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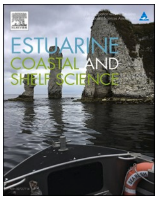

# Root decomposition in coastal wetlands of Southeast Queensland, Australia

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ABSTRACT

Root decomposition is a key coastal wetland ecological process. Despite this, there are limited empirical studies on root decomposition. In this study, we investigated the effect of species, root size and burial habitat on root decomposition of supratidal tree species (*Casuarina glauca*, *Melaleuca quinquenervia*), and intertidal mangrove (*Avicennia marina*) and saltmarsh species (*Sarcocornia quinqueflora*, *Sporobolus virginicus*) in Southeast Queensland, Australia. Decomposition curves for all tested factors indicated a plateau in remaining root mass by the end of the experiment; the plateau was therefore inferred to indicate the “expected liable fraction”. Root decomposition rates and fractions of expected labile root biomass of supratidal and intertidal species were not significantly different. The percentage mass remaining of fine roots ($<2$ mm) of woody species varied by species, but that of coarse roots (2–20 mm) did not vary among species. Decomposition rates and expected labile fractions of roots of intertidal species were not significantly different between burial in the same habitat (“at home”) versus in habitats dominated by other species (“away”). Overall, we found lowest variation in percentage mass remaining, followed by expected labile fractions and root decomposition rates across species and habitats after 14 months. The mean root decomposition rate using two-pool asymptotic models was $0.0169 \pm 0.0019$ day$^{-1}$; the mean expected labile fraction was $28.3 \pm 1.0$ %. These experimental root decomposition results across the intertidal to supratidal zone provide insights to the drivers of decomposition rates in coastal wetlands that can be used in ecological models.

## 1. Introduction

Vegetated coastal wetlands, such as intertidal mangroves and saltmarshes, and tidally influenced supratidal freshwater forests comprised of *Casuarina* and *Melaleuca* forests (hereafter “supratidal forests”) deliver critical ecosystem services (Adame et al., 2024a; Barbier et al., 2011). Importantly, coastal wetlands can sequester up to three times more carbon than terrestrial forests per hectare (Taillardat et al., 2018) and maintain surface elevation with respect to sea levels (Krauss et al., 2014; Lovelock et al., 2015; Saintilan et al., 2020). Carbon accumulation within coastal wetlands occurs in three pools – the aboveground biomass, belowground biomass, and soil organic carbon (Duarte et al., 2005). The interactions between these three pools and with variation in environmental conditions are mediated by biogeochemical processes (Lovelock and Reef, 2020). In particular, decomposition of organic matter is suppressed by the saline, waterlogged, and anoxic soil conditions unique to coastal wetlands (Chapman et al., 2019). The burial of dead roots could be the main source of organic matter input into the soil organic carbon pool (Kristensen et al., 2008), likely contributing up to $23 \pm 5$ Tg C yr$^{-1}$ in mangrove soils, or about 90 % of total carbon burial in mangroves (Arnaud et al., 2023). With limited organic matter decomposition, organic matter accumulates and can contribute to soil volume (Cahoon et al., 2006; McKee et al., 2007). This upward transition of the land surface can maintain the position of coastal wetlands within the tidal frame – an important response to rising sea levels (Rogers et al., 2019). Finally, the decomposition process cycles nutrients, particularly nitrogen and phosphorous, back into the environment to support productivity (Middleton and McKee, 2001; Reddy et al., 2022).

Knowledge of wetland root decomposition rates and belowground dynamics is limited to few species from select geographies (Adame et al., 2017; Adame et al., 2024b; Arnaud et al., 2023; Ouyang et al., 2017). Substantial variability in root decomposition rates among wetland species have been documented (Huxham et al., 2010; Perry and Mendelssohn, 2009). In intertidal mangrove and saltmarsh roots, higher C:N ratios of mangrove roots compared to saltmarsh roots results in more

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rapid decomposition of mangrove roots than those of saltmarshes (Simpson et al., 2021). Although there are no studies on the decomposition rates of supratidal tree roots, roots of woody supratidal tree species lack air-filled tissues (aerenchyma), and the high proportion of woody tissue in supratidal roots of 2–20 mm diameter (pers. obs.) indicates that they contain high lignin content, which reduces decomposition rates (Morris et al., 2016).

Root size classes may further moderate variation in root decomposition rates among species. Roots of different size classes can have different tissue compositions and physiochemical properties (Arnaud et al., 2024). For mangrove roots, coarser roots have been found to breakdown more rapidly than finer roots (Belize, *Rhizophora mangle*, fine: ≤2.5 mm, coarse: >2.5 mm (McKee et al., 2007); Australia, *Avicennia marina*, fibrous roots: assumed to be < 2 mm, main roots: 10–20 mm (Van der Valk and Attiwill, 1984)). This has been hypothesised to be due to high levels of aerenchyma within coarser roots that may increase the surface area of organic matter for microbial processing (Lovelock et al., 2017), and may lead to higher rates of decomposition in coarse compared to fine root fractions in mangrove species. Conversely, given increasing proportions of woody tissue in coarser roots of supratidal forest species, opposing patterns may be expected.

Apart from the influence of species and corresponding root sizes, the effect of habitat is also an important control on decomposition (Trevathan-Tackett et al., 2021). Some empirical evidence exists for different rates of root decomposition across the intertidal zone (e.g. Hayes et al., 2017b for mangrove roots, but see Middleton and McKee (2001)). Proxies for root decomposition studies, such as the use of leaf litter and tea bag index decomposition studies, are more common than those of root decomposition and reveal up to two-fold difference in decomposition rates among habitats observed (Friesen et al., 2018; Middleton and McKee, 2001; Trevathan-Tackett et al., 2024). This may be attributed to variation in environmental conditions like soil water content and nutrient availability, and to the presence of different soil microbial communities that mediate decomposition (Allison et al., 2013). For example, the structure of microbial communities in mangrove soils are strongly associated with soil salinity (Hu et al., 2023). With large differences in salinity regimes between mangroves and saltmarshes (e.g. high salinity in some high intertidal saltmarshes due to limited tidal inundation and high evaporation compared to lower intertidal mangroves; Lovelock et al. (2019)), variation in microbial communities across the intertidal zone may be pronounced (Barreto et al., 2018; Chuvochina et al., 2021).

