



Seagrass Species Identity Drives Leaf Litter Decomposition Across a Naturally Occurring Phosphorus Gradient

Alexandra L. Bijak¹ · Ashley R. Smyth^{1,2} · Savanna C. Barry³ · Charles W. Martin⁴ · Cloud A. Spengler¹ · Laura K. Reynolds¹

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Abstract

Decomposition is one of several controls on carbon storage in seagrass meadows, but the relative importance of environmental conditions and seagrass species identity in driving decomposition is unclear. We first investigated direct environmental effects on decomposition by measuring percent mass lost of standardized litter, green and rooibos (red) tea, incubated in meadows spanning a naturally occurring phosphorus gradient for up to 2 years; we then investigated indirect effects by measuring percent mass lost of seagrass leaf litter sourced from these meadows and incubated in a single location for up to 2 months. We tested the effect of species identity on decomposition by incubating litter from two seagrass species, the larger-bodied *Thalassia testudinum* and the smaller-bodied *Halodule wrightii*. We found evidence for both direct and indirect environmental effects on decomposition: the green tea decay rate was lowest at the phosphorus-limited site (0.011 d^{-1}), and *T. testudinum* litter decay rate was lowest for leaves collected from the phosphorus-limited site (0.017 d^{-1}). Species identity had a stronger effect on leaf litter decomposition, where mean leaf litter decay rates were consistently greater for *T. testudinum* ($k = 0.022 \pm 0.002 \text{ SE}$) compared to *H. wrightii* ($k = 0.010 \pm 0.001 \text{ SE}$). This finding was unexpected because *T. testudinum* meadows are typically associated with higher sediment carbon stocks than meadows dominated by other species and suggests that *T. testudinum* may promote carbon storage by producing above- and belowground litter in quantities that accrue as sediment carbon despite fast initial leaf litter decay rates, or through other mechanisms, such as particle trapping by the seagrass canopy.

Keywords Seagrass · *T. testudinum* · *H. wrightii* · Decomposition · Carbon cycling

Introduction

Decomposition of organic matter is an integral part of carbon and nutrient cycling, affecting soil carbon pools as a potential carbon loss pathway (Amundson, 2001) and regenerating

nutrients required for primary and secondary production (Vitousek & Sanford, 1986). Given plant litter is the primary source of soil organic matter, plant traits play an important role in decomposition. In terrestrial and freshwater systems, leaf litter quality in terms of chemistry (e.g., elemental composition or lignin concentration) can vary substantially by species (Aerts, 1997; Cornelissen, 1996; Hobbie, 1996; Madritch & Hunter, 2004) so that species identity is often a strong predictor of decomposition rates (Cornelissen, 1996; McLaren & Turkington, 2010). Environmental conditions, such as nutrient availability, can further limit decomposition within soils in terrestrial systems (McClaugherty et al., 1985) and within the water column in aquatic systems (Ardón et al., 2021; Costello et al., 2022; Tiegs et al., 2024; Woodward et al., 2012). Yet the relative importance of environmental conditions and species-linked traits in driving decomposition is less clear, especially in coastal ecosystems, such as seagrass meadows, that host wide within-species variation in plant traits (Arnaud-Haond et al., 2012).

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✉ Alexandra L. Bijak
abijak@ufl.edu

¹ Soil, Water, and Ecosystem Sciences, University of Florida, Gainesville, FL 32611, USA

² Soil, Water, and Ecosystem Sciences, Tropical Research and Education Center, Homestead, FL 33031, USA

³ Nature Coast Biological Station, University of Florida, Cedar Key, FL 32625, USA

⁴ Dauphin Island Sea Lab and University of South Alabama, Dauphin Island, AL 36528, USA

Seagrass meadows contain globally significant amounts of carbon in underlying sediments (Duarte et al., 2005; Fourqurean et al., 2012), where organic matter that escapes decomposition can be buried and stored for long periods of time (Cebrian, 2002; McLeod et al., 2011). Seagrass litter is one of many sources of organic matter that contributes to the pool of stored carbon in meadows, and the relative contribution of autochthonous organic carbon varies widely across meadows (Kennedy et al., 2010). Variation in seagrass productivity and traits, whether by species or environmentally induced, likely affects litter quality and decomposition. Seagrass plant structure differs by species (Larkum et al., 2006), and seagrasses also exhibit plasticity in terms of size and tissue elemental composition that vary within species across different environments (Barry et al., 2017; Bricker et al., 2011; Duarte, 1990, 1992). Aside from influencing litter quality, environmental conditions, including nutrient availability, temperature, sediment conditions (e.g., texture and oxygen availability), and microbial activity, can promote or inhibit decomposition in seagrass meadows (Macreadie et al., 2017; Trevathan-Tackett et al., 2021, 2017a, 2017b). Identifying both environmental conditions and plant characteristics that drive decomposition in meadow sediments can improve our understanding of the role of seagrasses in coastal carbon cycling, but studies demonstrating how within- and between-species variation in litter quality affects decomposition in different environments are lacking.

