

Competition and abiotic stress affect the size of mangroves near their geographic range limit

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Abstract

Aims

Studies of competition in mangroves are mostly limited to seedlings and artificial settings like forestry projects. We conducted the first experimental study of intraspecific competition among adult mangroves in a natural mangrove forest to examine how important competition is in determining tree size compared with abiotic conditions.

Methods

We conducted a study near Port Aransas, Texas, USA, which is near the geographical limit of mangroves and dominated by monospecific stands of “scrub” form black mangroves, *Avicennia germinans*. We thinned ten plots to create a gradient of mangrove cover, and quantified the effects of mangrove cover on the growth of tagged mangroves from 2013 to 2019, and the mangrove canopy height in 2019.

Important Findings

The relative growth rate of tagged mangroves declined as mangrove cover increased, and plants in the plot with 100% mangrove cover did not grow, indicating that they had attained their maximum size. In plots with reduced mangrove cover, plant height increased sharply, with plants in the plot with 11% mangrove cover growing ~ 52% taller over six years. Canopy height was ~ 30% taller in the plot fringe than in the interior, and canopy height in both fringe and interior declined as mangrove cover increased. Measures of leaf chlorophyll

concentration and light interception suggested that plants were primarily limited by nitrogen. Our results showed that scrub mangroves compete strongly despite being limited by abiotic conditions, and that the importance of competition was greater in magnitude than that of abiotic differences between the fringe and interior.

Key words: competition; adult mangrove; nutrient limitation; growth response; scrub mangrove; geographical limit

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Introduction

Competition is an important driver of community structure and dynamics in plant communities worldwide (Goldberg 1990; Kunstler *et al.* 2016). A large number of studies have shown that the uptake of limited resources, such as sunlight, water and nutrients, by plants can interfere with the growth and vitality of their neighbors (Gurevitch *et al.* 1992). Most experimental studies of competition, however, have been done with small, short-lived species, because of the logistical difficulties in working with large, long-lived taxa. For example, most studies of competition among trees have relied on correlative approaches (Uriarte *et al.* 2004; Berger *et al.* 2008; Lasky *et al.* 2015), experimental studies with seedlings (Barot and Gignoux 2003), or experimental studies of adults in artificial contexts such as forestry plantations (Forrester *et al.* 2013). Relatively few studies exist in which adult tree density has been experimentally manipulated in a natural setting (but see Meyer *et al.* 2008; Rozendaal *et al.* 2020).

Competition among adult mangrove trees is likely to be an important driver of community structure. Mathematical models of mangrove forests include intense competitive interactions among trees (Berger and Hildenbrandt 2000; Berger *et al.* 2008; Piou *et al.* 2008), and correlative studies support the hypothesis that mangrove trees compete strongly with immediate neighbors (Krauss *et al.* 2008; Chen *et al.* 2013). Experimental studies, however, have largely been confined to seedlings and juveniles, and are often conducted in the context of afforestation projects rather than natural mangrove stands (Chen *et al.* 2013; Pranchai *et al.* 2018). Mangrove seedlings can compete strongly with each other (Cardona-Olarte *et al.* 2006; Zhu *et al.* 2020), but in stressful habitats they also often facilitate survival of conspecifics (Toledo *et al.* 2001). To our knowledge, there have been no experimental studies of competition among adult mangroves in natural settings.

A long-standing debate has focused on the impact of competition in structuring plant communities as a function of the severity of the abiotic environment. This debate is complex, but opinions generally fall into one of two camps. One perspective is that competition plays a similar role in plant communities irrespective of system productivity, but that the mechanisms by which plants compete change with abiotic stress (Tilman 1989). The opposing view is that competition is a predominant force within plant communities in productive environment, but decreases when environmental severity increases and productivity decreases (Grime 1979). Some of the disagreement between these views comes from a failure to distinguish between the intensity (i.e., absolute magnitude) and importance (i.e., magnitude relative to other processes) of competition (Grace 1991; Brooker *et al.* 2005). The debate is relevant to mangrove forests in that the two perspectives differ in their predictions about the role of competition among plants in low-productivity stands, such as for scrub growth forms of mangroves.

The geographical limit of mangroves is set by cold temperatures or drought (Osland *et al.* 2017). As a result of cold and drought, mangroves near their geographical range limits have are often shorter, wider, and more shrub-like relative to their tropical counterparts growing in benign environments (Osland *et al.* 2014). In addition to this geographical variation in height, mangroves also often vary in height within a site. Mangroves are usually tall at the water's edge (the fringe habitat) and shorter in the interior of mangrove stands, a pattern that reflects spatial differences in environmental factors, including nutrient dynamics, salinity, and tidal inundation (Feller *et al.* 2003; Lovelock *et al.* 2004). For example, in South Africa, the height of *Avicennia marina* plants varies between fringe and interior habitats due to nutrient (N and P) limitation in the interior (Naidoo 2009; Anton *et al.* 2020).

Many studies have documented how abiotic conditions affect mangrove size across elevational gradients (McKee *et al.* 2012; Krauss *et al.* 2014) and geographically (Osland *et*

al. 2017) but none have compared this with competition. We experimentally studied competition among adult mangroves near the high-latitude and high-salinity end of their geographic distribution in Texas. Mangroves here occur in monospecific stands and typically exhibit scrub morphology, rarely exceeding of two meters in height. The north-west coast of the Gulf of Mexico is an arid region with periodic hard freezes, and it is generally thought that the range limit and small size of mangroves in this area is set by a combination of cold, drought, and salinity stress (Madrid *et al.* 2014; Osland *et al.* 2014). The scrub growth form of mangroves in the western Gulf of Mexico may also reflect nutrient limitation, as suggested by strong responses of mangroves to experimental nutrient inputs (Weaver and Armitage 2018). We asked whether intraspecific competition was important in structuring the size distribution of plants at this site. Alternatively, given the abiotic context, mangrove size might be primarily controlled by abiotic conditions. We addressed this by quantifying the effects of mangrove cover on mangrove growth in a long-term experiment near Port Aransas, Texas. We experimentally manipulated mangrove cover in 10 plots at a relatively large spatial scale and measured growth as a response variable. In addition to measuring growth, we measured an index of plant nitrogen concentration and available light, since competition among plants would most likely be for either nitrogen or light, and we also measured the soil porewater salinity and soil water content. We tested two hypotheses. 1) Reducing mangrove density will reduce competition, leading to increased growth rates. However, if plants facilitate each other, growth rates might decline at low mangrove cover. 2) Alternatively, if plant growth is primarily limited by abiotic conditions, competition will be weak, and responses to mangrove density manipulations will be minor.