The combination of species root traits and habitats gives rise to the home-field advantage hypothesis, which postulates that soil microbes responsible for decomposition in a particular habitat are specialised to break down litter originated from the same "home" habitat, compared to litter translocated from "away" habitats (Ayres et al., 2009; Pugnaire et al., 2023). The boundaries of coastal wetland vegetation types are projected to shift in response to global change variables (Campbell et al., 2022; Friess et al., 2022), altering the areal extent and species dominance of the ecotone over time. Increasing temperatures can lead to latitudinal range expansion of mangroves which have limited cold tolerance (Cavanaugh et al., 2014; Duke, 1990; Osland et al., 2017), while sea-level rise can lead to the landward migration of coastal wetlands, where mangroves may be able to outpace and eventually replace saltmarshes at the ecotone (Saintilan et al., 2019). The potential interaction of species root litter quality and habitats on root decomposition has not yet been widely assessed in coastal wetlands (Simpson et al., 2021), although there is still no consensus from the few existing studies. For example, it has been shown in mesocosms that soil respiration rates were significantly higher in marshes than mangroves (Geoghegan et al., 2021). Conversely, leaf litter studies in mangroves have also found that hydrological conditions exert a larger effect on decomposition rates than microbial communities (Dhaou et al., 2022). The ongoing encroachment of mangroves into saltmarshes and resultant shifts in vegetation dominance in the saltmarsh-mangrove ecotones may have substantial influence on carbon sequestration, surface elevation changes, and nutrient cycling.

Here, we conducted two decomposition experiments exploring controls on decomposition in intertidal mangrove, and saltmarsh, and tidally influenced supratidal freshwater forest habitats. Specifically, we investigated variation in the decomposition of root litter over variation in 1) plant species, 2) root size (for woody species only), and 3) habitat, where we used roots deployed at home and away habitats for mangroves and saltmarshes. We assessed the following hypotheses:

1. Roots from supratidal tree species decompose slower and are more recalcitrant than roots from intertidal species.
2. Fine roots of supratidal tree species decompose faster and are less recalcitrant than coarser roots. The converse is anticipated for mangrove species, where fine roots decompose slower and are more recalcitrant than coarser roots.
3. Decomposition rates of mangrove and saltmarsh roots are faster in "home" habitats compared to "away" habitats, reflecting adaptations of the soil microbial community to root litter of species which grow in the habitat.

## 2. Methods

### 2.1. Preparation of decomposition bags

Moreton Bay, Southeast Queensland (−27.367, 153.277) is situated in the subtropical region of Australia. Decomposition experiments were performed on roots of supratidal forest species and intertidal mangrove and saltmarsh species collected from natural remnant wetlands (Supplementary Table 1). Roots of supratidal species (*Casuarina glauca* and *Melaleuca quinquenervia*) were oven dried at 60 °C for two days. Intertidal mangrove and saltmarsh species (*Avicennia marina*, *Sarcocornia quinqueflora*, and *Sporobolus virginicus)* were air dried for one week. A subset of air-dried roots from each intertidal species were further dried in the oven at 60 °C for two days to estimate a conversion ratio from air-dried to oven-dried dry weight so that weights of all samples could be standardised. Although oven drying likely results in more uniform root moisture content with increased efficiency, the higher temperature can produce a lignin-like substance and consequently reduce decomposition rates (Moorhead et al., 1988); air drying at ambient temperature was therefore the alternative method for obtaining a standardised weight.

For all three experimental objectives, dried roots were packed in decomposition bags made of 1.5 mm flexible nylon mesh and measuring 10 by 10 cm (Middleton and McKee, 2001). The mesh size excluded macrodetritivores such as crabs. Root decomposition bags of supratidal species contained either fine (<2 mm), small (2–5 mm) or coarse (5–20 mm) roots. Root decomposition bags of *A. marina* contained either fine roots (<2 mm) or small and coarse roots (2–20 mm). Lastly, root decomposition bags of saltmarsh species contained roots and rhizomes because it was difficult to collect sufficient saltmarsh root biomass (hereafter collectively "roots", <2 mm). It is noted that this categorisation includes roots with different functions (Pregitzer et al., 2002). Each bag contained a known weight (~2 g) of root material. Weights were measured with an analytical balance (Mettler Toledo ML204T/00) with a precision of 0.0001 g but were recorded to the nearest 0.01 g.

### 2.2. Experimental design and deployment of decomposition bags

To account for the potential effect of soil depth on soil redox potential (Middleton and McKee, 2001) and thus oxygen availability and decomposition (Lovelock et al., 2017), bags were buried at two depths; at 30 cm and just below the soil surface (represented as 0 cm in Results).

To assess root decomposition among species, root samples of all species were deployed in their own habitat types. Roots of supratidal *C. glauca* were deployed in Deception Bay Conservation Park (−27.175, 153.025) and Boondall Wetlands (−27.338, 153.081); roots of supratidal *M. quinquenervia* were deployed in Boondall Wetlands (−27.340, 153.077) and McCoy's Creek (−27.835, 153.358) (Fig. 1A). Roots of intertidal species were deployed in Tinchi Tamba Wetlands Reserve (Fig. 1A). Each replicate consisted of sub-replicates, for four incubation periods of ~50 days, 100 days, 6 months, and either 14 months for roots of supratidal species or 12 months for roots of intertidal species. To assess the effect of root size on root decomposition of woody species, 640 decomposition bags were deployed in their respective habitats to investigate the effects of species and root size (*C. glauca*: 3 size classes * 8 replicates * 2 depths * 4 incubation periods; *M. quinquenervia*: 3 size classes * 12 replicates * 2 depths * 4 incubation periods; *A. marina*: 2 size classes * 5 replicates * 2 depths * 4 incubation periods; *S. quinqueflora*: 1 size class * 5 replicates * 2 depths * 4 incubation periods; *S. virginicus*: 1 size class * 5 replicates * 2 depths * 4 incubation periods). To standardise root size classes of all woody species samples, small and coarse root size classes of supratidal species were combined as coarse roots for data analysis.

Thirdly, to assess the effect of habitat on root decomposition, we conducted a reciprocal transplant experiment at Tinchi Tamba Wetlands (Fig. 1B), where *A. marina*, *S. quinqueflora*, and *S. virginicus* roots were buried in at "home" and one or two "away" habitats (Ayres et al., 2009; Pugnaire et al., 2023). For example, within a mangrove-dominated habitat, mangrove material would be considered "at home", while introduced saltmarsh material would be "away". 240 additional decomposition bags were deployed in "away" habitats (*A. marina*: 2 away habitats * 2 size classes * 5 replicates * 2 depths * 4 incubation periods; *S. quinqueflora* and *S. virginicus*: 1 away habitat * 2 species * 5 replicates * 2 depths * 4 incubation periods).

We measured 10 replicates of oxidation reduction potential (ORP) at 0 cm and 30 cm at all sites using a handheld soil ORP probe. As ORP did not vary with vegetation and depth, it was not included in subsequent analyses (Supplementary Table 2).

### 2.3. Retrieval of decomposition bags

A total of 30 decomposition bags containing roots of intertidal species were lost by the end of the experiment (Supplementary Table 3). Upon retrieval at the end of each incubation period, new roots that grew into the litter bags (lighter colour and more turgid than decomposing roots) were removed. The remaining root material was washed over a 500 nm sieve, then oven dried at 60 °C for two days and weighed. To further account for unwanted root growth into the decomposition bags, 19 bags (6 *C. glauca*, 2 *M. quinquenervia*, 9 *A. marina*, 1 *S. quinqueflora*, 1 *S. virginicus*) that gained weight from the initial deployment were excluded from analysis.