Nutrient availability in seagrass meadows may affect decomposition in two ways: by limiting microbial remineralization of any type of organic matter deposited within a meadow and by shaping the nutrient stoichiometry (i.e., carbon:nitrogen:phosphorus) of seagrass tissues that eventually become litter. Nutrient availability impacts on litter quality and decomposition in seagrass meadows are likely similar to those observed in freshwater ecosystems, where nitrogen and phosphorus availability are common predictors of decomposition (Webster & Benfield, 1986). Higher nitrogen and phosphorus content in plant litter can increase microbial remineralization rates in any ecosystem (Fenchel & Blackburn, 1979; Goldman et al., 1987). Yet there are key differences in controls on decomposition in marine sediments: sulfate reduction, rather than nitrate reduction or methanogenesis, is the dominant process controlling remineralization in marine sediments due to the abundance of sulfate in seawater (Jørgensen, 1982), and marine systems have historically been considered limited by nitrogen rather than phosphorus availability (Nixon et al., 1996). The effects of nitrogen availability on coastal plant decomposition have been more intensively studied, though phosphorus limitation can still occur in marine systems (Conley et al., 2009), especially in tropical and subtropical seagrass meadows. However, there has been limited research on the effects of phosphorus availability on decomposition in seagrass meadows.

We examined the roles of phosphorus availability and species identity in driving decomposition in subtropical seagrass meadows. In subtropical meadows where multiple species co-exist, we hypothesized species differences in litter quality to have small effects on decomposition relative to site-specific differences in litter quality, because previous work has found subtle taxonomic variation in leaf tissue recalcitrance (Trevathan-Tackett et al., 2017a, 2017b) but wide variation in leaf tissue nutrient content within species across different environments (Duarte, 1990, 1992). To test our hypothesis, we assessed the direct effects of phosphorus availability on the decomposition of standardized litter and then assessed the indirect effects of phosphorus availability via its influence on seagrass litter quality and decomposition. We exploited a naturally occurring phosphorus gradient in the northeastern Gulf of Mexico (Florida, USA) to conduct two litter bag experiments, where standardized litter, green and rooibos (red) tea, was deployed at sites spanning the gradient, and seagrass leaf litter of two species collected from sites spanning the gradient was deployed at a single site. This approach enabled us to compare both site differences driving in situ decomposition as well as to parse intrinsic species- vs. site-driven differences in seagrass litter quality and decomposition.

Methods

Study Area

Our study was conducted along a naturally occurring phosphorus gradient in the north-central Gulf Coast of Florida, USA, where comprehensive water quality and seagrass monitoring data show that water column total phosphorus as well as seagrass tissue phosphorus content decreases from north to south (Barry et al., 2017, 2024; Frazer et al., 1998; Jacoby & Frazer, 2013, 2015). To control for other potential sources of variation in seagrass litter quality and decomposition rates, we selected three sites in seagrass meadows along the phosphorus gradient that were similar in other water column characteristics, including depth, temperature, salinity, dissolved oxygen, total nitrogen, and irradiance at the bottom depth (Table S1; Fig. 1). At these sites, the mean percent of surface irradiance reaching bottom depths exceeds reported thresholds for seagrasses in Florida's Gulf Coast, indicating seagrasses are not light-limited (Barry et al., 2017; Choice et al., 2014). We included an additional site (Seahorse Key) outside of the documented gradient that is more balanced in terms of nitrogen and phosphorus concentrations and was used as the seagrass litter incubation location (Table S1; Fig. 1).

Seagrass traits vary along the phosphorus gradient, where leaf length, width, and phosphorus content increase with

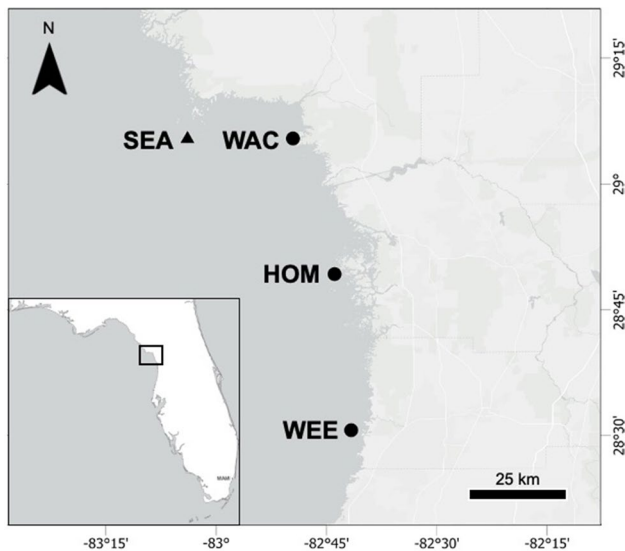


Fig. 1 Map of study sites along the naturally occurring phosphorus gradient (circles), where long-term total phosphorus water column concentrations decrease from north to south (WAC, Waccasassa; HOM, Homosassa; WEE, Weeki Wachee), and the additional seagrass litter incubation site (triangle; SEA, Seahorse Key)

total phosphorus while shoot density decreases with total phosphorus, though total biomass is similar across the gradient (Barry et al., 2017). The two most common seagrass species in the study area exhibit intrinsic differences in traits that reflect contrasting life histories: the climax species *Thalassia testudinum* is large, slow-growing, and has low nutrient demands, while the pioneering species *Halodule wrightii* is small, fast-growing, and has high nutrient demands (Kilminster et al., 2015). In the first experiment, we deployed standardized litter (i.e., green and red tea) in *T. testudinum*-dominated meadows at each site along the phosphorus gradient, and in the second experiment, we incubated *T. testudinum* and *H. wrightii* leaves collected from each site in a *T. testudinum*-dominated meadow at a single site, Seahorse Key.

