Estuarine, Coastal and Shelf Science 229 (2019) 106409

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: http://www.elsevier.com/locate/ecss

Carbon and nutrient fluxes from seagrass and mangrove wrack are mediated by soil interactions

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ARTICLE INFO

Keywords:
Leaf litter
Halodule wrightii
Rhizophora mangle
Blue carbon
Soil organic matter

Regional Index Terms:
USA
Florida
Indian river lagoon

ABSTRACT

Shoreline accumulation of vegetative wrack may contribute nutrient subsidies for primary or secondary production, detritivore food-web support, habitat provision, and sediment stabilization. This study addresses a knowledge gap in the literature by going beyond quantification of carbon (C) and nutrient flux potentials to investigate the biogeochemical interaction between wrack and shoreline soil. Results from a year-long shoreline survey of wrack type and abundance in Mosquito Lagoon, FL, were combined with a two-month intact core experiment observing the interaction of mangrove and seagrass leaves with organic and mineral shoreline soils. Experimental treatments were subjected to tidal cycles; at low tide, measurements were made of soil respiration and drainage water nutrient content. A measure called Soil Interaction with Litter Effect (SoILE) is introduced to quantify the suppression or enhancement of C and nutrient fluxes from a combination of wrack with shoreline soils compared to the potential fluxes of wrack and soil separately.

Monthly mean (±1 S.E.) accumulation of wrack dry mass in Mosquito Lagoon was $37.65 \pm 2.99\ g\ m^{-2}$. Unusually high values ($72.16 \pm 13.74\ g\ m^{-2}$) occurred in September 2017 following Hurricane Irma. In a comparison of seagrass and mangrove leaves and organic and mineral soils, seagrass leaves were the greatest source of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) by factors of 24 and 13, respectively. Seagrass also had the highest fluxes of dissolved organic carbon (DOC) and CO_2 by factors of 2 and 2.7, respectively. The most common effect of combining wrack and soil was to suppress the magnitude of DOC and CO_2 fluxes. There were few differences between combined and additive fluxes of DIN and SRP; the DIN flux was suppressed from the combination of seagrass with organic soil, and the SRP flux was enhanced from the combination of mangrove leaves with mineral soil. Suppression and enhancement of SoILE values were likely both attributable to a “smothering” effect caused by the physical interaction of vegetation with the soil surface that altered redox conditions. Wrack accumulation on restored living shorelines is likely to have a two-fold positive effect of subsidizing nutrients for primary production by shoreline plants and contributing to an increase in soil carbon by interacting with soils to result in a net suppression of DOC and CO_2 effluxes.

1. Introduction

Wrack, which consists of vegetative organic material (Colombini and Chelazzi, 2003; Orr et al., 2005) as well as debris discarded from human activity (Ryan and Moloney, 1993; Hoffmann and Reicherter, 2014), provides important ecosystem services to coastlines around the world. Vegetative wrack may include trees and woody debris, leaf litter, saltmarsh and mangrove detritus, macroalgae (i.e., seaweed) including kelp, and seagrass (Ochieng, and Erftemeijer, 1999; McLachlan and McGwynne, 1986; Orr et al., 2005). The amount of wrack on a shoreline can vary substantially both in space (depending on a shoreline's proximity and connectivity to vegetated habitats) and time (depending on seasonality of storms, ocean currents and vegetation senescence) (Koop and Field, 1980; Colombini and Chelazzi, 2003).

Abbreviations: SoILE, Soil Interaction with Litter Effect; SOM, soil organic matter; DIN, dissolved inorganic nitrogen; SRP, soluble reactive phosphorus; DOC, dissolved organic carbon; MBC, microbial biomass carbon; RM, *Rhizophora mangle*; HW, *Halodule wrightii*; OS, organic soil; MS, mineral soil; MR, mineral soil + *Rhizophora mangle*; MH, mineral soil + *Halodule wrightii*; OR, organic soil + *Rhizophora mangle*; OH, organic soil + *Halodule wrightii*.

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https://doi.org/10.1016/j.ecss.2019.106409
Received 3 June 2019; Received in revised form 20 September 2019; Accepted 8 October 2019
Available online 9 October 2019
0272-7714/

The intertidal nature of shorelines means that they undergo periods of wetting and drying, warming and cooling, and variation in redox conditions, all of which may contribute to physical, chemical, and biological alteration of the wrack and soil organic matter (SOM). The cycling and potential stability of wrack and soil C and nutrients will vary between wrack and soil types, depending on biogeochemical and physical variables such as scarcity or abundance of metabolic resources, redox conditions, bulk density, and composition of the microbial pool among others (Rossi and Underwood, 2002). On unvegetated shorelines, wrack can insulate the soil, preventing evaporative salinity increases and preserving soil moisture content (Haslam and Hopkins, 1996; Pennings and Richards, 1998). Evidence from terrestrial forests has shown that adding litter C to the soil can stimulate microbial activity in the soil and increase the loss of the soil C content via the priming effect (Fontain et al., 2004; Kuzyakov, 2010; Sayer et al., 2011). However, such evidence has not been demonstrated for coastal shorelines where the addition of wrack has had variable impacts on the soil organic content, in some cases leading to increased C burial rates rather than acceleration of soil respiration (Keuskamp et al., 2015; Sanders et al., 2014) and in others there was no change SOM or nutrient content (Chapman and Roberts, 2004).

Wrack provides important ecological functions for shorelines that otherwise exist as extreme ecotones exposed to variable wind and wave energy, intense solar radiation, and salt stress (Colombini et al., 2000). Wrack vegetation subsidizes food webs (Koop and Field, 1980) and contributes to macrofaunal abundance and diversity (Macmillan and Quijon, 2012). However, wrack contributes to alternative, less-desirable outcomes that require coastal managers to prioritize between services. For example, in the context of tourism, wrack removal is often seen as a necessary management tactic to remove unsightly and malodorous material (Chapman and Roberts, 2004), even if doing so causes negative ecological impacts (Llewellyn and Shackley, 1996). In addition to this annoyance-factor for humans, there is evidence that excessive wrack can be stressful for rooted shoreline vegetation, sometimes leading to plant death (Bertness and Ellison, 1987).

There are several trade-offs to consider regarding the fate of wrack and soil-derived carbon and nutrients. First, nutrients may provide a benefit by fertilizing coastal macrophyte growth (Chapman and Roberts, 2004) and increasing blue carbon via photosynthetic uptake of CO_2. Alternatively, nutrients may fertilize or prime microbial activity (Koop et al., 1982; Kuzyakov, 2010), increasing the efflux of CO_2 from the soil and decreasing the blue carbon soil stock (Sayer et al., 2011). These nutrients and C may also decrease water quality and contribute to harmful algal blooms in surface waters. On shorelines with a high sedimentation rate, wrack and its associated C and nutrients may be buried and either contribute to leaching of nutrients to groundwater or be sequestered from short-timescale biogeochemical cycling (Rossi and Underwood, 2002; Colombini and Chelazzi, 2003). In terrestrial environments, litter falls to the soil in the same location where it was produced. Tides and waves, including those associated with large storms, are unique shoreline variables that affect the import and export of vegetative litter, alteration of aerobic and anaerobic conditions, and rates of leaching and respiration. The concept of "home-field advantage" posits that rates of litter mass loss are greater in a vegetation's local environment than when deposited elsewhere (Ayres et al., 2009), which suggests that wrack is likely to be more stable on shoreline soils than in its locations of origin. Conversely, wrack may be less stable because of intertidal wetting, drying, and physical agitation from wave energy.

Wrack has practical management considerations for coastal restoration practitioners who utilize vegetated living shorelines to replace hardened structures like seawalls (Gittman et al., 2015, 2016; Donnelly et al., 2017). It is unclear whether wrack deposits in these settings are a beneficial source of nutrients that may help restoration efforts be more successful. Additionally, wrack accumulation, in combination with root production by living vegetation, may contribute to the formation of SOM (Llewellyn and Shackley, 1996) on living shorelines where the substrate at the time of restoration is typically sandy, muddy, or even shelly for projects located near shell middens (Donnelly et al., 2017). The formation of SOM can take up to 20 years for restoration sites to reach equivalent amounts as natural reference sites (Osland et al., 2012; Davis et al., 2015) and is a good indicator of overall biogeochemical activity (DeLaune and Reddy, 2008).

While previous work has investigated potential rates of carbon and nutrient cycling related to wrack or shoreline soils separately, there has been less said about the interactions that occur between the two. This study was designed to identify whether the combination of vegetative litter and soil had an interactive effect (i.e. enhancement or suppression) on aqueous nutrient fluxes and soil respiration (CO_2 production). Hereafter, the term "additive" refers to the sum of the separately measured fluxes from vegetation and soil types, whereas "combined" refers to fluxes from with vegetation and soil measured together. A term called Soil Interaction with Litter Effect (SoILE) is defined to quantify the difference in fluxes from combined and additive treatments. A positive SoILE value indicates that the combined flux is greater than additive flux and equates to an enhancement effect. Conversely, a negative value indicates a suppression effect because the combined flux is less than the additive flux. The objectives of this research were to: (1) quantify the type and amount of wrack accumulating seasonally over the course of a year on shorelines of Mosquito Lagoon, FL, USA, (2) determine whether there is a biogeochemical interaction between wrack vegetation and shoreline soil for fluxes of C and nutrients, and (3) estimate the amount of C and nutrient fluxes produced by wrack on Mosquito Lagoon shorelines annually. These findings can be used to inform shoreline restoration practitioners about the potential value of removing or maintaining shoreline wrack deposits based on soil properties and desired ecosystem services. Additionally, these findings will add a marine shoreline investigation to the existing body of literature investigating the potential influence of vegetative litter for priming respiration in soils and sediments.

