Life on the leading edge: Phenology and demography of the red mangrove *Rhizophora mangle* L. at the northern limit of its expanding range

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**A R T I C L E   I N F O**

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**A B S T R A C T**

Mangroves are expanding northward along the eastern coast of Florida and invading saltmarsh communities along the tributaries and main channels of rivers that flow into the Intracoastal Waterway system. To investigate *R. mangle*’s demography, reproductive effort and survivorship of offspring were monitored for three years along the Matanzas River, northern Florida. Flowering was delayed, fruit production was year-round and hypocotyl production covered a longer period than for populations further south. If a propagule survived to the recruit stage, the individual was more likely to produce branches. In addition, if the propagule recruited in mud and in the low intertidal zone, then the individual was more likely to survive to the juvenile stage. Those propagules that eventually developed into juveniles had remained within one meter of the parent, had recruited in a vertical position and had larger hypocotyls. Two adults contributed 79% of the propagules that survived to the branched stage. These successful adults become the islands from which the population persists and expands along the leading edge of its distribution.

1. Introduction

The distribution of the red mangrove *Rhizophora mangle* L. has been expanding northward into *Spartina alterniflora* Loisel-dominated saltmarsh communities along the eastern coast of Florida (Lewis et al., 1985). Cavanaugh et al. (2015) reported that mangrove coverage expanding northward into *Spartina alterniflora* Loisel-dominated saltmarsh communities along the eastern coast of Florida (Lewis et al., 1985). Cavanaugh et al. (2015) reported that mangrove coverage doubled between 1984 and 2011 in northern Florida (29°–29.75°N). The northernmost range of mangroves along the western Atlantic coast is in Guana Tolomata Matanzas National Estuarine Research Reserve (GTM NERR), St. Johns’ County. The northernmost individual was recorded at 29.98° N, 81.33° W (pers. observ.) and more than one kilometer north of the individual reported (29.94° N, 81.32° W) by Williams et al. (2014).

The leading edge of distributional advances is influenced by a species’ dispersal ability and tolerance to environmental conditions that differ relative to the center of their distributions. The persistence of *R. mangle* populations is entirely dependent on the survivorship of seedlings to reach adulthood due to an absence of vegetative reproduction (McKee, 1995; Sengupta et al., 2005). *Rhizophora mangle* has a viviparous life cycle in which hypocotyls develop from fruits that remain attached to the parent tree for up to six months (Gill and Tomlinson, 1971). Upon release, the hypocotyl separates from the fruit (therein referred to as a propagule) and then has the potential to remain viable while drifting in the water column for months before settling (Rabinowitz, 1978), but more typically, establishes close to the parent (Sengupta et al., 2005). For example, after 4 weeks, 77% of *R. mangle* propagules remained within 25 cm of the release point and did not disperse any further from a stand studied in Panama (Sousa et al., 2007).

This three-year study provides the first comprehensive and long-term investigation of *R. mangle*’s reproductive success and survivorship at the northern extent of its range. Given the latitudinal variability in parameters such as reproductive output, propagule size and age at maturity (Proffitt and Travis, 2014; Dangremond and Feller, 2016), we predicted that phenology of flowers and fruit production, reproductive effort and success and growth rates would differ from a population of *R. mangle* at the leading edge relative to more southern populations along the eastern coast of Florida. To compare reproductive phenological patterns with published studies, we measured the timing, production and survivorship of flowers and fruits from reproductive adults. To compare recruit establishment and survival, we measured growth and timing of node, leaf and branch development from tagged individuals.

To understand recruitment success, orientation and microhabitat conditions (sediment and canopy characteristics) were also recorded. Only three of thirteen phenology studies for this species occurred for greater than a one-year period and were conducted in Panama (Cerón-Souza et al., 2014; 1.5 years), Belize (McKee, 1995; 2.5 years) and southern Florida, (Gill and Tomlinson, 1971; 2 years). Studies conducted for one...
year cannot test for annual and seasonal variability in phenology and demography of a species. Six other studies were included to broaden geographic comparisons from Brazil (Fernandes, 1999; Duke and Pinzón, 1992; Menezes et al., 1997; Mehlig, 2006), Panama (Sousa et al., 2007), Columbia (Sánchez-Núñez and Mancera-Pined, 2011), Belize (Ellison and Farnsworth, 1993), Mexico (Hernández et al., 2011) and Florida (Sengupta et al., 2005; Ewe, 2007). No published study included the entire suite of measurements that were utilized in this investigation.