Methods

Our manipulative field experiment took place on Harbor Island, Port Aransas, Texas (27.86° N, 97.08° W; Fig. 1a). Harbor Island is located within a tidal delta (Sherrod and McMillan 1981), in a microtidal setting (0.27 m mean tidal range) that receives an average of 900 mm precipitation per year. Harbor Island tidal wetlands are currently dominated by black mangroves (*Avicennia germinans*), but vegetation has fluctuated between salt marsh and mangrove dominance over past decades, with mangrove and marsh vegetation coexisting across a patchy landscape. Black mangroves were known from Harbor Island as early as the 1930s (Sherrod and McMillan 1981). The population was severely damaged by hard freezes in 1983, 1987 and 1989 but rapidly recovered (Sherrod and McMillan 1985). More recent, less-severe freeze events (2010, 2018) have damaged leaves but not stems, and plants regrew leaves within a growing season (Osland *et al.* 2020). Thus, mangroves were common in the area for at least two decades before our experiment start, and had been present for at least seven decades.

In 2012, we demarcated ten large plots (Fig. 1b), each 42 m (perpendicular to the water's edge) × 24 m (parallel with the water's edge). Before we manipulated vegetation cover, all plots had similar elevation, soil characteristics and vegetation communities dominated by black mangrove with ~ 10% salt marsh vegetation that was predominantly *Batis maritima*, *Sarcocornia* sp., *Salicornia bigelovii*, with small patches of *Spartina alterniflora* (Guo *et al.* 2017). In summer 2012, plot-level mangrove cover was manipulated by removing all aboveground mangrove biomass from appropriate numbers of 3 × 3 m cells, mimicking the scale of patchiness in the natural environment (authors' personal observation), to create plots ranging from 0% to 100% nominal mangrove cover (0%, 11%, 22%, 33%, 44%, 55%, 66%, 77%, 88%, and 100%). Below-ground biomass was not directly manipulated, and we observed live pneumatophores extending into cleared cells throughout

the duration of the study, indicating that mangrove below-ground biomass was present in some “cleared” cells. Plots were arrayed in three blocks, with a wide range of mangrove densities represented in each block. In total there were $14 \times 8 = 112$ cells in each experimental plot (Fig. 1c), and each cell was either cleared of mangroves or left intact to facilitate maintenance. We maintained the cover treatments with periodic clipping and weeding of the cleared 3×3 m cells each year. We defined the first four rows of cells at the front of the plot, where plants tended to be taller, as the “fringe”, the back four rows of plots as the “back”, and the remaining six rows of plots as the “middle” of the plot. The middle and back together made up the plot “interior”.

In June of 2013, we tagged four individual mangroves in each plot except for the 0% mangrove plot. Each tagged plant was in the middle of a 3×3 m cell. The tagged plants were all in the interior habitat—the middle and back of each plot (Fig. 1c). We measured their height and canopy dimensions (the widest crown section, CD_1 , and the widest section perpendicular to the first section, CD_2). The two crown diameter measurements were used to calculate crown area via the equation for an ellipse: crown area = $[(CD_1)/2] * [(CD_2)/2] * \pi$. Crown area and height were integrated into a single estimate of volume via the following equation: volume = crown area * height (Osland *et al.* 2014). We repeated the measurements annually through November 2019.

Because mangroves were taller at plot fringe than in the interior, we supplemented the measurements of tagged plants with measurements of the overall canopy height at the fringe and back of each plot. We measured canopy height (defined as the height of the tallest plant in each cell) on May 2012, before mangrove cover in the plots was manipulated, and again on November 2019, measuring the height of the mangrove vegetation in six cells in the fringe of each plot (except for the 0% mangrove plot) and six cells in the back of each plot. We

averaged the readings to give a single value from the fringe and a single value from the back of each plot for each date.

To gain an understanding of what abiotic factors and resources might be limiting to mangroves at the site, and how these resources changed with mangrove density, we measured porewater salinity, soil water content, chlorophyll content of leaves and light interception by the canopy. We measured soil water content and porewater salinity of surface soils (top 10 cm) on eleven dates between June 2012 to March 2015, using standard gravimetric and rehydration techniques (Supplementary Fig. S1). We measured chlorophyll content of leaves on each tagged plant in October 2017, August 2018 and November 2019 using a CCM-200 meter (Opti-Sciences, Tyngsboro, Massachusetts, USA); the unit-less values obtained from this type of meter correlate well with leaf nitrogen content (Richardson *et al.* 2002). We measured three leaves per tagged plant and averaged these values to give a single value per plant; we then averaged values from replicate tagged plants to give a single value per plot.

We measured light intensity on 29 November 2019, using a SunScan Canopy Analysis System SS1, Delta-T Devices Ltd, Cambridge, UK. This unit has a 1 m wand with multiple PAR sensors whose readings are averaged to give a single integrated value. We measured light above and below (~ 10 cm above the ground) the canopy in five mangrove cells in the fringe of each plot and five mangrove cells in the back of each plot. We calculated the proportion of light intercepted by the vegetation for each cell using the formula: proportion of light intercepted = (light intensity above the canopy - light intensity at the soil surface) \times light intensity above the canopy \times 100%, and averaged replicate values to give a single value from the fringe and a single value from the back of each plot.

Data analyses

We calculated relative growth rate (RGR) of tagged mangroves based on plant canopy height, canopy area and plant volume, as $RGR = [Ln(\text{final size}) - Ln(\text{initial size})] / (t_1 - t_0)$, where t_0 and t_1 are the time in years when the experiment started and ended. We averaged RGR values for the replicate plants from each plot, omitting six plants that died, to give a single RGR value based on each measurement for each plot. We similarly calculated RGR of canopy height, using average final and average initial canopy heights in the fringe and back of the plots. In both cases, we used linear regression to evaluate the effect of mangrove cover on the relative growth rate (RGR) of tagged mangrove trees in each plot.

