

Original Research Paper

Examining the Density Gradient Along the *Rhizophora mangle* Propagule

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Abstract: Mangroves grow in tropical regions around the globe, but these dense forests have been declining due to agriculture, industry, and climate change. While of great ecological and economic importance, mangrove restoration is costly and has high failure rates. More research is needed to determine how these plants function. Mangrove propagules are not seeds but the seedlings themselves that grow on the parent tree until they reach maturity and fall. They are water dispersed, floating horizontally in seawater and vertically in brackish water. This study investigated the change in density longitudinally along the *Rhizophora mangle* propagule. Propagules were cut into one-centimeter sections and the density of each section calculated. The data shows that the density of the propagules increases from the plumule end to the radicle end until around 80-90% of the length of the propagule, at which point the density decreases. This density gradient is consistent with a propagule floating vertically with the radicle end below the plumule end. A cross-section of the propagule shows an inner medulla surrounded by a cortex. Towards the radicle end of the propagule, the cortex sinks while the medulla continues to float.

Keywords: mangrove; propagule; density

Introduction

Growing along the coastlines in tropical and subtropical regions, *Rhizophora mangles*, or red mangroves, are easily recognized by their characteristic prop roots called rhizophores. These aerial roots allow the trees to survive inundation of the sea by absorbing water but excluding salt. *R. mangles* grow along the Gulf of Mexico, Florida, and up the Atlantic coastline (Florida Museum). These trees can grow to 30-80 feet tall, produce yellow flowers, and have 2-6 inches long, opposite, oval, or elliptic smooth edged, thick and leathery leaves (Encyclopedia Britannica, 2019; Florida Museum, 2019). *R. mangles* are part of a larger family of mangrove trees of which there are many varieties that grow in other tropical locations around the world. Mangroves cover 53,000 to 77,000 square miles globally and are ecologically important for their role in water purification, erosion control, and carbon storage. They also are an important habitat for many animals and insects (Feller, 2018). These habitats are so crucial that the destruction of one square mile of mangrove

forest could result in the loss of 275,000 pounds of fish per year (Feller, 2018).

Mangroves, and the soil they live in, are key players in carbon sequestration (Gennari, 2024; Sanderman et al., 2018). In particular, mangroves are often associated with “blue carbon” storage (Feller, 2018; *Mapping Ocean Wealth*, 2025; Choudhary et al., 2024; Leal & Spalding, 2024). Blue carbon refers to the carbon captured and stored by ocean and coastal ecosystems particularly in sediments beneath marine vegetation. As coastal plants die and decompose, much of their carbon becomes trapped in the ocean floor (US Department of Commerce, 2023). Although mangroves occupy less than two percent of marine environments, they are responsible for an estimated 10 to 15 percent of carbon burial in coastal ecosystems. A single acre of mangroves can sequester about 1,450 pounds of carbon, roughly equivalent to the emissions produced by driving a car 7,560 miles (Feller, 2018). The United Nations (2024) stated that mangroves store on average 1,000 tons of carbon per hectare and Siikamaki et al (2012) found that mangroves have the largest blue carbon pool at 6.5 billion tons.

Mangrove forests have been declining due to both human activity and natural causes (Leal & Spalding, 2024; Ellison & Farnsworth, 1996). The mangroves are declining at a rate greater than or equal to that observed for coral reefs and tropical rainforest (Liao et al., 2025) with 50% of mangroves at risk of collapse by 2050 (Global Mangrove Alliance, 2024). Climate change is having a negative impact on mangroves and their ability to store carbon (Chatting et al., 2022). Increased temperatures and the rise in sea level have decreased the worldwide population even though mangrove tree roots are capable of withstanding submersion and can accrete land mass by trapping sedimentation amongst their roots (Krauss et al., 2013). This is in part because higher sea levels cause roots to be submerged longer and result in a reduced growth rate. This decrease in growth rate counters growth benefits from other global change factors (Farnsworth & Ellison, 1997).

Mangrove restoration costs between \$3,000 and \$510,000 per hectare (Spurgeon, 1999). Due to the ecologically important role of mangroves, cities, countries, and organizations are willing to spend large amounts of money to restore these forests. The city of Mumbai spent \$5 million between 2012-2022, the World Bank spent \$35 million in the Philippines in 1984-1992, and Indonesia spent \$2.7 trillion in 2020-2024 on mangrove restoration (Shaham, 2025; Feller, 2018; Miller & Tonoto, 2023; Leal & Spalding, 2024). Unfortunately, these restoration projects have high failure rates due to the mangrove trees being planted in areas that are not conducive to their growth, lack of understanding regarding why mangroves disappeared in the first place, and the failure to monitor the sites after planting (Lewis, 2009). Despite the money spent on restoration and the research that has been done on mangroves, populations continue to decline worldwide. More must be learned about how their propagules function and disperse in order to improve the effectiveness of recovery efforts.

