Away-field advantage: mangrove seedlings grow best in litter from other mangrove species

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Plant community composition can impact ecosystem processes via litter feedbacks. Species variation in litter quality may generate different patterns of nutrient supply for plants that are dependent on litter inputs. However, it is not known whether plants grow faster in their own litter, litter from other species, or in litter mixtures from multiple species. To test whether litter identity and mixture status influenced mangrove seedling growth, biomass allocation, and stoichiometry, we performed mesocosm experiments. Two species of mangrove seedlings, *Avicennia germinans*, black mangrove and *Rhizophora mangle*, red mangrove, were exposed to all possible combinations of three mangrove litter types and were isolated from all other nutrient inputs. Litter treatments significantly altered seedling growth. Seedlings from both mangrove species grew most rapidly in litter from a different species rather than their own, irrespective of litter chemical quality, decomposition rate, and nitrogen release. Litter mixtures from white and black mangroves caused black mangroves to grow 65% more than expected. Litter treatments did not impact seedling root:shoot ratios or tissue C:N. Our finding that seedlings grow best in litter from other species may indicate a mechanism that helps sustain the coexistence of dominant species.

At the plant–soil interface, plants, microorganisms, and soil fauna interact to regulate ecosystem productivity via nutrient availability. Through litter production and nutrient release during decomposition, plants influence soil nutrient availability and soil communities, so that plants may exert a strong influence over the soil environment in which they exist (Menyailo et al. 2002, Chapman et al. 2006, Schweitzer et al. 2008, van der Heijden et al. 2008). However, we still have a limited understanding of how litter production by co-occurring plant species can cascade through soils and feed back to indirectly impact plant productivity (Nilsson et al. 2008). Though they are often difficult to detect, plant–soil feedbacks may be important for structuring and maintaining plant communities and driving nutrient cycling (Bever 1994, Ehrenfeld et al. 2005, Kulmatiski et al. 2008, van der Heijden et al. 2008, Ayres et al. 2009, Mangan et al. 2010, Pregitzer et al. in press). Because estuarine systems allow for tidal movement of litter, plants often grow among other plant species’ litters, rendering litter feedbacks in these ecosystems more complex and unpredictable than those in terrestrial systems where litterfall is more predictable based on overstory community composition. In this study, we examine 1) whether plant litter identity alters the growth of mangrove seedlings, and 2) whether mixing litter can have a positive influence on seedling growth.

Leaf litter from different plant species varies in both physical and chemical traits. Physical characteristics of litter such as water-holding capacity and morphology can alter soil microclimate. Chemical quality of litter regulates nutrient release from litter during decomposition and may alter salinity of soils. Soil microenvironment and nutrient availability may be particularly important for plant seedlings due to intense competition for resources such as light, water, and nitrogen (N). Leaf litter has been shown to impact seedling germination, establishment (Vellend et al. 2000, Padhy et al. 2000, Conway et al. 2002), and growth (Xiong and Nilsson 1999, Quested et al. 2003, Durrepaal et al. 2007).