We calculated the relative neighbor interaction intensity (RII) based on the RGR values for the mangrove trees using the formula $RII = (RH_{+N} - RH_{-N}) / (RH_{+N} + RH_{-N})$, where RH_{+N} and RH_{-N} were the RGR of plant height (or canopy area, or volume) for mangrove trees in the presence (+) and absence (-) of mangrove neighbors. Because we were interested in how RGR varied across the gradient of plot-level mangrove cover, we used the RGR of the single fastest growing tree in the 11% plot as the control or “without neighbor” value. Similarly, for canopy height, we calculated RII based on the RGR of canopy height, using data from the 11% plot as the “without neighbors” value. Negative RII values indicate competition and positive values indicate facilitation.

To evaluate the effect of abiotic factors on the growth of mangrove trees in the fringe versus the back of each plot, we calculated an abiotic effect index using the same general formula as RII, based on the canopy height in the fringe and back: abiotic effect index = $(H_b - H_f) / (H_b + H_f)$, where H_b and H_f are plant height for mangrove trees in the fringe and back. We did not calculate this index using the tagged trees, because none of them were located in

the fringe zone. Negative values indicate conditions are more stressful in the back of the plot and positive values indicate the reverse.

We used one-way analyses of covariance (ANCOVA) to compare plot-level mangrove cover (covariate) and location effects (fixed factor) on mangrove canopy height, RGR, RII and light interception. We ran all statistical analyses with R 3.5.2.

Results

The relative growth rate of tagged mangroves declined linearly as mangrove cover increased (Fig. 2). *A. germinans* plants in the unmanipulated plot (100% mangrove cover) were stable, with little to no growth over the six-year period between 2013 and 2019. In plots with reduced mangrove cover, plant height increased sharply (Fig. 2a, $R^2 = 0.80$), with plants in the 11% mangrove plot growing ~52% taller over six years, and plot-level mangrove cover explaining 80% of the variation in RGR. In contrast, RGR of canopy area was not significantly related to mangrove cover (Fig. 2c, $R^2 = 0.26$). Plant volume, estimated as canopy area \times height, decreased with increasing mangrove cover (Fig. 2c, $R^2 = 0.64$). Relative interaction intensity (RII) values based on plant height and volume were smallest (closest to zero) at low mangrove densities, and greatest (most negative) at high mangrove densities (Fig. 2b, f). RII based on canopy area did not differ as a function of plot-level mangrove cover (Fig. 2d).

Canopy height was ~ 24-30% taller in the fringe than in the back of plots (Fig. 3a). Canopy height declined as mangrove cover increased in both the fringe and back of the plots, with plot-level mangrove cover explaining 69-75% of the variation in canopy height. In the plot fringe, canopy height declined from ~ 245 cm at low mangrove cover to ~ 160 cm at

100% mangrove cover. In the back of the plots, canopy height declined from ~ 185 cm at low mangrove cover to ~ 110 cm at 100% mangrove cover. Thus, plants growing at low densities in the back of the plots grew as tall or taller (185 cm) as plants growing at normal, high densities, in plot fringe (160 cm). Relative growth rate (RGR) of canopy height and relative interaction intensity (RII) based on RGR of canopy height both declined as mangrove cover increased, with no difference between the fringe and the back of plots (Fig. 3b, c). The abiotic effect index was negative, indicating that conditions were more stressful in the back of the plots than in the fringe, did not vary as a function of mangrove cover (Fig. 3d), and was smaller than the RII based on RGR of canopy height (Fig. 3c).

Soil porewater salinity was higher in the interior (63-85 PSU) than in the fringe (52-66 PSU), but soil water content did not differ between zones (Supplementary Fig. S1, Table S1). Plot-level mangrove cover had no significant effect on soil porewater salinity and soil water content (Supplementary Fig. S1). Leaf chlorophyll concentration of mangroves was ~ 23% higher in plots with low mangrove cover than in plots with high mangrove cover, with plot-level mangrove cover explaining 59% of the variation (Fig. 4a). Light interception by vegetation did not differ between the fringe of plots and the back of plots (Fig. 4b). Light interception by mangroves increased by ~ 83% from ~ 88% in plots with high mangrove cover to ~ 96% in plots with low mangrove cover, with plot-level mangrove cover explaining 39-49% of the variation (Fig. 4b). Although the effect of mangrove cover on light interception was highly significant in the ANCOVA analysis, the less-powerful individual regressions for each zone considered separately were significant in only one case (Fringe, $P = 0.07$; Back, $P = 0.03$).

Discussion

We conducted the first experimental study of intraspecific competition among adult mangroves in a natural mangrove forest. Our results indicated that, at our study site near the range limit of *A. germinans* in Texas, the size of mangrove plants was strongly limited by competition, and also in the forest interior compared to the fringe by abiotic conditions.

Mangroves in the study plot that we did not manipulate (100 percent mangrove cover) showed no growth over the six-year period, indicating that they had reached their maximum size under ambient levels of intraspecific competition and abiotic stress. *A. germinans* has occurred at our study site since at least the 1930s, and increased in areal extent from then until large patches were killed by several hard freezes in the 1980s (Sherrod and McMillan 1981, 1985). Since those freeze events, mangrove areal extent has rebounded and now surpasses that recorded in 1979 before the freezes (Montagna *et al.* 2011; Armitage *et al.* 2015). In particular, almost all of Harbor Island was either dominated by mangroves in 1990 or had transitioned from marsh to mangrove by 2004-2010 (Montagna *et al.* 2011; Armitage *et al.* 2015). Thus, the areal extent of mangroves on the Texas coast is limited primarily by hard freezes, and increases in the absence of such events. In contrast, the size of individual plants must be limited by other factors, such as salinity and nutrient availability, and plants attain their maximum size of ~1-2 m in height within a few years or at most a decade.

When we reduced the cover of mangroves within our experimental plots, plants at low densities grew rapidly, increasing in height by ~52% after 6 years. To our knowledge, this is the first experimental study of intraspecific competition among adult mangroves in a natural setting. Observational studies from natural forests, however, have long indicated that mangroves are likely competing with conspecifics in dense stands (Pranchai *et al.* 2018). Similarly, experimental plantings of mangroves in afforestation projects find more rapid

growth at low density (Gedan and Silliman 2009), and models of tree growth in mangrove forests assume both intra- and inter-specific competition (Berger and Hildenbrandt 2000; Berger *et al.* 2008).