R. mangle propagates via propagule, which is the seedling, not the fruit or the seed (Tomlinson & Cox, 2000). These propagules emerge from the fruit of the tree, and their long, cigar-shaped bodies are extruded from the seed coat before it is abscised (Tomlinson and Cox, 2000), as seen in Fig. 1. After the propagule has fallen from the tree, it is dispersed via water. Once in the water, propagules need to float for one week in order to keep a critical water balance to maintain proper hormone function (Simpson et al., 2017). Leaves will then sprout from one end, the plumule, and roots will grow from the other end, the radicle (Tonné et al., 2017; Das, 2001).

The inside of the propagule has two main sections, the very center called the medulla, and the outer ring called the cortex. The cortex and medulla are made of starch and tannin cells. The medulla is more lacunose

with radial cells while the cortex is compact with thicker walls and chloroplasts (Tomlinson and Cox, 2000). The outside is the periderm, with the distinctive brown tip caused by increased tannins at the propagule's radicle end (Tomlinson and Cox, 2000). Along the periderm are lenticels, which allow oxygen to enter the propagule through cell sized breathing pores which can be closed during high tide to prevent water from entering (American Museum of Natural History, 2024).



Figure 1. Propagules growing from the fruit of the mangrove tree in Florida. Photo credit: Sytil Murphy

The propagules can survive while floating in the ocean for up to a year. They float horizontally when in seawater and vertically in brackish water (American Museum of Natural History, 2024) due to the density of the propagule in relation to the density of the seawater (Guppy, 1906). Brackish water is the ideal condition for mangrove growth. Floating vertically allows for the propagule to be oriented in the position that it will eventually grow, with radicle end down once the propagule lands upon a suitable substrate (American Museum of Natural History, 2024). There is potential for tidal sorting. Large propagules may not be able to reach higher ground due to their size unless assisted by a higher tide caused, for example, by a storm. Similarly, smaller propagules can disperse everywhere but cannot establish themselves in deeper water (Rabinowitz, 1978).

The buoyancy behavior is related to differences in density along the length of propagules from the plumule (leaf) end to the radicle (root) end (Davis, 1940; Tonné et al., 2017). The aerenchymatous cortex and pith tissues of the propagules affect their density and buoyancy (Tomlinson, 1994; Robert et al., 2009; Tonné

et al., 2016; Tonné et al., 2017). Tonné et al. investigated the relationship between density along the mangrove propagule and their floating orientation (Tonné et al., 2017) in the species *Bruguiera gymnorhiza*, *Ceriops tagal*, and *Rhizophora mucronate*.

This study investigates the longitudinal gradient change in density along the *R. mangle* propagule. It also explores whether there was a difference in density between the medulla and the cortex. Understanding the tissues responsible for the increased propagule density could help researchers to identify the biological mechanism behind this effect. It is possible that this could aid conservationists in preserving or providing ideal conditions for propagule dispersal and survival into adulthood.

Materials and Methods

Propagule acquisition and storage

Red mangrove trees flower in summer and autumn, with propagules sprouting in the summer (Red Mangrove — The Department of Environment and Natural Resources, 2014). Propagules fall from the tree and can be collected from the water and on beaches in the late summer. This project started in the early summer, requiring initial propagules to be sourced from Amazon resellers, with two batches purchased in Spring 2023. A third batch of propagules was obtained in late August, after being collected by a Florida resident from the ground on their property and mailed to Shepherd University following Hurricane Idalia. (Following regulations, none of the propagules used in this project were picked from mangrove trees.)

The propagules from the different batches were of various ages, some with roots and leaves while others had none. After arrival, propagules were stored in a 30-gallon aquarium tank with an Aqueon Quiet Flow 30 aquarium pump. Instant Ocean Sea Salt was added to the tap water according to manufacturer instructions to replicate ocean salinity. Propagules were inserted upright into Styrofoam blocks to keep them organized and away from the pump filter. In order to limit mold growth, black vinyl was applied to the glass sides of the aquarium, reducing the amount of light in the tank and propagules were inspected and wiped down as needed. Once propagules began developing mold, they were removed from the experiment since their texture became softer, affecting the density. In total, 27 propagules were analyzed.

