soon after germination. *Rhizophora mangle* seedlings, however, are readily seen both on their parents and after they have dropped. While still attached they can be counted and their phenotypic ratios calculated directly. From these data the genotypes of parents and offspring can be determined in the wild.

Chlorophyll-deficiency typically is inherited as a recessive trait. If a mangrove tree is heterozygous (Aa), the self-pollination of this tree will yield the classic 3:1 ratio of green : mutant offspring phenotypes (Fig. 1). Ratios in which the mutant class is different from 25% have a number of possible explanations: 1) the progeny resulted from a mixture of selfing and outcrossing; 2) the mutant embryos were aborted or abscised by the tree; 3) the mutant phenotype is caused by mutant alleles at two gene loci (AaBb) and if only aabb is mutant, then only 1/16 of the offspring will have the mutant phenotype; 4) the tree is a chimera; 5) the so-called mutant embryos are not due to the segregation of mutant alleles but rather are due to stress or pathogen induced developmental alterations in chlorophyll synthesis or degradation. Obviously, little can be concluded from ratios other than 3:1 without further study.

METHODS

As a result of its self-compatibility, self-fertilization and viviparous seedlings, *Rhizophora mangle* is an excellent species to check for the presence of mutations in natural populations. We conducted surveys on foot and by canoe along the shorelines of Pigeon Creek and Great Lake in June and August of 1988. Distance measurements were taken along the shore by means of an optical rangefinder, and specific positions were located on a large scale map by taking compass azimuths to conspicuous landmarks. Sampling locations were marked on a map in the field, and distances later corroborated using a Jandel "Sigma Scan" planimeter with an AT&T PC6300 in the laboratory. Fig. 2 shows the sampling tracks in Pigeon Creek and Great Lake. The shoreline covered in Pigeon Creek was 11.8 km, while in Great Lake it was 5.5 km. Salinities in both



Parent tree
Phenotype - Green
Genotype Aa - selfs =

		pollen 1/2A	1/2a
eggs	1/2A	1/4AA Green	1/4Aa Green
	1/2a	1/4Aa Green	1/4aa White

Seedlings found on parent tree

34 green
ratio 2.83:1
12 white
46

Fig. 1. Diagram of mangrove genetics.

bodies of water were determined with a hand-held AO optical salinometer/refractor. A sample of water from Great Lake was analyzed by the University of Massachusetts Microanalysis Laboratory.

We travelled by canoe as close as possible to the edges of the mangrove communities and scored mature seedlings still attached to parent trees to obtain some measure of frequency of chlorophyll-deficient seedlings. Since most mangrove trees in both areas were less than 3 meters tall, it was relatively easy to survey the entire mangrove front at the water's edge. Where water depths were not sufficient for canoeing, surveys were made on foot. When "mutants" were located, a careful count was made of all seedlings on that tree. The mutants were collected, along with a sample of normal seedlings, and each set was photographed *in situ*, and again at the Bahamian Field Station. Chi-square analyses were made on the date collected from each tree.

Mutant and normal seedlings were returned to the University of Massachusetts where they were grown in a warm greenhouse in the fall of 1988. The plants were placed into plastic pots containing fine-grained soil and kept in tubs of slightly saline water.

Color classes of mutant seedlings were determined by comparing them with standard color charts - Code des Couleurs (Klincksieck and Vallette 1908), and Munsell Color Charts for Plant Tissues (1977).