Our results showed that mangroves grew taller rather than wider when plot-level mangrove cover was reduced. Height increased up to 52% at low densities, but canopy area only 23%. This was a consequence of our experimental design. We did not isolate individual plants, but instead progressively freed up more and more 3 × 3 m patches of mangroves from competition. Thus, the individual tagged plants that we monitored were surrounded by multiple neighbors, even if overall mangrove cover in the 42 × 24 m plot was as low as 11%. Since all the plants in a particular 3 × 3 m cell likely grew larger when mangrove cover at the plot scale was reduced, the tagged plants were constrained by their neighbors to grow taller rather than wider. This result is consistent with previous findings that *A. germinans* plants with dense neighbors tended to be taller but had a smaller crown (Pranchai *et al.* 2018).

The height gradient within each plot was probably explained by variation in abiotic stress, but variation in mangrove growth and size among plots was probably explained by resource availability. Porewater salinity was higher in the interior of the plots than in the fringe, but did not vary among plots as a function of mangrove cover. The measured salinity values were hypersaline (up to 85 PSU averaged over 11 sampling dates), consistent with the notion that this site is stressful overall for mangrove growth. High soil porewater salinity is one factor that often correlates with differences in plant height between fringe and interior zones of mangrove forests (Cintrón *et al.* 1978; Lovelock *et al.* 2005). Soil water content did not differ between the interior of plots and the fringe, or among plots. Air and soil temperature in these plots showed a hump-shaped relationship with plot-level mangrove cover (Guo *et al.* 2017), but growth responses to mangrove cover were linear, not hump-shaped. We conclude, therefore, that the growth response to thinning was due to increased

resource availability. We did not measure the availability of resources such as soil nitrogen in the plots, and did not separately manipulate the availability of different resources. As a result, we can only speculate about which resources were most affected by competition among *A. germinans* plants. Leaf chlorophyll concentration, a proxy for leaf nitrogen concentration (Croft *et al.* 2017; Li *et al.* 2018), decreased as mangrove cover increased, suggesting that plants growing at high densities were nitrogen-limited. We note, however, that leaf chlorophyll content can reflect a number of factors in addition to soil nitrogen availability, such as climate (drought, precipitation), soil characteristics and soil microbes (Li *et al.* 2018); however, we have no reason to believe that these confounding factors might have varied systematically across the study plots. Consistent with this hypothesis, a fertilization experiment near our study site found that nutrient enrichment (Nitrogen plus Phosphorus, $0.342 \text{ g N m}^{-2} \text{ day}^{-2}$ and $0.108 \text{ g P m}^{-2} \text{ day}^{-1}$) increased mangrove height by $\sim 46\%$ over four years (Weaver and Armitage 2018). Moreover, this hypothesis is consistent with our observation that mangrove root systems (as indicated by visible pneumatophores) extended far beyond the plant canopies, suggesting that plants were vigorously foraging for below-ground resources. In our experiment, mangroves in low-density plots blocked more light than mangroves in high density plots. Presumably this reflected an increase in leaf area index, although we did not measure this. In any case, it suggests that growth of plants in high density plots was not primarily limited by light, because plants in low density plots were able to thrive despite creating more shade.

We worked with relatively short, scrub mangroves. Mangrove scrub (or “shrub”) morphologies can result from various abiotic conditions, including drought stress, freeze stress, salinity stress, nutrient limitation, and hydrological isolation (Lugo and Snedaker 1974; Feller *et al.* 2003; Lovelock *et al.* 2004). In the absence of freeze events and where freshwater and nutrients are abundant, *A. germinans* trees can grow to 30 m in height (Suárez

and Medina 2005; Menezes *et al.* 2008). However, *A. germinans* plants at our study site, near the geographic range limit of mangroves, are shorter, wider, multi-stemmed, and more shrub-like than their tropical counterparts growing in resource-rich environments (Osland *et al.* 2014). Moreover, plants in the interior are more stunted than plants growing in the fringe, a pattern commonly seen elsewhere and usually attributed to nutrient limitation in the interior of the forest (Feller *et al.* 2003; Naidoo 2009; Anton *et al.* 2020). The Western Gulf of Mexico is an arid region with periodic hard freezes, and it is generally thought that the range limit and small size of mangroves in this area is set by cold and drought stress (Osland *et al.* 2013, 2014; Gabler *et al.* 2017). Our results, and a past fertilization experiment (Weaver and Armitage 2018), however, show that nutrient limitation also constrains mangrove growth in our study area. Although these results don't address the factors setting the range limit of mangroves, they do show that nutrient availability interacts with cold and drought stress to affect the growth of mangroves near their geographic range limit.

Ecologists have long argued about how the importance of competition should vary along productivity gradients, with Grime (1979) suggesting that competition should decrease as environmental severity increases, and Tilman (1989) arguing that competition should play a similar role in all plant communities irrespective of system productivity. At least some of this debate was due to a failure to clearly distinguish between the intensity of competition and its importance relative to other factors (Grace 1991; Brooker *et al.* 2005). Later theories of facilitation posited that interactions among species might switch from negative to positive as abiotic stress increased (Bertness and Callaway 1994). Our experiment was not designed to address these issues because we only worked at a single site; however, we did find that mangrove plants competed strongly in our study site in Texas where they were severely stunted by abiotic stress. Moreover, abiotic stress (inferred from tree canopy height, and measured soil porewater salinity) was higher in the interior of the plots than in the fringe, but

the intensity of competition was similar in the interior and the fringe. At the same time, the value of the abiotic effect index was considerably smaller than the value of RII based on canopy height, showing that competition was greater than the abiotic effect index. The most negative value of the abiotic effect index was not a statistical outlier, but even if it is dropped, the relationship between the abiotic effect index and mangrove cover is still not significant. Thus, our results show that competition among mangroves can be intense even when plants are severely stunted, that the intensity of competition does not change across a local stress gradient near the geographic range limit of the plants, and that at this site, the intensity of competition was greater than the effect of the local abiotic stress gradient between forest fringe and interior.