2. Methods

2.1. Site description

Field observations of wrack accumulation and collection of soil and vegetation for experimental analyses took place in Mosquito Lagoon, the northernmost of a series of lagoons that comprise the Indian River Lagoon (IRL) estuarine ecosystem. The IRL covers approximately 250 km along the Atlantic coast of Florida, is an "Estuary of National Significance" and is one of the largest and most biodiverse estuaries in the United States (IRLNEP, 2008). The lagoon is situated behind a chain of barrier islands along the east coast of Florida, including Canaveral National Seashore (CANA) where this research was conducted. Mosquito Lagoon is a microtidal system with tidal amplitudes on the order of 0–5 cm, and seasonal water level variations that exceed tidal ranges (Smith, 1987; Walters et al., 2001). Surface water salinity in the lagoon ranges from 25 to 45 and the mean water depth is 1.7 m (Barber et al., 2010). Flora of the lagoon includes three different species of mangroves: black mangroves (*Avicennia germinans*), white mangroves (*Laguncularia racemosa*), and red mangroves (*Rhizophora mangle;* RM), all found in abundance across the network of more than 100 islands within the estuary (Garvis et al., 2015). Other common flora include the seagrass *Halodule wrightii* (HW) found in the subtidal zone, and *Spartina alterniflora* found in the middle to upper intertidal zone (Manis et al., 2015). Both mangrove and salt marsh plants are salt tolerant species that are used for stabilizing estuarine shorelines against erosion, including Native American shell middens in the IRL (Manis et al., 2015; Donnelly et al., 2017).

2.2. Field surveys of wrack accumulation

Field surveys were conducted every two weeks from June 1, 2017 to

May 30, 2018 to collect wrack samples from three locations along the eastern shoreline of Mosquito Lagoon in CANA (Fig. 1). At each location, five randomly placed 0.25m × 0.25m quadrats were deployed at the high tide line along three adjoining 50-m lengths of shoreline. All the wrack within each quadrat was placed in a plastic bag labeled with the collection date, collection site, and quadrat number (1–5). Bags were transported back to the lab within 6 h and processed immediately.

The wrack was separated into the following categories: HW (seagrass), mangrove leaves, unclassified leaves, wood, roots, green algae, red algae, *Spartina alterniflora* (smooth cordgrass), mangrove propagules, red mangrove flowers, and unclassified vegetation. Mangrove leaves that were readily identifiable by species were grouped together rather than separately because of the small individual cumulative masses. Uncategorized leaves likely also included mangrove leaves, but because of degradation state and similarity with other upland leaf types, this group was broadly categorized to include unidentifiable leaves. Uncategorized vegetation included any group whose cumulative dry mass from all sites, quadrats and sampling times was less than 5 g. The uncategorized vegetation category included acorns, pine needles, reeds, upland plant stems, seagrape leaves, and saw palmetto fronds.

The initial wet-weight of each group was obtained by hand-drying the sample with paper towels to remove all external water. This weight was recorded in grams to the hundredths decimal place. Groups were subsequently placed in labeled aluminum tins in a drying oven for 24–48 h until constant weight was observed, after which the dry weight of each group was recorded.

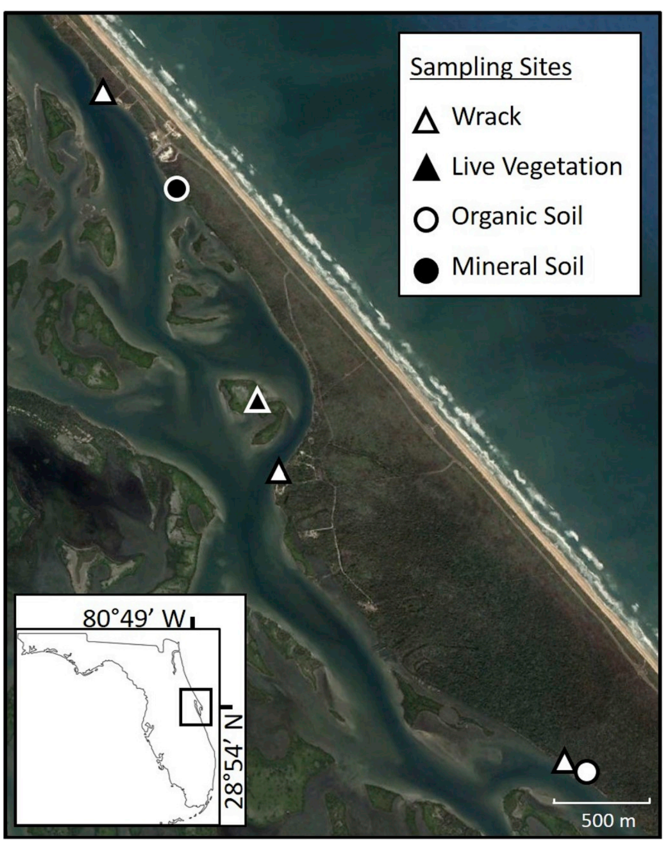

Fig. 1. Location of wrack, live vegetation, and soil sampling sites in Mosquito Lagoon, Canaveral National Seashore, FL USA. For wrack collection, the northern site is Turtle Mound, the middle site is Eldora House, and the southern site is Castle Windy.

2.3. Intact core experimental study

2.3.1. Experimental design and sample collection

Leaves of RM and HW were used as representative wrack types, and field-collected mineral and organic soils (MS and OS, respectively) were used for the intact core experiment. The HW and OS represent labile sources of C and nutrients, while the RM and MS represent more refractory sources with less nutrient availability. Soil samples were collected in June 2018 from two shoreline sites where mangroves are growing in Mosquito Lagoon (Fig. 1). Six push cores (6.9 cm wide x 10 cm long) were collected for destructive analysis (three from each site) and 24 cores were collected for experimental intact core analysis (12 from each site, including four replicates for each treatment). The incubation cores were 10 cm wide and 15 cm long (including 5 cm of open headspace) and remained intact throughout the duration of the study. Soil at the northern site consisted of siliciclastic sand. Vegetation growing at this location consisted of isolated, small (<1 m tall) red and black mangroves within the intertidal shoreline. The southern site had a sandy fringing berm approximately 5 m wide behind which was a lower elevation back-basin with predominantly organic soil where the cores were collected. Vegetation at this site consisted of red and black mangroves that were 1.5–2.0 m in height, with stem densities of 2–4 m^{-2}, as well as a dense understory of seedlings.

Fresh vegetation samples were harvested from the field. Live RM leaves were collected from shoreline trees and HW leaves were collected by clipping above the sediment surface. Vegetation was placed into gallon size airtight bags and returned to the lab on ice. Freshly harvested vegetation was used rather than existing shoreline wrack to ensure highest nutrient content, least degradation, and consistency among samples. Our use of soil cores without crab burrows and freshly harvested seagrass and mangrove leaves excludes the degradative influence of invertebrates on shoreline wrack. Therefore, the results of this study pertain only to the flux differences that occur as a result of biogeochemical interactions between wrack and soil and does not account for alterations to wrack composition that occur because of macro-biotic influences.

Intact cores and fresh leaves were randomly assigned to four experimental treatments: soil only, vegetation only, soil + HW, and soil + RM leaves. Hereafter these treatments will be referred to as: OS (organic soil), MS (mineral soil), OR (organic soil plus RM), OH (organic soil plus HW), MR (mineral soil plus RM), and MH (mineral soil plus HW). All results are presented by normalizing to the mass of dry organic matter to account for differences in mass between treatments. The average mass of seagrass used in the HW treatments was 14.7 ± 1.8 g wet, (3.0 ± 0.4 g dry); the average mass of leaves in the RM leaf treatments was 12.1 ± 0.9 g wet, (3.8 ± 0.3 g dry).

2.3.2. Characterization of soil and vegetation for experimental study

Upon return to the lab, the bags with extruded soil cores were weighed for wet soil weight. Soil and vegetation were dried in an oven (70 °C) until constant weight was achieved for calculations of moisture content and soil dry bulk density (soil dry mass divided by initial wet volume of the soil core). After drying, soil and vegetation samples were homogenized with a Spex 8000 mixer/mill (Spex Sample Prep, Metuchen, NJ, USA). Organic matter content was measured using loss-on-ignition (LOI) measurements at 550 °C for 3 h (Dean, 1974). Measurements of total C, total N, and organic C were conducted using an Elementar vario MICRO select (Elementar Analytical, Langenselbold, Germany). For organic C, sediment was de-carbonated by fumigation with 12 N HCl in a desiccator for 6 h (Harris et al., 2001). Total P was measured following the protocol of Andersen (1976) by digesting combusted samples in 1 M HCl and colorimetrically analyzing the digestant with a SEAL AQ2 Automated Discrete Analyzer (Seal Analytical, Mequon, WI) using EPA method 365.1 Rev. 2.0 (USEPA, 1993).

Analysis of soil samples for microbial biomass C (MBC) was begun within 24 h of field collection. The chloroform fumigation procedure

(Vance et al., 1987) was used to measure MBC as the difference between fumigated and non-fumigated samples. Homogenized, wet soil samples of 2.5 g were weighed into duplicate sets of 40 mL centrifuge tubes. The first set was placed in a glass desiccator and exposed to pure chloroform for 24 h. Second, both fumigated and non-fumigated centrifuge tubes were filled with 25 mL 2 M KCl, then shaken for 1 h to suspend the soil in solution. Samples were subsequently centrifuged, decanted and vacuum filtered (0.45 μm), then acidified for preservation. Measurement of TOC for both fumigated and non-fumigated treatments was conducted using a Shimadzu TOC-L Analyzer (Kyoto, Japan). The TOC from the non-fumigated treatment represents total extractable C. Microbial biomass C was calculated as the difference between fumigated TOC and non-fumigated TOC divided by the dry soil mass and multiplied by a factor of 2.22 (Joergensen, 1996). At the conclusion of the experiment, MBC was also measured in the soils of the intact cores.

2.3.3. Leachate nutrient fluxes

A hole was drilled at the base of each intact PVC core to facilitate simulation of tidal drainage; holes were plugged with a rubber stopper during simulated high tide. For the vegetation treatments, vegetation was held in an open nylon screen 2 cm above the drainage hole to enable aerobic exposure during low-tide conditions. In practical terms, these measurements from isolated vegetation samples are analogous to conditions when wrack is deposited, draped or perched on elevated structures along the waterline such as docks, low hanging branches, pneumatophores, and oyster bag breakwaters used for shoreline restoration projects. Site surface water from Mosquito Lagoon was collected in June and July of 2018, and used to fill the intact cores to a depth of 2 cm above the soil or vegetation surface to mimic the micro-tidal conditions of the region. Cores were filled and drained to simulate one high and one low tide every 48 h from June 13 to August 15, 2018. Each of the intact cores was housed inside a larger PVC chamber to collect the drained tidal water. The volume of leachate water was recorded for each core throughout the study because of variation in drainage rate between soil types. The average volume of leachate collected from each core was 664 ± 16 mL for the vegetation-only treatments, and 216 ± 15 mL for the soil-based treatments. Leachate was subsequently filtered (0.45 μm) and acidified for preservation until analysis. All intact cores were kept in the dark between tidal manipulations and measurements to prevent photosynthetic activity.