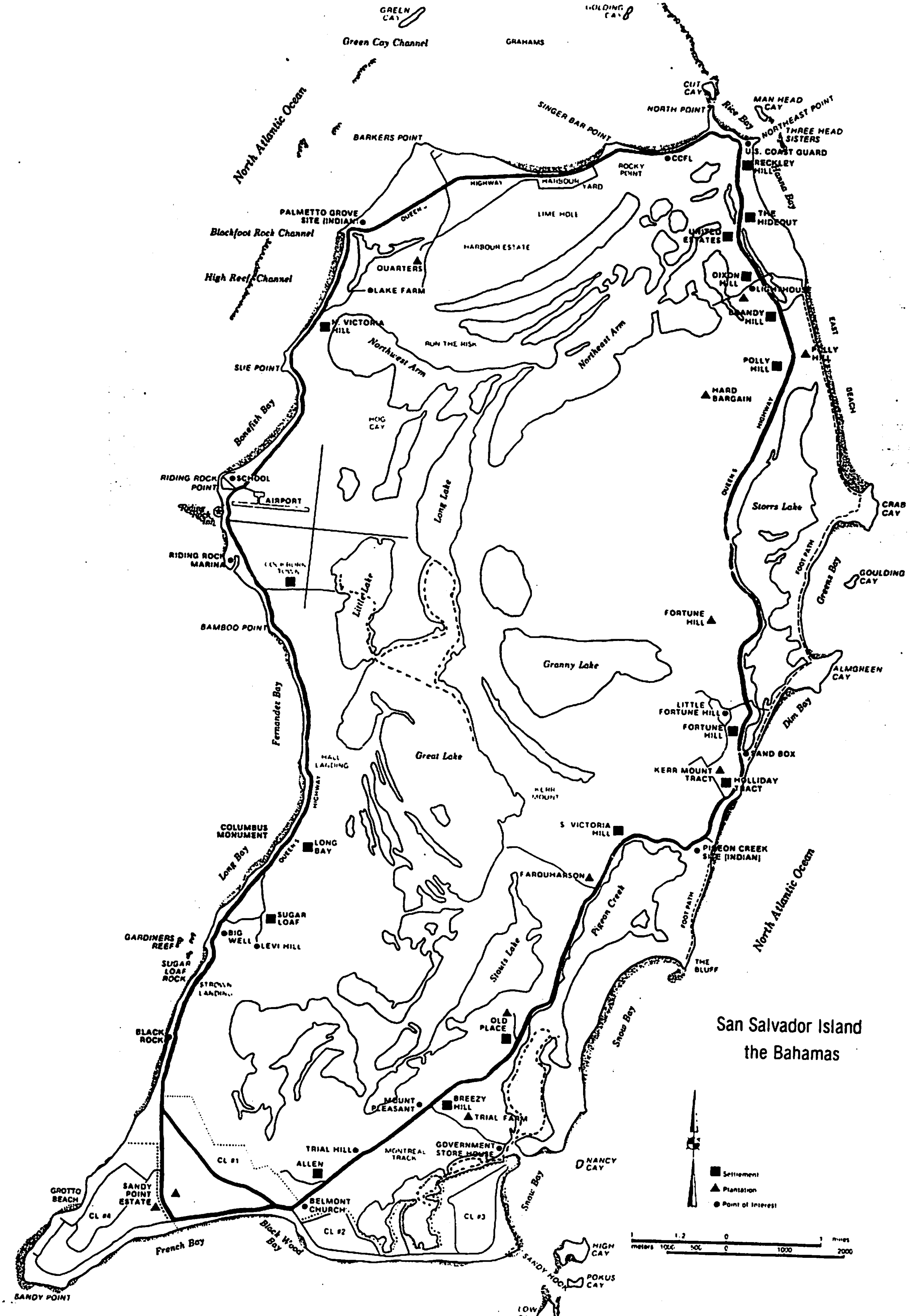


Fig. 2. Map of San Salvador showing mangrove surveys, 1988.

RESULTS AND DISCUSSION

Mutant seedling surveys

Data from Pigeon Creek and Great Lake were published in Klekowski and Godfrey (1989) *Nature* article and will be summarized here. (Colored photograph 1 illustrates the first albino seedling found in Pigeon Creek.) A total of 27 trees were found bearing chlorophyll-deficient seedlings, which range in color from almost pure white to bright yellow, orange, and red. Of these, 23 trees had very low Chi-square values (.01 to .93) when the numbers of green and mutant seedlings ("white") found on each tree were compared to an expected ratio of 3 to 1. The average ratio of green to mutant seedlings for these 23 was actually 3.02 to 1. Three other trees had high Chi-square values (2.3 to 2.95) and may represent chimeras. Even so, when these were included with the previous trees, the overall average ratio of green to mutant was 3.11 to 1. One tree showed a ratio of 27 to 1 (Chi-square = 7.5) and probably was a chimera.