Negative plant–soil feedbacks, in which plants grow more slowly in soils cultured under a conspecific, have been documented in many ecosystems (reviewed by Kulmatiski et al. 2008). These ecological patterns may be caused by an accumulation of soil-based enemies (Bever et al. 1997). Conversely, positive plant–soil feedbacks confer advantages to conspecific juvenile plants via soil culturing with beneficial organisms (Bever et al. 1997). Fewer studies have documented plant–litter feedbacks; however, researchers have shown that litter decomposes most rapidly when in the presence of the plant species that generate that litter type (Gholz et al. 2000, Vivanco and Austin 2008, Ayres et al. 2009, 2010), otherwise known as a ‘home-field advantage’. Both feedback studies and these ‘home-field advantage’ to decomposition studies may have important implications for plant succession and species coexistence. Yet, not much is known about whether conspecific litter production can confer productivity advantages to the species studied. Similar to a positive plant–soil feedback based on soil organisms, if plants grow best in their own litter, perhaps their offspring (and thus seedlings) are likely to persist in the parental habitat.
Although much is known about mixed litter decomposition and mixed litter nutrient release (Gartner and Cardon 2004, Hättenschwiler et al. 2005, Wärdle et al. 2006, Meier and Bowman 2009, Wärdle et al. 2009), only one study, to our knowledge, has found that mixtures of plant litter alter plant growth synergistically (Nilsson et al. 2008). Recently, Nilsson et al. (2008) investigated the impact of varying litter diversity and plant diversity on plant growth and other ecosystem parameters in a pot experiment. They found that individual substrates altered plant growth and that some litter mixtures generated different plant growth patterns than would be expected from the component litters. Non-additive litter decomposition and nutrient release are commonly found (Gartner and Cardon 2004), thus it is important to examine the implications of these interactions for plant productivity. Because seedlings have diverse and high nutrient demands, synergisms that occur during mixed litter decomposition may be particularly important for their growth.

Because mangrove ecosystems have only a few dominant species (Smith and Duke 1987), direct investigations of plant litter feedbacks that involve the full complement of mangrove species are possible. Further, understanding mangrove seedling productivity in habitats with various species assemblages will inform current restoration efforts, necessary due to the massive losses of mangroves to coastal development (Valiela et al. 2001). Mangroves do not often employ vegetative reproduction and therefore rely on seedling establishment for forest regeneration (Tomlinson 1986). Mangrove seedling success is partly driven by salinity, tidal action, and availability of nutrients (McKee 1995a, b, Krauss et al. 2008), but perhaps the most important variable regulating growth after establishment is availability of resources to allow stem elongation, and thus access to light and avoidance of tidal inundation. Litter may be particularly important for providing the bulk of nutrients available for elongation in mangrove ecosystems that have isolated nutrient cycles, like inland mangrove stands in Florida (Twilley et al. 1986) and in some intertidal mangrove systems (Bouillon et al. 2003). In their tropical habitats, mangroves produce litterfall and grow continuously throughout the year. Various natural combinations of relatively few species (often three in the neotropics) occur naturally over small areas. Mangroves commonly exhibit zonation, with red mangrove *Rhizophora mangle* most frequently occurring along the coast and black mangrove *Avicennia germinans* dominating in the interior of islands or landward side of coastal mangroves. Though litter of a certain species is generally concentrated in the zone where that litter occurs, tidal flushing can move litter from all dominant mangrove species, thereby rendering litter mixtures common across the intertidal zone. Thus, it is likely that co-occurring mangrove species, via their varied litter quality, have differential impacts on the growth of seedlings outside their own species. In particular, red mangrove litter may commonly be ‘washed into’ the black mangrove zone. The magnitude of tidal inundation determines the frequency of litter mixture but also the importance of litter as a nitrogen source for mangroves and adjacent ecosystems (Twilley et al. 1986). Because these forested wetlands serve as fish nurseries for adjacent coral reefs (Mumby et al. 2004), stabilize coastlines, and provide important terrestrial inputs of energy and nutrients to offshore ecosystems (Granek et al. 2009), understanding potential feedback influences on plant productivity and ecosystem regeneration is essential.

In this study we investigated how mangrove litter identity and diversity affect mangrove seedling growth and stoichiometry in mesocosms containing seedlings, sand, microbial inoculum and litter. By using sand as a substrate and deionized water, we were able to remove all exogenous nutrient inputs other than those available to seedlings via litter and stored propagule resources. Although the species used in this study are halophytes, they grow equally well in freshwater. This study’s novelty lies in our integrative approach, linking plant community composition to microbially-mediated decomposition and resultant seedling productivity.

We address the following questions: 1) does mangrove litter identity influence mangrove seedling growth? 2) Do seedlings grow best in the presence of their own litter? 3) Do mixed-litter additions result in mangrove growth that is different from expected growth rates? We hypothesize that black mangrove litter, which has the highest N, will decompose fastest, release the most N, and increase mangrove seedling growth, regardless of seedling type. We hypothesize that mangrove litter mixtures will generate faster than expected seedling growth due to a diversity of available resources.

