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A comparison of mangrove and marsh influences on soil respiration rates: A mesocosm study

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ABSTRACT

Due to reductions in freeze events, mangroves have been rapidly encroaching into previously salt marsh-dominated coastal wetlands along the northeastern shores of Florida, USA. This shift in dominant wetland vegetation type may have significant implications for belowground processes such as soil organic matter decomposition and respiration. Using a full factorial greenhouse mesocosm experiment, we investigated the effects of plant type (no plant, *Avicennia germinans*, or *Spartina alterniflora*) and soil type (sand, mangrove-derived soil, or marsh-derived soil) on estimated heterotrophic soil respiration rates. While we predicted that *A. germinans* mangrove seedlings would increase heterotrophic respiration, we found that mangrove seedlings did not increase heterotrophic respiration when compared to control (no plant) treatments. Additionally, we found that heterotrophic respiration was higher in marsh-derived soils than in mangrove-derived soils for both control and mangrove plant treatments. Our findings suggest that the stage of mangrove invasion and the level of root development may influence changes in heterotrophic soil respiration.

1. Introduction

Coastal wetlands, such as salt marshes and mangrove forests, are efficient carbon (C) sinks due to high rates of sediment C capture, high primary productivity per area, and low decomposition rates (Rabenhorst, 1995; Mcleod et al., 2011; Taillardat et al., 2018). In northern Florida, reduced frequency of freeze events has permitted mangroves, which have been historically restricted to the tropics and subtropics, to encroach into established temperate salt marsh ecosystems (Stevens et al., 2006; Krauss et al., 2011; Saintilan et al., 2014; Cavanaugh et al., 2014, 2019). This shift in dominant vegetation type could have a significant impact on soil C storage in these coastal wetlands due to potential changes in root activity and litter composition. Root inputs can strongly influence soil C storage in terrestrial systems (Cheng and Coleman, 1990; Dijkstra and Cheng, 2007; Bird et al., 2011; de Graaff et al., 2014; Lange et al., 2015), but we lack an understanding of how these changes in dominant plant functional type may affect soil C storage in coastal wetlands.

Salt marshes span coastlines from the arctic to the subtropics and are dominated by herbaceous vegetation, while mangrove forests exist largely in the tropics and subtropics and are dominated by woody vegetation (Mitsch and Gosselink, 2007). Mangroves such as *Avicennia germinans* are salt-tolerant trees that occupy a narrow fringe along coastlines located approximately between 32.3°N and 38.9°S (Bunting et al., 2018). At higher latitudes, herbaceous salt marsh species such as *Spartina alterniflora* dominate owing to the freeze intolerance of mangroves (Kangas and Lugo, 1990). Once released from temperature constraints, established mangroves tend to outcompete temperate salt marsh plant species for light, nutrients, and space due to advantages in reproduction, perennial aboveground structure growth, shading, and high root biomass production (Kangas and Lugo, 1990; Simpson et al., 2013, 2019; Osland et al., 2013; Doughty et al., 2016). The expansion of mangroves into temperate salt marshes has been observed in New Zealand, southern Australia, South America, and the Gulf and Atlantic coasts of the USA (Saintilan et al., 2014). This expansion is expected to increase in areas such as the southeastern USA, where small changes in winter climate factors (such as mean annual minimum temperature and number of days below freezing) have been predicted to increase mangrove expansion into salt marshes (Osland et al., 2013). Some studies have shown how this expansion of woody mangroves into herbaceous salt marshes may fundamentally alter the structure and function of these coastal ecosystems (Kelleway et al., 2016). However, less is known about how mangrove and marsh vegetation influence soil respiration rates and how a shift in dominant plant species will

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ultimately alter belowground C cycling (Kelleway et al., 2016; Yando et al., 2016; Barreto et al., 2018).

In addition to allocthonous sediment inputs, rates of soil C sequestration in coastal wetlands are largely determined from the balance of soil respiration and primary production (Choi and Wang, 2004; Saintilan et al., 2013). Soil C accumulates when the rate of C deposited into the system as sediment and organic matter (OM) exceeds the rate of C lost as CO_2 through soil respiration (McKee, 2011). Soil respiration is a combination of root respiration and heterotrophic soil respiration (henceforth termed 'heterotrophic respiration') that results from microbial decomposition of OM. Herbaceous marsh species such as *S. alterniflora* produce different litter than woody mangroves and therefore contribute OM of different qualities to the soil, which can influence decomposition rates (Taylor et al., 1989; Enríquez et al., 1993). Lignin content, in particular, can have a significant impact on litter decomposition rates. Lignin concentration is inversely related to litter decomposition rate due to the recalcitrance of its chemical structure to microbial decay (Melillo et al., 1982; Austin and Ballaré, 2010). For example, root tissues of the mangrove *A. germinans* have been found to have approximately 13% (seedlings) and 27% (adult trees) lignin content by weight (Chapman, unpublished data), while root tissues of *S. alterniflora* contain approximately 9% lignin (Benner et al., 1987, 1991). Therefore, OM in soils containing mangrove-derived plant litter may decompose more slowly than OM in soils dominated by herbaceous marsh-derived plant inputs, thereby reducing heterotrophic respiration rates.