The total number of seedlings counted in our measured sampling tracks in Pigeon Creek was 4,747. These were tallied in groups of 10, with enough distance along the shore before the next group was counted to ensure that individual trees were being sampled. This was necessary because one could not easily separate trees that were close together due to their spreading growth patterns. The approximate number of trees sampled was 475, of which 14 could be classified as heterozygotes. Using the mutation-selection equilibrium equation for the case of complete selfing, a mutation rate of 0.0074 mutations per haploid genome was calculated. This rate is about 25 times greater than values calculated from published data for the annuals *Hordeum vulgare* and *Eagopyrum esculentum* (see Klekowski and Godfrey, 1989). The frequency of heterozygous trees containing the chlorophyll-deficient seedlings to homozygous plants on this particular survey was 2.9 percent. Figure 3 and colored photograph 4 shows the mangrove habitat and examples of mutant seedlings in Pigeon Creek. This habitat is a typical Bahamian coastal lagoon, open to the sea and tidal.

In Great Lake, a hypersaline lake with no opening to the sea, 9 mutant-bearing trees were found out of approximately 40 scored along 5.5 km of shoreline, giving an unusually high frequency of 22.5 percent. Here the number of heterozygous trees per km of shoreline was somewhat higher than in Pigeon Creek: 1.6 versus 1.3. However, unlike Pigeon Creek, the distribution of red mangroves along the shoreline of this salt lake was very spotty, with most trees occurring as individuals rather than in a dense community as in more suitable locations. We found only about 7 trees/km that bore seedlings, while in Pigeon Creek we sampled 40 trees/km within a nearly continuous band of healthy, reproducing *Rhizophora*. The calculated mutation rate for Great Lake was 0.0563 mutations per haploid genome per generation, which was nearly an order of magnitude greater than for Pigeon Creek. These preliminary data suggest that there is a substantially greater occurrence of mutant-bearing trees within the open mangrove community of Great Lake compared to the dense Pigeon Creek vegetation.

The Great Lake mangroves grow on sandy barrier beaches scattered along both sides of the lake, as well as on rocky shores a meter or more above the water level (Fig. 4). In such an unusual location for red mangroves, seedlings apparently started within small depressions in the limestone rock where rain water could accumulate. Trees around the lake are very short, usually not much more than 2 m tall. Those with mutant seedlings were found on the rocks as well as on sandy sites. Mutant seedlings showed a wide range of color types, including bright orange and deep vermillion as well as yellow and white (Fig. 5 and colored photograph 2).

Because there were relatively few samples from Great Lake, further surveys are needed before we can say with confidence that the mutation rate is truly as high as our preliminary data suggest. If it is as high, then we have found an exceptionally mutagenic natural environment. The very short stature of mangroves and their unusual inclination to grow above the actual water level on rocky shores suggests that Great Lake is indeed a severe habitat for even this very salt-adapted species.

During a brief survey in 1989, more trees with mutant seedlings were found in Great Lake, Little Lake, a swamp along the road at Fernandez Bay, Reckley Hill Pond, an Oyster Pond. The new Great Lake tree was located next to ones found during our 1988 survey on "UV Point" with a 3.5:1 ratio of green to mutant seedlings (see the discussion about reproductive variations below). Another tree from Little Lake had long yellow seedlings and a perfect 3:1 ratio (Fig. 6 and

Fig. 3a. Overview of Pigeon Creek mangrove community.

Fig. 3b. First mutant (albino) seedling found in Pigeon Creek.

Fig. 3c. 3:1 ratio on one branch of a tree--seedling was yellow.