Tea Decomposition Experiment

We deployed green and red tea (Lipton© by Unilever) at each site along the phosphorus gradient and the additional site in Seahorse Key (Fig. 1) in July 2017 to test the effects of environmental conditions on the decomposition of standardized litter. The green tea represents a more labile form of organic matter, i.e., water-soluble, relative to the red tea, which represents a more recalcitrant form of organic matter, i.e., high lignin content (Keuskamp et al., 2013; Trevathan-Tackett et al. 2024). The tea was packaged in the original woven nylon bag (pyramid: 5 cm × 5 cm × 5 cm) with a 0.25-mm mesh size (Mori et al., 2021). Initial tea mass was

calculated as the difference between the total weight of the tea in the bag and the mean empty bag weight (mean = 0.20 g and standard error of the mean (SE) = 0.002 g, $n = 40$ empty bags). At each site, we buried both green and red tea bags to 10 cm depth, with 4 replicates within each of 4 plots, so that $n = 4$ for each tea type at each site and retrieval time. The tea bags were collected approximately 3, 6, 12, and 24 months after deployment, and 67% and 70% of green and red tea bags were recovered, respectively. Recovered samples were rinsed and cleared of sediment and then dried to a constant weight in a drying oven at 60 °C. For each sample, we calculated percent mass lost of tea:

$$\text{Percent mass lost} = \frac{(mass_{initial} - mass_{final})}{mass_{initial}} * 100 \quad (1)$$

For each tea type, we estimated litter decay rates using an exponential decay model:

$$\text{Proportion mass remaining} = e^{-tk} \quad (2)$$

where litter decays at a constant rate (k , d^{-1}) over time (t , days).

Due to the limited recovery of standardized litter samples at each retrieval, we calculated a single decay rate, k , per site and therefore could not statistically compare k across sites (for both types of tea, replication was low at $n = 1$ or $n = 2$ for 50% of all site-by-retrieval combinations). An analysis of covariance (ANCOVA) allowed us to assess site differences in percent mass lost while controlling for retrieval time as a covariate (“Anova” function in the “car” package in R version 4.3.3; Fox & Weisberg, 2019; R Core Team, 2024) using type II sum of squares to account for unequal sample sizes across sites. We used Quade’s procedure to perform a nonparametric ANCOVA because data for both green and red tea violated assumptions of normality and equal variances across groups (Bonate, 2000; Quade, 1967). Briefly, the Spearman correlation coefficient between percent mass lost and retrieval time ranks was used to predict percent mass loss deviation rank scores, and a one-way analysis of variance (ANOVA) was then performed on the residual deviation rank scores for percent mass lost with site as the fixed effect. We performed pairwise comparisons across sites using estimated marginal means of the residual deviation rank scores in the “emmeans” package (Lenth, 2024).

Seagrass Litter Decomposition Experiment

We collected fresh *H. wrightii* and *T. testudinum* leaf tissue from at each site along the phosphorus gradient and the additional site in Seahorse Key (Fig. 1) in June 2022 to compare decomposition between the two species across collection sites. Leaf tissue was refrigerated (4 °C) until processed, and all samples were processed within 72 h

of collection. Seagrass leaves were rinsed and cleared of epiphytes by gently scraping leaves with a razor blade. Leaves were then cut into 4-cm-long segments and dried in a drying oven at 60 °C for at least 48 h. We apportioned ~0.5 g (mean = 0.46, SE = ± 0.007 g) of dry leaf tissue from each site-species combination into empty synthetic (polypropylene/polyethylene) rectangular tea bags (7 × 9.5 cm) with a nonuniform mesh size of < 1 mm. Seagrass litter bags were deployed in six replicate 1 × 1 m plots within nearshore subtidal seagrass meadows in Seahorse Key (water depth = 1 m). We randomly distributed litter bags across replicate plots so that there were two for each site-species combination placed within each plot: one for the earlier (24-day) and one for the later (63-day) retrieval. Bags were spaced at least 15 cm apart and were buried within the rhizosphere to a depth of 10 cm. During each retrieval, we were unable to recover two bags. Upon return to the laboratory, samples were rinsed and dried in a drying oven at 60 °C for at least 1 week before we measured the dry weight of each litter bag. We calculated percent mass lost of seagrass litter for each sample (Eq. 1) and decay rates, k , for each replicate plot (Eq. 2).

We used a two-way ANOVA to assess the effects of site and seagrass species, as well as their interaction, on k . We performed pairwise comparisons using Tukey's post hoc test and calculated partial effect sizes (η_p^2) for both main and interaction effects. k was arcsine-square root transformed to meet ANOVA assumptions of normality and equal variances between groups.

Additional seagrass leaves were collected from each site to measure total carbon, nitrogen, and phosphorus content ($n = 6$ replicates of ~100 *H. wrightii* leaves and ~50 *T. testudinum* leaves) and specific leaf area ($n = 10$ leaves). Percent carbon and nitrogen of dry leaves were determined using an ECS 8020 Elemental Analyzer (NC Technologies), and percent phosphorus was determined using a Shimadzu UV-2450 spectrophotometer following a modified colorimetric method (Solórzano & Sharp, 1980) at Florida International University's Blue Carbon Analysis Laboratory. We calculated carbon-to-nitrogen (C:N) and nitrogen-to-phosphorus ratios (N:P) based on molar mass. We calculated specific leaf area ($\text{cm}^2 \text{g}^{-1}$) as the leaf surface area (length × width) divided by the dry leaf mass. We compared differences in nutrient content and ratios across sites, species, and their interaction using ANOVA and Tukey's post hoc test. Specific leaf area data violated the assumption of heterogeneity of variances across groups, so we used an aligned rank transform ANOVA (Wobbrock et al., 2011) and post hoc contrast tests using the "ART-C" procedure (Elkin et al., 2021) via the "ARTool" package (Kay et al., 2021).