Vegetation type in coastal wetlands has the potential to significantly impact heterotrophic respiration through root activity. Increased heterotrophic respiration could be caused by mechanisms such as O_2-driven priming due to root oxygen loss (Brix, 1994; Wolf et al., 2007) or substrate-induced priming due to the production of root exudates (Bais et al., 2006; Blagodatskaya and Kuzyakov, 2008; Haichar et al., 2014). Both *A. germinans* and *S. alterniflora* have well-developed aerenchyma and leak oxygen into the surrounding soils and rhizosphere (Teal and Kanwisher, 1966; Mendelssohn and Postek, 1982; McKee et al., 1988; Maricle and Lee, 2002; Pi et al., 2009; Hogarth, 2015). Though we do not know the difference in oxygen delivery between the two plants, mangrove-dominated soils have been observed to possess more putatively aerobic bacteria than salt marsh-dominated areas (Barreto et al., 2018). This suggests that mangroves may have a greater capacity for root oxygen loss than marsh plants such as *S. alterniflora*, which could increase wetland heterotrophic respiration as mangroves encroach into salt marshes (Wolf et al., 2007; Kirwan and Blum, 2011). However, little is known about how mangrove and marsh roots may specifically contribute to differences in heterotrophic respiration.

Despite previous studies on biomass changes in mangrove-marsh ecotones, it remains unclear how net soil C storage in these transitional wetland ecosystems will be affected by mangrove encroachment. While soil respiration rates in mangroves and salt marshes have been compared *in situ*, they have not been compared in a way that can isolate the effects of plants from the soils in which they occur. Using plants and soils from a mangrove-marsh ecotonal system in Northeast Florida, we investigated how mangrove encroachment may influence heterotrophic respiration in coastal wetlands. We performed an *ex situ* greenhouse mesocosm experiment in which we cross-planted *A. germinans* seedlings and *S. alterniflora* plugs in mangrove-derived and marsh-derived soils. We hypothesized that (1) both mangrove and marsh plants would increase heterotrophic respiration relative to unplanted soil, and that (2) mangrove seedlings would increase heterotrophic respiration more than marsh plants. Improving our understanding of belowground C cycling within shifting mangrove-marsh ecotones could potentially lead to more accurate predictions of C storage across a broader scale of coastal wetland systems (Holmquist et al., 2018).

2. Methods

2.1. Site description

Soil and plant samples were taken from tidal wetlands within the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM), located north of St. Augustine, Florida (30.11 N, 81.37 W; Fig. 1). GTM is 50 miles south of the current known northern range limit of Florida mangrove populations (Williams et al., 2014). At the sample collection sites, mean tidal range is approximately 50 cm and salinity is approximately 25 psμ (NOAA National Estuarine Research Reserve System, 2019). These sites are dominated by the C_4 perennial grass, *S. alterniflora*, and the C_3 mangrove species, *A. germinans*. The soil contains a top layer of predominantly OM and silty soil with an underlying layer of silty clay. Preliminary data from these sites found that total organic soil C does not significantly vary between mangrove-dominant and marsh-dominant sites.

2.2. Plant and soil collection

A. germinans seedlings and *S. alterniflora* plugs were collected from GTM and allowed to acclimate to greenhouse conditions at Villanova University for three months. Mangrove-derived and marsh-derived soils were collected from plots near and within GTM from established monocultures of *A. germinans* and *S. alterniflora*, respectively. These plots contain soils that, through a pilot study conducted at Villanova University, have been identified to contain soils with ^{13}C signatures consistent with dominant input from C_3 (mangrove) and C_4 (marsh) plants ($\delta^{13}C$ −25‰ and $\delta^{13}C$ −15‰, respectively).

2.3. Mesocosm design

We established a full factorial experiment in which we randomly assigned combinations of three plant types (control/no plant, *A. germinans*, or *S. alterniflora*) and three soil types (C-free sand, mangrove-derived soil, or marsh-derived soil) to greenhouse mesocosms (Fig. 2). Plant-free pots served as baselines for soil respiration rates without plant influences. Sand pots contained no OM and should have heterotrophic respiration rates close to zero. Therefore, the sand pots served as baselines for plant respiration alone. Each treatment contained ten replicates (n = 10), with the exception of the sand + plant-free control treatment (n = 5), for a total of 85 mesocosms.