Within mangrove forests, conspecific and interspecific neighbors can act as competitors or facilitators following disturbances; the nature of the interaction depends on the species identity and the nature of the disturbance (Uriarte *et al.* 2004). Some evidence exists that mangrove seedlings may facilitate each other's survival under harsh conditions (Toledo *et al.* 2001), leading to the suggestion that mangrove afforestation projects could be more successful if seedlings were planted in clumps to maximize survival rather than evenly spaced to minimize competition (Gedan and Silliman 2009). We found no evidence for facilitation in our experiment. Our methods were not ideal to test facilitation because our design did not isolate single plants, but only small groups of plants in 3×3 m cells; however, at this spatial scale we found no evidence for net facilitation (i.e., RII was never positive). Previous studies have typically found facilitation when comparing single plants to small groups of plants (Toledo *et al.* 2001; Gedan and Silliman 2009), and it may be that we did not observe it because we worked at the wrong spatial scale. Alternatively, facilitation in mangroves may be most important at the seedling stage (McKee *et al.* 2007; Huxham *et al.* 2010), which was bypassed in our experiment.

One caveat to our results is that the measurements of leaf chlorophyll content and growth of tagged trees were conducted only in the interior of the plots. The measurements of the abiotic stress effect, then, were based only on the canopy height of the 3×3 m mangrove cells. However, measurements of RGR based on height of tagged trees and on canopy height of the 3×3 m cells were almost identical in the interior (compare Fig. 2a with Fig. 3b), so we don't think conclusions would have changed if we had also measured growth of tagged trees in the fringe.

In conclusion, we conducted the first experimental study of intraspecific competition among adult mangroves in a natural mangrove stand. Although our finding that mangroves compete is perhaps not surprising, it is somewhat unexpected that mangroves compete so strongly at a site where they are severely stunted by abiotic stress. Moreover, the importance of competition was greater in magnitude to the importance of the abiotic stress difference between the fringe and interior of the habitat. These results emphasize that mangrove forests are strongly structured by competition, even in locations where plants are severely stunted by abiotic stress.

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References

- Anton A, Almahasheer H, Delgado A, et al. (2020) Stunted mangrove trees in the oligotrophic central red sea relate to nitrogen limitation. *Front Mar Sci* 7: 597.
- Armitage AR, Highfield WE, Brody SD, et al. (2015) The contribution of mangrove expansion to salt marsh loss on the Texas Gulf Coast. *PLoS One* 10: e0125404.
- Barot S, Gignoux J. (2003) Neighbourhood analysis in the savanna palm *Borassus aethiopum*: interplay of intraspecific competition and soil patchiness. *J Veg Sci* 14: 79–88.
- Berger U, Hildenbrandt H. (2000) A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. *Ecol Model* 132: 287–302.
- Berger U, Piou C, Schiffers K, et al. (2008) Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. *Perspect Plant Ecol* 9: 121–135.
- Bertness MD, Callaway RM. (1994) Positive interactions in communities. *Trends Ecol Evol* 9: 191–193.
- Brooker R, Kikvidze Z, Pugnaire FI, et al. (2005) The importance of importance. *Oikos* 109: 63–70.
- Cardona-Olarte P, Twilley RR, Krauss KW, et al. (2006) Responses of neotropical mangrove seedlings grown in monoculture and mixed culture under treatments of hydroperiod and salinity. *Hydrobiologia* 569: 325–341.

- Chen L, Peng S, Li J, et al. (2013) Competitive control of an exotic mangrove species: restoration of native mangrove forests by altering light availability. *Restor Ecol* 21: 215–223.
- Cintron G, Lugo AE, Pool DJ, et al. (1978) Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* 10: 110–121.
- Croft H, Chen J, Luo X, et al. (2017) Leaf chlorophyll content as a proxy for leaf photosynthetic capacity. *Glob Change Biol* 23: 3513–3524.
- Feller IC, McKee KL, Whigham DF, et al. (2003) Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry* 62: 145–175.
- Forrester DI, Elms SR, Baker TG. (2013) Tree growth-competition relationships in thinned *Eucalyptus* plantations vary with stand structure and site quality. *Eur J Forest Res* 132: 241–252.
- Gabler CA, Osland MJ, Grace JB, et al. (2017) Macroclimatic change expected to transform coastal wetland ecosystems this century. *Nat Clim Change* 7: 142–147.
- Gedan KB, Silliman BR. (2009) Using facilitation theory to enhance mangrove restoration. *AMBIO* 38: 109–109.
- Goldberg DE. (1990) Components of resource competition in plant communities. In Grace JB, Tilman D (eds). *Perspectives on Plant Competition*, San Diego: Academic Press, 27–49.
- Grace JB. (1991) A clarification of the debate between Grime and Tilman. *Funct Ecol* 5: 583–587.
- Grime JP. (1979) *Plant Strategies and Vegetation Processes*. London: John Wiley and Sons.

- Guo H, Weaver C, Charles SP, et al. (2017) Coastal regime shifts: rapid responses of coastal wetlands to changes in mangrove cover. *Ecology* 98: 762–772.
- Gurevitch J, Morrow LL, Wallace A, et al. (1992) A meta-analysis of competition in field experiments. *Am Nat* 140: 539–572.
- Huxham M, Kumara MP, Jayatissa LP, et al. (2010) Intra-and interspecific facilitation in mangroves may increase resilience to climate change threats. *Philos T R Soc B* 365: 2127–2135.
- Krauss KW, Lovelock CE, McKee KL, et al. (2008) Environmental drivers in mangrove establishment and early development: a review. *Aquat Bot* 89: 105–127.
- Krauss KW, McKee KL, Lovelock CE, et al. (2014) How mangrove forests adjust to rising sea level. *New Phytol* 202: 19–34.
- Kunstler G, Falster D, Coomes DA, et al. (2016) Plant functional traits have globally consistent effects on competition. *Nature* 529: 204–207.
- Lasky JR, Bachelot B, Muscarella R, et al. (2015) Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. *Ecology* 96: 2157–2169.
- Li Y, He N, Hou J, et al. (2018) Factors influencing leaf chlorophyll content in natural forests at the biome scale. *Front Ecol Evol* 6: 64.
- Li Z, Tian D, Wang B, et al. (2019) Microbes drive global soil nitrogen mineralization and availability. *Glob Change Biol* 25: 1078–1088.
- Lovelock CE, Feller IC, McKee KL, et al. (2004) The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Funct Ecol* 18: 25–33.