**Material and methods**

**Site description**

In October 2006, propagules, litter and soil samples were collected in Florida from mangrove stands at an island (hereafter referred to as T-9) in the Merritt Island National Wildlife Refuge near Titusville, and at a mosquito impoundment (hereafter referred to as MI-23) in the Avalon State Recreation Area on the lagoonal side of North Hutchinson Island near Ft. Pierce (described in Feller et al. 2003a). The Merritt Island site was also formerly impounded to control mosquito populations. The dike surrounding the impoundment was removed in 2000 to re-establish a natural hydrological exchange. Mangrove forests at the former mosquito impoundment MI-23 were reconnected to the Indian River Lagoon 1974 through a breach and culverts that re-established hydrological exchange. Propagules were collected from both sites in order to ensure 1) a sufficient number of propagules and 2) phenotypic variation in the population of mangroves. The mangrove community at both collection sites consisted of all three dominant mangrove species: black mangrove, white mangrove *Laguncularia racemosa*, and red mangrove. Propagules and litter from all three species were collected at each site and combined.

**Mesocosm design and material collection**

Mesocosms were comprised of pots containing germinants, sand, inoculum and litter. Seven germinants of each mangrove species (n = 7) were exposed to each of the seven litter treatments for a total of 98 plant–litter mesocosms (49 for black mangroves and 49 for red mangroves). Sand-only (2), plant only (n = 7 for each mangrove species), and litter-only
controls (n = 3 for each treatment) were also included in the experiment (135 pots total).

Mangrove propagules, which undergo development from flower to germinated seedling while still attached to adult trees, were collected by hand from >30 individual black, white, and red mangrove trees at both T-9 and MI-23. Mature propagules were chosen that were ready to abscise. A subset of these propagules was planted at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland. White mangrove propagules had an extremely low viability rate and thus were removed from the study. All propagules were weighed and measured for length, and germinants were selected based on a uniform propagule length and weight. A subset of propagules was set aside for initial nutrient analyses. After eight weeks, germinants (one in each pot) were planted in standard one-gallon (3.8 l) nursery pots filled with sterilized sand and grown on tables in a greenhouse at SERC. Pots were placed in individual dishes (~0.5 l) of distilled water and water levels in the dishes were maintained in order to ensure complete soil saturation. Distilled water (50 ml) was poured over the litter surface of each mesocosm once a week to attempt to simulate tidal flushing of the litter and allow for leaching of nutrients to occur. The initial placement of mesocosms in the greenhouse was randomized, and mesocosms were moved to new random locations on greenhouse tables monthly over six months of seedling growth.

We also collected senescent leaf litter from red, black and white mangroves from the two mangrove sites described above. We only chose leaves for which the abscission layer had fully formed, therefore rendering them easy to pluck from the tree. Litter was bulked by species and was air-dried before being applied to the mesocosms. A subset of each initial litter type was set aside for nutrient analyses.

We collected soil inoculum from MI-23 to insure that a native microbial community was available to decompose litter in the mesocosms. We collected three soil cores using a 30-ml syringe (2-cm ø) that had been cut and sharpened at the tip, resulting in cores 10 cm deep. We took cores 25 cm from the base of mangroves in three previously established sites in the fringe zone where the litter was collected. Because these soils are often saturated, each of these cores was a sediment–seawater slurry. We stored soil cores in a cooler in the field and then refrigerated them until the inoculum was applied to the mesocosms. We bulked the three soil cores together and added half of each core to 500 ml of distilled water to create a soil slurry. Two ml of the slurry was added to each litter treatment and plant control. Any nutrients added via the soil inoculum were negligible due to the dilution with water and therefore would not contribute to seedling growth.