The mesocosms, housed in the Villanova University greenhouse (Villanova, PA), were constructed using 30 cm sections of 7.62 cm diameter PVC pipe. Pipes were sealed on the bottom using PVC caps and PVC cement. Ports were drilled approximately 5 cm from the bottom to allow for water drainage after daily inundation with artificial seawater. The mesocosms were lined at the bottom with fiberglass insulation and 450 mL of C-free sand in order to prevent the drainage ports from clogging. To increase drainage and prevent toxic H_2S build-up in the mesocosms (Pezeshki et al., 1991a; Lamers et al., 2013; Zhang et al., 2017), both types of soil were mixed with sand in a 1:2 soil-to-sand ratio. Then, each mesocosm received 1 L of a designated soil type. Lastly, mangrove seedlings and marsh plugs were planted in mesocosms containing their designated soil types. Daily greenhouse temperatures ranged between 22 °C and 27 °C over the course of the experiment (approximately nine months in total). Mesocosms were watered daily with a saline nutrient stock solution containing 0.42 mM NH_4NO_3, 1.2 mM KNO_3, 0.69 mM $Ca(NO_3)_2$, 0.1 mM NaH_2PO_4, 0.05 mM Fe-EDTA, and 500 mM NaCl (Instant Ocean® Sea Salt) (Hayes et al., 2017). Mesocosm porewater salinity was maintained at 25 psμ, based on pore water salinities measured in the field sites at GTM. In order to clear the mesocosms of excess toxic sulfides at the beginning of the experiment, the mesocosms were flushed daily with nutrient solution using a 60 mL syringe.

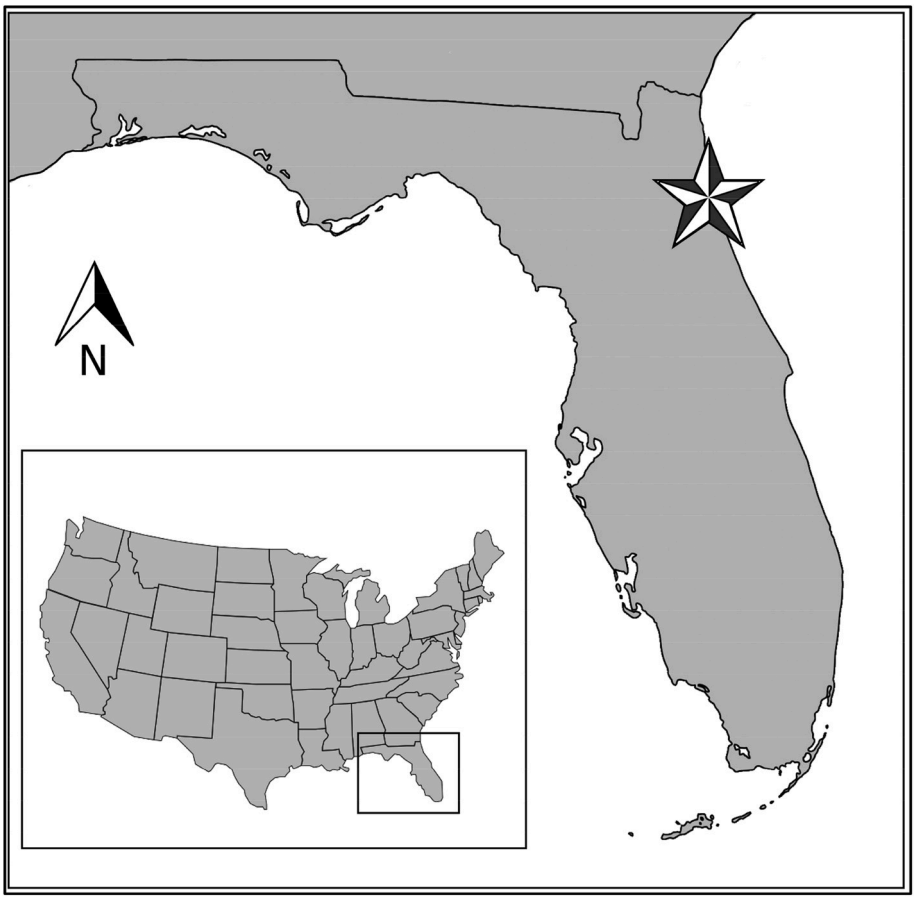

Fig. 1. Map depicting the location of the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM), which lies along the northeastern coast of Florida, approximately 50 miles south of the state's northernmost mangrove.