- Lovelock CE, Feller IC, McKee KL, et al. (2005) Variation in mangrove forest structure and sediment characteristics in Bocas del Toro, Panama. *Caribb J Sci* 41: 456–464.
- Lugo AE, Snedaker SC. (1974) The ecology of mangroves. *Annu Rev Ecol Evol S* 5: 39–64.
- Madrid EN, Armitage AR, López-Portillo J. (2014) *Avicennia germinans* (black mangrove) vessel architecture is linked to chilling and salinity tolerance in the Gulf of Mexico. *Front Plant Sci* 5: 503.
- McKee KL, Rogers K, Saintilan N. (2012) Response of salt marsh and mangrove wetlands to changes in atmospheric CO₂, climate, and sea level. In Middleton BA (ed). *Global change and the function and distribution of wetlands*, Dordrecht: Springer, 63–96.
- McKee KL, Rooth JE, Feller IC. (2007) Mangrove recruitment after forest disturbance is facilitated by herbaceous species in the Caribbean. *Ecol Appl* 17: 1678–1693.
- Menezes MPM, Berger U, Mehlig U. (2008) Mangrove vegetation in Amazonia: a review of studies from the coast of Pará and Maranhão states, north Brazil. *Acta Amazon* 38: 403–420.
- Meyer KM, Ward D, Wiegand K, et al. (2008) Multi-proxy evidence for competition between savanna woody species. *Perspect Plant Ecol* 10: 63–72.
- Montagna PA, Brenner J, Gibeaut J, et al. (2011) Coastal impacts. In Schmandt J, North GR, Clarkson J (eds). *The Impact of Global Warming on Texas*, Austin: University of Texas Press, 96–124.
- Naidoo G. (2009) Differential effects of nitrogen and phosphorus enrichment on growth of dwarf *Avicennia marina* mangroves. *Aquat Bot* 90: 184–190.

- Osland MJ, Day RH, Hall CT, et al. (2017) Mangrove expansion and contraction at a poleward range limit: climate extremes and land- ocean temperature gradients. *Ecology* 98: 125–137.
- Osland MJ, Day RH, Hall CT, et al. (2020) Temperature thresholds for black mangrove (*Avicennia germinans*) freeze damage, mortality and recovery in North America: refining tipping points for range expansion in a warming climate. *J Ecol* 108: 654–665.
- Osland MJ, Day RH, Larriviere JC, et al. (2014) Aboveground allometric models for freeze-affected black mangroves (*Avicennia germinans*): equations for a climate sensitive mangrove-marsh ecotone. *PLoS One* 9: e99604.
- Osland MJ, Enwright N, Day RH, et al. (2013) Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biol* 19: 1482–1494.
- Piou C, Berger U, Hildenbrandt H, et al. (2008) Testing the intermediate disturbance hypothesis in species- poor systems: a simulation experiment for mangrove forests. *J Veg Sci* 19: 417–424.
- Pranchai A, Jenke M, Vogt J, et al. (2018) Density-dependent shift from facilitation to competition in a dwarf *Avicennia germinans* forest. *Wetl Ecol Manag* 26: 139–150.
- R Development Core Team. (2018) R: a language and environment for statistical computing, version 3.5.2. R Foundation for Statistical Computing, Vienna, Austria.
- Richardson AD, Duigan SP, Berlyn GP. (2002) An evaluation of noninvasive methods to estimate foliar chlorophyll content. *New Phytol* 153: 185–194.

- Rozendaal DM, Phillips OL, Lewis SL, et al. (2020) Competition influences tree growth, but not mortality, across environmental gradients in Amazonia and tropical Africa. *Ecology* 101: e03052.
- Sherrod CL, McMillan C. (1981) Black mangrove, *Avicennia germinans*, in Texas: past and present distribution. *Contrib Mar Sci* 24: 115–131.
- Sherrod CL, McMillan C. (1985) The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. *Contrib Mar Sci* 28: 129–140.
- Suárez N, Medina E. (2005) Salinity effect on plant growth and leaf demography of the mangrove, *Avicennia germinans* L. *Trees* 19: 722–728.
- Tilman D. (1989) Competition, nutrient reduction and the competitive neighbourhood of a bunchgrass. *Funct Ecol* 3: 215–219.
- Toledo G, Rojas A, Bashan Y. (2001) Monitoring of black mangrove restoration with nursery-reared seedlings on an arid coastal lagoon. *Hydrobiologia* 444: 101–109.
- Uriarte M, Canham CD, Thompson J, et al. (2004) A neighborhood analysis of tree growth and survival in a hurricane- driven tropical forest. *Ecol Monogr* 74: 591–614.
- Weaver CA, Armitage AR. (2018) Nutrient enrichment shifts mangrove height distribution: implications for coastal woody encroachment. *PloS One* 13: e0193617.
- Zhu D, Hui D, Wang M, et al. (2020) Light and competition alter leaf stoichiometry of introduced species and native mangrove species. *Sci Total Environ* 738: 140301.

Figure Legends

Figure 1. The study site was located a) in the Gulf of Mexico, near Aransas Bay, Texas, United States. The 42 m × 24 m study plots (demarcated with dashed lines) were located b) on Harbor Island, in three blocks (demarcated with solid lines); percent values indicate maintained mangrove cover in each plot. The image was taken in 2013 shortly after the study began. c) Schematic of a representative plot depicting mangrove (gray) and marsh (no shading) patches (3 m × 3 m), X symbols indicate four tagged trees.

Figure 2. Relative growth rate (RGR) of tagged mangrove trees from June 2013 to November 2019 based on (a) height ($R^2 = 0.80$, $P = 0.001$), (c) canopy area (no significant pattern), and (e) volume ($R^2 = 0.64$, $P = 0.01$); and RII (relative interaction intensity) based on RGR (b) RII (RGR of height, $R^2 = 0.81$, $P = 0.001$), (d) RII (RGR of canopy area, no significant pattern), (f) RII (RGR of volume, $R^2 = 0.62$, $P = 0.01$) as a function of nominal plot-level mangrove cover (grey shadow represents 95% confidence interval).