Ten grams of litter (in all possible mixtures) were added to each of the mesocosms. This amount of litter was determined based on the natural litterfall rate scaled by the area of the pot. The mangrove litter treatments consisted of red, white, black, red + black, white + black, red + white, and red + black + white litter, and no litter, and seven replicates of each treatment were employed. The initial mass of individual species’ litter placed on the sand was equal to 10 g (air-dried) divided by the number of species.

Seedling growth measurements

Mangrove growth was measured at 3-week intervals over the course of the experiment. Multiple parameters of seedling growth were measured, including the leaf length of the newest fully mature leaf, total leaf number, total seedling height, and shoot length and number of leaf nodes. Previous studies (Feller 1959) have shown that shoot elongation and internodal length are the best metrics of mangrove growth. We report growth as total shoot length (the sum of all nodes and internodes) at the duration of the experiment (Fig. 1) but analyzed total shoot length increases over time (obtained during each three-week sampling interval) using repeated measures analyses.

After allowing the seedlings to grow for six months, all litter was removed from the sand, minimizing sand contamination as much as possible. We then took a 15 cm deep soil core (3 cm ø) halfway between plant main stem and the edge of pot. Leaves were harvested before cutting off the top (shoot) of the plant at the level where it transitioned between above- and below-ground. Sand was rinsed from seedling roots using a 1 mm sieve to minimize loss of small/ fine roots. Roots, leaves and stems were oven-dried at 65°C and weighed separately. Stems and leaf samples were bulked together for shoot analyses.

Litter decomposition and nitrogen release

Litter was removed from the sand and rinsed over a size 4 sieve to remove sand particles. Litter was dried at 65°C for 24 h and weighed. Proportion mass loss is calculated as initial mass minus final mass loss divided by initial mass loss. Expected mass losses for mixed litters are determined by calculating the average mass loss of the two component litters.
in the mixture. Nitrogen release from litter was determined by subtracting final % N from initial % N and dividing the difference by initial % N.

**Chemical analyses**

Seedling shoot (leaves and stems) and root tissues and mesocosm litter were ground to a fine powder using an IKA grinding mill. Concentrations of carbon (C) and N in ground tissue, litter, and mesocosm sand were determined with an elemental analyzer. A subset of propagules (10 per species) and initial litter (three subsamples per species) were also oven-dried, ground with the IKA mill and analyzed for C and N concentrations.

**Statistical methods**

Total shoot length (an index for growth) for each species (red and black mangrove) was analyzed using repeated-measures MANOVA with time and litter treatment as the main effects. In a separate analysis, the impact of single species litter treatment on total growth over the course of the experiment was examined using repeated measures ANOVA and post hoc contrasts were performed to examine the differences between the various single litter treatments. Feedback ratios were calculated by dividing total growth (shoot elongation) in home litter by total growth (shoot elongation) in away litter (Brinkman et al. 2010).

Expected growth rates of seedlings exposed to mixed litter were calculated using the average growth rate of seedlings (shoot length) exposed to each component litter. Two individual seedlings were paired (e.g. a black mangrove seedling with red mangrove litter and a black mangrove seedling with black mangrove litter) randomly to calculate these expected growth rates. Differences between expected and observed seedling growth rates were analyzed using matched pairs t-tests.

Total biomass of roots and shoots within each seedling experiment (red mangrove and black mangrove) was analyzed using ANOVA with initial propagule weight as a covariate. A student’s t post hoc test was performed to compare the impacts of the various litter treatments on seedling biomass. Total N and C:N of individual biomass components were analyzed using ANOVA. All univariate statistics were performed using JMP IN 5.1 (SAS Inst., Cary, NC, USA). Statistical significance was determined at α = 0.1.

Litter treatment influences on litter mass loss, % of initial litter N released, and total N mass released were analyzed using a one-way ANOVA within each seedling experiment (red mangrove and black mangrove). The observed mass loss and N release of litter mixtures was compared to expected mass loss of litter mixtures using post hoc contrasts.