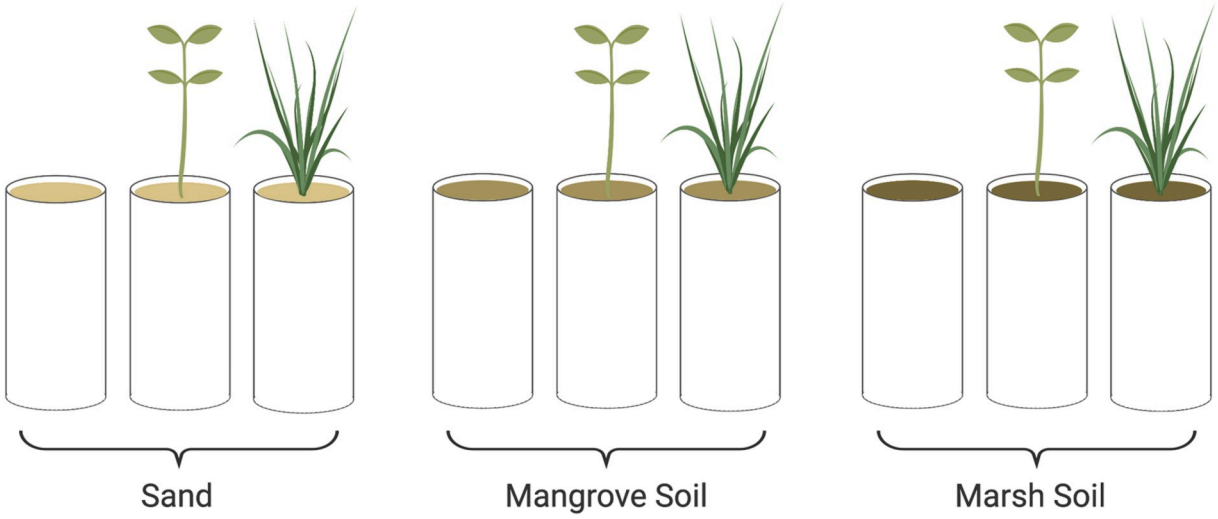

Fig. 2. Experimental design diagram illustrating the nine mesocosm treatment combinations of plant type (control/no plant, *A. germinans*, or *S. alterniflora*) and soil type (sand, mangrove-derived soil, or marsh-derived soil). Each treatment combination had ten replicates (n = 10), with the exception of the sand + control (no plant) treatment, which consisted of five replicates (n = 5). Created using BioRender.com; 2019.

2.4. Total soil respiration measurements

Total CO_2 respiration rates in each mesocosm were measured across four time points approximately one month apart. ^{13}C isotopic signatures of respired CO_2 in the mesocosms were also measured each month, but due to inconclusive results, these values were not analyzed (see Supplemental Information). To obtain total respiration rates from the 85 experimental mesocosms at each time point, subsets of 15 mesocosms were sampled per day across six days. During measurements, mesocosms were capped with airtight, opaque PVC chambers with sealable outlet fittings (Fig. 3A). Reusable adhesive putty was packed around the ports and caps in order to further reduce potential for gas leakage. Then, the