2. Materials and methods

2.1. Growth

Growth of adults, juveniles, recruits and propagules was measured from individuals located at Summer Haven Island, northeastern Florida (29.68° N, 81.22° W). Individuals were tagged with numbered cable ties. The heights of tagged adults (≥1.5 m tall), juveniles (branched individuals < 1.5 m tall that were not reproductive), recruits (unbranched individuals with nodes) and propagules (unbranched individuals without nodes) were measured monthly from July 2013 to June 2016. Heights of adults were measured to the nearest centimeter with a PVC pole marked off in 5-cm increments. Juvenile heights were measured to the nearest 0.1 cm with a flexible measuring tape. The lengths of the hypocotyl and growing axis were measured monthly from propagules also using a flexible measuring tape to the nearest 0.1 cm.

2.2. Reproductive effort

Monthly production of flower buds, flowers, fruits and hypocotyls was recorded from twenty-four tagged adults. The lengths of the fruits and emerging hypocotyls were measured to the nearest 0.1 cm. If > 20 fruits or hypocotyls were observed on an adult, then 20 individuals were selected randomly and measured to the nearest 0.1 cm. The mean lengths of the fruits and hypocotyls per adult were calculated per month.

2.3. Survivorship, growth and mortality of propagules, recruits and juveniles

Propagules and recruits were tagged with numbered cable ties and the closest adult, numbered as SH (Summer Haven) #, was noted. The orientation of the propagules (horizontal, vertical, or angled) and the presence of roots were recorded monthly. Tagged recruits were measured monthly for lengths of the released hypocotyl and growing axis, numbers of nodes and numbers of leaves. Evidence of damage (loss of the growing tip or hypocotyl, or scrapings along the hypocotyl or growing axis) and desiccation were recorded. Tagged individuals that were not relocated were presumed to have dispersed with tidal exchange or storm surge (Sousa et al., 2007).

2.4. Statistical analyses

To determine whether reproductive effort differed among adults throughout the study, the non-parametric Kruskal-Wallis test was used for comparing among seasons and the Mann-Whitney non-parametric test was used for comparing between years. Non-parametric tests were used due to unequal sample sizes. The unit of replication was the adult tree. Variables tested were monthly numbers of flower buds, flowers, fruits and hypocotyls per adult.

Because hypocotyl length can predict survivorship of fallen propagules (Ewe, 2007), a Mann-Whitney non-parametric test was used to investigate differences between tagged hypocotyl lengths from those that (i) died, were not located, or were damaged versus (ii) those that reached the recruit stage. The unit of replication was the nearest adult. In addition, a goodness of fit analysis was used to test whether the number of hypocotyls for two categories of hypocotyl length (≤25.0 cm and > 25.0 cm) differed between those propagules that had died and those that had survived to the recruit and juvenile stages. A square root transformation was applied to satisfy the assumption of parametric statistics.

Because survivorship can be predicted by length of the growing axis and by node and leaf production rates, non-parametric tests were used to compare individuals that reached the recruit stage and those that reached the juvenile stage. A Kruskal-Wallis non-parametric test was used to compare individuals that were first tagged as propagules and developed into (i) recruits that died, were not located, or were damaged, (ii) recruits that did and (iii) did not reach the juvenile stage (i.e. develop branches). The last recorded measurements for recruits that died, were not located, or were damaged were used in the analyses. If significant differences were observed among the three groups, then pairwise comparisons were conducted with Mann-Whitney non-parametric tests.

For those recruits that were first tagged as recruits, differences in growth rates of the growing axis and production rates of nodes and leaves were compared with Mann-Whitney non-parametric tests between (i) a combined group of recruits that died and (ii) did not reach the juvenile stage. The last recorded measurements were used for recruits that died, were not located, or were damaged. Recruits that remained as recruits (n = 4 individuals) were combined with the group of dead, were not located and damaged recruits. Variables measured were maximum number of nodes, nodes per growing axis (number of nodes per cm), maximum number of nodes produced per day during the growing period, mean number of nodes produced during the period that the recruit was observed, maximum number of leaves per adult and maximum length (cm) of the growing axis.