### 2.4. Data analysis

Decomposition curves were modelled using the asymptotic function:

$$\frac{y_t}{y_0} = a\exp(-kt) + 1 - a \tag{1}$$

and exponential function:

$$\frac{y_t}{y_0} = \exp(-kt) \tag{2}$$

where $y_t$ is the remaining dry weight of roots at time $t$, $y_0$ is the initial dry

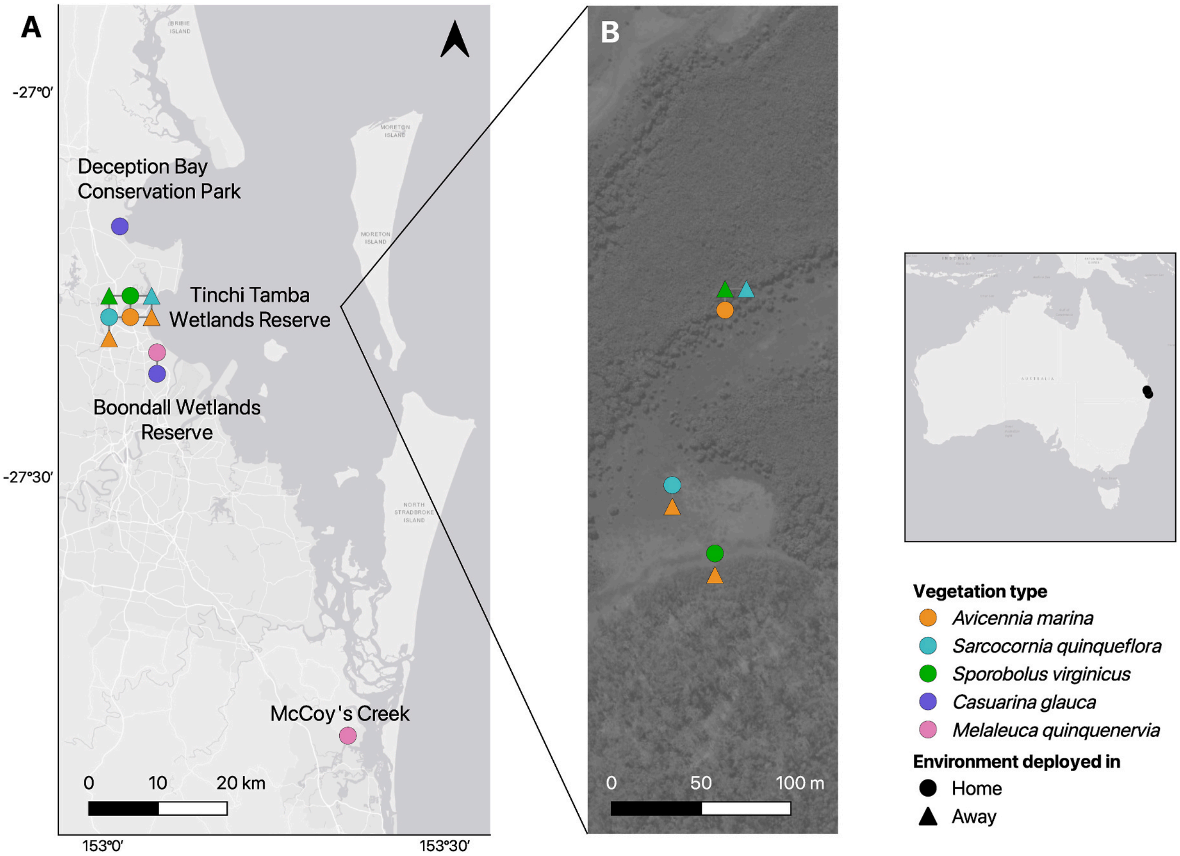

**Fig. 1.** (A) Roots of supratidal (*Casuarina glauca* and *Melaleuca quinquenervia*) and intertidal species (mangrove: *Avicennia marina*, saltmarshes: *Sarcocornia quinqueflora* and *Sporobolus virginicus*) were buried in their respective habitats to investigate the effects of species and woody root size. (B) Reciprocal transplant experimental design for mangrove and saltmarsh roots to investigate the effect of habitat. Inset map shows the study area on the eastern coast of Australia. Base maps obtained from Esri and Queensland Globe.

weight of roots, $k$ is the decomposition rate, and $a$ is the expected labile fraction (Keuskamp et al., 2013; Simpson et al., 2023). The asymptotic model partitions early and long-term decay rates, while the exponential model assumes a constant decay rate (Trevathan-Tackett et al., 2024). The models were fitted separately for each combination of 1) plant species and root size, and 2) for intertidal species, home/away burial habitat. All statistical analyses were performed in R version 4.1.1 ((R Core Team, 2024). The asymptotic and exponential decay models were fitted using *stat::nls()*. Values were reported as mean ± 1 standard error (SE). Comparisons of asymptotic against exponential decay model fits were performed using *stats::anova()*. To compare decomposition rates ($k$) and expected labile fractions ($a$), Welch's t-tests were performed using *stats::t.test()* after checking for data normality with Shapiro-Wilk tests using *stats::shapiro.test()*.

To analyse the effect of species and root size (woody species only) on the shape of root decomposition curves, percentage remaining root mass ($\frac{y_t}{y_0}$) was modelled as a linear mixed-effects model, with species, root size and incubation period as categorical fixed effects, while depth nested within site were assigned as random slopes to account for non-independent measurements in space. To analyse the effect of habitat on the shape of intertidal root decomposition, percentage remaining root mass ($\frac{y_t}{y_0}$) was also modelled as a linear mixed-effects model, with species-root size (coded as a combination, since species and root size are not independent when saltmarsh only has one root size class), home/away burial habitat and incubation period as categorical fixed effects, while depth was assigned as random slopes. Models were fitted using *lme4::lmer()* (Bates et al., 2015). Singularity in linear mixed-effects models was checked using *lme4::isSingular()*. Model assumptions of normality and homoscedasticity of residuals were checked using diagnostic plots generated from *sjPlot::plot_model()* (Supplementary Fig. 1–2). Model comparison between linear mixed-effects models and linear regression without random effects using *stats::anova()* indicated that the inclusion of random effects reduced residuals. Pairwise comparisons were performed using *emmeans::emmeans()* (Lenth, 2024) and *multcomp::cld()*. Values were reported as marginal means ± 1 standard error (SE) unless stated otherwise.

## 3. Results

### **Hypotheses 1 and 2.** Comparison of root decomposition among species and root sizes

Our assessment found that asymptotic decomposition curves fit the data better than exponential decomposition curves (Fig. 2; Table 1).

