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## Sacrificial leaf hypothesis of mangroves

### Background

Extensive research into the halophytic nature of mangroves has led to as many myths about their physiology as there are documented facts. One of the most common myths is the sacrificial leaf hypothesis. As leaves of *Rhizophora mangle* (red mangrove) develop and mature, the ones farthest from the apical tip turn yellow before abscission. According to the hypothesis, this is an adaptive consequence in which excess salt is accumulated in the old leaves which are later shed. This supposedly reduces the overall concentration of salt in the tree. Tomlinson (1986) suggested that leaf loss may serve as a useful mechanism for reducing salt concentration in mangroves. As leaves age, they become repositories for salt that would otherwise accumulate in other plant tissues (Hogarth, 1999; Saenger, 2002).

### Materials and methods

This hypothesis was tested by sampling leaves of *R. mangle* growing at the perimeter of hypersaline lakes of San Salvador, Bahamas. Four trees of *R. mangle* were sampled using 13 clusters and 64 leaves. For comparison, a tree of *Avicennia germinans* (black mangrove) was included, using four different clusters for a total of 19 leaves.

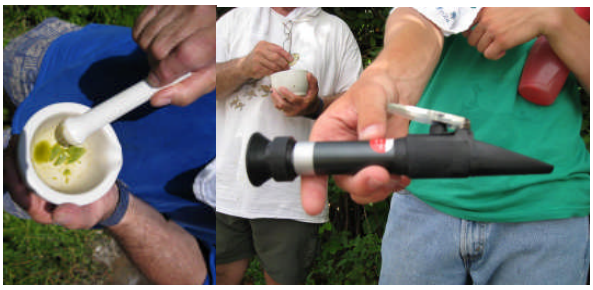

Fig. 2. Grinding mangrove leaf with a mortar and pestle (a) and optical salinity refractometer (Huake Instruments, Model: RHS-10ATC) for reading relative salinity (b)

Five leaves, including the yellow leaf, were sampled per cluster. The distance of each leaf from the apical leaf tip was measured. Leaves were ground individually in a mortar and pestle (Fig. 2a). After adding a fixed volume of water, their salt contents (ppt) were read using an optical salinity refractometer (Fig. 2b).

### Results and discussion

It was observed that these sacrificial leaves were typically the farthest from the apical tip of a stem although there were some exceptions (Fig. 1).

Fig. 1. A yellow leaf of *Rhizophora mangle*

Our results showed that yellow leaves did not have more salt than green leaves (t-test Prob>|t| is 0.7402). Anecdotal observations showed that yellow leaves were frequently drier than green leaves. It was clear that they were senescent leaves prior to abscission from the branch. There appears to be no adaptation for salt sequestration as a mechanism for the reduction of overall salt content of the plant. However, there was an increase in the salt content of green leaves in relation to their distance from the apical tip (t-Test Prob>|*t*| is 0.0067). This corresponds with research done on *R. mangle* shoots grown in high concentrations of NaCl (Werner & Stelzer, 1990).

Anecdotal observation showed that distal green leaves were also slightly more succulent. We believe that this succulence may directly correlate with the increase in salinity. Researchers have suggested that succulence correlates with leaf age in *Rhizophora* (Tomlinson, 1986). According to Tomascik *et al.* (1997), succulence in leaves of mangroves is a consequence of the presence of a well-developed, large celled, water storing layer of hypodermis as well as strongly developed palisade mesophyll tissue and small intercellular space volume. Werner and Stelzer (1990) observed such an increase in the hypodermis in NaCl treated plants.

We suggest that salt accumulation in the leaves is simply a part of the photosynthetic usage of water in the leaves. As water flows through and is transpired by the leaves, the salt left behind becomes more concentrated and potentially toxic. Increasing succulence helps to dilute the salt that has accumulated in the leaves (Tomascik *et al*. 1997). Similarly, Smith *et al.* (1989) observed such an increase in succulence with leaf age and a corresponding increase in salt concentration in *Conocarpus erectus*. Our comparison of *R. mangle* and *A. germinans* showed no difference in the leaf salinity. The fact that we did not observe a similar increase in succulence and salt sequestering in *A. germinans* may be a function of the species being a salt excreter (Smith *et. al.*, 1989).

## Conclusion

Our findings did not support the sacrificial leaf hypothesis in the sense that such a function serves as a survival strategy to lower salt accumulation in mangrove plants. There is no deliberate act of salt sequestration in yellow (senescent) leaves of the red or black mangroves. Our analysis did reveal that there is a correlation between the salinity and leaf position in green (normal) leaves of *R. mangle* and *A. germinans*. Additionally, these older leaves are generally more succulent. This increase in salinity is a consequence of leaf age and eventual leaf loss does little or nothing to assist in survival in the saline environment.

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**L. Joseph Gray[1)], Kristie Shubin[2)], Hays Cummins[3)], Donna McCollum[3)], Tyler Bruns[3)] & Eleanor Comiskey[3)]**

1) *Notre Dame Academy Park Hills, Kentucky, USA*

E-mail: grayj@ndapandas.org

2) *California State University, Fullerton, California, USA*

E-mail: dkshubin@mac.com

3) *Miami University, Oxford, OH, USA*