**Results**

**Initial litter C:N**

Black mangrove litter applied in the mesocosm experiment had the lowest average C:N at 59.13 (SE = 0.57). Red mangrove litter and white mangrove litter had average C:N ratios of 68.63 (SE = 2.20) and 87.88 (SE = 1.70), respectively. Black mangrove litter had an average initial N concentration of 0.75%. Red mangrove litter had initial [N] of 0.65% and white had litter with 0.44% [N].

**Seedling growth**

Black mangrove seedling growth, as measured by total shoot length, was significantly different over the course of the experiment (repeated measures) due to litter treatment (all mixed and single litter treatments, model p = 0.03, F = 2.53, DF = 7, litter treatment p = 0.03. Time was a significant factor (p < 0.0001), but there was no significant time by treatment interaction. Black mangrove seedling growth over the course of the experiment was significantly impacted by single species litter treatments (repeated measures p = 0.075, F = 2.67, DF = 3; Fig. 1A). Post hoc contrasts showed that black mangrove seedlings growing in red mangrove litter had significantly higher average growth than those growing black mangrove litter (their own, p = 0.06), thereby providing evidence for a negative plant-litter feedback. The feedback ratio of home growth to away growth for black mangroves is 0.63. Shoot elongation was larger for black mangroves growing in red litter vs. no litter (p = 0.01). Black mangrove seedlings exposed to mixed litter did not grow differently than those growing in single species litter (p = 0.15). However, the among-pairs analysis showed that seedlings growing in mixtures of white and black mangrove litter grew significantly faster than the expected growth rate for this litter combination (p = 0.08). A follow-up t-test showed that observed growth was significantly higher than expected growth for black mangrove seedlings growth in the white–black litter mixture (p = 0.05; Fig. 2A).

Red mangrove seedling growth (as measured by shoot length) differed due to litter treatment over the course of the experiment (model p = 0.0001, F = 5.98, DF = 7, litter treatment p < 0.0001). There were significant time and time × treatment interactions. Red mangrove seedling shoot length was significantly impacted by the presence of the different single species litter treatments (repeated measures p < 0.001, F = 12.05, DF = 3; Fig. 1B). Post hoc contrasts showed that red mangrove seedlings growing in black mangrove litter have significantly higher growth than seedlings growing in their own (red mangrove) litter (p < 0.01), providing evidence for a negative plant–litter feedback. The feedback ratio of growth in their own litter divided to growth in black mangrove litter is 0.77. Red mangroves growing in black litter also grew faster than those growing in no litter (p < 0.0001) or in white mangrove litter (p = 0.01). Red mangrove seedling growth was not significantly different from expected when seedlings were grown in mixed litter (p = 0.26; Fig. 2B).

**Seedling biomass**

Litter treatments had no significant effect on stem biomass, leaf biomass, shoot biomass or total biomass for either species of mangrove seedling. Black mangrove seedling root mass and root:shoot ratios were not significantly changed due to litter treatment. However, red mangrove seedling root biomass was altered by litter amendments (p = 0.001, F = 10.03, DF = 8; Table 1). Red mangrove seedlings growing in black
Table 1. Plant tissue stoichiometry and growth allocation patterns after six months of exposure to litter treatments. Average plant shoot C:N, root C:N, shoot biomass, root biomass and root:shoot ratios are shown for both seedling species exposed to all litter treatments. Litter components are indicated by a single letter or a combination of letters representing the three mangrove species: R (red mangrove), B (black mangrove), W (white mangrove). Seedlings exposed to the ‘No litter’ treatment were grown in sand without any litter added. An (∗) at the beginning of a row indicates that the seedling is growing in its own or ‘home’ litter. Superscripted letters next to average values indicate significant differences at $p < 0.05$. Comparisons were only made between treatments applied to the same mangrove species.