Three types of aqueous nutrient measurements were conducted: (1) extractable nutrients from the destructible cores at the beginning of the experiment, and from the intact cores at the conclusion of the experiment, (2) lagoon surface water (for use in tidal treatments of intact cores), and (3) leachate collected from the intact cores. Extractable nutrients include constituents dissolved in pore-water and ionically complexed with soil particles, and were measured simultaneously with the MBC samples treated with KCl, described in the previous section. The nutrients measured were DOC, NO_3^-, NH_4^+, and ortho-PO_4^{3-} (SRP). For the leachate collected from the intact core study, NO_3^- and NH_4^+ were summed and reported as dissolved inorganic Nitrogen (DIN). Colorimetric analysis of samples was conducted with a SEAL AQ2 Automated Discrete Analyzer (Seal Analytical, Mequon, WI) using EPA Methods 353.2 Rev. 2.0, 350.1 Rev. 2.0, and 365.1 Rev. 2.0, respectively, for NO_3^-, NH_4^+, and PO_4^{3-} (USEPA, 1993). Cumulative nutrient flux for each tidal manipulation was calculated by multiplying leachate nutrient concentration (mg L^{-1}) by the volume of leachate (mL) that was collected from each core for the respective tidal cycle. Nutrient fluxes are reported in units of mg dry OM^{-1} where OM is comprised of the dry mass of vegetation added at the beginning of the experiment plus the mass of dry SOM in each core.

2.3.4. CO_2 fluxes

Fluxes of CO_2 from the intact cores were measured using a LI-COR 8100 (LI-COR Biosciences, Lincoln, NE) during low tide conditions over the course of six weeks. For time series, fluxes are reported in units of μmol CO_2 g^{-1} dry OM hr^{-1}; units for the cumulative fluxes were mol CO_2 kg^{-1} dry OM, where OM is comprised of the dry mass of vegetation in each core plus the mass of dry SOM present in the top 1 cm of soil. This soil normalization quotient was used assuming the diffusion of microbial CO_2 occurs from the top 1 cm of sediment during simulated low tides (approximating the depth of diffusion of O_2 into the soil) and represents a conservative estimate (DeLaune and Reddy, 2008).

The offset depth between the soil surface and top of the PVC tube (used for calculation of headspace volume) was measured by averaging three measurements in each core to account for any unevenness of the soil surface. A mass:volume relationship (g: cm^3) was determined for both vegetation types based on a water volume displacement measurement, so that the mass of vegetation added to each intact core could be subtracted from the headspace volume. For HW, the conversion was volume $= 1.28 \times$ mass $+0.91$ ($R^2 = 1.00$) and for RM the conversion was volume $= 1.00 \times$ mass $+ 0.89$ ($R^2 = 0.99$).

2.4. Data analysis

All statistical analyses were conducted using IBM SPSS Statistics Version 25. Differentiation of physicochemical characteristics of OS and MS at the beginning of the experiment was determined using independent t-tests ($\alpha = 0.05$). Comparisons of wrack accumulation by season were conducted using Welch's 1-Way ANOVA (which is robust to heteroscedasticity) followed by Games-Howell post hoc comparisons. For the intact core experiment, 1-way ANOVA with post-hoc Tukey comparisons were conducted on the individual and combined treatments. Assumptions of normal distribution and homogeneity of variance of the dependent variables (nutrients, DOC, and CO_2 fluxes), were tested using the Shapiro-Wilk and Levene's tests. When variables failed to meet either assumption, data were log-transformed (SRP and DIN) or cube-root transformed (DOC). A modified Thompson Tau test was used to identify outliers for measurements of leachate and CO_2 after normalization to dry mass of OM for each sampling date. Data presented throughout are mean ± standard error unless stated otherwise.

Simple linear and non-linear regression were used to compare mean CO_2 fluxes as a function of time for each treatment (4 replicates per treatment). The integral of each curve was calculated for the length of the study time under low tide conditions to determine the total mean flux of CO_2 from each individual treatment; uncertainties were reported based on the variability between the integrals of the four replicates.

The combined and additive fluxes were calculated separately for each of the combined-treatment cores to quantify the effect of the biogeochemical interaction between soil and vegetative wrack (aka litter). First, the combined flux was calculated as:

$$CT_{cf} = (V_m + SOM_m) \times CT_{mf} \qquad \text{Eq. 1}$$

where CT represents each combined treatment replicate, V represents mangrove or seagrass vegetation, and SOM represents soil organic matter. For the subscript terms, *cf* is the cumulative combined flux for each tidal cycle (in units of mg or mol), *m* is dry mass, and *mf* is the cumulative observed mass flux for each tidal cycle (in units of mg per dry kg of vegetation plus SOM).

Second the additive flux of the same combined-treatment replicate cores was calculated as:

$$CT_{af} = \left(V_m \times V_{mf}\right) + \left(SOM_m \times SOM_{mf}\right) \qquad \text{Eq. 2}$$

where the subscript term *af* is the cumulative additive flux for each tidal cycle (in units of mg or mol). Paired t-tests were conducted to determine if there were significant differences between the combined and additive fluxes for each C and nutrient constituent. Assumptions of normal distribution and homogeneity of variance were tested (and confirmed) using the Shapiro-Wilk and Levene's tests.

The Soil Interaction with Litter Effect (SoILE) was calculated as:

$$SoILE = \mu \pm \delta\left(\left(CT_{cf} - CT_{af}\right) \div CT_{af}\right) \quad \text{Eq. 3}$$

where μ is the cumulative mean flux of the four replicates for each treatment and δ is the 95% confidence interval. The 95% C.I. was used to determine if a SoILE value was significantly different from zero. The SoILE value represents the percentage by which the combined fluxes increased or decreased compared to the additive fluxes.

3. Results

3.1. Wrack mass by type and season

Monthly accumulation of dry mass of all wrack types on the shorelines of Mosquito Lagoon was 31.79–43.51 $g\,m^{-2}$ (95% C.I.). However, there was substantial monthly variability. The lowest monthly mean (±1 S.E.) values of 1.60 ± 0.78 and $3.45 \pm 1.07\,g\,m^{-2}$ were observed in August and July, respectively (Fig. 2A). The highest monthly mean values of 72.16 ± 13.74 and $114.82 \pm 18.04\,g\,m^{-2}$ occurred in September and January. The high values in September coincide with the occurrence of Hurricane Irma (Cangialosi et al., 2018). There were significant differences between seasons ($p < 0.001$), with the lowest accumulation of $6.62 \pm 1.42\,g\,m^{-2}$ in summer of 2017, and the highest accumulation of $68.93 \pm 7.76\,g\,m^{-2}$ in winter of 2017–2018 (Fig. 2B). Autumn and spring accumulations were not statistically different ($p = 0.942$). Alternatively, if the high September rates were classified as anomalous due to the influence of Hurricane Irma and were withheld from the analysis, then the mean autumn accumulation decreased from $35.20 \pm 5.68\,g\,m^{-2}$ to $16.72 \pm 3.83\,g\,m^{-2}$ and was not different from the summer accumulation ($p = 0.070$).

The largest annual dry wrack contributor was HW, with a total of $647.82 \pm 9.85\,g\,m^{-2}\,yr^{-1}$ (Fig. 3). This was over three times greater than the next largest contributor, black mangrove propagules, with a total of $198.99 \pm 8.32\,g\,m^{-2}\,yr^{-1}$. When grouped together, algae (red and green) and leaves (mangrove and uncategorized) were the largest next two contributors at 183.89 ± 53.10 and $205.01 \pm 48.23\,g\,m^{-2}\,yr^{-1}$, respectively. Accumulation of HW was approximately the same during

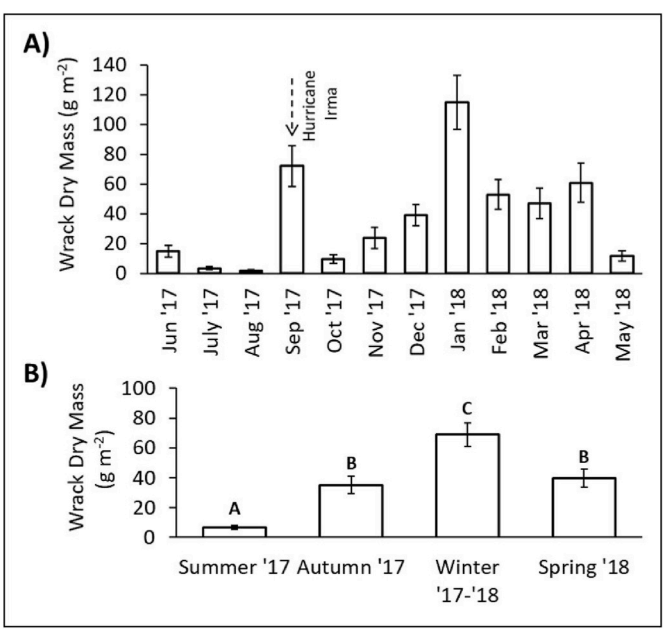

Fig. 2. Mean (±1 S.E.) mass of wrack accumulation per square meter by A) month from June 2017 to May 2018, and B) season from summer 2017 to spring 2018. The high mass of wrack in September 2017 (panel A) coincided with the occurrence of Hurricane Irma. Different capital letters in panel B represent significant differences ($p < 0.05$) between seasons (Welch's asymptotically distributed F (3,243) = 35.4, $p < 0.001$).