Growth rates (cm per year) were compared among (i) juveniles that were first tagged as juveniles, (ii) first tagged as propagules and (iii) first tagged as recruits, using Kruskal-Wallis non-parametric tests. Mann-Whitney non-parametric tests were used to compare growth rates between those first tagged as propagules versus those first tagged as recruits.

3. Results

3.1. Reproductive effort

Flower bud production differed among seasons (H = 255.77, p < 0.001) and between years (W = 59238.50, p < 0.001). Mean (± 1 SE) monthly numbers of flower buds ranged from no buds recorded in March 2014, June 2014, and May 2015, to a mean maximum of 254.6 ± 33.9 buds per adult in August 2015 (Fig. 1). The greatest percentage of adults with flower buds (≥75% of the 24 adults) occurred in the summer months of July–September.

Trees produced flowers throughout the year with production differing among seasons (H = 89.10, p < 0.001; Fig. 1) and between years (W = 61044.50, p = 0.001). Mean monthly numbers of flowers ranged from no flowers in June 2014 to a mean maximum of 49.9 ± 11.8 flowers per adult in September 2015 (Fig. 1). The greatest percentage of adults with flowers (≥75% of the 24 adults) occurred in summer months, with greatest representation in September of 2014 and 2015. Flower production was 45.9 ± 4.9% of flower buds per adult.

Fruit production differed among seasons (H = 20.71, P < 0.001) and between years (W = 62919.00, p = 0.022, Fig. 1). The mean monthly numbers of fruits ranged from 3.5 ± 1.6 fruits per adult in January 2014 to a mean maximum of 24.2 ± 7.8 fruits per adult in October 2014. The greatest percentage of adults with fruits (≥75% of the 24 adults) occurred in October–January 2015 and September–November 2016. Fruit production was 40.0 ± 6.0% of flowers per adult. Mean maximum fruit lengths were recorded in September and July, with 2.7 ± 0.1 cm per adult (n = 11 adults) and 2.5 ± 0.1 cm per adult (n = 15 adults), respectively.

A seasonal production of hypocotyls was also evident (Fig. 1). The
greatest numbers were recorded in June–October with a mean maximum of 20.8 ± 6.7 hypocotyls per adult in September 2015 (Fig. 1). Significant differences were observed among seasons (H = 74.78, p < 0.001), but not between years (W = 65354.00, p = 0.424). Hypocotyl production was 32.0 ± 5.8% of fruits per adult. Mean lengths were 25.1 ± 1.7 cm per adult (n = 11 adults) and 24.9 ± 0.4 cm per adult (n = 10 adults), in November 2014 and October 2015, respectively.

### 3.2. Propagule survivorship, growth and mortality

Propagules were recorded on the ground during the colder months. From 11 adults, 92% of the 270 tagged propagules were first recorded in the months of October–March, with 37% tagged in December. Roots were observed from 41 propagules after 119.1 ± 14.0 days. Propagules that reached the recruitment stage were more likely to be found in the vertical position. Of the 86 propagules that produced nodes, 6% had remained in the horizontal position, 35% began in the horizontal or angled position and moved to a vertical position and 56% had remained in the vertical position. By comparison, 87% of the 185 propagules that did not develop nodes remained where they were first located for 94.9 ± 5.9 days. Of the 45 propagules that were not located after the first record, 59% went missing from March–May, 50% showed evidence of herbivory and 12% showed evidence of desiccation.

Survivorship of propagules to the recruit stage was also indicated by mean hypocotyl length. Mean hypocotyl lengths was on average > 3 cm longer for those propagules that produced nodes (length: 29.3 ± 0.7 cm) as compared to the propagules that had died, were not located, or were damaged (length: 25.5 ± 0.4 cm; W = 22087.00, p < 0.001; Table 1). Propagules that survived to recruit stage were more likely to have a hypocotyl > 25.0 cm as compared to those that had died (X² = 7.81, p = 0.005). The percentage of individuals > 25.0 cm was 51% for those that died, were not located, or were damaged and 71% for those that survived and developed nodes (Fig. 2a).