Results

Tea Decomposition Experiment

Site influenced green tea decomposition: percent mass lost and decay rates for green tea were lowest at the site with the lowest phosphorus concentrations, Weeki Wachee (Tables 1 and 2; Table S2; Fig. 2). Percent mass lost of green tea differed between Weeki Wachee and other sites, except for Waccasassa ($F(3, 44) = 7.12$, p -value < 0.001; Table 2; Table S2). Overall, sites differed by less than 10% across all retrieval times, where the lowest percent mass lost for green tea at Weeki Wachee was $77.1 \pm 6.4\%$ (median $\pm$ interquartile range) and highest at the site in the middle of the phosphorus gradient, Homosassa, at $86.3 \pm 2.4\%$ (Fig. 2). Percent mass lost of red tea was lowest at Waccasassa ($33.1 \pm 12.1\%$) though differences between sites were small (Tables 1 and 2; Fig. 2). Retrieval time was a significant covariate where percent mass lost generally increased with retrieval time for both tea types (green: $\rho = 0.42$, p -value = 0.003; red: $\rho = 0.85$, p -value < 0.001; Fig. S1). The mean percent mass lost for green tea across all sites and retrieval times was $81.9 \pm 1.9\%$ (mean $\pm$ SE here and subsequently throughout), which was twofold greater than the mean percent mass lost for red tea at $38.2 \pm 2.4\%$. Mean decay rates across all sites were an order of magnitude greater for green ($k = 0.010 \pm 0.001$) compared to red tea ($k = 0.0022 \pm 0.0002$; Table 1).

Seagrass Litter Decomposition Experiment

Site, seagrass species, and their interaction influenced seagrass litter decay rates (Table 3; Table S3-S4; Fig. 3). Decay rates were lower for litter from both species collected from Weeki Wachee and Waccasassa compared to litter collected from other sites along the gradient, and there was strong evidence that *T. testudinum* decay rates were lowest at the more phosphorus-limited site, Weeki Wachee, compared to more phosphorus-enriched sites further north (Fig. 3; Table S3-S4). Yet the effect of species was stronger than the effect of site on decay rates (site $\eta_p^2 = 0.75$; species $\eta_p^2 = 0.94$; Table 3). Decay rates differed between *H. wrightii* and *T. testudinum* litters ($F(1, 36) = 590.56$, p -value < 0.001;

Table 1 Decay rates for green tea (k_g) and red tea (k_r) by site

Site	k_g	k_r
SEA	0.014	0.002
WAC	0.013	0.002
HOM	0.015	0.001
WEE	0.011	0.001

Table 2 Quade's ANCOVA results for standardized litter (green and red tea) residual percent mass lost deviation rank scores explained by site. Residual deviation rank scores are the difference between observed deviation rank scores and scores predicted by retrieval time (covariate)

Source of variation	Degrees of freedom	Sum of squares	Mean squares	<i>F</i>	<i>p</i> -value
Green tea					
Site	3	2486.00	828.67	7.12	< 0.001
Residuals	44	5121.00	116.39		
Red tea					
Site	3	534.28	178.09	2.99	0.040
Residuals	49	2917.60	59.54		