**Table 1**

Model coefficients and model fit comparisons of asymptotic and exponential root decomposition curves for coastal wetland species and two different root size classes for woody species. Values are shown as mean ± 1 standard deviation (SD).

| | $k_{\text{asymptotic}}$ | $a$ | $k_{\text{exponential}}$ | Model fit | Replicates |
|---|---|---|---|---|---|
| *Casuarina glauca*, coarse | 0.0126 ± 0.0029 | 0.1708 ± 0.0136 | 0.0006 ± 0.0000 | $F_{(1,\ 121)} = 44.5$, $p < 0.001$ | 123 |
| *Casuarina glauca*, fine | 0.0156 ± 0.0041 | 0.2675 ± 0.0222 | 0.0011 ± 0.0001 | $F_{(1,\ 60)} = 35.0$, $p < 0.001$ | 62 |
| *Melaleuca quinquenervia*, coarse | 0.0106 ± 0.0015 | 0.2536 ± 0.0134 | 0.0009 ± 0.0000 | $F_{(1,\ 177)} = 108.9$, $p < 0.001$ | 179 |
| *Melaleuca quinquenervia*, fine | 0.0202 ± 0.0058 | 0.4095 ± 0.0337 | 0.0022 ± 0.0002 | $F_{(1,\ 87)} = 45.1$, $p < 0.001$ | 89 |
| *Avicennia marina*, coarse | 0.0201 ± 0.0066 | 0.2629 ± 0.0237 | 0.0013 ± 0.0002 | $F_{(1,\ 34)} = 46.0$, $p < 0.001$ | 36 |
| *Avicennia marina*, fine | 0.0110 ± 0.0027 | 0.3978 ± 0.0372 | 0.0019 ± 0.0002 | $F_{(1,\ 34)} = 26.7$, $p < 0.001$ | 36 |
| *Sarcocornia quinqueflora* | 0.0450 ± 0.0207 | 0.3664 ± 0.0249 | 0.0023 ± 0.0003 | $F_{(1,\ 36)} = 88.3$, $p < 0.001$ | 38 |
| *Sporobolus virginicus* | 0.0212 ± 0.0037 | 0.4468 ± 0.0204 | 0.0025 ± 0.0003 | $F_{(1,\ 37)} = 120.0$, $p < 0.001$ | 39 |

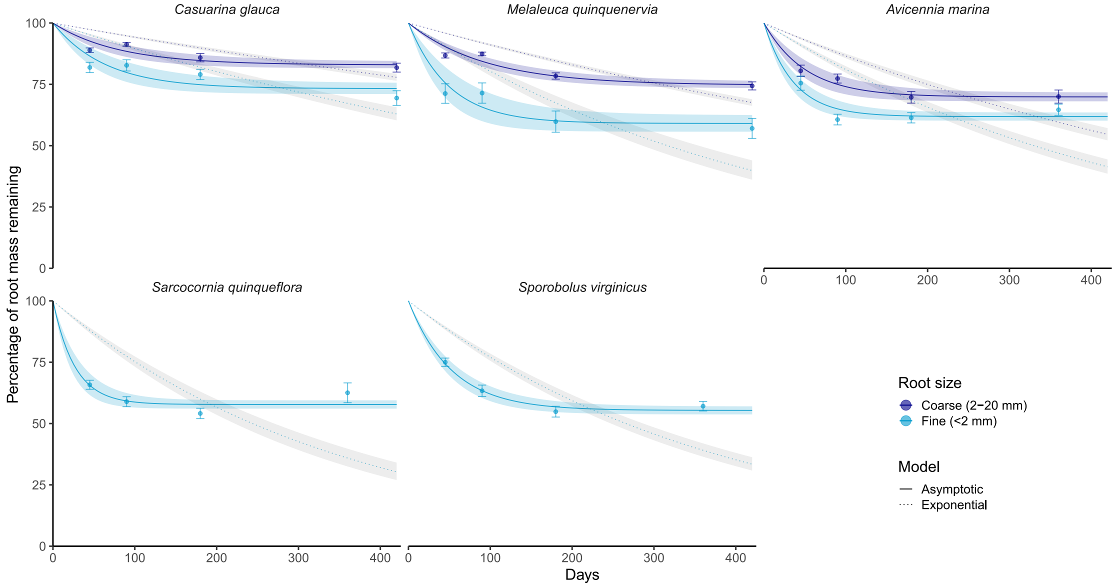

**Fig. 2.** Decomposition curves fitted for coastal wetland species and two woody root size classes, as asymptotic $\frac{y_t}{y_0} = a\exp(-kt) + 1 - a$ and exponential $\frac{y_t}{y_0} = \exp(-kt)$ curves, where $k$ represents decomposition rates, and $a$ represents fraction of root biomass that was expected to be labile. Decomposition curve coefficients and model fit comparisons are provided in Table 1. Values are shown as mean ± 1 standard error (SE).

Asymptotic root decomposition rate ($k$) of supratidal species tended to be slower than that of intertidal species (Table 1), but the difference was not significant ($t(3.5) = -1.3$, $p = 0.28$). The fractions of expected labile root biomass ($a$) of supratidal and intertidal species were not significantly different ($t(5.7) = -1.5$, $p = 0.19$; Table 1). Comparing between woody species (*C. glauca*, *M. quinquenervia* and *A. marina*) and saltmarsh species (*S. quinqueflora* and *S. virginicus*), there were no significant differences in decomposition rates ($t(1.0) = -1.5$, $p = 0.37$), but the expected labile root fractions of roots of woody species was smaller than for saltmarsh species ($t(3.1) = -2.1$, $p = 0.13$; Table 1). Overall, using asymptotic decay models, the root decomposition rates ($k$) of all coastal wetland species examined here had a mean value of 0.0169 ± 0.0019 day$^{-1}$, and expected labile fraction of root biomass had a mean value of 28.3 ± 1.0 %.

Although there were no significant differences between fine roots and coarse roots in decomposition rates ($t(4.0) = 0.3$, $p = 0.78$) and expected labile fractions ($t(3.4) = 2.4$, $p = 0.09$) of woody species (*C. glauca*, *M. quinquenervia* and *A. marina*; Table 1), the decomposition curves were different (Fig. 2). The percentage root mass remaining $(\frac{y_t}{y_0})$ depended on root size (Fig. 2; Table 2). For coarse roots, there were no significant pairwise differences among mean percentage root mass remaining of the three woody species at all time periods (Table 2). For fine roots, there were significant pairwise differences between *C. glauca* and *M. quinquenervia* at 6 months, but at 14 months the difference was no longer significant (Table 2). For all three woody species, there was more coarse root biomass remaining than fine roots at the end of the experiment (Table 2).