<table>
<thead>
<tr>
<th>Litter treatment</th>
<th>Shoot C:N</th>
<th>Root C:N</th>
<th>Shoot biomass</th>
<th>Root biomass</th>
<th>Root:shoot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black mangrove</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No litter</td>
<td>32.32 (2.43)</td>
<td>37.73 (6.38)</td>
<td>0.54 (.06)</td>
<td>0.30 (.05)</td>
<td>0.54 (.04)</td>
</tr>
<tr>
<td>R</td>
<td>40.61 (2.29)</td>
<td>54.03 (2.92)</td>
<td>0.57 (1.1)</td>
<td>0.42 (0.6)</td>
<td>0.78 (0.08)</td>
</tr>
<tr>
<td>B∗</td>
<td>34.57 (3.63)</td>
<td>47.69 (6.22)</td>
<td>0.33 (0.09)</td>
<td>0.23 (0.07)</td>
<td>0.48 (0.14)</td>
</tr>
<tr>
<td>W</td>
<td>39.73 (0.50)</td>
<td>53.41 (4.15)</td>
<td>0.53 (0.09)</td>
<td>0.53 (0.10)</td>
<td>0.69 (0.19)</td>
</tr>
<tr>
<td>RB</td>
<td>36.36 (2.15)</td>
<td>48.01 (5.98)</td>
<td>0.65 (0.08)</td>
<td>0.44 (0.05)</td>
<td>0.69 (0.07)</td>
</tr>
<tr>
<td>RW</td>
<td>22.73 (2.15)</td>
<td>51.24 (3.97)</td>
<td>0.58 (0.07)</td>
<td>0.41 (0.05)</td>
<td>0.72 (0.06)</td>
</tr>
<tr>
<td>WB</td>
<td>39.33 (3.37)</td>
<td>47.67 (3.59)</td>
<td>0.58 (0.08)</td>
<td>0.44 (0.06)</td>
<td>0.85 (0.15)</td>
</tr>
<tr>
<td>RWB</td>
<td>36.72 (1.26)</td>
<td>53.93 (4.67)</td>
<td>0.49 (0.12)</td>
<td>0.36 (0.11)</td>
<td>0.61 (0.13)</td>
</tr>
<tr>
<td>Red mangrove</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No litter</td>
<td>70.24 (2.99)</td>
<td>63.76 (2.15)</td>
<td>5.76 (3.1)</td>
<td>0.58 (0.06)</td>
<td>0.10 (0.01)</td>
</tr>
<tr>
<td>R∗</td>
<td>75.03 (2.65)</td>
<td>65.20 (2.49)</td>
<td>6.23 (0.83)</td>
<td>0.88 (0.14)</td>
<td>0.14 (0.1)</td>
</tr>
<tr>
<td>B</td>
<td>75.93 (4.85)</td>
<td>74.34 (3.91)</td>
<td>5.40 (5.8)</td>
<td>1.05 (1.0)</td>
<td>0.23 (0.06)</td>
</tr>
<tr>
<td>W</td>
<td>82.11 (1.80)</td>
<td>69.17 (1.83)</td>
<td>6.12 (0.56)</td>
<td>0.94 (0.08)</td>
<td>0.15 (0.00)</td>
</tr>
<tr>
<td>RB</td>
<td>81.00 (2.65)</td>
<td>71.29 (3.12)</td>
<td>7.26 (1.1)</td>
<td>1.08 (1.1)</td>
<td>0.15 (0.1)</td>
</tr>
<tr>
<td>RW</td>
<td>82.24 (2.72)</td>
<td>70.32 (2.03)</td>
<td>5.98 (0.07)</td>
<td>0.89 (0.07)</td>
<td>0.15 (0.1)</td>
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<tr>
<td>WB</td>
<td>77.10 (4.90)</td>
<td>66.90 (2.85)</td>
<td>6.45 (0.47)</td>
<td>1.10 (1.1)</td>
<td>0.15 (0.1)</td>
</tr>
<tr>
<td>RWB</td>
<td>74.64 (2.69)</td>
<td>66.85 (2.62)</td>
<td>8.66 (0.72)</td>
<td>1.02 (0.14)</td>
<td>0.15 (0.1)</td>
</tr>
</tbody>
</table>

Figure 2. Average mangrove seedling growth (total shoot length) in response to mixed litter treatments. Error bars indicate SE. The left panel shows black mangrove growth in response to all possible mixtures and the right panel shows red mangrove growth in response to all possible mixtures. The components of the litter mixtures are indicated by combinations of single letters representing the three mangrove species: R (red mangrove), B (black mangrove), W (white mangrove). The (∗) indicates a significant difference at $p < 0.05$.