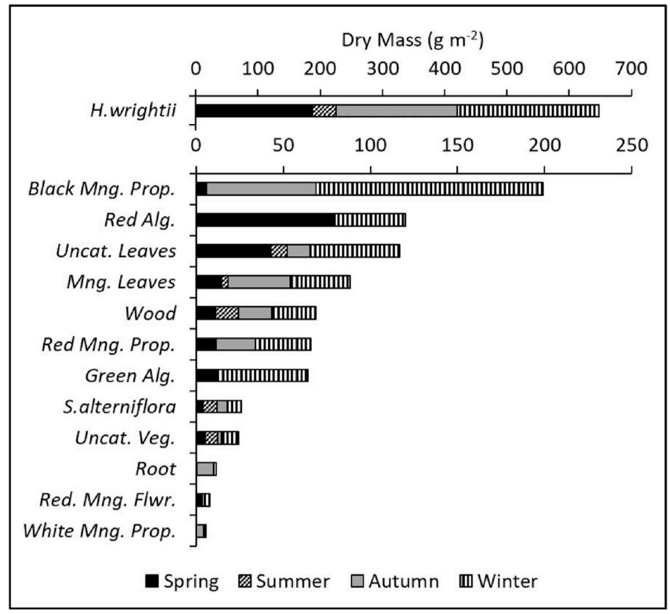

Fig. 3. Mean annual wrack composition by season. Note the separate scale for *H. wrightii*.

the spring, autumn, and winter seasons, but was negligible during the summer. Red and green algae accumulation was most prominent during winter and spring, with negligible presence during summer and autumn. Leaves were found during all seasons, but with the lowest abundance during summer. Mangrove propagules were mostly found during autumn and winter, coinciding with the annual dispersal period, with low or negligible presence in spring and summer.

3.2. Physicochemical characteristics of experimental soil and vegetation samples

Vegetation characteristics were measured for single, dry homogenized samples to establish qualitative differences between mangrove and seagrass vegetation used in the intact core experiment. The mangrove leaves had greater OM (92.1 vs. 49.9%) and organic C (44.64 vs. 20.69%) as a percentage of total mass, whereas the seagrass leaves were higher in TN (1.76 vs. 1.21%), TP (1.73 vs. 1.02 $mg\,g^{-1}$) and MBC (42.61 vs 0.0 $mg\,g^{-1}$) (Table 1). The OC:TN of mangroves was higher than that of seagrass (43.07 vs. 13.71), whereas the TN:TP was similar for both (26.23 and 22.47).

Soil organic content of the organic site was approximately six times greater than that of the mineral site soil ($p = 0.005$) (Table 1). This was accompanied by four-fold greater moisture content ($p = 0.004$) and lower dry bulk density ($p = 0.02$). There was no significant difference in OC content ($p = 0.054$). No IC content was detected (less than 0.00%), and therefore all subsequent references are to OC. The mean difference between replicates of OC was 0.40 ± 0.15%. The OS had higher values of TN ($p = 0.02$), TP ($p < 0.001$), and MBC ($p < 0.009$). No difference was detected between soil types for extractable NH_4^+ ($p = 0.49$), NO_3^- ($p = 0.08$), or SRP ($p = 0.21$), but the OS had five times more extractable DOC than the MS did ($p = 0.03$).

3.3. Leachate nutrient fluxes

3.3.1. Dissolved inorganic nitrogen (DIN)

In the IRL surface water used for tidal treatments, the concentration of NH_4^+ was 0.08 $mg\,l^{-1}$ in June and July, and the concentration of NO_3^- was below detection. All subsequent DIN fluxes have these surface water concentrations subtracted. The majority of the DIN flux from HW leaves occurred in the first two weeks with values as high as 704–747 $mg\,kg^{-1}$,

Table 1
Average (±1 S.E.) physicochemical properties of vegetation and soils. For soils, different letters indicate significant difference between types; levels of significance indicated by * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$), and ns (not significant). No uncertainty estimates were available for vegetation because measurements were made from a single homogenized sample. (n/a = not available, and b/d = below detection).

Property	*R. mangle* Leaves	*H. wrightii* Leaves	Organic Soil	Mineral Soil	Soil Difference
Moisture (%)	68.2	79.6	41.4 (5.2)	9.6 (0.5)	**
DBD (g cm^{-3})	n/a	n/a	0.86 (0.11)	1.46 (0.05)	*
OM (%)	92.1	49.9	11.2 (1.7)	1.4 (0.3)	**
OC (%)	44.64	20.69	5.76 (2.04)	0.35 (0.06)	ns
TN (%)	1.21	1.76	0.32 (0.08)	0.01 (0.00)	*
TP (mg g^{-1})	1.02	1.73	0.70 (0.01)	0.19 (0.02)	***
MBC (mg g^{-1})	0.00	42.61	2.49 (0.16)	0.59 (0.02)	**
OC:TN (mol mol^{-1})	43.02	13.71	18.58 (0.55)	103.50 (58.02)	ns
TN:TP (mol mol^{-1})	26.23	22.47	9.89 (2.48)	1.70 (0.62)	*
Extr. NH_4^+ (mg kg^{-1})	n/a	n/a	0.50 (0.50)	3.12 (3.12)	ns
Extr. NO_3^- (mg kg^{-1})	n/a	n/a	b/d	2.32 (0.69)	ns
Extr. SRP (mg kg^{-1})	n/a	n/a	1.48 (0.51)	0.67 (0.19)	ns
Extr. DOC (mg kg^{-1})	n/a	n/a	167.36 (25.61)	32.89 (7.97)	**

DBD dry bulk density, *OC* organic carbon, *TN* total nitrogen, *TP* total phosphorus, *MBC* microbial biomass carbon, & *Extr.* Extractable.

which subsequently decreased sharply and were not different from zero after three weeks (Fig. 4A). For the individual soil and vegetation treatments, the cumulative flux of DIN was greatest from the HW treatments (1912.0 ± 331.7 mg kg^{-1}), and there was no difference in fluxes from RM, OS, and MS treatments (range: 9.24–74.02 mg kg^{-1}) ($p < 0.001$) (Fig. 5A). The total DIN flux from RM leaves was negligible throughout the study, with the exception of a pulse of 68.44 ± 34.65 mg kg^{-1} at the end of the second week (Fig. 4A). The DIN flux was low with no difference between soil types (9.24 ± 2.38 and 42.95 ± 14.33 mg kg^{-1} for OS and MS, respectively) (Fig. 5A). Although the difference between OS and MS cumulative DIN fluxes was not significant, the relatively strong DIN flux from the MS treatment was due to an early pulse of NO_3^- (data not shown). No further NO_3^- was detected during the study, likely because the experimental tidal regime shifted the system toward anaerobic conditions. Summing the NO_3^- and NH_4^+ fluxes into DIN compensated for shifts in redox status that may have artificially influenced the speciation of inorganic N.

For the combined treatments, the cumulative flux of DIN was greatest from the MH treatments (241.21 ± 31.40 mg kg^{-1}), and there was no difference in fluxes from OH, OR, and MR treatments (range: 14.74–52.66 mg kg^{-1}) ($p = 0.002$) (Fig. 5B). The majority of the DIN flux from MH cores occurred in two of the first three sampling days with values of 80.40 ± 18.01 mg kg^{-1} and 123.78 ± 16.82 mg kg^{-1}, but were otherwise not different from zero during the study (Fig. 4D).

3.3.2. *Soluble reactive phosphorus (SRP)*

The concentration of SRP was below detection in the IRL surface water used for tidal treatments. The cumulative flux of SRP from the individual treatments was greatest from HW (412.13 ± 91.84 mg kg^{-1}), statistically equivalent for RM and OS (29.43 ± 5.01 and 15.14 ± 3.56 mg kg^{-1}, respectively), and least for MS (4.72 ± 0.45 mg kg^{-1}) ($p < 0.001$) (Fig. 5A). Compared to DIN for which the efflux was largest at the beginning of the study followed by sharp declines, the timing of SRP fluxes varied by treatment (Fig. 4B). For example, the SRP flux from HW was dominated by an initial pulse of 352.94 ± 98.10 mg kg^{-1} followed by a drop to near zero for the remainder of the study. However, the RM, OS, and MS treatments all saw gradual or sharp increases over time.

While there were several differences in the SRP flux from the individual treatments, there was no difference between combined treatments ($p = 0.27$) (Fig. 5D). Fluxes of SRP from the combined treatments ranged from 19.92 ± 2.27 mg kg^{-1} for MR and 36.10 ± 9.89 mg kg^{-1} for OR. The previously noted trend of increasing SRP fluxes over time for the individual vegetation and soil treatments was especially pronounced for the combined treatments where the maximum values occurred on days 27 (OR), 34 (MR and OH), and 44 (MH) before all trending to near zero by the end of the study (Fig. 4E).

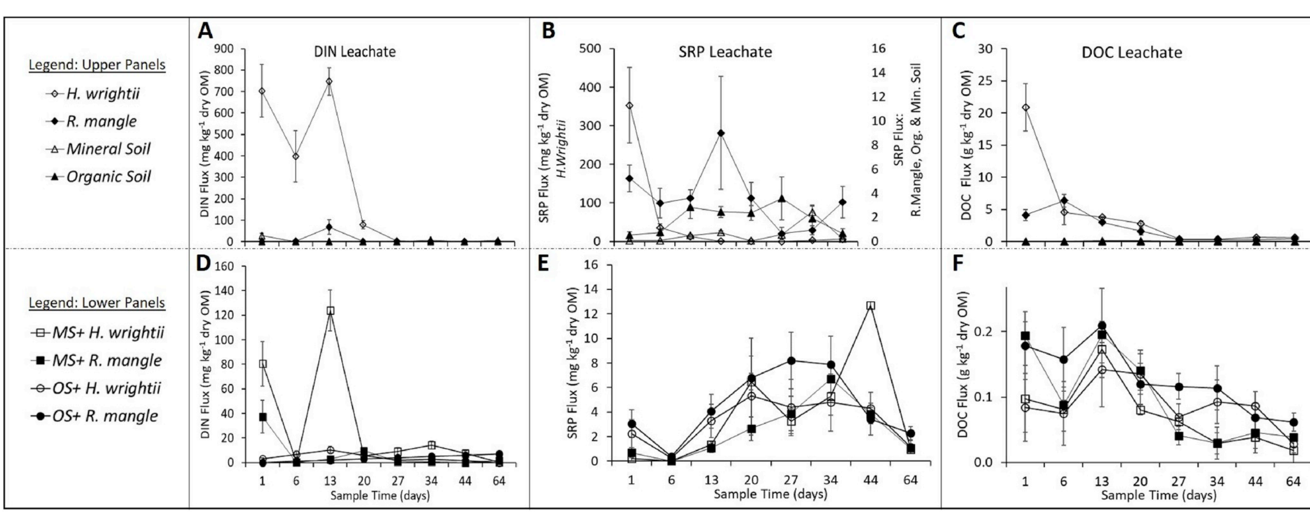

Fig. 4. Time-series of mean leachate fluxes for A,D) dissolved inorganic nitrogen (DIN), B,E) soluble reactive phosphorus (SRP), and C,F) dissolved organic carbon (DOC). Upper panels depict vegetation-only and soil-only fluxes, and lower panels depict fluxes from combined treatments. Note scale differences between upper and lower panels.