Propagules that did not develop nodes (n = 185 individuals) remained where they were first located for 94.9 ± 5.9 days. Of the 45 propagules that were not located after the first record, 59% went missing from March–May, 50% showed evidence of herbivory and 12% showed evidence of desiccation.

### 3.3. Tagged propagules: recruit survivorship, growth and mortality

Of the 86 tagged propagules that developed nodes, 31 died, were not located, or were damaged, 31 remained as recruits and 24 produced branches to become juveniles (Table 1). The first node developed fully by 136.5 ± 13.6 days (n = 48 individuals). A greater percentage of propagules developed into recruits during the spring (47% of propagules measured) and summer (34%) months as compared to winter (10%) and autumn (10%) months (n = 62 individuals). Of the 31 propagules that did not reach the juvenile stage, 39% were not located and assumed absent from the area, 29% showed evidence of herbivory, 23% had a dead tip and 10% had been snapped at the tip of the growing axis or along the hypocotyl.

Although mean hypocotyl lengths were greater for those tagged propagules that reached the recruit stage, mean hypocotyl lengths were not significantly different among the three recruit categories: those that (i) produced branches, (ii) remained as recruits, or (iii) died, were not located, or were damaged (H = 1.61, p = 0.448; Table 1). Similarly, surviving recruits that were first tagged as propagules were not more likely to have hypocotyls > 25.0 cm (78% of tagged propagules) as compared to those that had died, were not located, or were damaged (74% of tagged propagules; X² = 0.18, p = 0.670; Table 1; Fig. 2b).

Recruits that did not produce branches throughout the study were more likely to be taller than those that had produced branches to become juveniles, or had died, were not located, or were damaged (square root transformation, H = 14.85, p = 0.001; Table 1). However, growth rates for the growing axis (mm/day/individual) were significantly different among the three categories of recruits that were first tagged as...
The number of leaves was lower for recruits that died, were not located, or were damaged compared to those that did not die, disappear, or become damaged. The maximum growth rate was almost twice as fast for those recruits that produced branches as compared to those that remained as recruits (W = 341.00, p = 0.008).

Recruits having twice the rate as those that remained as recruits (W = 678.00, P = 0.008; square root transformation, p < 0.001; Table 1), with those recruits that developed branches and the combined group of individuals that remained as recruits, died, were not located, or were damaged (W = 681.20, p = 0.009; Table 1).

Comparison of recruit hypocotyl lengths, growing axis lengths, growth rates and production of nodes and leaves from individuals first tagged as propagules. Results in bold indicate a significant difference (p < 0.05). n = number of tagged individuals.