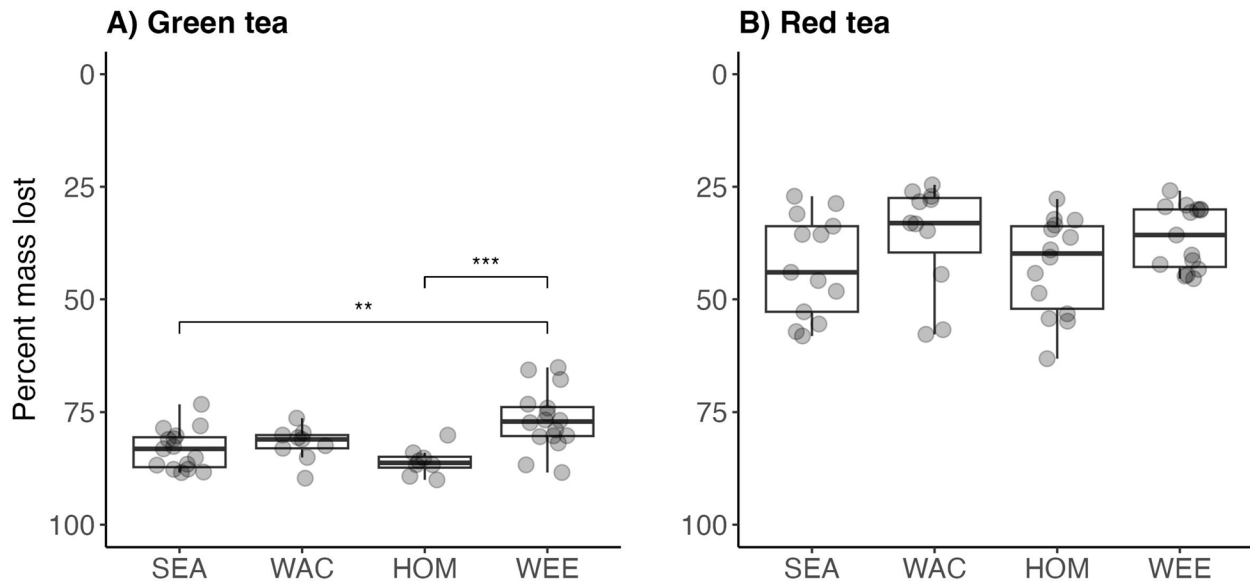


Fig. 2 Percent mass lost of **A** green and **B** red tea across all retrieval times (3, 6, 12, and 24 months) at each site (SEA, Seahorse Key; WAC, Waccasassa; HOM, Homosassa; WEE, Weeki Wachee). The boxes display the median value with the 25th and 75th percentiles, and the whiskers display the 25th percentile $-1.5 \times \text{IQR}$ and the 75th percentile $+1.5 \times \text{IQR}$ (IQR, interquartile range). Stars above

horizontal lines indicate statistically significant differences ($\alpha < 0.05$) between sites based on pairwise comparisons of residual deviation rank scores using Quade's procedure to account for retrieval time as a covariate (* = p -value < 0.05 , ** = p -value < 0.01 , and *** = p -value < 0.001)

Table 3 ANOVA results for seagrass litter percent mass lost and decay rates explained by site, seagrass species, and their interaction. Partial effect sizes for main and interaction effects are reported as η_p^2

Source of variation	Degrees of freedom	Sum of squares	Mean squares	<i>F</i>	<i>p</i> -value	η_p^2
Site	3	4.73E-03	1.58E-03	36.57	< 0.001	0.75
Species	1	2.55E-02	2.55E-02	590.56	< 0.001	0.94
Site*species	3	6.50E-04	2.20E-04	5.02	0.005	0.30
Residuals	36	1.60E-04	4.30E-05			

Table 3), where rates were consistently greater for *T. testudinum* litter (Table S3; Fig. 3): *T. testudinum* mean decay rates (0.02 ± 0.002) were double that of *H. wrightii* (0.01 ± 0.001).

Seagrass leaf morphology and tissue chemistry also differed between sites and species and by their interactive effects (Table 4.; Table S5). *H. wrightii* had a greater specific leaf area than *T. testudinum* at all sites except for

Waccasassa, though the effect size of species was modest ($\eta_p^2 = 0.06$) relative to that of site ($\eta_p^2 = 0.49$; Table 4). Within sites, *H. wrightii* leaves had consistently higher C:N than *T. testudinum* (Table S5). For both species, C:N varied slightly but not systematically across sites along the phosphorus gradient and were lowest at Seahorse Key. Leaf total phosphorus decreased from north to south along the phosphorus gradient for both species, mirroring long-term water

Fig. 3 Decay rates by site (SEA, Seahorse Key; WAC, Waccasassa; HOM, Homosassa; WEE, Weeki Wachee) and seagrass species shown by color (light green, *H. wrightii*; dark green, *T. testudinum*). Error bars represent SE and letters denote statistically significant ($\alpha < 0.05$) site and species differences

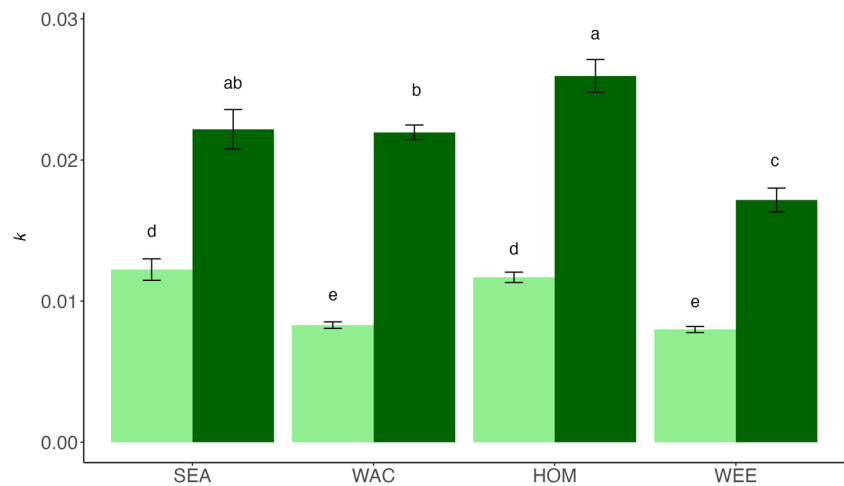


Table 4 Mean values ($\pm$ SE) for seagrass litter specific leaf area and percent carbon, nitrogen, and phosphorus for each site (SEA, Seahorse Key; WAC, Waccasassa; HOM, Homosassa; WEE, Weeki Wachee) and seagrass species