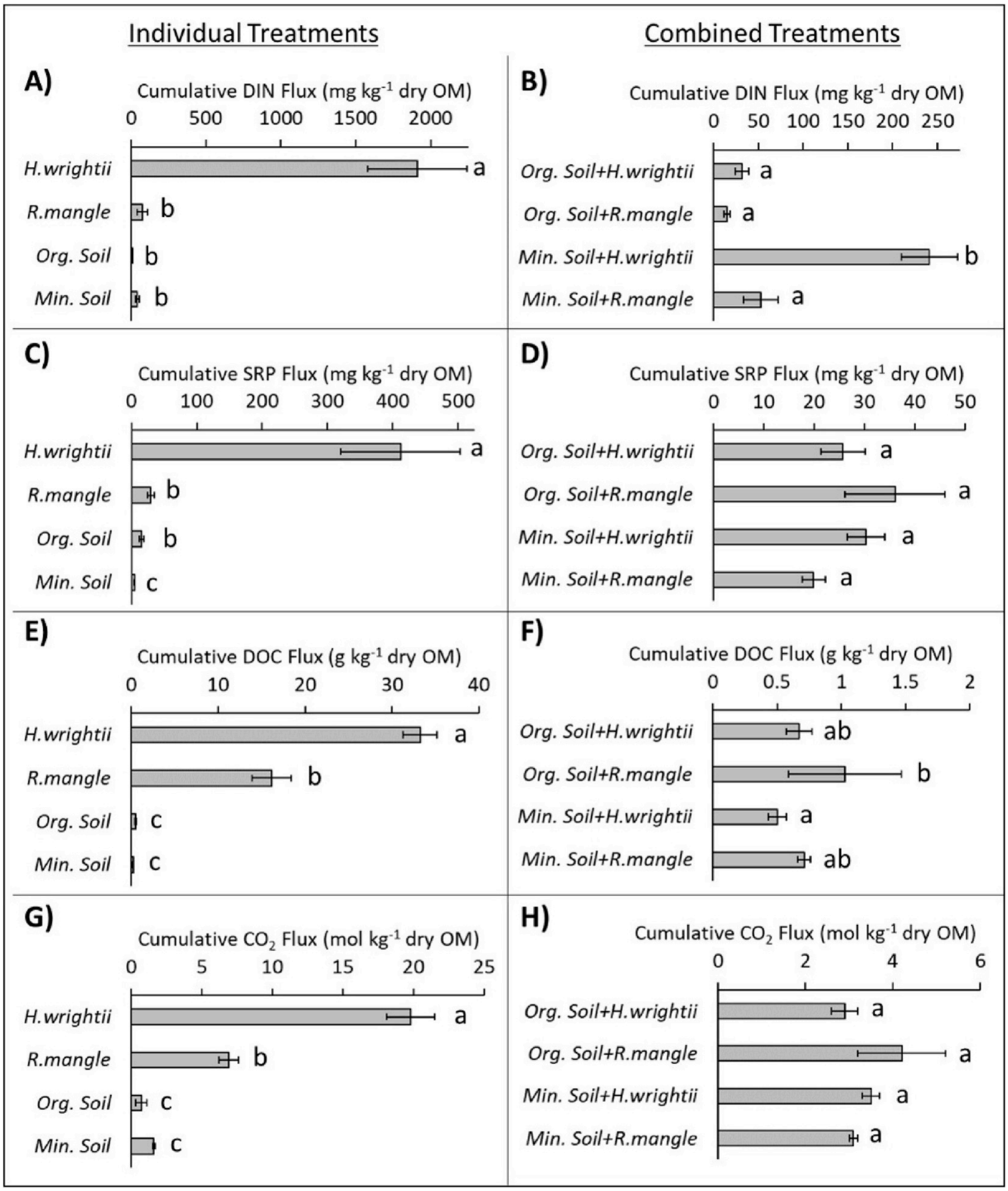

Fig. 5. Mean (±1 S.E.) cumulative fluxes per kg of dry vegetation and/or soil organic matter for: A) & B) dissolved inorganic nitrogen (DIN), C) & D) soluble reactive phosphorus (SRP), E) & F) dissolved organic carbon (DOC), and G) & H) CO_2 for vegetation and soil types (left-side panels) and combined vegetation + soil treatments (right-side panels). Note: the scale size decreases from the left-side to right-side panels for all rows. Different letters within a panel indicate significant differences ($p < 0.05$).

3.3.3. *Dissolved organic carbon (DOC)*

In the IRL surface water used for tidal treatments, the concentration of DOC was 9.95 mg L^{-1} in June and 12.00 mg L^{-1} in July. All subsequent DOC fluxes have these surface water concentrations subtracted. The cumulative flux of DOC was greatest from the HW treatments (33.21 ± 1.91 mg kg^{-1}), followed by RM (16.17 ± 2.24 mg kg^{-1}), and was least for the OS and MS treatments (0.50 ± 0.07 and 0.23 ± 0.30 mg kg^{-1}, respectively) ($p < 0.001$) (Fig. 5E). Both HW and RM had strong initial DOC fluxes that declined and remained near zero by the end of the third week of sampling (Fig. 4C).

For the combined treatments, the DOC flux was lowest from MH (0.50 ± 0.07 mg kg^{-1}) and greatest from OR (1.03 ± 0.44 mg kg^{-1}), however these two were not different from OH and MR (0.67 ± 0.10 and 0.71 ± 0.05 mg kg^{-1}, respectively) (Fig. 5F). Although the scale is much reduced compared to the individual vegetation and soil treatments, each of the combined treatments saw decreasing DOC fluxes over the course of the study (Fig. 4F).

3.4. *CO_2 fluxes*

The HW leaves had the highest cumulative CO_2 flux of 19.8 ± 1.7 mol kg^{-1} dry OM, followed by RM (6.9 ± 0.7 mol kg^{-1}), then OS and MS which were not different from one another (0.7 ± 0.4 and 1.6 ± 0.1 mol kg^{-1}, respectively) ($p < 0.001$) (Fig. 4G). The HW treatments began with the highest mean CO_2 fluxes observed from all measurements, equating to 149.4 ± 29.1 μmol g^{-1} dry OM hr^{-1}, then decreasing logarithmically ($R^2 = 0.72$) to 9.7 ± 0.1 μmol g^{-1} hr^{-1} on day 44 at the conclusion of the study (Fig. 6A). The RM leaves produced an initial flux of 23.1 ± 0.9 μmol g^{-1} hr^{-1} followed by an exponential decrease ($R^2 = 0.47$) to 10.1 ± 3.6 μmol g^{-1} hr^{-1} on day 44 (Fig. 6B).

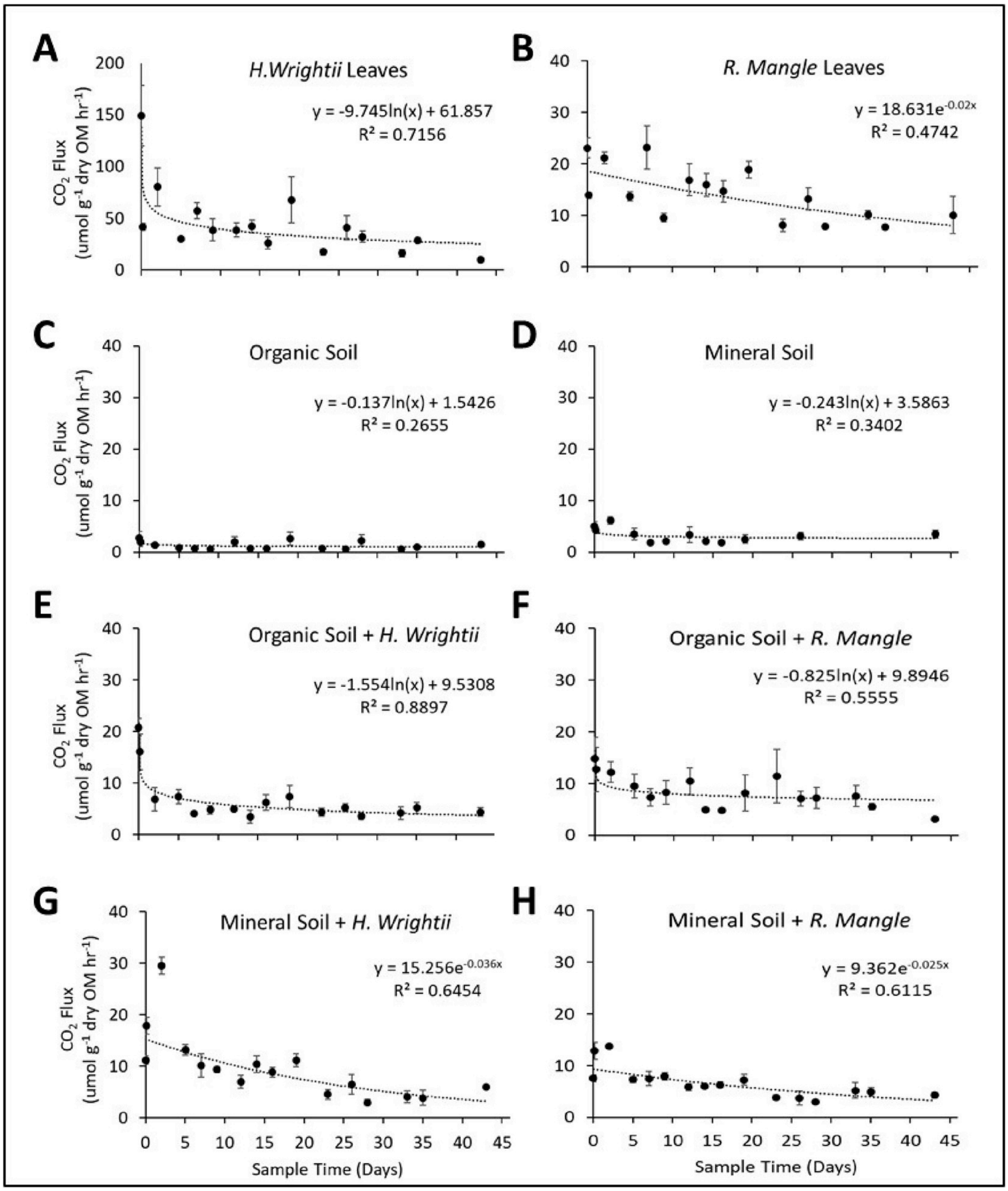

Fig. 6. Time-series of mean CO_2 fluxes and best-fit curves for each vegetation type, soil type, and vegetation-soil combination type. Note scale difference for panel A.