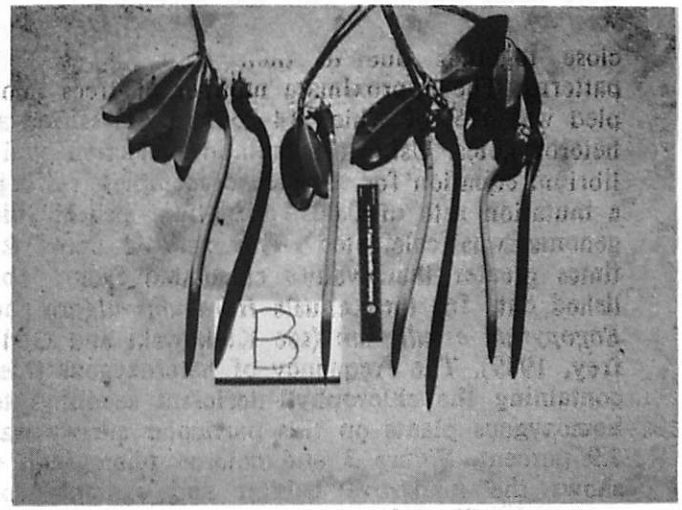


Fig. 3d. Long, yellow mutants (lighter color in photo) from tree B, Pigeon Creek.

Fig. 4a. Beach mangrove community in Great Lake.

Fig. 4b. Rock mangrove community in Great Lake.

Fig. 5a. Red mutant seedlings in Great Lake.

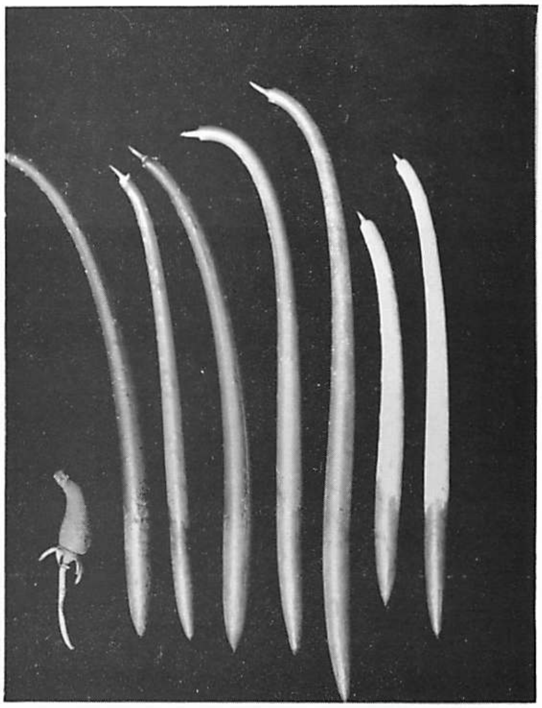


Fig. 5b. Mutant seedlings in Great Lake: right two = yellow, middle two = orange, left three = green.

Fig. 6a. Yellow mutants on tree 89-LL-1, Little Lake, '89.

Fig. 6b. Total collection from tree 89-LL-1.

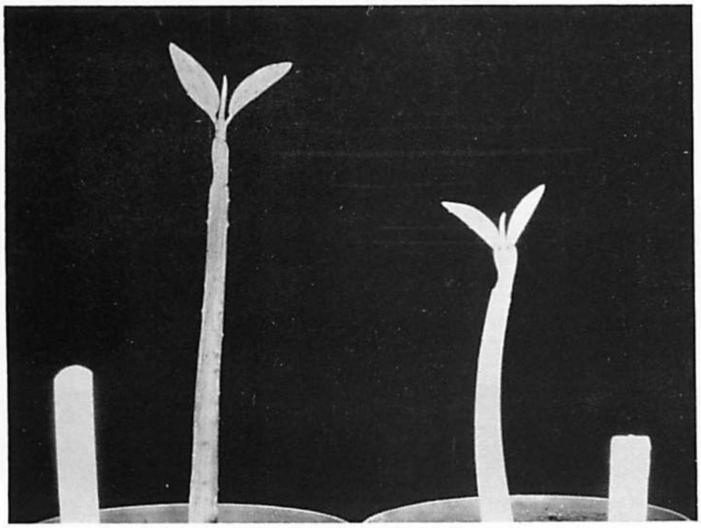


Fig. 7. Mutant and normal seedlings in greenhouse, '88; left, normal; right, mutant.