**Hypothesis 3**. Comparison among habitats– reciprocal transplant experiment of intertidal plant roots

Asymptotic curves provided better fits than exponential curves for decomposition of biomass in different habitats (Fig. 3; Table 3). There were no significant differences in asymptotic root decomposition rate ($k$) ($t(5.6) = -0.4$, $p = 0.72$) and expected labile fractions ($a$) ($t(5.9) = -0.8$, $p = 0.46$) of intertidal mangrove and saltmarsh roots buried in their home habitats to that of roots buried in away habitats.

The habitat in which root biomass was deployed had a slight influence on root decomposition curves (Fig. 3; Table 4). For coarse *A. marina* and saltmarsh roots (*S. quinqueflora* and *S. virginicus*), there were no significant pairwise differences in remaining root mass $(\frac{y_t}{y_0})$ between roots buried in the home habitat and in away habitats at all time periods (Table 4). Fine *A. marina* roots buried in away habitats had significantly less remaining root mass than roots buried in the home habitat at 1.5 months and 3 months, but the difference was not significant after 3 months (Table 4).

**Table 2**

Percentage remaining root biomass of woody species at time periods. Compact display letters in superscript indicate pairwise comparisons at each time period; shared letters indicate no significant differences. Model estimates are shown as marginal means ± 1 standard error (SE). Mass loss in grams in parentheses; values are shown as mean ± 1 standard deviation (SD).

| | 1.5 months | 3 months | 6 months | 12 months | 14 months |
|---|---|---|---|---|---|
| *Casuarina glauca*, coarse | 86.4 ± $3.1^{b}$ (0.2 ± 0.1) | 88.8 ± $3.2^{b}$ (0.2 ± 0.1) | 83.3 ± $3.2^{b}$ (0.3 ± 0.2) | | 79.3 ± $3.2^{b}$ (0.4 ± 0.2) |
| *Casuarina glauca*, fine | 79.4 ± $3.7^{ab}$ (0.4 ± 0.2) | 80.3 ± $3.7^{ab}$ (0.3 ± 0.2) | 76.5 ± $3.7^{b}$ (0.4 ± 0.2) | | 67.0 ± $3.7^{a}$ (0.6 ± 0.2) |
| *Melaleuca quinquenervia*, coarse | 88.2 ± $2.9^{b}$ (0.3 ± 0.1) | 88.8 ± $2.9^{b}$ (0.3 ± 0.1) | 80.1 ± $2.9^{b}$ (0.4 ± 0.2) | | 76.4 ± $3.0^{b}$ (0.5 ± 0.2) |
| *Melaleuca quinquenervia*, fine | 72.7 ± $3.3^{a}$ (0.6 ± 0.4) | 72.7 ± $3.3^{a}$ (0.6 ± 0.4) | 61.5 ± $3.3^{a}$ (0.4 ± 0.2) | | 59.0 ± $3.4^{a}$ (0.9 ± 0.4) |
| *Avicennia marina*, coarse | 84.9 ± $5.5^{ab}$ (0.3 ± 0.1) | 78.1 ± $5.3^{ab}$ (0.4 ± 0.1) | 72.5 ± $5.3^{ab}$ (0.5 ± 0.2) | 75.7 ± $5.5^{b}$ (0.4 ± 0.1) | |
| *Avicennia marina*, fine | 90.9 ± $5.5^{ab}$ (0.2 ± 0.1) | 69.6 ± $5.3^{ab}$ (0.5 ± 0.1) | 67.2 ± $5.3^{ab}$ (0.6 ± 0.2) | 61.1 ± $5.5^{a}$ (0.7 ± 0.2) | |

## 4. Discussion

### 4.1. Root decomposition of supratidal and intertidal species

In this study, the overall asymptotic decomposition rate of coastal wetland plant roots was 0.0169 ± 0.0019 day$^{-1}$. Assuming that global mangrove fine root mortality is at equilibrium with the production rate of 3.0 ± 0.8 Mg C ha$^{-1}$ year$^{-1}$ (Adame et al., 2024b; Arnaud et al., 2023) and using the overall asymptotic decomposition derived here, limited decomposition rates could account for about 2.2 ± 0.6 Mg C ha$^{-1}$ year$^{-1}$ in accumulation of dead roots. Results also suggested that coastal wetland root decomposition rates in the study region were not significantly different among the five species assessed. Additionally, there were no significant differences in the expected labile fraction of root biomass among the five species. Although supratidal and intertidal plants are adapted to their respective ecological niche across coastal wetland gradients such as hydroperiod, nutrient availability, and salinity (Adame et al., 2024a), and are therefore expected to have potentially large variation in root chemistry composition (Arnaud et al., 2024; Ola and Lovelock, 2021), species-specific root traits that often influence rates of root decomposition may have been masked by the overwhelming influence of variation in hydro-edaphic conditions that are characteristic of coastal wetlands of the region (Hill et al., 2021).

Possible explanations for the homogeneity of decomposition rates across the species studied include similar climate within the small study region (Trevathan-Tackett et al., 2024), levels of oxygen availability (Lovelock et al., 2017), and levels of phenolic inhibition of decomposition (Friesen et al., 2018). Under anaerobic conditions that often occur in coastal wetlands, the enzymic latch mechanism describes reduced catalytic activity of phenol oxidase that can lead to increased concentration of phenols, which are inhibitors of hydrolase enzymes (Freeman et al., 2001). In turn, the reduced activity of hydrolase reduces decomposition of organic matter, contributing to soil organic matter accumulation in mangroves (Kim et al., 2021; Saraswati et al., 2016) and possibly other coastal wetland habitats, although other processes (e.g. tidal flushing, leaching, bioturbation) can also be important (Friesen et al., 2018).

### 4.2. Fine roots (<2 mm) of woody species decompose faster and have smaller expected recalcitrant fractions than coarse roots (2–20 mm)

Coarse roots decomposed less than fine roots across all the woody species in our experiments. Contrary to experimental results on *A. marina* root decomposition from temperate Australia (where 'fibrous' roots were <2 mm, and 'main' roots were 10–20 mm (Van der Valk and Attiwill, 1984)), our results contradicted our working hypothesis that larger, more aerenchymatous mangrove roots could decompose more rapidly compared to fine roots (Lovelock et al., 2017). Instead, our results are consistent with the study of Huxham et al. (2010) who found that coarse roots (>3–9 mm diameter) of *A. marina* decomposed more slowly than fine roots (≤3 mm diameter) in a period of 12 months in Gazi Bay, Kenya. Although coarser roots may contain soft tissue (such as aerenchyma in *A. marina* roots, and the papery outer covering of *M. quinquenervia* roots), their surface area:volume ratio decreases as root size increases, decreasing exposure to microbial mineralisation. A high proportion of woody root tissue in larger roots that contain more stable compounds, reduce susceptibility to microbial attack (Lallier-Vergès et al., 2008; Sarkanen and Ludwig, 1971). Different composition of biological compounds, such as higher lignin content (Arnaud et al., 2024; Carrasco-Barea et al., 2022; Ola and Lovelock, 2021), low C:N ratio (Bosire et al., 2005; Huxham et al., 2010), and high total phenolic