Organic soils produced an initial flux of 2.7 ± 1.3 μmol g^{-1} hr^{-1} followed by a weak logarithmic decrease ($R^2 = 0.27$) to 1.5 ± 0.4 μmol g^{-1} hr^{-1} on day 44 (Fig. 6C). Mineral soil fluxes began at 5.0 ± 0.9 μmol g^{-1} hr^{-1} and decreased logarithmically ($R^2 = 0.34$) to 3.5 ± 0.8 μmol g^{-1} hr^{-1} at the conclusion of the study (Fig. 6D).

There was no difference between the cumulative CO_2 fluxes from the combined treatments ($p = 0.49$), with values that ranged from 2.9 ± 0.3 μmol g^{-1} hr^{-1} (OH) to 4.2 ± 1.0 μmol g^{-1} hr^{-1} (OR) (Fig. 5H). The OH treatments began with mean CO_2 fluxes of 20.8 ± 1.7 μmol g^{-1} dry OM hr^{-1}, then decreased logarithmically ($R^2 = 0.89$) to 4.4 ± 0.8 μmol g^{-1} hr^{-1} on day 44 (Fig. 6E). The OR leaves produced an initial flux of 14.9 ± 4.0 μmol g^{-1} hr^{-1} followed by a logarithmic decrease ($R^2 = 0.56$) to 3.1 ± 0.4 μmol g^{-1} hr^{-1} on day 44 (Fig. 6F). The MH treatments produced a mean initial flux of 11.2 ± 0.8 μmol g^{-1} hr^{-1} followed by an exponential decrease ($R^2 = 0.66$) to 5.9 ± 0.2 μmol g^{-1} hr^{-1} on day 44 (Fig. 6G). The MR treatments began at 7.5 ± 0.7 μmol g^{-1} hr^{-1} and decreased exponentially ($R^2 = 0.61$) to 4.3 ± 0.5 μmol g^{-1} hr^{-1} at the conclusion of the study (Fig. 6H).

3.5. Combined and additive fluxes

There were no differences ($p > 0.05$) between combined and additive fluxes of for six out of eight comparisons of DIN and SRP (Fig. 7A and B). The exception for DIN was the OH treatment, where the mean additive flux of 8.23 ± 1.34 mg was greater than the mean combined flux of 4.96 ± 1.06 mg ($p = 0.001$). For SRP, the mean combined flux from the MR treatment was 0.82 ± 0.10 mg, which was greater than the mean additive flux of 0.26 ± 0.02 mg) ($p = 0.008$). There was no difference between the combined and additive DOC fluxes for the OR treatment, but the mean additive fluxes were greater than the mean combined fluxes for the OH, MH and MR treatments ($p = 0.01$, 0.001, and 0.001, respectively) (Fig. 7C). The qualitative relationship between additive and combined fluxes was the same for CO_2 as for DOC, with p values for the OH, MH, and MR treatments of 0.002, 0.001, and 0.005, respectively (Fig. 7D). Overall, there were no differences between mean combined and additive fluxes of any of the four constituents from the OR treatments.

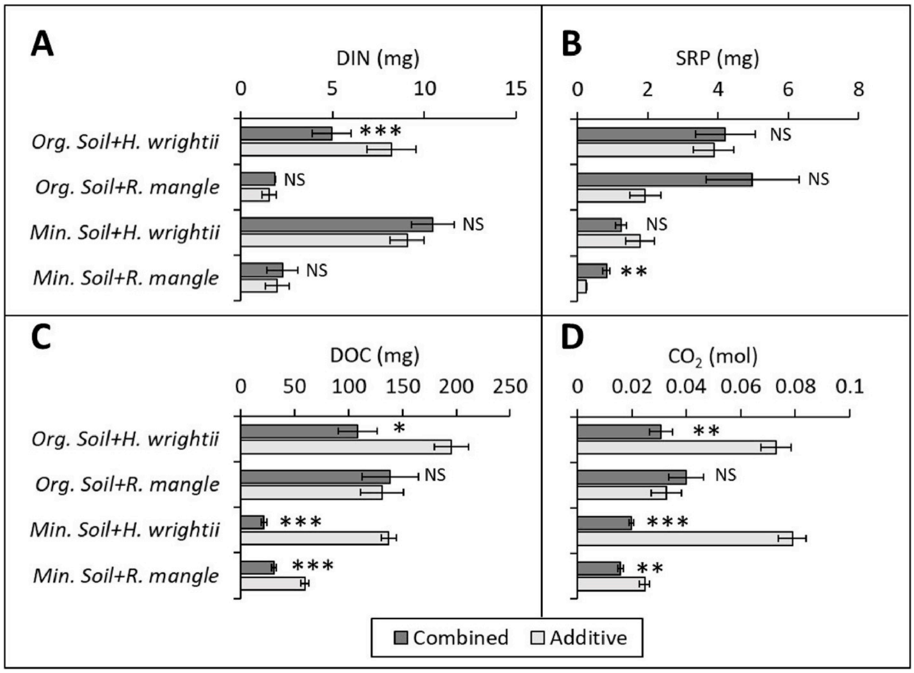

Fig. 7. Comparison of mean (±1 S.E.) combined and additive fluxes from the combined-treatment cores.

The difference between combined and additive fluxes equates to a wide range of SoILE values (Fig. 8). On average, DIN fluxes were suppressed by 41 ± 10% (95% C.I) from the OH treatment, whereas each of the other treatments varied widely but were not different from zero (Fig. 8A). There was no consistent suppression or enhancement of SRP fluxes from the MH, OH and OR treatments, however the MR treatment exhibited an enhanced flux of 224 ± 105% (95% C.I.) (Fig. 8B). Fluxes of DOC from the MR, MH and OH combined treatments were suppressed by 48 ± 5%, 84 ± 9%, and 45 ± 25% (95% C.I.) (Fig. 8C). Similarly, fluxes of CO_2 from the combined treatments were suppressed in the MR, MH and OH treatments by 35 ± 8%, 75 ± 4%, and 58 ± 14% (95% C.I.) (Fig. 8D).

3.6. Post-experiment soil properties

At the conclusion of the experiment, phyico-chemical properties of the intact cores were compared to one another and to the pre-experiment destructible cores to assess the homogeneity of the two

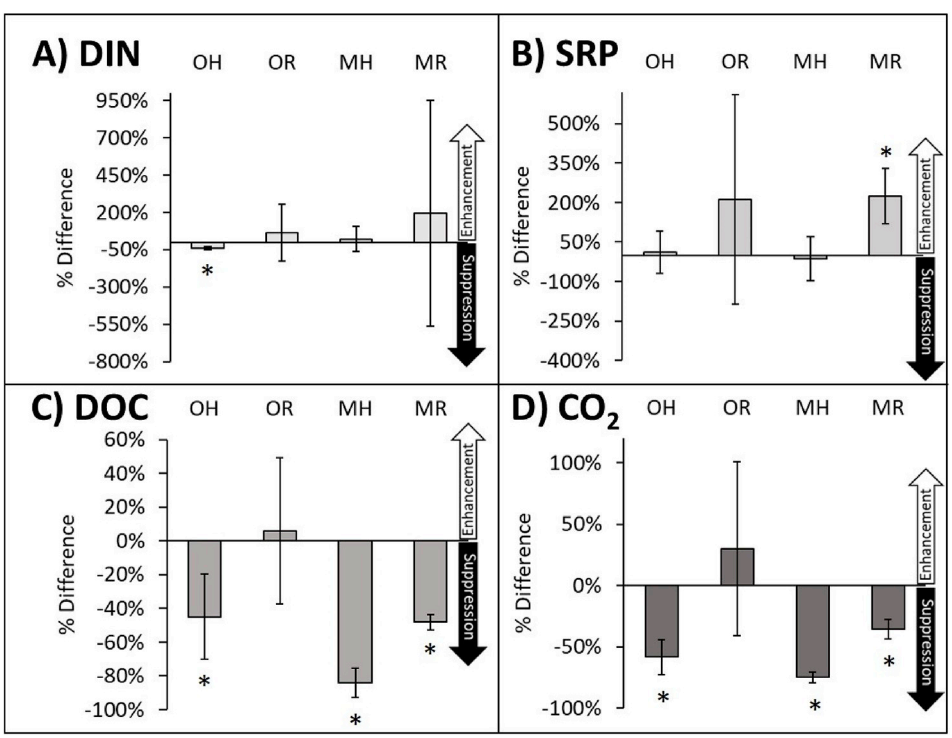

Fig. 8. Soil Interaction with Litter Effect (SoILE) values for A) DIN, B) DOC, C) SRP, and D) CO_2. Error bars are the 95% confidence interval of the difference between additive and combined fluxes of the combined treatment cores. Asterisks indicate SoILE values that are significantly different from zero ($p < 0.05$).

soil types throughout the study. For both DBD and moisture content, there were significant differences between organic and mineral soils throughout the study, and no significant differences within each soil type as a result of vegetation treatment type (i.e., presence or absence of vegetation) (Table 2). The DBD of the mineral soil treatments increased slightly from $1.46 \pm 0.05\ g\ cm^{-3}$ in the pre-experiment destructible cores to $1.78 \pm 0.03\ g\ cm^{-3}$ in the post experiment incubation cores ($p = 0.002$); there was no significant change in the organic soil cores ($p = 0.321$) (Table S1). Similarly, there was a significant increase in soil moisture content of the mineral cores from $9.63 \pm 0.52\%$ to $19.53 \pm 0.65\%$ ($p < 0.001$), but no significant change in the moisture content of the organic soil cores (Table S1). There was no significant change in TC or TN content of the soils over the course of the study (Table S1).