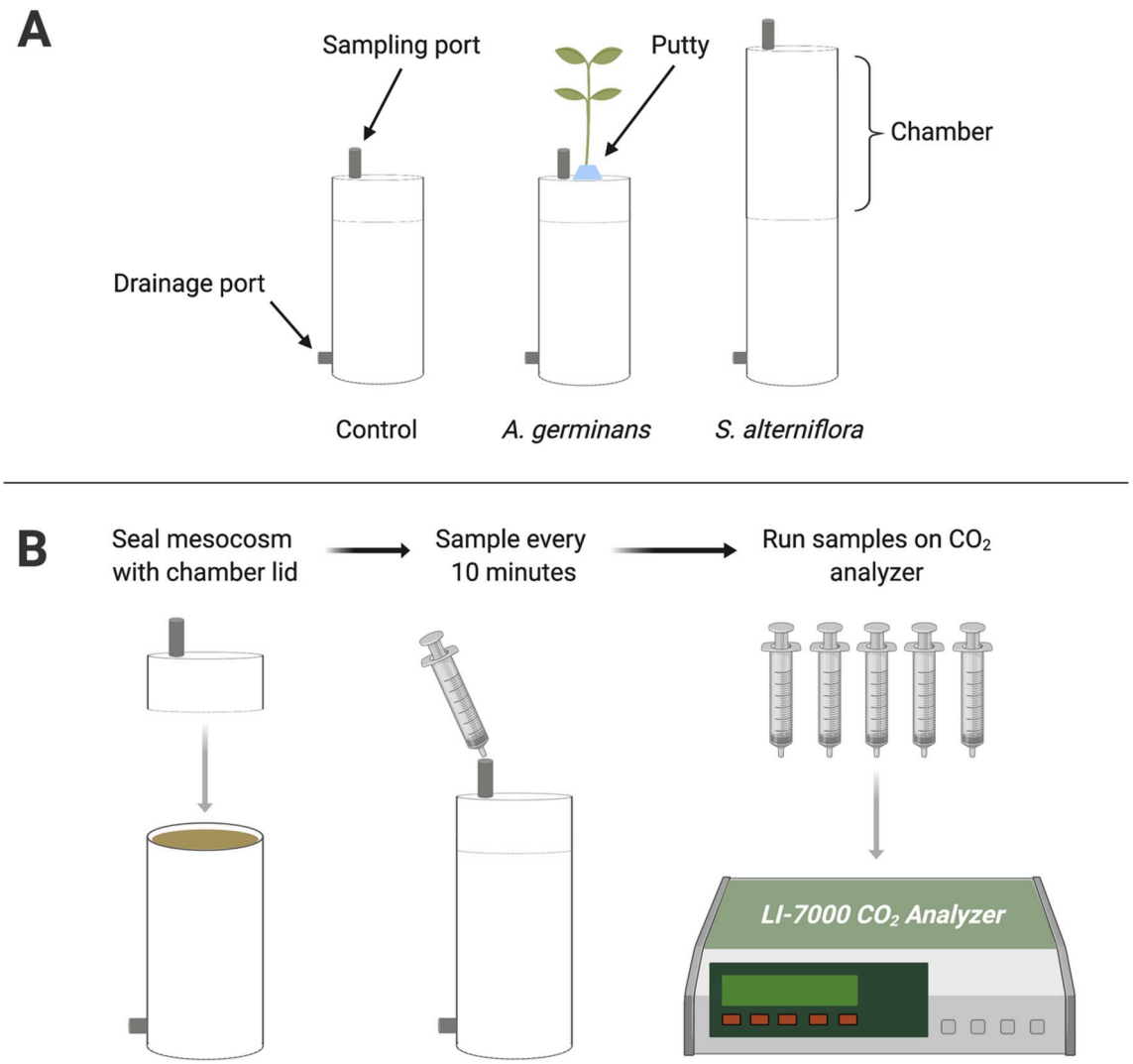

Fig. 3. Schematic diagram illustrating the respiration measurement methods. (A) Chamber setup for each plant treatment type during respiration sampling. The smaller respiration chambers placed on the control (no plant) and *A. germinans* pots captured belowground respiration, while the larger chambers on the *S. alterniflora* pots captured both aboveground and belowground respiration. (B) Simplified order of events during mesocosm respiration rate sampling. Created using BioRender.com; 2019.

ports were sealed using stopcocks attached to the outlet fittings. Temperatures in the greenhouse were monitored continuously using a HOBO External Temperature/RH Sensor Data Logger (Onset Computer Corporation, Bourne, MA).

The PVC chamber types varied between the two plant types. Mangrove plant pots were capped with small chambers that measured belowground respiration (soil + root respiration, also referred to as 'total soil respiration' in this paper), while marsh plant pots were capped with large chambers that encompassed both aboveground (plant) respiration and belowground respiration. The chambers covering the marsh plants blocked all light during respiration measurements, preventing photosynthesis. We aimed to exclude aboveground respiration in order to estimate heterotrophic respiration alone. While we could accomplish this by creating a gas-tight seal around the mangrove stem using putty, this could not be achieved with structure of *S. alterniflora* stems, which represents an important limitation of this study. We had originally aimed to use the ^{13}C signatures to accomplish accurate partitioning of plant and heterotrophic respiration, but as described above, this was inconclusive due to carbonate contamination of the isotopic signal.

Once sealed, the mesocosms were allowed to sit for approximately 10 min to allow for CO_2 accumulation. To measure respiration rates, 10 mL syringes were first filled with 2 mL ambient air to inject into the mesocosms to replace displaced gas volume. At 10-min intervals, headspace gas within the mesocosms was mixed using the 10 mL syringe and 2 mL of headspace gas was removed. Five samples were collected for each mesocosm, representing a total of 40 min of sampling per mesocosm (Fig. 3B). Upon completion of sampling, CO_2 concentrations within the syringes were measured by injecting samples into an LI-7000 CO_2/H_2O Gas Analyzer, (LI-COR Biosciences, Lincoln, NE). Standards of 1000 ppm, 5000 ppm, and 25,000 ppm CO_2 were used to create a standard curve to convert peak values into ppm CO_2. Rates were then adjusted for headspace volume, soil area, ambient air dilution, and air temperature. Total respiration rates were expressed as μg C m^{-2} s^{-1}.