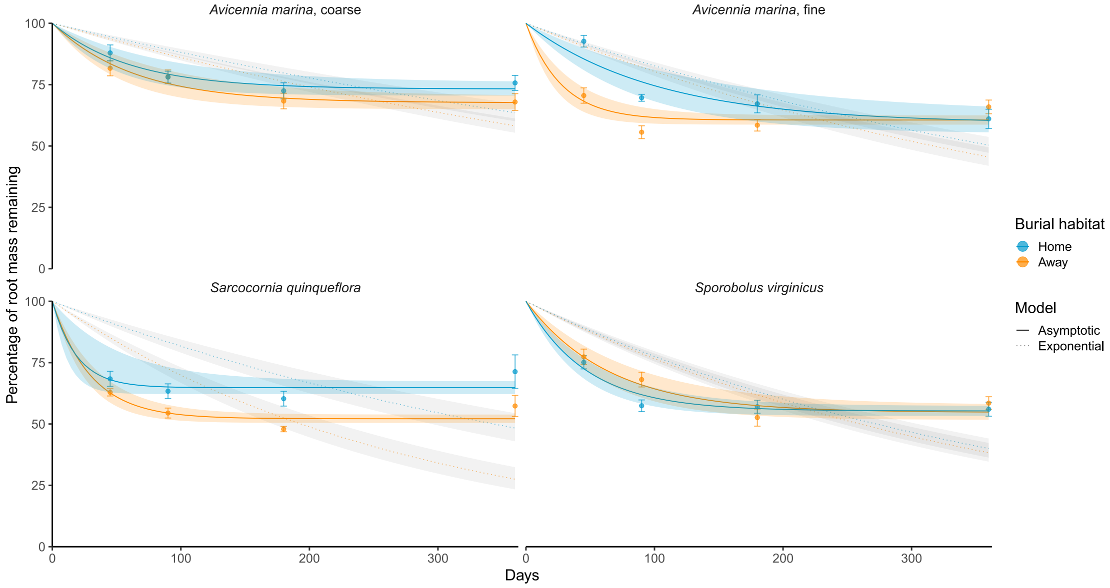

**Fig. 3.** Decomposition curves fitted for *Avicennia marina, Sarcocornia quinqueflora, and Sporobolus virginicus*, and root size class, as asymptotic $\frac{y_t}{y_0} = a\exp(-kt) + 1 - a$ and exponential $\frac{y_t}{y_0} = \exp(-kt)$ curves, where $k$ represents decomposition rates, and $a$ represents the fraction of biomass that was expected to be labile. Asymptotic and exponential decomposition curve coefficients for away habitats are provided in Table 2. Values are shown as mean ± 1 standard error (SE).

**Table 3**
Model coefficients and model fit comparisons of asymptotic and exponential root decomposition curves for coastal wetland species in away habitat(s). Values for roots buried in home habitats are the same as in Table 1. Values are shown as mean ± 1 standard deviation (SD).

| | | $k_{asymptotic}$ | $a$ | $k_{exponential}$ | Model fit | Replicates |
|---|---|---|---|---|---|---|
| *Avicennia marina*, coarse | Away | 0.0203 ± 0.0059 | 0.3171 ± 0.0233 | 0.0015 ± 0.0001 | $F_{(1, 74)} = 46.6$, $p < 0.001$ | 76 |
| | Home | 0.0201 ± 0.0066 | 0.2629 ± 0.0237 | 0.0013 ± 0.0002 | $F_{(1, 34)} = 46.0$, $p < 0.001$ | 36 |
| *Avicennia marina*, fine | Away | 0.0400 ± 0.0113 | 0.3942 ± 0.0179 | 0.0022 ± 0.0002 | $F_{(1, 77)} = 197.0$, $p < 0.001$ | 79 |
| | Home | 0.0110 ± 0.0027 | 0.3978 ± 0.0372 | 0.0019 ± 0.0002 | $F_{(1, 34)} = 26.7$, $p < 0.001$ | 36 |
| *Sarcocornia quinqueflora* | Away | 0.0336 ± 0.0062 | 0.4787 ± 0.0172 | 0.0036 ± 0.0005 | $F_{(1, 35)} = 246.3$, $p < 0.001$ | 37 |
| | Home | 0.0450 ± 0.0207 | 0.3664 ± 0.0249 | 0.0023 ± 0.0003 | $F_{(1, 36)} = 88.3$, $p < 0.001$ | 38 |
| *Sporobolus virginicus* | Away | 0.0169 ± 0.0033 | 0.4484 ± 0.0269 | 0.0027 ± 0.0003 | $F_{(1, 35)} = 75.6$, $p < 0.001$ | 37 |
| | Home | 0.0212 ± 0.0037 | 0.4468 ± 0.0204 | 0.0025 ± 0.0003 | $F_{(1, 37)} = 120.0$, $p < 0.001$ | 39 |

content (Pradisty et al., 2021), are likely the causes of the increased resistance to decomposition in larger roots, as has been suggested for variation in decomposition rates of mangrove leaf tissues (Kristensen et al., 2008).

Root decomposition may contribute to better mechanistic understanding of soil elevation changes in coastal wetlands. Soil elevation changes per unit time is a function of autocompaction and the addition of mineral and organic matter (Rogers and Saintilan, 2021); specifically, the standing biomass of roots is a result of the production and preservation rates of dead organic matter (Conroy et al., 2025). Decomposition is therefore one of the controls on soil volume; while there are no reports of elevation loss of supratidal forests when they experience mass tree mortality, decomposition of mangrove roots has been documented to cause rapid declines in surface elevation and peat collapse (Bennion et al., 2024; Cahoon et al., 2003; Lang'at et al., 2014). Our results indicate that there were similar percentage mass of coarse and fine roots remaining with decomposition among woody species, but comparative estimates of root zone volume changes following tree mortality of supratidal forests versus mangroves may also require the proportion of each root size class in total root volume. The distribution of root biomass per size class can be obtained from soil cores and excavation plots, although such work is laborious (Adame et al., 2017) and has not been documented for *C. glauca* and *M. quinquenervia*. As soils of *M. quinquenervia* and *C. glauca* can be highly organic particularly in the root zone (Adame et al., 2020; Kelleway et al., 2021), further research could assess the effects of decomposition rates and biomass distribution among root size classes on elevation change in supratidal forests.

### 4.3. Root decomposition at home and away habitats

Results from the reciprocal transplant experiment revealed no significant differences in root decomposition rates and the expected labile fraction of root mass between home and away habitats across the intertidal species and different root sizes. Results here did not demonstrate a positive home-field advantage effect (Ayres et al., 2009; Pugnaire et al., 2023), likely because environmental variables and root litter quality may interact synergistically and exert non-linear effects on decomposition coefficients (Stagg et al., 2017). Since root litter quality of each species is the same between habitats, differences in the remaining root mass in different habitats could be influenced by a combination of microbial community structure and hydro-edaphic characteristics, and the average litter quality in the habitat (Freschet et al., 2012; Stagg et al., 2017).