There were significant differences in MBC content between the organic and mineral soils at the end of the study, but no differences within soil type (Table 2). Values for extractable NH_4^+ and DOC were below detection for all post-experiment cores, as were values for extractable NO_3^- from the MH, OR, and OH treatments (Table 2). There was no difference between extractable NO_3^- concentrations in the OS, MS and OH treatments. There was substantial variability in extractable SRP concentrations, ranging from $0.74\ mg\ g^{-1}$ in the MH treatment, to $6.35\ mg\ g^{-1}$ in the OS treatment.

4. Discussion

4.1. Wrack benefits to living shorelines

The presence of wrack on living shorelines represents a two-fold benefit as (1) a subsidy of DIN and SRP that can be used for primary production by shoreline plants, and (2) as a net suppression of DOC and CO_2 fluxes compared to the fluxes that would occur in the absence of the interaction between wrack and soil. These results show that a large mass of wrack accumulates on these shorelines over the course of the year, with the seagrass HW being the primary contributor (Figs. 2 and 3). Additionally, HW was shown to be a labile and strong source of DIN, SRP, DOC and CO_2 by a wide margin compared to mangrove leaves and the two soil types examined here (Figs. 4 and 5). The subsidies provided by this wrack would not occur on hardened or armored shorelines that use concrete wave-breaks for shoreline stabilization at the cost of ecological.

Connectivity between the marine and upland environments. In cases where wrack has no shoreline on which to settle, the entire potential leachate flux (Fig. 5A, C, E) will be introduced to surface waters, although the efflux of gaseous CO_2 may be reduced for permanently submerged vegetative litter. The fluxes from the separate vegetation and soil treatments support previous findings (Lavery et al., 2013; Rossi and Underwood, 2002; Liu et al., 2019; Prasad et al., 2019), and also demonstrate the importance of accounting for the interaction between soil and wrack when reporting on the impact of wrack to shoreline carbon and nutrient budgets.

4.2. SoILE indications of suppression and enhancement

This dataset indicates that the flux of DIN was suppressed from the combination of organic soil and seagrass, while the flux of SRP was enhanced from mineral soil combined with mangrove leaves (Fig. 8B). It should be noted that there was substantial suppression and enhancement of DIN and SRP from the other soil-vegetation treatments, but without a consistent statistical trend. There was no evidence of enhanced fluxes of carbon from either soil type with the addition of wrack (Fig. 8C and D), instead there was a strong indication of suppressed carbon fluxes.

We propose that the interaction of vegetation with the soil surface leads to a “smothering” effect that alters redox conditions and decreases available surface area for bio-physical activity, contributing to both negative and positive SoILE values (Fig. 9). As the experimental study progressed, visible physical interactions occurred with the vegetation and both soil types. For the OS treatments, the vegetation was seen adhering to the other vegetation and to the soil surface. This was confirmed during the dismantling of the cores at the conclusion of the study, when the leaves were firmly adhered to the soil. This physical connection decreased the exposed surface area of the vegetation and soil available for the physical leaching of nutrients and microbial nutrient mining and respiration. In the sandy MS treatments, the vegetation litter slowly became buried in the sand over the duration of the study. This was particularly the case for the HW leaves. Such burial would contribute to preservation of the leaves and suppression of their degradation products. We propose that the effect of the physical interaction of the vegetation to the soil surface combined with the tidal regime to cause this “smothering” effect and anaerobism in the cores.

The suppression of DIN from the OH treatment was likely to have occurred as a result of N removal via denitrification in the organic soils. The greatest source of DIN from the individual soil and vegetation types was from the seagrass HW (Figs. 5A and 6A). This flux occurred primarily in the form of NO_3^- rather than NH_4^+ (data not shown). When the HW was combined with the two soil types, there was a strong initial pulse of NO_3^- from the MH treatments, but not from the OH treatments. Soil moisture can be a proxy indicator of soil anaerobism. The mineral, sandy soils drained much more quickly than the OS treatments during each tidal efflux, with the water often draining completely from the soil surface within less than 15 min, indicative of greater potential for aerobic conditions to return to these soils during low tide conditions. Also, the organic soil had an initial moisture content of 41.4% compared with only 9.6% in the mineral soil (Table 1); mean soil moisture values increased to 53.4% and 17.9%, respectively for both soil types by the end of the study (Table 2). This indicates that experimental tidal conditions increased moisture (and anaerobic conditions) compared to initial field conditions, but similar changes may occur in these soils under natural seasonal variability in water levels. This suggests that the

Table 2
Average (±1 S.E.) soil properties of intact cores at the conclusion of the experiment. Different letters within a row indicate significant difference; levels of significance indicated by * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$), and ns (not significant). (n/a = not available, and b/d = below detection).

Property	No wrack treatment		HW wrack treatment		RM wrack treatment		
	Organic Soil	Mineral Soil	Organic Soil	Mineral Soil	Organic Soil	Mineral Soil	Difference
DBD ($g\ cm^{-3}$)	0.65 (0.07)a	1.80 (0.10)b	0.79 (0.06)a	1.77 (0.04)b	0.70 (0.14)a	1.78 (0.02)b	***
Moisture (%)	53.4 (2.9)a	17.9 (1.6)b	48.9 (1.4)a	21.1 (0.6)b	57.4 (6.5)a	19.6 (0.1)b	***
OC (%)	8.20 (0.83)a	0.49 (0.21)b	10.33 (0.67)a	1.66 (0.25)c	13.72 (2.30)a	0.85 (0.06)b	***
TN (%)	0.45 (0.04)a	0.00 (0.00)b	0.59 (0.09)a	0.02 (0.02)b	0.67 (0.16)a	0.00 (0.01)b	
MBC ($mg\ g^{-1}$)	1.62 (0.20)a	0.40 (0.03)b	1.23 (0.16)a	0.47 (0.04)b	1.97 (0.46)a	0.34 (0.02)b	***
Extr. NH_4^+ ($mg\ kg^{-1}$)	b/d	b/d	b/d	b/d	b/d	b/d	n/a
Extr. NO_3^- ($mg\ kg^{-1}$)	0.01 (0.26)	0.10 (0.17)	1.18 (1.07)	b/d	b/d	b/d	ns
Extr. SRP ($mg\ kg^{-1}$)	6.35 (2.26)a	0.92 (0.07)bc	3.81 (1.10)ab	0.74 (0.17)c	3.08 (0.36)abc	1.32 (0.15)bc	**
Extr. DOC ($mg\ kg^{-1}$)	b/d	b/d	b/d	b/d	b/d	b/d	n/a

DBD dry bulk density, *MBC* microbial biomass carbon, & *Extr.* Extractable.

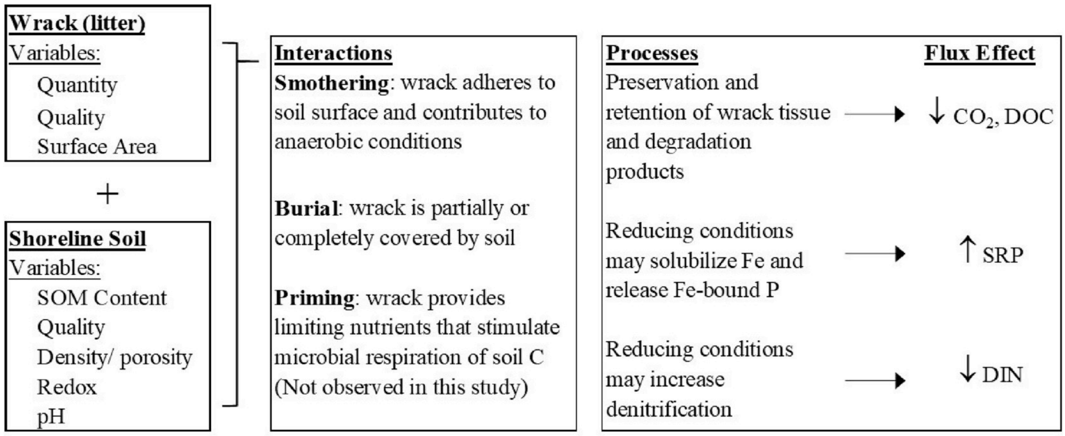

Fig. 9. Conceptual model of potential wrack-soil interactive processes influencing fluxes of DIN, SRP, DOC, and CO_2.

more reducing conditions of the organic soils can remove seagrass N from the environment, possibly via denitrification, whereas the sandy, mineral soils can return to aerobic conditions during low tide conditions and may simply convey the nitrate to the surface water. We note that mangrove leaves and both soil types all produced low fluxes of DIN (Fig. 5A). The large variability in DIN SoILE values for the MR treatment was because DIN fluxes from mangrove leaves, while very small, varied by a factor of 57, contributing to large percentage differences between additive and combined fluxes.

The enhanced flux of SRP from the MR treatment is also likely a function of altered redox conditions in the soils caused by both a smothering effect from the leaves and from the tidal regime. The increased flux of SRP over time (mirrored by high extractable SRP in the post experiment soils; Table 2) is likely driven by the onset of anaerobism in the cores, whereby reducing conditions convert insoluble Fe^{3+} to soluble Fe^{2+} leading to the simultaneous release of Fe-bound P (DeLaune and Reddy, 2008). This observation is important for intertidal wetlands like those in microtidal Mosquito Lagoon where seasonal water level changes are more substantial than daily tidal ranges (Smith, 1987), and the prospect of strongly different seasonal redox conditions is likely. This suggests that soils in the lagoon may be a source of SRP in the high-water season. It is also important to note that this study used soils devoid of vegetation. On a vegetated living shoreline, the likelihood of nutrient export from wrack to surface water would be less because of the assimilation by plants. While the HW vegetation was a strong source of SRP on its own (Fig. 5C), when combined with both organic and mineral soils, there was substantial variability leading to no clear trend of suppression or enhancement (Fig. 8B).

The concept of "blue carbon" focuses on the stocks of C present in coastal wetland ecosystems that include mangroves, saltmarshes, and seagrasses (Nellemann et al., 2009). Although terrestrial forest research has documented a priming, or enhancing, effect of soil C loss following the addition of leaf litter to the soil (Fontaine et al., 2004; Sayer et al., 2007), such findings were not observed for these tidally-manipulated observations. Instead, these data indicate that addition of wrack to the soil contributes to an increase in the retention of C in the form of both DOC and CO_2 (Fig. 8C and D). This research documents the importance of quantifying exchange of litter between neighboring blue-carbon communities within coastal ecosystems. For example, litter that is shed and exported as wrack to a regional shoreline will efflux its C and nutrients outside the location where it was initially fixed as plant OM. Similarly, if wrack from a nearby ecosystem is deposited on a mangrove or marsh shoreline, the suppression of SoILE values seen in this dataset suggest that not only will the wrack add to the soil C and nutrients stores, but there will be an overall increase greater than would be expected from analysis of the vegetation and soil separately.