Propagule measurements and observations

Each propagule was cut into approximately 1-cm long section using a razor blade and numbered with a Sharpie, with the plumule end being marked as section 1, as shown in Fig. 2. Red mangrove propagules change in color from green at the plumule end to brown at the radicle end. The color of each section was noted as being green, color shift (where the color is changing from green to brown), and brown. Sections 1-15 of the propagule shown in Fig. 2 are green, while the color shifts from green to brown in sections 16 and 17 and sections 18-20 are brown. For each section, the cortex's outer diameter, the medulla's outer diameter, and its length were measured with a digital caliper. Each section was placed in deionized (DI) water to observe if it floated or sank.

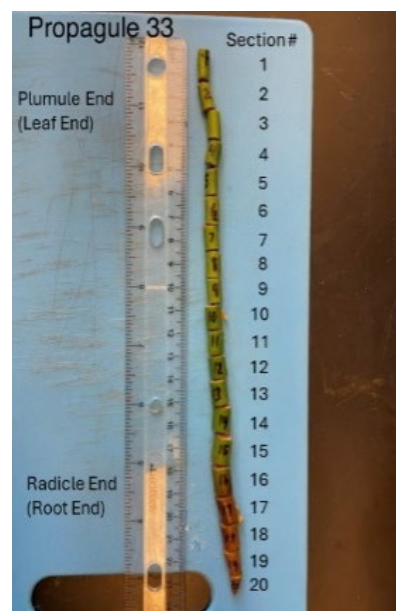


Figure 2. Centimeter long sectioning of mangrove propagule number 33. The plumule end is marked as section number 1 and the sections are numbered in ascending order to the radicle end (section number 20 in this propagule). Note the change in color from green to brown in sections 16 and 17. Photo Credit: Marissa Mohn

Propagule sections are not uniformly shaped. Therefore, the volume was measured using a pycnometer which allows for the accurate measure of the volume of irregularly shaped objects by measuring the mass of displaced fluid (Measurement Canada, 2017). The pycnometer used in this study has a nominal volume of 50 mL (Fig. 2) and was purchased on Amazon. Mass measurements were made with a Scout Pro 2,000-gram Ohaus balance.

The mass of each propagule section was measured before and after being placed in the pycnometer, which was a straight-sided stainless-steel cup with lid and a hole to allow water displacement (Fig. 3) to monitor

water absorption by the propagule sections during submersion.

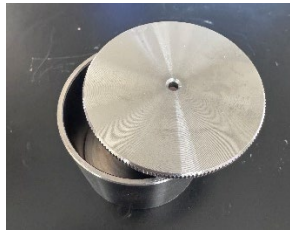


Figure 3. Pycnometer used in this study. Photo credit: Sytil Murphy

In select propagules, the medulla was removed from the cortex using metal rings approximately the size of the medulla by pressing the metal ring down on the boundary between the two and then pulled out, like using a cookie cutter. The four metal rings used were 2.5 cm in height and with diameters of 0.8 cm, 0.6 cm, 0.4 cm, and 0.3 cm. After the medulla was removed, it was placed in a glass of DI water to see if it floated or sank. Then the cortex was placed in a glass of DI water to check if it floated.

Results

Effect of submersion on propagule sections

Since the propagule sections were not uniformly shaped, volume was more accurately calculated using pycnometers than with calipers alone. This required submerging the sections into water. However, it was unknown if the sections would absorb any water during pycnometer measurements since their edges had been cut during sectioning, which removed the periderm barrier from the top and bottom sides of the sections. To determine any water absorption, measurements were taken before and after the sections were placed in the pycnometer for the first six propagules. The average percent change in length was 0.10% and had a correlation coefficient of 0.9996 (Fig. 4). The average percent change in radius was 0.89% and had a correlation coefficient of 0.997 (Fig. 5). The two outliers in this figure are from sections at either the top or bottom of the propagules, where the propagule shape is the most non-uniform and are most likely due to measuring at a slightly different position within the segment. The average percent change in mass was 3.57% and had a correlation coefficient of 0.9978 (Fig. 6). The trendlines associated with Figs. 4-6 were all forced to have a y-intercept of 0, as it makes physical sense that a section with no dry measurement would have no wet measurement. All measurements collected did not show significant changes after hydration,

indicating that the pycnometer measurement, despite submersion in water, did not significantly alter the propagules. Therefore, after the first six propagules, radius, mass, and length data were taken only before being submerged.