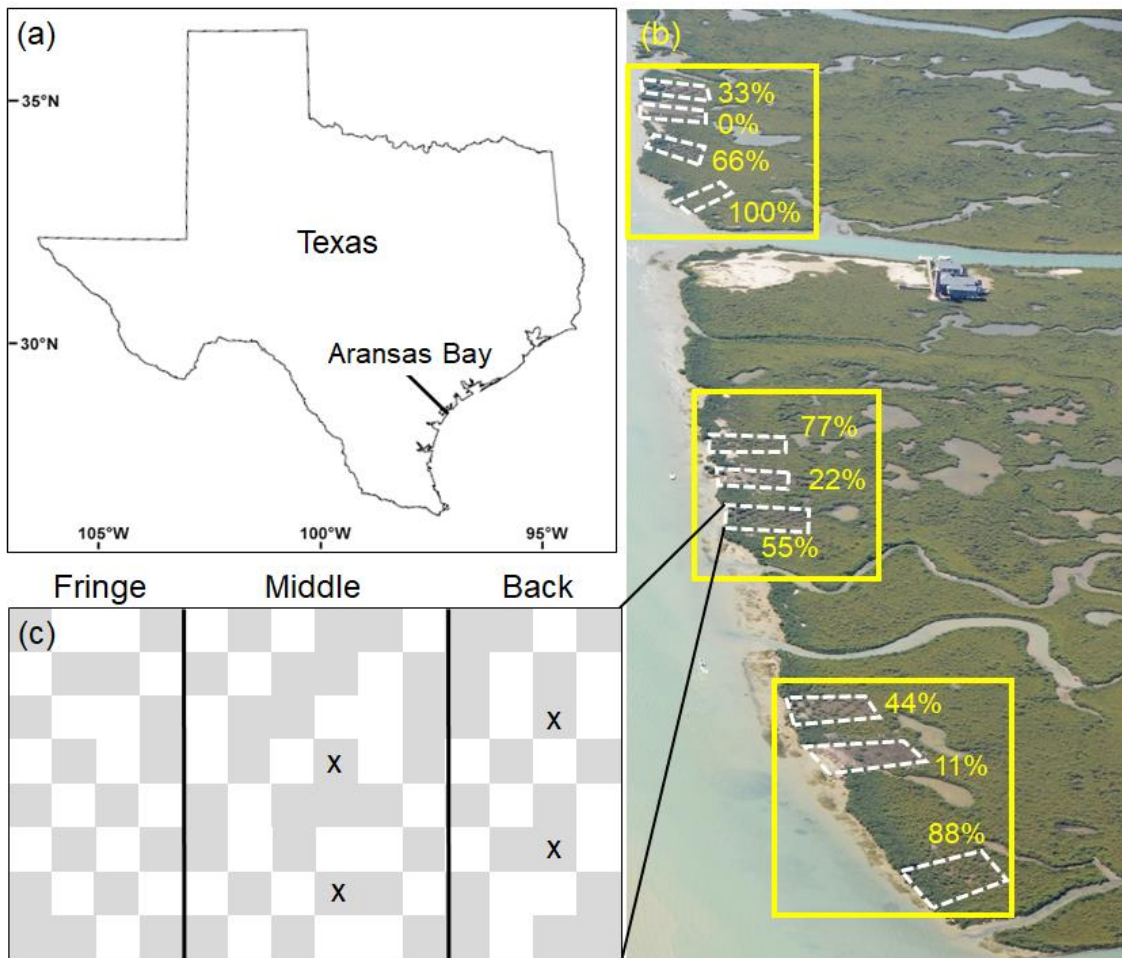
Figure 3. (a) Height of the mangrove canopy (ANCOVA: Mangrove cover, $F_{1, 98} = 102.7$, $P < 0.001$; Location: $F_{1, 98} = 110.3$, $P < 0.001$; Mangrove cover × Location: $F_{1, 98} = 1.1$, $P = 0.30$), (b) relative growth rate (RGR, based on canopy height, ANCOVA: Mangrove cover, $F_{1, 96} = 16.8$, $P < 0.001$; Location: $F_{1, 96} = 0.14$, $P = 0.71$; Mangrove cover × Location: $F_{1, 96} = 3.0$, $P = 0.09$), (c) RII based on RGR of canopy height, (d) abiotic effect index based on the height difference between canopy height of mangrove in the fringe and back of each mangrove plot as a function of nominal plot-level mangrove cover (ANCOVA comparing

abiotic effect index with RII based on RGR of canopy height: Mangrove cover, $F_{1,21} = 19.2$, $P = 0.0002$; Index: $F_{2,21} = 6.1$, $P = 0.008$; Mangrove cover \times Index: $F_{2,21} = 5.4$, $P = 0.013$).

Figure 4. Effect of nominal mangrove cover on potentially-limiting resources. (a) leaf chlorophyll content of tagged mangrove trees ($R^2 = 0.59$, $P = 0.02$), (b) light interception by mangrove canopy in the fringe and the back of plots (ANCOVA: Mangrove cover, $F_{1,86} = 26.4$, $P < 0.001$; Location: $F_{1,86} = 1.7$, $P = 0.19$; Mangrove cover \times Location: $F_{1,86} = 0.0$, $P = 0.98$).