Site	Species	SLA (cm ² g ⁻¹)	TC (% dry weight)	TN (% dry weight)	TP (% dry weight)	C:N	N:P
SEA	<i>H. wrightii</i>	345.6 ($\pm$ 45.8)	39.45 ($\pm$ 0.03)	2.42 ($\pm$ 0.04)	0.16 ($\pm$ 0.009)	19.03 ($\pm$ 0.31)	33.00 ($\pm$ 2.03)
	<i>T. testudinum</i>	292.5 ($\pm$ 8.2)	38.60 ($\pm$ 0.44)	2.50 ($\pm$ 0.03)	0.18 ($\pm$ 0.009)	18.00 ($\pm$ 0.21)	30.85 ($\pm$ 1.92)
WAC	<i>H. wrightii</i>	185.7 ($\pm$ 6.0)	39.32 ($\pm$ 0.20)	1.72 ($\pm$ 0.09)	0.14 ($\pm$ 0.004)	26.84 ($\pm$ 1.23)	26.63 ($\pm$ 0.74)
	<i>T. testudinum</i>	275.9 ($\pm$ 8.3)	37.22 ($\pm$ 0.18)	1.78 ($\pm$ 0.03)	0.14 ($\pm$ 0.002)	24.39 ($\pm$ 0.48)	27.37 ($\pm$ 0.29)
HOM	<i>H. wrightii</i>	356.1 ($\pm$ 25.3)	40.72 ($\pm$ 0.12)	1.97 ($\pm$ 0.02)	0.08 ($\pm$ 0.003)	24.16 ($\pm$ 0.27)	54.66 ($\pm$ 1.99)
	<i>T. testudinum</i>	338.1 ($\pm$ 18.2)	38.70 ($\pm$ 0.09)	2.14 ($\pm$ 0.03)	0.11 ($\pm$ 0.006)	21.10 ($\pm$ 0.28)	44.49 ($\pm$ 2.21)
WEE	<i>H. wrightii</i>	400.8 ($\pm$ 16.6)	40.35 ($\pm$ 0.28)	1.72 ($\pm$ 0.01)	0.08 ($\pm$ 0.002)	27.43 ($\pm$ 0.34)	49.05 ($\pm$ 1.37)
	<i>T. testudinum</i>	255.4 ($\pm$ 10.9)	38.66 ($\pm$ 0.21)	2.05 ($\pm$ 0.03)	0.05 ($\pm$ 0.001)	22.01 ($\pm$ 0.31)	86.07 ($\pm$ 2.53)

column total phosphorus concentrations (Table S1), and N:P values were lowest and highest at the northern and southern sites along the gradient, respectively (Table 4).

Discussion

Our findings indicate that species identity can have stronger effects on decomposition than environmental conditions. In our study, phosphorus availability appeared to limit the decomposition of labile standardized litter deployed at the low phosphorus site as well as the decomposition of *T. testudinum* leaves collected from the low phosphorus site; however, species identity had the largest effect on seagrass decay rates. *T. testudinum* litter decayed faster than *H. wrightii* litter, counter to our expectation that the larger-bodied seagrass would produce relatively recalcitrant leaf litter compared to the smaller-bodied seagrass. The finding that *T. testudinum* decays quickly was also unexpected because meadows dominated by *T. testudinum* often contain high densities of sediment organic carbon. We found further evidence of decoupling between decomposition and carbon storage: the low phosphorus site with the lowest green tea and *T.*

testudinum leaf litter decay rates also contained the lowest sediment carbon densities along the phosphorus gradient, according to a previous study (Barry et al., 2018). We would have expected sites with lower decomposition rates to store more carbon; however, carbon accumulation and burial in seagrass meadows are complex processes dependent upon several factors beyond decomposition dynamics.

Our findings indicate environmental variability, including nutrient availability, can affect decomposition in seagrass meadows in two ways: by modulating site conditions that affect decomposition regardless of litter provenance and by influencing seagrass leaf chemistry and ultimately litter quality. In our study, environmental conditions directly influenced decomposition, where we observed differences in the decomposition of standardized litter deployed across the phosphorous gradient. While decomposition did not clearly differ across sites for the more recalcitrant litter type (red tea), the decay rate of the more labile litter type (green tea) was lowest at Weeki Wachee ($k = 0.011 \text{ d}^{-1}$; Table 1), the site with the lowest water column phosphorus concentrations, although percent mass lost of green tea was similar between Weeki Wachee and Waccasassa (Table S2; Fig. 2). In a large-scale study conducted across the range of *T.*

testudinum, nitrogen availability (as indicated by seagrass leaf N:P) positively affected green but not red tea decay rates over a 4-month incubation period (Fourqurean et al., 2023). Red tea decomposition may be less impacted by nutrient availability due to the differences in tea composition: green tea contains more water-soluble compounds while red tea contains more lignin compounds (Keuskamp et al., 2013). Green tea buried in seagrass sediments may undergo substantial leaching early on in decomposition, followed by a process that can be influenced by nutrient availability—the microbial breakdown of relatively labile compounds, such as hemicellulose and cellulose (Duddigan et al., 2020; Trevathan-Tackett et al., 2021). Degradation of relatively recalcitrant compounds in red tea, however, may be more limited by oxygen conditions, temperature, or other sediment properties (Marley et al., 2019; Trevathan-Tackett et al., 2021).