1

2

3

4

Fig. 1 First Albino seedling found in Pigeon Creek, 1988. *Photo P. Godfrey*

Fig. 2 Red mutant found along shore of Great Lake. *Photo E. Klekowski*

Fig. 3 Yellow mutants found on a tree near Little Lake, Cockburn Town. Ratio of green seedlings to yellow on this tree was exactly 3:1. *Photo P. Godfrey*

Fig. 4 *Rhizophora mangle* vegetation along Pigeon Creek, San Salvador Island, The Bahamas. *Photo P.Godfrey* colored photograph 3). However, a tree found near Fernandez Bay and another in Reckley Hill Pond had seedling ratios that did not fit the expected 3:1 pattern. Any one or combination of the factors described in the introduction might have produced these results.

Salinity

Salinity measurements in Great Lake made with an optical salinometer gave values around 55 ppt on August 19 and 21, 1988. For comparison, salinities in Pigeon Creek a few days before were around 36 ppt. The following is a laboratory analysis of water from Great Lake:

Sodium	37,500	ug/ml	(37.5 ppt)
Magnesium	4,075	"	(4.1 ppt)
Calcium	1,200	"	(1.2 ppt)
Potassium	17,200	"	(17.2 ppt)
Chloride	31,770	"	(31.7 ppt)
Total salts	76,265	"	(76.3 ppt)

This laboratory analysis gave a somewhat higher total salinity than that measured in the field with a refractometer; and the reason for this discrepancy is not known at present. The data show that sodium content was more than 3.5 times that of normal sea water. [Odum (1971) lists sodium content of sea water as 10.7 ppt.]

In June of 1989, refractometer readings in Great Lake ranged between 68 ppt and 70 ppt. There was substantially more rain in the spring of 1988 and this resulted in lower salinity values compared to 1989. Granny Lake and Little Granny Lake, which also have scattered *Rhizophora* trees along their shorelines, were checked in June, 1989, and these had salinities of 95 ppt and 65 ppt respectively. Little Lake, which is attached to Great Lake through a small boat channel, had a salinity of 53 ppt. Red mangroves nearly ring the shore of Little Lake and Occur on both rock and sand substrates in denser communities than in Great Lake. On the eastern shore of Little Lake is a tall and well-developed stand of *Rhizophora* quite unlike those usually seen on San Salvador Island.

Reproductive variations: 1988-89

An important factor which bears on sampling mangrove seedling production was found in June of 1989, when sites surveyed the previous year were rechecked. A tree bearing mutant seedlings was found in Great Lake next to two which had seedlings in 1988, but not a year later. The 1989 sample did not have seedlings the year before. These three trees are probably related, but their genetic connections would not have been noticed had they been sampled only once. In addition, one large tree found along the highway to United Estates near the Navy Dock, which bore mutant seedlings in 1988, did not have any seedlings in 1989. Another 1988 mutant-bearing tree nearby was just beginning to produce seedlings, but none could be identified as abnormal as they embryos were too young. In addition, we found that only about a third of all mangrove trees checked were bearing progeny regardless of genetic types. This suggests that cycles exist in *Rhizophora* reproduction, and should be considered when studying the biology of this species on San Salvador. It is also important to return over several years to sites containing heterozygous trees if one is trying to determine their actual number in the population.

Phenotypic Color Variations

Mutant seedlings were found to show considerable color variations, some of which were consistent on particular trees. It was possible to classify these phenotypes using a standard color chart. The phenotypic variations could be groups within a certain range of shades for each major color series. The following represents an initial classification of mangrove phenotypes by color:

1. True albino: these are pure white, or a shade of white, with no other colors present.
2. Cream or yellow-white: light tinges of yellow mixed with white, which probably could be classed as "albino". Code des Couleurs #78C or D, Munsell 7.5YR 8/6 or 8/4.
3. Crimson series from a deep shade to pink: the crimson or carmine reds are a purer shade compared to orange-reds found in #6 below. Colors on any particular seedling ranged from a deep crimson to light pink, some with a light yellow hue added. Coded des

Couleurs #2, Munsell 2.5R 4/10.