<table>
<thead>
<tr>
<th>Produced branches</th>
<th>Remained as recruits</th>
<th>Died, were not located, or were damaged</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hypocotyl length</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(i) Mean length (cm) ± 1 SE</td>
<td>(i) 31.0 ± 1.2</td>
<td>(i) 28.1 ± 1.2</td>
</tr>
<tr>
<td>(ii) Range (cm)</td>
<td>(ii) 20.5–43.6; n = 24 from 5 adults</td>
<td>(ii) 12–39; (ii) 13.1–40.6</td>
</tr>
<tr>
<td>Growing axis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(i) Mean maximum length (cm) ± 1 SE</td>
<td>(i) 20.9 ± 1.5</td>
<td>(i) 20.9 ± 1.5</td>
</tr>
<tr>
<td>(ii) Range (cm)</td>
<td>(ii) 11.6–32</td>
<td>(ii) 11.5 ± 1.7</td>
</tr>
<tr>
<td>(iii) Growth rate (mm/day) ± 1 SE</td>
<td>(iii) 0.41 ± 0.11</td>
<td>(iii) 0.43 ± 0.12</td>
</tr>
<tr>
<td>(iv) Days observed ± 1 SE</td>
<td>(iv) 352.2 ± 55.2; n = 21</td>
<td>(iv) 352.2 ± 55.2; n = 21</td>
</tr>
<tr>
<td>Nodes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(i) Mean maximum number ± 1 SE</td>
<td>(i) 5.4 ± 0.7</td>
<td>(i) 6.3 ± 0.4</td>
</tr>
<tr>
<td>(ii) Range</td>
<td>(ii) 1–14</td>
<td>(ii) 1–12</td>
</tr>
<tr>
<td>(iii) Mean nodes per cm ± 1 SE</td>
<td>(iii) 0.4 ± 0.06; n = 22</td>
<td>(iii) 0.3 ± 0.03; n = 31</td>
</tr>
<tr>
<td>(iv) Mean maximum node per cm ± 1 SE</td>
<td>(iv) 0.018 ± 0.0021</td>
<td>(iv) 0.011 ± 0.008</td>
</tr>
<tr>
<td>(v) Mean node per day ± 1 SE</td>
<td>(v) 0.018 ± 0.0021</td>
<td>(v) 0.001 ± 0.0008</td>
</tr>
<tr>
<td>(vi) Mean days observed ± 1 SE</td>
<td>(vi) 297.1 ± 62.9; n = 14</td>
<td>(vi) 464.5 ± 35.9; n = 19</td>
</tr>
<tr>
<td>Leaf number</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(i) Mean maximum number ± 1 SE</td>
<td>(i) 8.3 ± 0.7 leaves</td>
<td>(i) 8.1 ± 0.7 leaves</td>
</tr>
<tr>
<td>(ii) Range</td>
<td>(ii) 2–12 leaves; n = 24</td>
<td>(ii) 2–13 leaves; n = 31</td>
</tr>
</tbody>
</table>

3.4. Tagged recruits: recruit survivorship, growth and mortality

Of the 45 recruits that were first tagged as recruits, 29 produced branches, 12 died as recruits and 4 remained as recruits. Of the 12 recruits that did not survive to juvenile stage, 42% were not located from where they were first tagged, 25% showed evidence of herbivory and 17% had snapped along the growing axis.

Like patterns observed in tagged propagules that ultimately developed branches, mean hypocotyl length was approximately 5 cm longer for those that survived and produced branches as compared to the combined group of individuals that remained as recruits, died, were not located, or were damaged (W = 792.50, p = 0.003; Table 2). Survival of recruits was more likely to have hypocotyls > 25 cm as compared to those that had died (X^2 = 11.11, p = 0.001, Table 2; Fig. 2c). The percentage of individuals > 25.0 cm was 25% for those that died and 79% for those that survived.

Individuals that were first tagged as recruits and later produced branches appeared to be persisting but not thriving as compared to those that were first tagged as propagules (Tables 1 and 2). Maximum lengths were not significantly different between recruits that developed branches and the combined group of individuals that remained as recruits or died, were not located, or were damaged (W = 405.50, p = 0.380; Table 2). Similarly, growth rates were not different between those that produced branches and the combined group of individuals that remained as recruits, died, were not located, or were damaged (W = 290.50, p = 0.688; Table 2) and were almost a quarter the growth rate of tagged propagules that produced branches (Table 1).

The maximum numbers of nodes and leaves per individual were not significantly different between those recruits that later produced branches and the combined group of individuals that remained as recruits, died, were not located, or were damaged (W = 418.50, p = 0.001; Table 2) and were almost a quarter the growth rate of tagged propagules that produced branches (Table 1). However, node production rates were greater for those that later produced branches. The mean maximum number (calculated during a period of growth) and mean number (calculated during the period that each individual was monitored) of nodes per day were significantly greater for those recruits that developed branches (maximum node production rate: W = 212.50, p = 0.004; mean node production rate: W = 286.00, p = 0.001; Table 2).

3.5. Juvenile survivorship and growth

During the study period, 6 of the 24 adults produced propagules that eventually reached the juvenile stage (Fig. 3). During the juvenile stage, tagged recruits (9.5 ± 1.1 cm per year) and tagged propagules (9.2 ± 1.2 cm per year) grew at a similar rate (H = 131.50, p = 0.609; Fig. 4). Adults grew 24.2 ± 2.1 cm per year and juveniles grew 31.2 ± 4.8 cm per year (Fig. 4).