It is unclear whether low water column phosphorus concentrations directly limited decomposition of labile litter in seagrass meadows in our study, as has been observed for other systems. For example, increases in water column nutrient concentrations often lead to faster decomposition rates in streams (Ferreira et al., 2015; Kominoski et al., 2015; Manning et al., 2015), and in coastal marshes, water column phosphorus availability can affect decomposition by driving microbial biomass and activity (Rejmánková & Houdková, 2006). Litter buried beneath the sediment surface decayed less at the low phosphorus site in our study, indicating that sediment porewater phosphorus concentrations may have been limiting for the seagrass sediment microbial community. Nutrient availability in seagrass sediment porewater in part relies on remineralization (Hemminga & Duarte, 2000), so if decomposition is limited, nutrient regeneration within the sediments is also limited. An earlier study in Florida Bay did not find any influence of water column nutrient availability on decomposition within seagrass sediments, where water column N:P values were comparable to values measured from our study sites (Fourqurean & Schrlau, 2003). Florida Bay contains more carbonates compared to the sites in our study, and carbonate-rich sediments, especially those with fine grain size, can bind phosphorus through adsorption and precipitation, further limiting its availability within the porewater (Gaudette & Lyons, 1980; Kitano et al., 1978). The relative importance of water column nutrient availability in driving decomposition may therefore depend on other environmental conditions, including sediment properties.

Water column phosphorus availability clearly varied among our study sites, though we did not control for sediment properties that may have affected decomposition of the standardized litter. The sites are influenced by freshwater sources to varying degrees: Seahorse Key is influenced by the Suwanee River, a blackwater river with a mean discharge of $272.4 \text{ m}^3 \text{ s}^{-1}$, while the other sites are influenced by smaller, spring-fed rivers, with mean discharges ≤ 10.0

$\text{m}^3 \text{ s}^{-1}$ (USGS, 2022). River discharge and meadow proximity to rivers influence the delivery of sediment and land-based organic matter (Ewers Lewis et al., 2018), which may in turn interact with localized hydrodynamics to influence sediment properties, such as sediment bulk density. Sediments in Seahorse Key and the most phosphorus-limited site, Weeki Wachee, were higher in density ($\sim 1.0\text{--}1.5 \text{ g cm}^{-3}$) while sediments in the other sites along the phosphorus gradient were lower in density ($< 1.0 \text{ g cm}^{-3}$) (Barry et al., 2018; Bijak et al., 2023). Sediment bulk density is tightly linked with grain size and porosity, and all affect sediment permeability and oxygen levels (Wilson et al., 2008), which strongly control decomposition. Past studies have also found wide variation in percent sediment organic carbon across sites: 1.0% in Weeki Wachee, 8.7% in Homosassa, 2.8% in Waccasassa, and 0.6% in Seahorse Key (Barry et al., 2018; Bijak et al., 2023). Porewater nutrient concentrations and sediment texture would provide more information on nutrient availability within sediments, but characterizing sediments was beyond the scope of our study. We suspect both site differences in sediment properties and water column phosphorus availability affected decomposition of the standardized litter.

Environmental variability, including nutrient availability, also affected decomposition indirectly through the conditions under which seagrass leaves grew and their effect on litter quality. While decay rates were consistently higher for *T. testudinum* compared to *H. wrightii* litter, the decay rates for each species differed across collection sites. Notably, the decay rates were lowest for *T. testudinum* litter collected from Weeki Wachee, the site with the lowest leaf total phosphorus concentrations, while decay rates were lowest for *H. wrightii* litter collected from both Weeki Wachee and Waccasassa (Table 3; Table S3; Fig. 3). Previous work along the phosphorus gradient suggested that phosphorus availability in the region does not meet seagrass nutrient demands based on leaf elemental composition (Barry et al., 2017), given that N:P values > 30 can indicate phosphorus limitation in seagrass (Atkinson & Smith, 1983; Fourqurean & Zieman, 2002; Fourqurean et al., 2005). Seagrass leaves in Weeki Wachee exhibited high N:P for *H. wrightii* (49.05 ± 1.37) and *T. testudinum* (86.07 ± 2.53 ; Table 4), and we therefore infer that seagrass at this site is especially phosphorus-limited, which may inhibit its decomposition relative to seagrass collected from less phosphorus-limited sites (Enríquez et al., 1993). Further, low phosphorus availability may also impact seagrass litter quality through the production of anti-herbivore defenses. In a prior study, seagrass in Weeki Wachee had higher leaf fiber content, lower specific leaf area, and higher condensed tannins than more northern sites along the phosphorus gradient (Roth et al., 2024)—all of which are characteristics that render litter more recalcitrant (Klap et al., 2000; Liu et al., 2018; Zak et al., 2019).

Whether water column phosphorus availability more so than porewater phosphorus availability caused the differences in seagrass leaf nutrient content found here and in secondary metabolites found in other studies is unclear because seagrasses can absorb nutrients directly from the water column through their leaves (Gras et al., 2003; Lee & Dunton, 1999; Short, 1987; Touchette & Burkholder, 2000) and the relative uptake rates through leaves vs. roots can vary (Lee & Dunton, 1999; Lee et al., 2007). Total phosphorus in the water column appears to be a good indicator of nutrient availability for seagrasses in the study area, given leaf nutrient concentrations change with total phosphorus concentrations in our study (Table 4.; Table S1) and above-to-belowground biomass ratio increases with phosphorus concentrations from Weeki Wachee to Waccasassa (Barry et al., 2017). Our findings that *T. testudinum* litter grown under the low-phosphorus conditions had the lowest phosphorus content and decayed the least over shorter burial periods (~ 1–2 months) and a labile standardized litter decayed slowest at the low-phosphorus site over longer burial periods (up to 2 years; Table 1) provide evidence that environmental variation in site conditions, including but not limited to water column phosphorus availability, can affect both seagrass litter quality and the process of decomposition.