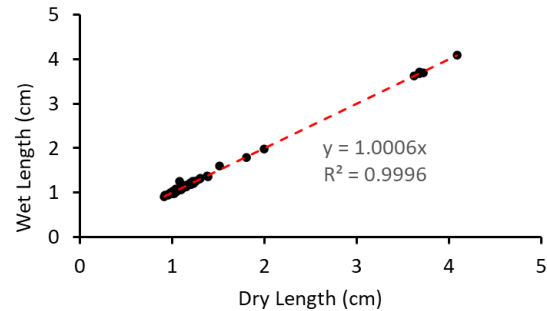


Figure 4. Propagule section length measurements before (dry) and after (wet) being submerged in water. N = 88

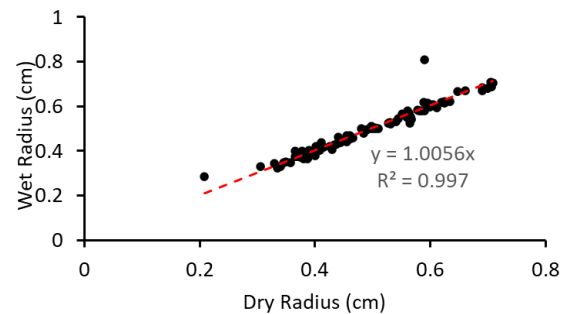


Figure 5. Propagule section radius measurements before (dry) and after (wet) being submerged in water. N = 88

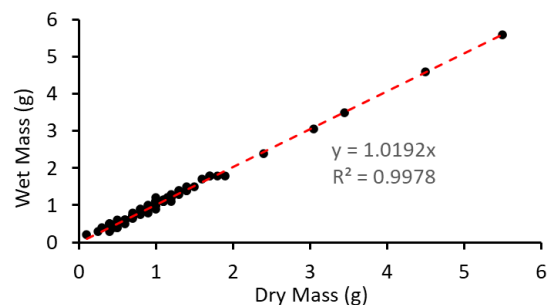


Figure 6. Propagule section mass measurements before (dry) and after (wet) being submerged in water. N = 88

Density data

Each propagule was a different length. Therefore, in order to create a consistent data set across propagules, the percentage of the total propagule length of the center of each propagule section was determined. Low numbered sections near the plumule end of the propagule had a smaller length percentage than high numbered sections near the radicle end. Figure 7 shows the variation in density along the propagule's lengths.

A trendline fitted to the data, showing a generally positive correlation (i.e. the density increases from the plumule end to the radicle end of the propagule), however, due to the scatter in the data the correlation coefficient was low (0.2001). Despite our observations that many sections near the radicle end sank, we rarely observed densities greater than 1.0 g/cm^3 . It is unclear why this occurred but could be related to measurement error or the propagule's physical properties. It is acknowledged that there are many sources of error with this first data set, some in the control of the researchers while others were not.

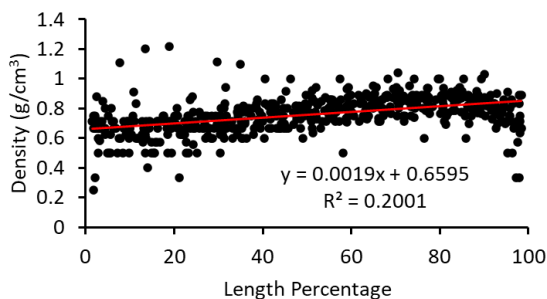


Figure 7. Propagule density variation as a function of the length percentage. The trendline (red) shows a positive slope but has a low correlation coefficient due to the scatter in the data as well as the downward turn at the plumule end.

It has been reported that the age of the propagules affects the density and the position in which they float (Tonné, 2017). In this study, the age of the samples varied; some propagules had leaves and roots while others were younger. Presumably, due to this variation in propagule developmental age or degradation due to mold/decomposition, some of the propagules did not display an increase in density longitudinally.

Because controlling for propagule age or quality was not possible with the first data set and given that the results were promising, measurements were made on a second data set. The second data set was taken in August of 2024 and consisted of twenty-nine propagules obtained from a beach off the western coast of Florida. All measurements were made in Florida, ensuring the propagules were as fresh as possible. The same protocol used for the first data set was followed in the analysis of this second data set.

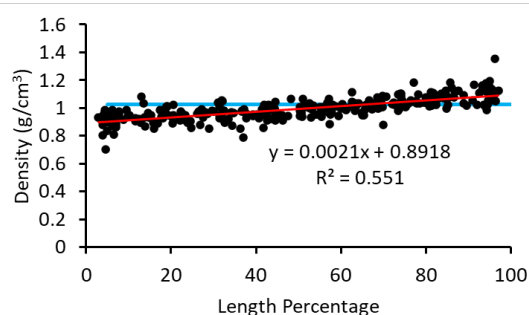


Figure 8. Propagule density variation as a function of the length percentage for the August 2024 data set. A linear trendline (red) shows an increase in density along the propagule's length. The blue line is constant at 1.205 g/cm^3 , the density of salt water.