Two adults produced 54% of the propagules that survived to the recruit stage. Greatest recruit and juvenile survivorship was from the same two adults that had the greatest propagule survivorship (Fig. 3). Of the 24 tagged propagules that developed branches, 46% and 33% were beneath two adults. The remaining five individuals were found beneath four other adults (Fig. 3).

Surviving propagules, recruits, juveniles and adults were more likely to be growing in mud as compared to sand. The ratios of tagged individuals located in mud versus sand were 3.8 for adults (n = 24 individuals), 5.4 for juveniles (n = 58 individuals) and 3.3 for recruits (n = 43 individuals). Ratios for dead propagules (n = 186 individuals) and recruits (n = 40 individuals) were 1.2 and 1.5, respectively.
Juveniles were more likely to be growing beneath a *R. mangle* canopy (67%) than under *Avicennia* sp. (8%) or in the open (25%), and in the lower intertidal zone as compared to the mid-intertidal zone (64% versus 36%, respectively). Fewer adults (32%) were growing in the low intertidal zone as compared to mid-intertidal zone (68%).

4. Discussion

Reproductive success of a northeastern Florida *Rhizophora mangle* population at the edge of its distribution was less limited by reproductive effort than by recruitment success. The population of adults produced fruits and hypocotyls for a longer period than estimates accounted by Gill and Tomlinson (1971) from southern Florida populations. However, recruit and juvenile survivorship was lower at Summer Haven than had been reported from more southern populations and these differences may be related to microhabitat conditions under the parent canopy. Rabinowitz (1978) reported an estimated 50% survivorship after 338 days in Panama mangrove stands and McKee (1995) reported 90% survivorship after one year in a Belizean mangrove. In this study, from 6 adults, survivorship was 60% and 25% of the 199 tagged propagules that reached the recruit and juvenile stage, respectively. Propagules that ultimately developed branches were more likely to have longer hypocotyls, and to have settled in a vertical orientation and in a muddy substratum.

4.1. Reproductive effort

Reproductive adults from the northern population were more successful in producing propagules than from southern populations. Gill and Tomlinson (1971) reported that approximately 7% of flowers developed fruits from populations surveyed in Biscayne Bay, southern Florida, as compared to 40% in this study. In Brazil near the equator, 2% of flowers produced mature propagules (Menezes et al., 1997) as compared to 13% from this study. Development from flower to propagule release took 203 days in Brazil as compared to approximately 300 days in our study population (Mehlig, 2006). In addition, more than twice the fruits in our study (32%) produced hypocotyls as compared to 13% in a Brazilian population (Mehlig, 2006) and < 10% in a southern Florida population (Gill and Tomlinson, 1969), indicating differences in reproductive success between the leading edge population and southern populations.

Timing of flower maturation was comparable to southern Florida populations, occurring during seasonally hot and rainy conditions (Fernandes, 1999, Table 3). Production was greatest from June–October, a pattern comparable to Biscayne Bay and Indian River mangroves (Gill and Tomlinson, 1971; Sánchez-Núñez and Mancera-Pined, 2011). By comparison, no evidence of seasonality was observed in a Panama population at 8°N (Cerón-Souza et al., 2014). Proffitt and Travis (2014) suggested that cold stress may increase the tendency of trees to flower. In our study population, flowering was not significantly different between years, but significantly different between months within a year. Cavanaugh et al. (2014) reported that mangrove cover decreased during periods of extreme cold events (< −4 °C) along the northeastern coast of Florida. The absence of extreme cold events may explain why flowering patterns did not differ among years (https://www.wunderground.com).

Timing of fruit production and propagule abscission occurred during the rainy (> 100 mm per month) season for both northern and southern populations, indicating synchronicity in the production and release of propagules (Table 3). However, the northern population had a longer period in peak fruit production, occurring during the months of May–Dec, than the period recorded for the southern population, occurring during the months of August–Sept (Gill and Tomlinson, 1969, 1971). By comparison, populations closer to the center of *R. mangle*’s latitudinal distribution showed no seasonality in propagule production (Cerón-Souza et al., 2014).