2.5. Growth and biomass measurements

Plant heights, diameters, and leaf/stem counts were measured monthly coinciding with each of the respiration sampling time points. After respiration rates were measured at the last time point, the plants were destructively harvested to determine final aboveground biomass (AGB, shoots) and belowground biomass (BGB, roots). Shoots were removed at soil level, sorted into stems and leaves, placed in paper bags to oven dry for at least 48 h at 60 °C, and then weighed. Soils were sieved

using 1.00 mm and 4.75 mm sieves, then roots were washed to remove soil and placed in coin envelopes. Roots were then dried for 48 h at 60 °C and weighed. The final biomass data was then used in the heterotrophic respiration rate calculations and for AGB:BGB comparisons.

2.6. Estimated heterotrophic respiration calculations

After collecting total respiration rates, estimated heterotrophic respiration rates for mangrove plant treatments were calculated by subtracting estimated plant respiration from total soil respiration. To estimate mangrove root respiration, we first subtracted the average total respiration measured in the baseline sand pots (0.867 μg C m^{-2} s^{-1}) from the total respiration measured sand + mangrove plant pots. Then, we predicted mangrove root respiration rates in the mangrove-derived soil and marsh-derived soil pots by fitting the sand + mangrove plant respiration rate values to a least squares linear model, using AGB and BGB as prediction factors (predicted mangrove root respiration = 0.11037 + (0.87045 x BGB) – (0.07043 x ABG); $R^2 = 0.58$). Marsh plant respiration rates were also calculated, but since the aboveground respiration could not be distinguished from belowground respiration, they could not be accurately adjusted for biomass respiration and were therefore excluded from our final analyses. Heterotrophic respiration rates for control (no plant) treatments were simply the measured total soil respiration values. Heterotrophic respiration rates were only calculated for the last time point because biomass, which was used to calculate predicted root respiration rates, could only be measured at that the final time point.

2.7. Statistical methods

To determine the effects of treatment on heterotrophic respiration rates, the data was log-transformed to more closely align with assumptions of normality and equal variance. Then, factorial ANOVA tests were performed on linear models of the data, using plant type, soil type, and plant:soil interaction as fixed factors. Specific effects of plant and soil types were determined using Tukey's *post hoc* HSD tests. All statistical analyses were conducted in R version 3.6.2 (R Core Team, 2019).

2.8. Study limitations

This study possesses a few limitations, and the results should be interpreted with these limitations in mind. One limitation in the experiment is the lack of a tidal regime that would more accurately represent daily tidal changes in the field. Another limitation is that daily flushing of the mesocosms was required at the beginning of the experiment to prevent the newly transplanted mangrove seedlings and marsh plugs from dying due to H_2S build-up. To account for this, all mesocosms, including control (no plant) treatment pots, were flushed at the same time (within 1 h) every day. The variable soil structure between the three soil types (sand, marsh, mangrove) could have contributed to differences in gas diffusion, and therefore oxygenation and anaerobic conditions of each soil type. It is possible that the sand, for example, could allow for higher rates of gas diffusion if the soil was not entirely saturated (Armstrong, 1980). While soils were kept saturated, there was no standing water on the soil surface when gas measurements were taken. Therefore, the soils may have had slight differences in soil saturation and gas diffusion at the soil surface. Finally, since the chambers used to measure respiration in marsh plant mesocosms encompassed both aboveground and belowground respiration, marsh plant root respiration could not be calculated, so only mangrove and control (no plant) treatments could be compared.

3. Results

When comparing all three plant treatments, plant type, soil type, and plant:soil interactions had significant effects on total respiration rates ($p < 0.001$, Fig. S1). Marsh plant treatments had the highest total respiration rates, largely because the respiration chamber encompassed both aboveground and belowground respiration. Total respiration rates were lowest in the sand treatments. Across the four sampling time points, the average total respiration rates remained relatively stable (Fig. S2). When comparing only mangrove and control (no plant) treatments, total soil respiration rates were significantly affected soil type ($p < 0.001$, Fig. 4A, Table 1).

Estimated heterotrophic respiration rates were statistically similar between the control (no plant) and mangrove plant treatments ($p = 0.326$), but statistically different between the mangrove soil and marsh soil treatments ($p < 0.001$, Fig. 4B, Table 1). Average estimated heterotrophic respiration rates were highest in the marsh soil + control (no plant) treatment (8.18 μg C m^{-2} s^{-1}) and lowest in the mangrove soil + mangrove plant treatment (2.91 μg C m^{-2} s^{-1}).

Plant type, soil type, and plant:soil had significant effects on both AGB (Fig. S3A) and BGB (Fig. S3B). Marsh plants had significantly higher BGB than mangrove seedlings. Both plant type and soil type had significant effects on AGB:BGB ratios ($p < 0.001$, Table S1), with the mangrove plants having significantly higher AGB:BGB ratios than the marsh plants (Fig. S4). Mean heights, diameters, and stem/leaf densities for both marsh and mangrove plants increased over time and generally did not differ between marsh and mangrove soil types (Fig. S5).