4.3. Regional implications

The wrack surveys and experimental observations were used to estimate the amount of C and nutrients produced from seagrass and mangrove leaf wrack along 1 km of shoreline and along the total length of shoreline in Mosquito Lagoon (1328.15 km). The mean annual accumulation of all leaves (mangrove plus unclassified leaves) was used as an upper level estimate. A wrack accumulation zone of 1 m was assumed as a conservative measure. The calculations for annual flux from the entire shoreline length of Mosquito Lagoon assumed that the substrate was either all OS or all MS because no estimate is available for the proportion of the lagoon shoreline occupied by each soil type.

Our combined treatment observations indicate that the combination of seagrass with mineral shoreline soil is a significantly greater source of DIN, and a marginally (though not significantly) greater source of SRP and CO_2 than the combination of seagrass with organic soil shorelines (Fig. 5B, D, & H), while the relationship is opposite for DOC (Fig. 5F). Therefore, assuming that all of Mosquito Lagoon shorelines are organic represents a low-end estimate for DIN, SRP and CO_2 fluxes, and assuming that all the shoreline is mineral represents the high-end estimate. The range of fluxes from HW in Mosquito Lagoon was 27.5 ± 6.9 to 207.4 ± 44.9 kg yr^{-1} for DIN, 22.4 ± 3.5 to 25.8 ± 5.7 kg yr^{-1} for SRP, and 2.6 ± 0.3 to 3.0 ± 0.6 Mmol yr^{-1} for CO_2 (Table 3). Because more DOC was released from the combination of seagrass with organic soil, a high-end estimate was derived from assuming all the shoreline was organic and the low-end from assuming all the shoreline was mineral. The total annual flux of DOC from HW in Mosquito Lagoon was estimated to be 430.2 ± 114.0 to 860.4 ± 87.0 kg (from MS and OS, respectively) (Table 3). The flux of DIN was higher from the combination of leaf wrack with mineral shorelines, whereas SRP, DOC, and CO_2 were higher from the combination of leaf wrack with organic shorelines. The range of DIN produced from leaf wrack in Mosquito Lagoon was 12.9 ± 2.6 to 45.6 ± 18.2 kg yr^{-1}. The total estimated annual fluxes from leaves were 17.2 ± 3.5 to 31.0 ± 8.6 kg for SRP, 602.3 ± 135.6 to 860.4 ± 344.4 kg for DOC, and 2.7 ± 0.5 to 3.6 ± 0.9 Mmol for CO_2 (assuming the shoreline was entirely MS or OS, respectively) (Table 3).

Ultimately, contextualizing the importance of these values requires a complete regional C and nutrient budget in order to assess their scale relative to other fluxes, both spatially and temporally. While these estimates project annual lagoon inputs, it is important to consider the timing of wrack accumulation and how pulses of nutrients may affect the health of the lagoon. For example, winter represents the greatest accumulation period for wrack, however this does not coincide with peak productivity of rooted vegetation. Similarly, events like Hurricane Irma in 2017 substantially elevated the September litter accumulation compared to usual summer and autumn fluxes (Fig. 2). This suggests that the storm caused an abnormally high flux of nutrients that may have

Table 3
Total flux of DIN, SRP, DOC, and CO_2 from 1 kg of dry wrack, 1 km of shoreline yr^{-1}, and total shoreline length of Mosquito Lagoon yr^{-1} assuming that 100% of shoreline is organic soil or 100% is mineral soil. Mean annual accumulation rates were 647.82 g m^{-2} yr^{-1} for HW and 205.01 g m^{-2} yr^{-1} for uncategorized and mangrove leaves combined (Fig. 3). Note that units increase with spatial scales.

Vegetation	Variable	1 kg dry wrack		Annual Flux km^{-1} shoreline		Annual Flux: Total Shoreline of Mosquito Lagoon	
		Organic Soil	Mineral Soil	Organic Soil	Mineral Soil	Organic Soil	Mineral Soil
Halodule Wrightii leaves	DIN	32 (8) mg	241 (31) mg	20.7 (5.2) g	156.1 (33.8) g	27.5 (6.9) kg	207.4 (44.9) kg
	SRP	26 (4) mg	30 (4) mg	16.8 (2.6) g	19.4 (4.3) g	22.4 (3.5) kg	25.8 (5.7) kg
	DOC	1 (0.1) g	0.5 (0.1) g	647.8 (65.5) g	323.9 (85.9) g	860.4 (87.0) kg	430.2 (114.0) kg
	CO_2 (Atm.)	3 (0.3) mol	3.5 (0.2) mol	1.9 (0.2) kmol	2.3 (0.4) kmol	2.6 (0.3) Mmol	3.0 (0.6) Mmol
Rhizophora Mangle leaves	DIN	15 (3) mg	53 (19) mg	9.7 (1.9) g)	34.3 (13.7) g	12.9 (2.6) kg	45.6 (18.2) kg
	SRP	36 (10) mg	20 (2) mg	23.3 (6.5) g	13.0 (2.6) g	31.0 (8.6) kg	17.2 (3.5) kg
	DOC	1 (0.4) g	0.7 (0.1) g	647.8 (259.3) g	453.5 (102.1) g	860.4 (344.4) kg	602.3 (135.6) kg
	CO_2 (Atm.)	4.2 (1) mol	3.1 (0.1) mol	2.7 (0.6) kmol	2.0 (0.4) kmol	3.6 (0.9) Mmol	2.7 (0.5) Mmol

added to high nutrient concentrations in stormwater run-off (Lapointe and Matzie, 1996; Dillon and Chanton, 2005), or conversely the wrack nutrient flux may have been diluted by the high volume of precipitation associated with the storm (Cangialosi et al., 2018).

4.4. Management recommendations

Shoreline managers have the option of leaving wrack in place or manually removing it, depending on the short and long-term objectives that range from prioritization of tourism, providing habitat and food-web support, and restoration. The temporal variability of wrack deposition coupled with variable physical structure and nutritional quality means that active planning is needed to align wrack types with shoreline management objectives. Depending on the amount and type of litter deposition, there is potential for the smothering effect to alter elemental cycling in surface soils and add stress to rooted shoreline plants. It can be surmised that while seagrass is a strong source of nutrients, mangrove leaves may be more effective at creating anaerobic soil conditions, although conclusions regarding the extent of smothering by different types of wrack require additional research. Intentional, manual addition of wrack may serve management objectives of enhancing blue carbon or restoring natural wetland function. Though contrary to the priming hypothesis, these data gave strong evidence that the addition of wrack to shoreline soils led to the net suppression of DOC and CO_2 effluxes, contributing to an increase in soil blue carbon. If management goals include restoration of a “living shoreline”, then the evidence of smothering and early burial of wrack suggest that wrack contributes to SOM formation, a process that takes several decades to achieve natural reference conditions (e.g., Osland et al., 2012). Conclusions and recommendations are less clear regarding an interactive effect on nutrient fluxes, but these data suggest the smothering effect may have an amplifying effect on the release of SRP from the combination of wrack and soil. For managers of P-limited ecosystem shorelines, this suggests that wrack may be a vehicle to stimulate release of P to the ecosystem. Conversely, encouraging anaerobic conditions with the use of wrack may be a means of increasing DIN removal via denitrification.

Mosquito Lagoon has been the focus of extensive restoration efforts that utilize mangrove and salt marsh vegetation to stabilize vulnerable shorelines (Walters et al., 2017; Donnelly et al., 2017). These planting efforts often involve shelly substrates because their intended purpose is to stabilize and prevent further erosion of Native American shell middens. We assume that the SOM content will be lower and porosity will be greater than that of the MS used in our experiment, which may lead to enhanced NO_3^- efflux from wrack at these sites. This NO_3^- may be taken up by the living shoreline plants, but it may also be exported to the lagoon surface water. Similar interactions should occur on other coarse mineral sediment shorelines around the world. If so, this demonstrates the long-term benefits of living shoreline establishment on these shelly shorelines, and the gradual accumulation of below-ground organic soils capable of maintaining anaerobic, reducing conditions for denitrification.

5. Conclusions

The accumulation of marine and terrestrial wrack along shorelines is a natural pathway of carbon and nutrient cycling in coastal ecosystems. Accelerating sea-level rise and increasing storm frequency are likely to increase the amount, timing and types of wrack accumulation as evidenced by the high wrack inputs from Hurricane Irma observed in this dataset (Fig. 2A). These wrack-driven subsidies are important to understand in the context of how they may exacerbate coastal zone eutrophication and associated algal blooms and anoxia. This study addresses a knowledge gap in the literature by going beyond the quantification of the C and nutrient flux potentials from wrack to investigate the biogeochemical coupling with shoreline soil types. We define a measure called the Soil Interaction with Litter Effect (SoILE) to quantify the suppression or enhancement of C and nutrient fluxes from wrack with shoreline soils compared to the potential fluxes of wrack and soil separately. While the effect of combining vegetative litter with soil varied, there was evidence of significant suppression of DIN, DOC and CO_2 fluxes and enhancement of SRP fluxes. We propose that the physical interaction of vegetation with the soil contributes to variable SoILE values due to a “smothering” effect that drove changes in redox chemistry that affect denitrification, soil respiration, and Fe-bound P solubility. The observations from this research suggest that wrack on living shorelines is likely to offer a two-fold benefit by (1) providing a subsidy of DIN and SRP to support mangrove and salt marsh primary production, and (2) suppressing fluxes of DOC and CO_2 compared to the fluxes that would occur in the absence of the interaction between wrack and soil.

Declaration of competing interest

All authors declare that there are no conflicts of interest regarding the publication of this paper.

Acknowledgements

This work was funded by a Coupled Natural-Human Systems grant (Award #1617374) from the National Science Foundation. JLB was supported by P3 post-doctoral funding from the University of Central Florida. Thanks to Dr. G. McClenachan for calculating the total shoreline length of Mosquito Lagoon, and to the many UCF undergraduate student field assistants. We are grateful to Canaveral National Seashore for providing access to the field sites.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.106409.

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