4. Greenish-yellow to yellow: a mixture of light greens and yellows in various hues suggesting the bleaching of chlorophyll as the seedling grows. Pure yellow is shown on the lower portions of the seedling, with greenish-yellow and light green at the fruit. This class proved difficult to score because of low penetrance. Code des Couleurs #251, Munsell ?, and Code des Couleurs #181, Munsell 2.5Y 8/8.

5. Pure yellow: seedlings totally yellow with few, if any other shades, and about the same size as normal plants. This color phase was the most common and easily located among the normal seedlings. Code des Couleurs #181, Munsell 2.5Y 8/8 or 8/10.

6. Orange to deep red: seedlings similar in shape and size to #4 but grading from shades of orange to scarlet or vermillion reds, quite unlike the reds in #3 since they contain yellow pigments. Orange - Code des Couleurs #127, Munsell 5 YR 6/10; red-orange - C. des C. # 102, Munsell 1OR 6/10; red- C. des C. #28, Munsell 5R 5/10.

These different color groupings suggest that many pathways are involved in mutations for color deficiency, as described for barley mutations by Gustafsson (1940). The color groupings above fit into several of his suggested classifications for chlorophyll mutations: Type #1 = I "Albina"; Type #5 = II "Xantha"; Type #4 = IV "Viridis". Some of these phenotypic color variations may also be linked to other abnormal characteristics such as size, shape, time of abscission, and so forth. Further work on pigmentation could lead to a more precise description of the compounds and pathways involved in chlorophyll-deficiency of mangrove seedlings.

It is possible that some of these variations follow the type of Mendelian inheritance we have found while others do not. For example, it is known that the development and enhancement of anthocyanin pigments, which are water soluble and usually located in cell vacuoles, can be caused by environmental stress such as bright light. Tissues containing anthocyanins become redder as levels of light increase, particularly with the shorter wavelengths such as ultraviolet. When chlorophyll is lacking, these pigments become much more visible. Such may be the case for color classes #3 and #6 above. We have observed that even normal seedlings are distinctly reddish-green after they have been attached to their parents for several months.

Greenhouse Experiments

Plants brought back to the greenhouse began growth soon after placement in soil and standing water. Normal seedlings grew well, and after 8 months were about 0.5 m tall, with several sets of leaves. Mutant seedlings also sprouted roots and leaves, and most were still alive after three months, but usually had only one set of leaves (Fig. 7). The mutant seedlings began dying after 3-4 months, and by 8 months nearly all had perished while the controls continued growing steadily. In some cases, albino hypocotyls produced normal leaves, and these plants survived, but only for a time.

Two general categories of mutant phenotypes have been found. All of the mutant seedlings formed by a tree will have either a chlorophyll-deficient hypocotyl and epicotyl, or a chlorophyll-deficient hypocotyl and green epicotyl. The majority of heterozygous trees produced the former, but in three instances trees had embryos with the latter mutant phenotype [trees BB, N, and CC in Klekowski and Godfrey (1989)]. The mutant embryos of BB and N expired after 10 months of growth in the greenhouse. The mutant embryos of CC are still alive after 12 months, but have formed pale green leaves and are growing slowly. The growth characteristics of CC are such that seedlings would probably not survive competition in their natural habitat.

It is clear that substantial food reserves, derived from the parents, were present in the hypocotyls of the mutant seedlings and were able to keep them alive in a warm greenhouse for more than half a year. The nature of these reserves and the metabolism of mutant seedlings deserve further investigation.

History of San Salvador Island and Arrival of *Rhizophora*

San Salvador Island had its beginnings as an atoll during the Pleistocene with several submergences and exposures during this period. The present surface dates back to the Sangamon, when the most recent deposits were exposed (125,000 years B.P.). At this time, sea level was several meters higher than at present. During various stages of emergence and submergence, beaches and dunes were formed in what is now the interior of the island. The dune lines that existed 80,000 - 90,000 years ago have since hardened into limestone, with the intervening low lands between holding saline lakes. As the Wisconsin glaciation began, sea level dropped more than 100 meters, and San Salvador Island stood well above the sea, but was still surrounded by ocean water, unlike some portions of the Bahamas that were connected when sea level was at its low stand. The interior lakes dried up as the island's water table fell in conjunction with the falling sea level. Any mangroves present then would surely have died out, although they may have survived around the outer coastline. With the waning glaciers, sea level rose once again and eventually flooded the interior lowlands, creating the present lake system. The modern shoreline consisting of uncemented beaches and dunes began forming around 5-6,000 years ago. [The description above is based on Titus (1989).]