4.2. Indicators of recruit success

Irrespective of whether populations are located at the leading edge or towards the center of their distribution, *R. mangle* propagule dispersal was very localized with fallen propagules located either directly
Note: for analyses, recruits that remained as recruits were combined with the group of recruits that died, were not located, or were damaged. n = number of tagged individuals.

Comparison of hypocotyl lengths, growing axis lengths, growth rates and node and leaf production during the recruit stage. Results in bold indicate a significant difference (p < 0.05).

### Table 2

<table>
<thead>
<tr>
<th>Hypocotyl length</th>
<th>Produced branches</th>
<th>Remained as recruits</th>
<th>Died, were not located, or were damaged</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean length (cm) ± 1 SE</td>
<td>(i) 28.5 ± 0.8</td>
<td>(i) 23.7 ± 5.5</td>
<td>(i) 23.2 ± 1.8</td>
</tr>
<tr>
<td>Range</td>
<td>(ii) 17.2–35.0</td>
<td>(ii) 10.0–35.5 cm</td>
<td>(ii) 15.0–40.9</td>
</tr>
</tbody>
</table>

Comparison of months observed for reproductive stages between northern (N, this study) and southern (Gill and Tomlinson, 1971) Florida. n = > 60% reproductive adults of the 24 sampled monthly throughout the study period at Summer Haven.

<table>
<thead>
<tr>
<th>Flower buds</th>
<th>Flower open</th>
<th>Hypocotyl present</th>
<th>Propagules falls</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>S</td>
<td>S/N</td>
<td>N</td>
</tr>
<tr>
<td>S</td>
<td>S</td>
<td>S/N</td>
<td>S/N</td>
</tr>
</tbody>
</table>

Fig. 3. Proportion of surviving tagged propagules (white), recruits (hatched) and juveniles (striped) from 6 adults (SH1-6, SH = Summer Haven). Initial numbers of tagged propagules indicated below and numbers of surviving juveniles in boxes above.

Fig. 4. Mean annual heights (+ 1 SE) of adults (black with white, n = 27), tagged juveniles (black, n = 14), juveniles first tagged as recruits (white with black, n = 26) and juveniles first tagged as propagules (white, n = 23), measured in June, from 2013 to 2016.

Propagules were first recorded, with 62–92% of individuals rooting after approximately 133 days in Panama stands. At Summer Haven, propagules either remained under or near the parent tree, and rooted or were not located from the area within 120 days of observation. Given their elongated shape, propagules tend to get trapped in vegetation (e.g. *S. alterniflora* blades; Sousa et al., 2007) and thus, extreme high tides and storm events may be required to ensure that the propagules can be carried away by currents.

Propagules that settled in a vertical position by leaning against *S. alterniflora* blades or a mangrove prop root, or falling into a crab burrow when released were more likely to survive relative to those that had landed in a horizontal position. McKee (1995) reported that 60% of propagules that rooted in a vertical position had survived after 2.5 years as compared to 90% of propagules that had died in a horizontal position within a period of 1.5 years. In Summer Haven, only 13% of propagules survived that had settled and remained in the horizontal position after a mean period of 100 days, supporting the hypothesis that settlement orientation contributes to propagule survivorship.

In addition to settlement orientation, propagule mortality has been linked to herbivory and desiccation. McKee (1995) reported 17% of mortality due to herbivory and 17% due to desiccation. In Summer Haven, 50% of propagule mortality was due to herbivore damage (e.g. missing ends or scraping scars observed along the hypocotyl or growing axis) and 12% due to desiccation. McKee (1995) observed that propagules that rooted were just as likely to be damaged by crabs after 8 days. In this study, a greater number of individuals were damaged by herbivores during the propagule stage (72 individuals) than during the recruit stage (15 individuals) during a period of 11 months.