4. Discussion

This study examined how soil type and plant type could affect estimated heterotrophic respiration rates of coastal wetland ecosystems within newly established zones along the Floridian mangrove-marsh ecotone. We hypothesized that (1) mangrove and marsh plants would increase heterotrophic respiration relative to unplanted soil and (2) that mangrove plants would increase heterotrophic respiration more than marsh plants. We were unable to address our second hypothesis because aboveground respiration could not be separated from belowground respiration in marsh plant mesocosms using isotope partitioning as originally planned. However, we did find that - contrary to our first hypothesis - heterotrophic respiration did not differ between mesocosms with mangrove seedlings and mesocosms with no plants (bare soil). Our findings could be due to a number of reasons, such as reductions in microbial activity caused by mangrove root exudates or by low root biomass present at this early mangrove growth stage.

One possible explanation for the relatively low heterotrophic respiration rates in mesocosms with mangrove plants is that soil microbial activity may have been hindered through the release of chemicals from mangrove roots or mangrove soil litter. For example, heterotrophic respiration rates were lowest in the mangrove soil treatments. Mangrove litter often contains chemicals such as tannins, which are associated with decreasing bacterial counts (Sahoo and Dhal, 2009). It is also possible that the mangrove soil, which is largely comprised of mangrove litter, might have contained high amounts of chemicals like lignin that decreased rates of OM decomposition (and therefore, soil respiration).

A second possible explanation for the low heterotrophic respiration rates in mangrove mesocosms is that the mangrove root biomasses were too low to contribute to noticeable differences in respiration. At the seedling stage, oxygen-transporting systems in mangrove root structures may not be well developed, and therefore root oxygenation may be low (Pezeshki et al., 1991b, 1997). Previous findings have shown that total soil respiration is highest in established mangroves compared to marsh-dominated or transitional areas and is correlated with increased BGB (Simpson et al., 2019). Mueller et al. (2016), alternatively, found that AGB was a better predictor of increased SOM decomposition than BGB. This could be because O_2 enters through plant shoots first before being directed into roots, so more surface area of shoots could indicate more radial O_2 loss (ROL). Stem diameter has also been found to correlate with increased ROL (Tanaka et al., 2007). In the mesocosms, though, mangrove stem diameters were not different between soil types.

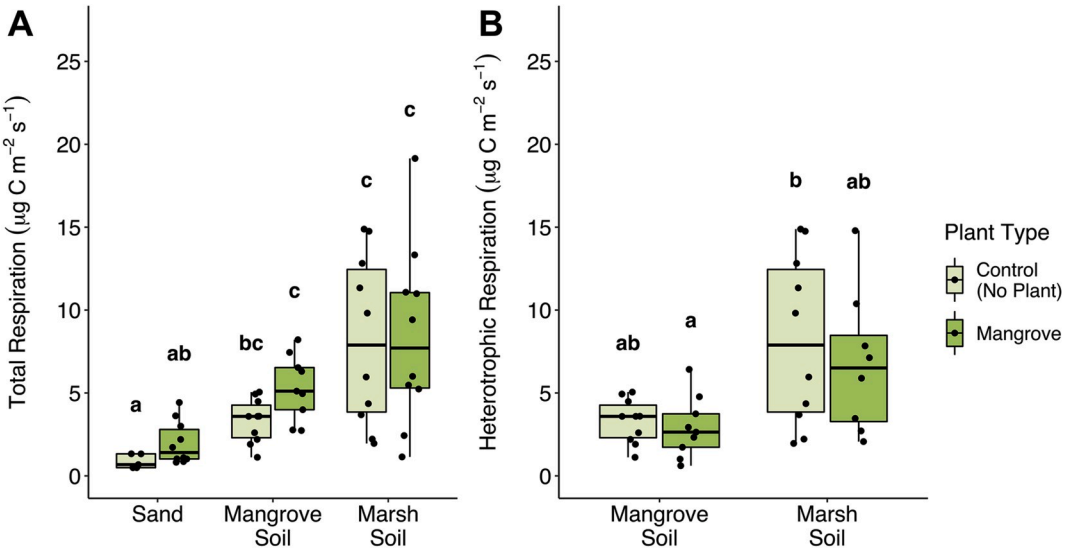

Fig. 4. Box plots representing the respiration rates calculated for control (no plant) and mangrove plant treatments. (A) Total soil respiration rates (μg C m^{-2} s^{-1}) in each of the three soil types. (B) Estimated heterotrophic respiration rates (μg C m^{-2} s^{-1}) of mangrove and marsh soil types. Lower and upper box boundaries represent the 25th and 75th percentiles, respectively, and the line inside the box is the median. The lower and upper error bars represent the 10th and 90th percentiles, respectively. All individual data points are plotted. Treatments with different letters have means that differ significantly (Tukey's HSD post-hoc test, $p > 0.05$).