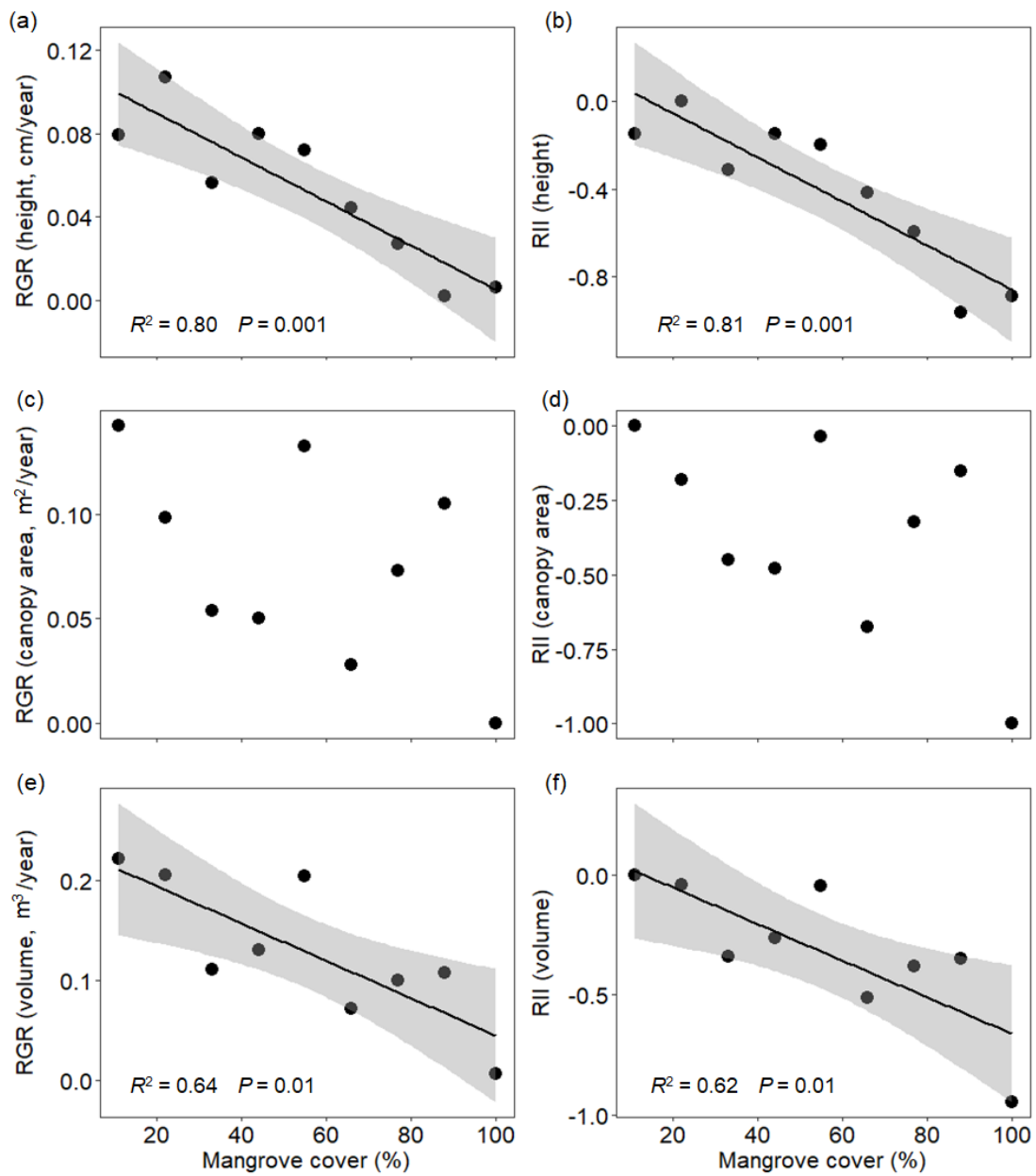
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Figure 1



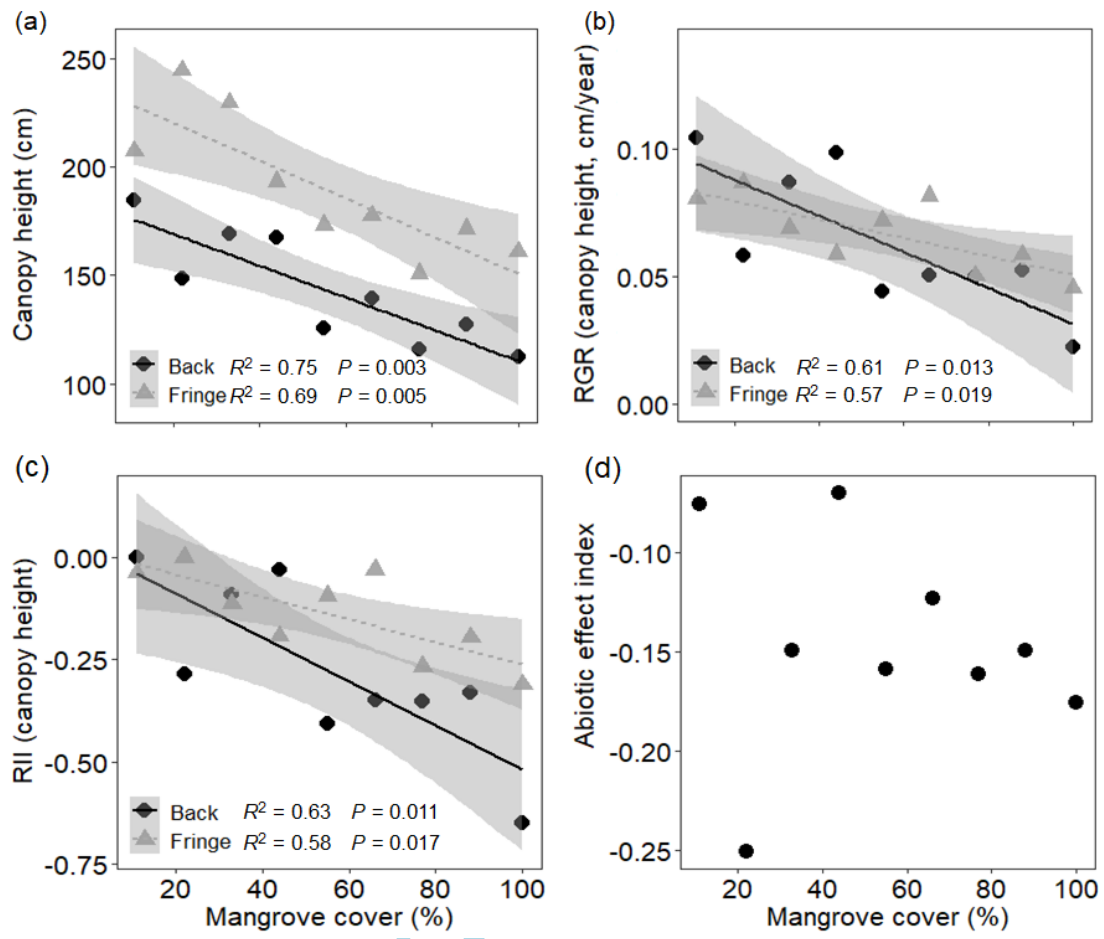
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Figure 2



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Figure 3



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Figure 4