Survivorship of *Rhizophora* propagules has been predicted by hypocotyl length. For example, De Ryck et al. (2012) suggested that the larger propagules had greater starch reserves, tolerance to herbivory, water and nutrient supplies and faster root growth relative to other
mangrove genera. Similarly, Ewe (2007) reported a positive relationship between survivorship and hypocotyl length, with lengths in the largest size class (17-20 cm) having 100% survivorship as compared to a mean survivorship of 59% across all size classes from a Florida population. Mean hypocotyl lengths of 25.1 ± 1.7 cm per adult from the Summer Haven population were comparable to those of other studies: 15–28 cm (n = 20) (Panama, Sousa et al., 2007), 23 cm (Belize, McKee, 1995) and reaching lengths of 30 cm (southern Florida, Gill and Tomlinson, 1969, 1971). Hypocotyl lengths were longer than those recorded by Ewe (2007; 3–20 cm, mean = 10 cm). Interestingly, Dangremond and Feller (2016) reported that mean hypocotyl lengths and percent flowering increased with latitude, reaching a mean of 34 cm from the GTM NERR, a greater mean length than was measured from the Summer Haven population located 2 km to the south. They had, however, collected the three longest propogules per adult. Despite the difference in collection methods, their results support the hypothesis that propagules with longer hypocotyls are more likely to develop into reproductive and even precocious adults (38% of individuals produced flowers within two years; Dangremond and Feller, 2016). In this study, only one of the 49 juveniles that was first tagged as a recruit or propagule produced a propagule and then became non-reproductive the next season. We suggest that a two-year old individual that becomes reproductive (Dangremond and Feller, 2016) is an unusual fate for most of the released propagules, which are typically smaller than 34 cm.

Annual node production and leaf numbers are indicators of vigor in R. mangle populations in Belize and Panama (Duke and Pinzón, 1992; Ellison and Farnsworth, 1993). At Summer Haven, maximum node production during the recruit stage was significantly greater for recruits that produced branches than for those that remained as recruits. Mean number of nodes was 4.6 nodes per year for those that remained as recruits, a rate comparable to shade plants (< 5 nodes per year in shady conditions; Duke and Pinzón, 1992). Recruits that developed branches produced 6.4 nodes per year, a rate comparable to sun plants (> 5 nodes per year in sun; Rabinowitz, 1975; Duke and Pinzón, 1992), which may be indicative of relatively more healthy individuals.

4.3. Conclusions

Cavanaugh et al. (2014) estimated that the range of R. mangle would extend northward 2.2–3.2 km per year over the next 50 years. Expansion of R. mangle populations at the leading edge of the distribution may be less limited by reproductive ability than by the physical challenges for propagules to disperse away from parent populations, given that most remained within meters of the parent, and to successfully recruit into S. alterniflora meadows, given that the grass blades act as barrier to prevent settlement in a vertical position (Sousa et al., 2007). The longer period of fruit production and propagule abscission relative to southern populations may promote monospecific stands and increase the potential for long-distance dispersal during extreme high tides and storm events.

From our observations, competition for space or top-down control by herbivores in the saltmarsh had not prevented the expansion of this species. Instead of predation and competition for space, Smith et al. (1994) suggest that facilitation occurs during the first few years of establishment. The density of seedlings was < 1.3 juveniles per m² at Summer Haven and was lower than the estimates of < 2.4 per m² from Biscayne Bay, Florida (Ball, 1980), suggesting a reduced potential for competition for resources as individuals colonize and establish in the saltmarsh community.

Populations living at the edge of their distribution are more vulnerable to local extinction if unable to tolerate extremes in physical conditions (Thullier et al., 2008). However, Proffitt & Travis (2014) predicted that self-fertilization would result in locally-adapted genotypes to temperate conditions. Rodriguez et al. (2016) described an increasing trend of winter minimum monthly temperatures from 1988 to 2013, which would support survivorship of mangrove individuals.

Throughout the study period, extreme cold events did not occur and the number of adults that produced offspring increased. In a northern Brazilian mangrove forest where seasonal dry periods are atypical, Fernandes (1999) suggested that variability in abiotic factors such as groundwater salinity may not necessarily coincide with the timing of reproductive events. Instead, a prolonged period of fruiting, as observed in this study, may be a function of physiological adaptations to promote reproductive success and colonization (Fernandes, 1999). In summary, R. mangle appeared to be tolerant to physical conditions at the leading edge of its distribution, to produce viable propagules and to sustain successive generations as it colonizes in saltmarsh communities.

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References