Unexpectedly, the larger species, *T. testudinum*, produced leaf litter that decayed faster—and we therefore infer is more labile—than leaf litter from the smaller species, *H. wrightii*. *T. testudinum* is a large-bodied, slow-growing climax species, while *H. wrightii* is a fast-growing pioneering species (Kilminster et al., 2015). Leaf chemistry, including lignin content, is generally responsible for observed species differences in litter degradation in seagrass meadows and other systems. Lignin strengthens plant cell walls and is typically more resistant to microbial degradation than other types of plant compounds (Derenne & Largeau, 2001). For this reason, larger seagrasses, especially those belonging to the *Posidonia* or *Thalassodendron* genera, can have high lignin content, similar to that of marsh plants (Trevathan-Tackett et al., 2015). However, past research has found only small differences in leaf lignin content between *T. testudinum* (e.g., 4.6% in Bjorndal, 1980) and *H. wrightii* (e.g., ~ 3% in Opsahl & Benner, 1993), and there is substantial overlap in leaf lignin content between their respective families, Hydrocharitaceae and Cymodoceaceae (Pfeifer & Clasen, 2020).

Species differences in other plant characteristics, such as leaf nutrient content or morphology, may instead be driving the faster decay of *T. testudinum* leaf litter. Litter elemental composition is a strong driver of decomposition because it largely determines whether microbial nutrient demands are met (Enríquez et al., 1993), and specific leaf area, independent of leaf chemistry, can promote decomposition simply by exposing the leaf surface to microbial activity (Liu et al.,

2018). In our study, specific leaf area did not systematically vary by species, though *H. wrightii* specific leaf area was more variable than *T. testudinum* specific leaf area across the phosphorus gradient sites (Table 4). More generally, *T. testudinum* leaves, due to their larger total leaf area and lifespan (Duarte, 1991), provide a better substrate for fungi than the smaller, shorter-lived leaves of *H. wrightii* (Mata & Cebrián, 2013), which may in part explain the faster decomposition of *T. testudinum* leaves. Leaf C:N was consistently higher in *H. wrightii*, suggesting *H. wrightii* litter is lower in quality and therefore decomposes more slowly (Table 4). While absolute C:N values varied across sites, the consistent differences we observed between *H. wrightii* and *T. testudinum* seem to be linked to intrinsic species differences in plant structure.

Implications for Seagrass Carbon Cycling

Species identity can be a strong determinant of litter decay within seagrass meadow sediments, while nutrient availability can limit the extent of decomposition across species. Interestingly, the most phosphorus-limited site where in situ decomposition rates were slowest contained the lowest surface sediment carbon stocks, according to previous work conducted along the phosphorus gradient (Barry et al., 2018). This apparent decoupling between decomposition rates and carbon storage has also been observed across the range of *T. testudinum* (Fourqurean et al., 2023); however, faster decomposition rates do not necessarily preclude carbon storage. For example, lignin in *T. testudinum* tissue can undergo extensive degradation within sediments, where it can still contribute up to ~ 50% of sedimentary carbon (Barry et al., 2018). Decomposition rate is only one among several factors, including hydrodynamics setting, sediment properties, and seagrass canopy particle trapping, that influence carbon stocks.

Our finding that *T. testudinum* leaves decayed quickly was at first counterintuitive, since *T. testudinum* meadows—and meadows dominated by large-bodied seagrasses more generally—typically store more carbon than meadows dominated by other species (Bijak et al., 2023; Kennedy et al., 2022; Piñeiro-Juncal et al., 2022). Yet we only included leaf tissue as seagrass litter and examined its decomposition over relatively short time scales (after 1–2 months of burial) that encompassed the earlier stages of decomposition (Blum & Mills, 1991). It is unclear if we would observe similar patterns over longer time scales because seagrass decomposition often follows a two-part decay model, where more labile material degrades quickly while more recalcitrant material degrades slowly (Fourqurean & Schlau, 2003; Suonan et al., 2024; Trevathan-Tackett et al., 2017a, 2017b). Non-photosynthetic tissues can also contribute to sediment carbon through the decay and burial of sheaths, rhizomes, and roots, which tend to be more refractory than leaf tissue (Trevathan-Tackett et al., 2017a, 2017b). However, the

contribution of seagrass tissue to meadow carbon storage in sediments varies widely and can be relatively small (Kennedy et al., 2010). Our findings suggest that *T. testudinum* meadows may achieve high levels of sediment carbon storage by producing and storing larger quantities of above- and belowground litter, despite relatively fast decay rates of leaf tissue, and/or by more effectively trapping external carbon sources. Future work should address species effects on both belowground tissue decomposition and sediment organic matter accumulation to clarify why *T. testudinum* is often associated with greater carbon storage despite its faster leaf decay rates.

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Author Contribution All authors contributed to the design of this study. C.W.M., L.K.R., and S.C.B. coordinated the collection of tea litter decomposition data, while A.L.B., C.A.S., and L.K.R. coordinated the collection of seagrass litter decomposition data. The first draft of the manuscript was written by A.L.B., and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability Data from this study are available in the Zenodo repository: <https://doi.org/10.5281/zenodo.15545202>.

Declarations

Ethics Approval and Consent to Participate Not applicable.

Consent for Publication Not applicable.

Competing interests The authors declare no competing interests.

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