Fig. 8 shows the variation in density along the propagule's lengths for the second data set. A comparison of the data in Figs. 7 and 8 shows that working with fresh propagules resulted in a much cleaner data set with much less scatter and without the downward "hook" at the radicle end, resulting in a higher correlation coefficient for a linear trendline (red line) fit to this data. The second data set also shows a clear demarcation where the density changes from less than to greater than 1.205 g/cm^3 (blue line), the density of salt water.

To better see the variation in the data, the length percentages were grouped into bins with a 5% range. In other words, all sections with a length percentage between 0 and 5% were grouped, as were those with length percentages between 5% and 10%, etc. for a total of 20 bins. The density of all sections within a given bin were averaged together. The result of this averaging is shown in Fig. 9. The trendline fit to the data in Fig. 9 has the same slope as that in Fig. 8 but with a correlation coefficient of 0.9124. Using the formula for the trendline fit to the data in Fig. 9, it was determined that the propagule density goes from below 1.205 g/cm^3 to above at 66%, which is in the 65% - 70% range bin.

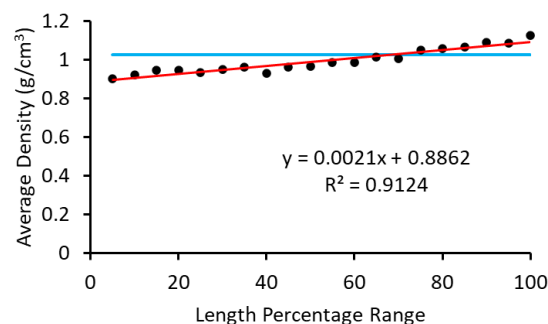


Figure 9. Average propagule density variation as a function of the length percentage range for the August 2024 data set. The trendline (red) is a linear fit to the data, showing an increase in density along the propagule's length. The blue line is constant at 1.205 g/cm^3 , the density of salt water.

As a first step towards determining if the changes in the radicle tissues were limited to the cortex, the medulla was removed from some sections of the first set of propagules. It was observed that the cortex would sink at the radicle end but float at the plumule end of the propagule (Table 1). Sometimes the cortex at the

radicle end would sink even if the section floated before the medulla was removed. This may indicate the density gradient is due to something in the cortex. Future research is needed to examine the cortical tissues and identify how they could generate the gradient

Table 1. Frequency of floating and sinking sections by section color for both whole sections and cortex only (with the medulla removed).

	Green		Color Shift		Brown	
	Float	Sink	Float	Sink	Float	Sink
Whole Section	224	33	17	9	68	22
Cortex Only	112	145	2	24	11	79

differential observed. This process was not repeated with the second data set but will be further investigated in the future.

Discussion

Mangrove populations are critical components of ecosystems worldwide. They are responsible for carbon absorption and support diverse species (Feller, 2018; *Mapping Ocean Wealth*, 2025; Choudhary et al., 2024; Leal & Spalding, 2024, US Department of Commerce, 2023). Despite this importance, their numbers continue to decline rapidly, and conservation efforts struggle to keep up. Mangrove reproduction is unusual, relying on propagules that drop from the adult trees and disperse by floating through water for up to a year before planting and maturing. The purpose of this study was to better understand the density changes in the propagules that support the floatation and distribution of these critical reproductive structures.

It is apparent from the data that there is a change in density longitudinally along the mangrove propagule that plays a role in its buoyancy. Since the radicle end has a brown periderm while the plumule end is green, and the cortex sinks even while the medulla floats at the radicle end, there may be a difference between the cortex in the radicle end and the cortex in the plumule end. Future research would be needed to better determine how the density is changing along the length of the propagule and what is causing the observed change,

This research on *R. mangle* propagules supports previous research done on other *Rhizophoracean* mangrove propagules done by Davis (1940) and research done on *R. gymnorhiza*, *C. tagal*, and *R. mucronate* propagules done by Tonné (2017). This previous research also showed that there is a density

gradient along the mangrove propagules (Tonné et al., 2017). This research has limitations that are outside the researchers control like salinity and temperature fluctuations, by using propagules in the second data set that were all gathered at the same time in the same place, the researchers have tried to mitigate the effect of these variables as much as they are able. And, while this research helps to answer the question of whether there is a change in density and where that shift in density occurs along the length of the propagule, more work is needed to understand how these densities are achieved within the plant tissues by looking more specifically at their biological and chemical compositions. Given the ecological and economical importance of mangroves, it is vital that more work be done to increase the success of restoration efforts. The more that is understood about mangrove propagules, the more effectively mangrove forests can be restored.

Acknowledgements

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