According to pollen data, *Rhizophora* was present in Granny Lake at least 5,000 years ago (Pacheco and Foradas 1986). Granny Lake is one of the interior salt lakes that was open to the sea during Lake Wisconsin times (about 15,000 years B.P.). The Pigeon Creek system formed within the last 10,000 years (Titus 1986). Present conditions of Pigeon Creek probably date back 3,000 years, and during this period it had only one inlet (Mitchell 1986). This would suggest that the mangroves in Pigeon Creek probably were established more than 3,000 years ago and have been locked in there ever since the barriers formed, with only a minor opportunity for any recruitment through the single inlet. There are no *Rhizophora* populations nearby, so seedlings would have had to arrive over the open sea from a very distant source, and then entered the narrow creek opening. It seems more likely that red mangroves got into Pigeon Creek before the barriers formed. That would mean they arrived prior to 3,000 yrs. B.P., and the population is probably of the same age as that in Granny Lake - at least 5,000 years old. The seedlings probably arrived when this coast of San Salvador was an open system, perhaps like the reefs and mangrove islands that now exist off Central America.

On the other hand, *Rhizophora mangle* populations in the other salt lakes of the interior, such as Great Lake, may be much older than 5,000 years, but if they are there is no evidence as to when they may have colonized these lakes. The geological record shows that unlike Pigeon Creek, these lakes were sealed off from the ocean for thousands of years. There is some evidence that a high stand of sea level might have flooded into the Granny Lake system around 5,000 years ago (Teeter, pers. comm.), allowing *Rhizophora* to enter the lakes at that time. Since red mangrove seedlings must travel by water, there is no way that new recruits could have entered these lakes from the sea, nor could any escape unless the old dune ridges were overtopped.

In any case these mangrove populations have been isolated for a very long time, allowing mutations to accumulate over many generations with no outside source of plants that were free of a heavy genetic load. We would expect to find high mutation rates in such highly inbred, isolated populations. San Salvador Island can provide an excellent opportunity to test the relationships between mutation rates, environmental stress, and the age of plants in the context of the geological history of *Rhizophora* habitats.

CONCLUSIONS

Red mangrove provides a good system for studying inheritance of recessive mutations in the field. Because this species is viviparous and produces large seedlings that remain attached to the parent for months, any deviations from the norm can be readily scored. It is self-fertile with no apparent out-crossing system, and, as a result, retains the recessive allele for chlorophyll-deficiency ("albinism"). Inheritance of this allele follows a Mendelian ratio of 3:1, indicating that trees containing albino seedlings are heterozygous for the recessive gene. Red mangroves possess a higher mutation rate than short-lived plants.

Several different color morphs could be identified - white, carmine red, green-yellow, yellow, orange and vermillion - suggesting that numerous pathways are involved with other abnormal phenotypic characteristics such as size and shape. Greenhouse studies showed that mutant seedlings could survive for many months on stored reserves obtained from the parent tree. This suggests that large quantities of stored materials are present in all seedlings and provide them with a major survival advantage under conditions where they might not be able to root for a relatively long time.

Rhizophora on San Salvador Island goes back at least 5,000 years. Individual populations locked within hypersaline lakes are probably thousands of years old and have not been exposed to external recruitment for a very long time. This would mean that genotypes within the closed saline environments of San Salvador have been accumulating mutations for an equally long time, and we would therefore expect the high mutation rates found. Since this species is so important to the ecology of tropical coastlines, any indications of genetic problems resulting from natural or anthropogenic stress and geological age should be of major concern to biologists.

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