Decomposition of saltmarsh roots buried in mangroves (i.e. away) were more rapid than expected by the home-field advantage hypothesis, which may be attributable to distinct microbial communities between wetland habitats (Barreto et al., 2018; Trevathan-Tackett et al., 2021) that have different metabolic capabilities (Liu et al., 2022). For example,

**Table 4**
Percentage remaining root biomass of intertidal species at time periods. Compact display letters in superscript indicate pairwise comparisons at each time period; shared letters indicate no significant differences. Model estimates are shown as marginal means ± 1 standard error (SE). Mass loss in grams in parentheses; values are shown as mean ± 1 standard deviation (SD). Mean values for mangrove roots buried in home habitats are the same as in Table 2.

| | | 1.5 months | 3 months | 6 months | 12 months |
|---|---|---|---|---|---|
| *Avicennia marina*, coarse | Away | 78.3 ± $3.1^{bcd}$ (0.4 ± 0.2) | 77.0 ± $3.1^{c}$ (0.4 ± 0.2) | 68.3 ± $3.0^{cd}$ (0.6 ± 0.3) | 67.9 ± $2.9^{ab}$ (0.6 ± 0.3) |
| | Home | 84.9 ± $4.2^{cd}$ (0.3 ± 0.1) | 78.1 ± $3.8^{c}$ (0.4 ± 0.1) | 72.5 ± $3.8^{d}$ (0.5 ± 0.2) | 75.7 ± $4.2^{b}$ (0.4 ± 0.1) |
| *Avicennia marina*, fine | Away | 69.1 ± $3.0^{ab}$ (0.6 ± 0.2) | 55.6 ± $3.1^{a}$ (0.8 ± 0.2) | 58.5 ± $3.0^{abc}$ (0.7 ± 0.2) | 65.9 ± $2.9^{ab}$ (0.6 ± 0.2) |
| | Home | 90.9 ± $4.2^{d}$ (0.2 ± 0.1) | 69.6 ± $3.8^{bc}$ (0.5 ± 0.1) | 67.2 ± $3.8^{bcd}$ (0.6 ± 0.2) | 61.1 ± $4.2^{ab}$ (0.7 ± 0.2) |
| *Sarcocornia quinqueflora* | Away | 62.7 ± $4.0^{a}$ (0.5 ± 0.1) | 54.4 ± $3.8^{a}$ (0.6 ± 0.1) | 47.9 ± $3.8^{a}$ (0.7 ± 0.0) | 57.3 ± $4.2^{a}$ (0.5 ± 0.2) |
| | Home | 68.4 ± $3.8^{ab}$ (0.4 ± 0.1) | 63.4 ± $3.8^{ab}$ (0.5 ± 0.1) | 60.3 ± $3.8^{abcd}$ (0.5 ± 0.1) | 67.7 ± $4.2^{ab}$ (0.4 ± 0.3) |
| *Sporobolus virginicus* | Away | 74.6 ± $4.0^{abc}$ (0.4 ± 0.1) | 68.1 ± $3.8^{abc}$ (0.6 ± 0.2) | 52.6 ± $3.8^{ab}$ (0.9 ± 0.2) | 58.5 ± $4.2^{a}$ (0.7 ± 0.1) |
| | Home | 75.1 ± $3.8^{abc}$ (0.4 ± 0.1) | 57.4 ± $4.2^{ab}$ (0.7 ± 0.1) | 57.0 ± $3.8^{abc}$ (0.7 ± 0.1) | 55.9 ± $3.7^{a}$ (0.8 ± 0.2) |

bacterial communities from mangrove sediment on Minjerribah, Moreton Bay were reported to be dominated by Deltaproteobacteria (Chuvochina et al., 2021), which are major decomposers (Holguin et al., 2001). Deltaproteobacteria was present in saltmarsh sediment but in lower abundance compared to within mangrove habitats (Chuvochina et al., 2021). Members of the Deltaproteobacteria that are capable of breaking down *S. quinqueflora* and *S. virginicus* roots may therefore be present in mangroves, but absent in hypersaline saltmarshes where *S. quinqueflora* and *S. virginicus* occur.

Enhanced initial decomposition of *A. marina* roots buried in saltmarshes (i.e. away) could be related to the higher soil redox potential (Clarke and Hannon, 1969), higher temperatures (Charles et al., 2020) and higher N:P ratio of high intertidal saltmarsh sediments compared to sediment conditions in mangroves (Lovelock et al., 2014). More rapid decomposition of fine mangrove roots in the saltmarsh soils occurred, despite the expected negative effects of high soil porewater salinity (Reddy et al., 2025; Zhang et al., 2021) and reduced microbial biomass in soils of high bulk density (Beylich et al., 2010), which are soil properties typical for saltmarshes in the region (Hayes et al., 2017; Lovelock et al., 2019), on root decomposition rates.

The overall decomposition rates within mangrove and saltmarsh habitats were similar, suggesting that the increasing encroachment of mangroves onto saltmarshes with climate change is unlikely to lead to substantial differences in decomposition rates (Henry and Twilley, 2013; Perry and Mendelssohn, 2009; Simpson et al., 2021). Nutrient cycling may be altered due to changes in the input of litter of varying quality (Simpson et al., 2021), and possibly due to the introduction of woody roots of *A. marina* with higher expected recalcitrance into saltmarsh soils that could increase the amount of root necromass input into the soil carbon pool. On a landscape scale, it may therefore be inferred that the soil carbon sequestration potential of the saltmarshes undergoing mangrove encroachment could increase via this pathway, as has been previously observed (Kelleway et al., 2016; Osland et al., 2012). However, the direction and magnitude of any changes to soil carbon with vegetation change could be variable among different species and systems (Doughty et al., 2016; Henry and Twilley, 2013; Perry and Mendelssohn, 2009).