Table 1
Respiration rates at the final timepoint for control (no plant) and *A. germinans* (mangrove) mesocosms in each soil treatment (sand, mangrove soil, and marsh soil). Values are means (±SE). Results of factorial ANOVA tests performed on log-transformed values are included at the bottom of the table. Bold text indicates significant effect ($p < 0.05$).

Treatment	Total Soil Respiration (μg C m^{-2} s^{-1})	Estimated Heterotrophic Respiration (μg C m^{-2} s^{-1})
Sand	0.87 (0.19)	–
Control (no plant)	1.98 (0.41)	–
A. germinans		
Mangrove Soil	3.31 (0.42)	3.31 (0.42)
Control (no plant)	5.34 (0.65)	2.33 (0.62)
A. germinans		
Marsh Soil	8.18 (1.62)	8.18 (1.62)
Control (no plant)	8.79 (1.22)	4.77 (1.15)
A. germinans		
Probability of > F	0.316	0.326
Plant Type	**< 0.001**	**< 0.001**
Soil Type	0.241	0.814
Plant:Soil		

Studies have found that C stocks tend to increase over time with increased mangrove age and expansion into salt marshes (Doughty et al., 2016; Kelleway et al., 2016; Simpson et al., 2019), so our findings may only reflect the conditions of initial mangrove encroachment, and not the conditions experienced in established mangrove stands.

In our mesocosms, AGB:BGB ratios for mangrove seedlings were significantly higher than the AGB:BGB ratios for marsh plants across all soil types. This observation that mangrove seedlings had higher AGB:BGB ratios than marsh plants provides some evidence to support a theory that mangroves invest more in AGB growth to shade out competitors (Janzen, 1985; Zhou et al., 2015). Therefore, while established mangroves may cause higher soil respiration than marshes, early stages of encroachment with young mangrove seedlings may have a smaller influence on soil respiration until they can establish larger rooting systems. It is notable how low the average root mass-specific respiration rates are for the mesocosm mangrove seedlings (0.002 ± SE 0.0008 μg C s^{-1} g^{-1}), especially when compared to root-specific respiration rates previously measured in *A. germinans* seedlings in anoxic conditions (~0.048 μg C s^{-1} g^{-1}, McKee, 1996).

We originally planned to distinguish plant and soil respiration rates using $\delta^{13}C$ signature partitioning, but the signatures could not be distinguished enough to use an isotopic partitioning equation to accurately determine the fraction of soil respiration (Fig. S6). This may have been due to the transformation of DIC into carbonate over the course of the experiment. Sulfate reduction is the dominant remineralization pathway in salt marsh sediments and can lead to carbonate formation. However, the high porewater salinity of the mesocosms may have prevented sulfate reduction from causing large amounts of carbonate formation (Bahr et al., 2005; Meister, 2013; Zhu and Dittrich, 2016). If carbonate material was present in our soils at the time of collection or formed during the experiment, it could have potentially dissolved and been released as CO_2 with highly enriched ^{13}C isotopic signatures that skewed our data (Tamir et al., 2011). However, soil carbonates do not always contribute strongly to CO_2 emissions. Setia et al., (2010) found that in saline soils with less than 10% calcium carbonate content, there was no significant influence of carbonate on CO_2 release. Therefore, depending on the soil type, future mesocosm or field respiration studies should take carbonate respiration into consideration when taking measurements and interpreting their results.

Our study highlights that the stage of mangrove encroachment into salt marsh ecosystems must be taken into account when predicting the impact on soil C storage, as young life-stage mangrove seedlings do not strongly influence heterotrophic respiration. Differences observed between mangrove forests and salt marshes may not appear until later life stages of mangroves, when mangrove plants are more established and possess more substantial rooting systems. Studies parsing out the specific effects of mangrove invasion on heterotrophic respiration specifically through SOM decomposition priming would be a valuable next step to move towards developing a better understanding of mangrove encroachment on wetland soil C storage. Ultimately, it is important to consider the level of mangrove encroachment in mangrove-marsh ecotones when predicting heterotrophic respiration rates and soil C storage of wetlands undergoing vegetation shifts.

CRediT authorship contribution statement

Emily K. Geoghegan: Formal analysis, Investigation, Data curation,

Writing - original draft, Writing - review & editing, Visualization, Project administration. **J. Adam Langley:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition. **Samantha K. Chapman:** Conceptualization, Methodology, Resources, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition, Project administration.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2020.106877.

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