### 4.4. *Asymptotic models provide better fit than exponential models*

Asymptotic decay models provided better fits than exponential decay models for our data. Although root decomposition studies are sparse in the literature, exponential decay models are often used for analysis (Simpson et al., 2023). On the other hand, asymptotic models follow a similar form but are constrained by the fraction of expected labile biomass (Keuskamp et al., 2013). Our estimate for the fraction of expected labile root mass of home-field mangrove fine roots (39.8 ± 3.7 %) corroborated an earlier study in the region (43 ± 2 %) (Hayes et al., 2017b). However, the expected refractory root mass of mangrove roots (60.2 %) is slightly higher than lignin and cellulose content measured in roots of ~200 day-old mangrove seedlings (48 %, Ola and Lovelock, 2021). We found that the expected recalcitrant fractions of roots were larger than the expected labile fractions, particularly for tree roots with diameter >2 mm. Hence, we found that the asymptote was important to reflect the preferential preservation of expected recalcitrant root mass, given the critical role of root inputs (regulated by root production, root mortality and root decomposition rates) for carbon sequestration and surface elevation changes (Arnaud et al., 2023; Cahoon et al., 2003; Kirwan and Megonigal, 2013; McKee et al., 2007; Saintilan et al., 2020). On the other hand, exponential models are unconstrained by an expected labile fraction and provide an overall decay rate (Gill et al., 2022). For example, the global average mangrove root decomposition rate calculated from exponential models is 0.002 ± 0.001 $\text{day}^{-1}$ (Simpson et al., 2023), which is an order of magnitude lower than the value observed here (0.0169 ± 0.0019 $\text{day}^{-1}$). Exponential decay models may be less useful in describing the differing behaviours of expected recalcitrant and expected labile fractions, which we expect to have different decomposition rates (Trevathan-Tackett et al., 2024). Future decomposition studies could estimate decay rates using both asymptotic and exponential models to assess the adequacy of different modelling approaches.

### 4.5. *Comparison with other studies and proxies*

The percentage remaining mass at each incubation period $\left(\frac{y_t}{y_0}\right)$, expected labile root fractions ($a$) and decomposition rates ($k$) among species and habitats here had different levels of variation (coefficients of variance of 16.3–22.5 %, 27.2 % and 50.8 % respectively), which demonstrated varying levels of empirical uncertainty about wetland root decomposition across a coastal wetland mosaic within the same locality.

Among proxies for root tissue in existing decomposition literature, standardised tea litter is likely to be the most useful for estimating root decomposition rates. Overall root decomposition rate (0.0169 ± 0.0019 $\text{day}^{-1}$) was comparable to local decomposition of green tea litter, which is used as a proxy for comparing decomposition of labile organic matter among sites (mangrove: 0.02 ± 0.00 $\text{day}^{-1}$, saltmarsh: 0.02 ± 0.00 $\text{day}^{-1}$; Supplementary Table 4; Trevathan-Tackett et al. (2021)). The expected recalcitrant fraction of roots of intertidal species (63.6 ± 1.5 %) was higher than the remaining mass of rooibos tea litter (buried in mangroves: 49.3 ± 1.1 %, buried in marsh: 50.1 ± 1.2 %; Supplementary Table 3), which is assumed to be a proxy for less labile organic matter (Trevathan-Tackett et al., 2021). The estimates of decomposition rates for tea proxies were derived from exponential decay models rather than asymptotic models (Trevathan-Tackett et al., 2021) which may contribute to differences observed between expected recalcitrant fractions here and remaining mass of rooibos tea litter. Conversely, global estimate of mangrove leaf litter decay rates (0.009 ± 0.0005 $\text{day}^{-1}$ estimated from exponential decay models; Simpson et al. (2023)) was substantially higher than the exponential decomposition of root tissue in the present study (0.0016 ± 0.0000 $\text{day}^{-1}$; Supplementary Table 4), likely reflecting the high labile fraction of leaves that are more susceptible to rapid mineralisation compared to root tissues (Middleton and McKee, 2001; Simpson et al., 2023). Taken together, the lack of empirical measurements of wetland root decomposition is best addressed by experimenting with field assessments of root tissue. Standardised tea bags are possibly suitable alternatives to the use of harvested roots in decomposition experiments, but root decomposition rates should not be substituted with leaf litter decomposition rates.

### *4.6. Limitations*

Although oven drying for preparation of root material reflects common practice in published literature (e.g. Huxham et al., 2010), air drying at ambient temperature is perhaps a more natural process to preserve root integrity. We accounted for root tissue moisture in the preparation of decomposition bags by oven drying and air drying, but applying factors (coarse *A. marina*: 0.847, fine *A. marina*: 0.903, *S. quinqueflora*: 0.863, *S. virginicus*: 0.913) to convert air-dried weight to oven-dried weight likely introduced errors to the converted weights. Future work could increase the root material enclosed within decomposition bags to reduce the effect of uncertainty around initial weights. Secondly, the root size classes here includes roots of different functions, and therefore likely having different anatomical and chemical make ups that may affect decomposition. From terrestrial studies, proximal fine roots ($<$2 mm) are more ephemeral, and primarily performs respiration and absorption, while distal, perennial roots are associated with storage and transport (Guo et al., 2008). Accordingly, distal roots have been shown to decompose slower than proximal roots in a mixed mangrove forest (Zhang et al., 2021). We also did not undertake composition analyses of the root material. Future work could investigate the effects of C:N and lignocellulose (e.g. Ola and Lovelock, 2021) on decomposition for each species and root size class, as well as carbon content analyses for carbon cycle calculations (Adame et al., 2024b; Arnaud et al., 2023).

### *4.7. Implications*

Nonetheless, root decomposition rates derived from this study are useful for ecological modelling. Experiments here investigated drivers of decomposition rates across a coastal wetland gradient, which could be applied to the parameterisation of ecological models, including predictive models that inform coastal wetland conservation and restoration. For example, root decomposition rates are a key control on surface elevation changes, which in turn determine resilience to sea-level rise (Lang'at et al., 2014). Particularly, supratidal forests of Queensland that are comprised of *Melalueca* sp. and *Casuarina* sp. have unique biodiversity (Hagger et al., 2025) but have been converted to agriculture or degraded in large areas across Queensland, resulting in many of the communities being listed as vulnerable and endangered (Rowland et al., 2023; Department of the Environment, 2025). Root decomposition rates can also be applied to modelling organic matter accumulation rates in wetland soils, which influences the magnitude of climate change mitigation potential (Lovelock et al., 2017). Further research on roots and belowground dynamics in coastal wetland soils can improve models of conserved or restored ecosystem services that include habitat, flood protection, nutrient cycling and carbon sequestration (Adame et al., 2024b).

## 5. Conclusion

Overall, this study contributed to the sparse literature on wetland root decomposition by investigating the effect of species, root size and burial habitat on root decomposition rates from five species typical of coastal wetlands. Root decomposition in Southeast Queensland's coastal wetlands follow similar patterns among intertidal and supratidal species. The results presented demonstrated the importance of verifying root decomposition in field assessments against commonly used proxies, and that implementation of asymptotic models and mass remaining are useful for projecting impacts of future coastal wetland change.

## CRediT authorship contribution statement

**Valerie Kwan:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Vicki Bennion:** Writing – review & editing, Investigation. **Matthew A. Hayes:** Writing – review & editing. **Catherine E. Lovelock:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

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## Declaration of competing interest

The authors declare no competing interests.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109547.

## Data availability

Data files and code to reproduce all other results and figures have been uploaded to Zenodo (10.5281/zenodo.17113618)

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