Mangrove litter had significantly more root biomass than those growing in red mangrove litter ($p < 0.05$; Table 1). Further, red mangrove seedlings growing in no litter had significantly lower root biomass than all other treatments ($p < 0.05$) and had a lower root:shoot ratio than seedlings amended with litter (model $p = 0.07$, post hoc $p < 0.05$).

**Seedling stoichiometry and soil nutrients**

The C:N ratio of black mangrove seedlings shoots or roots was not significantly altered by litter treatment. However, the C:N ratio of red mangrove shoots and roots were marginally, though not significantly, changed by litter treatments. The no litter treatment yielded somewhat lower C:N ratios of red mangrove shoots ($p = 0.12$; Table 1). Red mangrove seedlings growing in black mangrove litter had higher root C:N than those growing in red mangrove litter or no litter ($p = 0.11$).

Nitrogen levels in mesocosm soils were measured but were so low that they were undetectable by the CHN analyzer.

**Litter decomposition**

Litter type had a significant impact on litter mass loss in black mangrove mesocosms ($p = 0.0004$, $F = 5.75$, $DF = 6$) and...
red mangrove mesocosms ($p = 0.003$, $F = 4.13$, $DF = 6$; Fig. 3). Post hoc contrasts determined that red mangrove litter decomposed 67% slower than black mangrove litter in black mangrove mesocosms and 22% slower than black mangrove litter in red mangrove mesocosms ($p < 0.05$). Plant type also significantly impacted litter decomposition. Litter decomposing beneath black mangroves had significantly lower mass loss than litter decomposing beneath red mangroves ($p < 0.01$). However, there was no significant interaction between plant type and litter type in determining litter decomposition rate. Mixed red–black litter decomposed more quickly than expected in black mangrove mesocosms ($p < 0.05$) and was the only litter mixture that decomposed significantly different from expected rates according to post hoc contrasts. White–black litter mixtures seemingly decomposed more rapidly than expected, but this difference may not be statistically significant due to a lack of power.

**Nitrogen release from litter**

Litter treatments significantly differed in the proportion of initial N released from litter in both black mangrove mesocosms ($p = 0.001$, $F = 5.16$, $DF = 6$; Fig. 4A) and red mangrove mesocosms ($p = 0.06$, $F = 2.18$, $DF = 6$; Fig. 4B). Post hoc contrasts showed that red mangrove litter significantly released a higher percent of initial N than black mangrove litter ($p = 0.05$) and white mangrove litter ($p < 0.001$) in black mangrove mesocosms despite lower decomposition rates. In black mangrove mesocosms, red mangrove litter N released significantly more N than white mangrove litter but did not differ from black mangrove litter N release. There were no significant differences between observed and expected N release values for either mesocosm type. In order to understand the total mass of N available to the seedlings, we calculated N mass loss (((initial % N x initial mass) - (final % N x final mass)) / (initial % N x initial mass)) (Classen et al. 2007). Litter treatment significantly influenced total N mass released for both black mangrove

(p = 0.024, $F = 2.95$, $DF = 6$) and red mangrove mesocosms ($p = 0.10$, $F = 1.86$, $DF = 6$). Post hoc tests showed that there was no significant difference between red and black litter in total N mass released in black mangrove mesocosms or in red mangrove mesocosms, despite the large differences in percent of initial N released (Fig. 4A). Red–black litter mixtures released significantly more N mass than red–white and white–black litter mixtures in black mangrove mesocosms ($p < 0.05$; Fig. 4A). In the red mangrove mesocosms, white litter released significantly less total N mass than all other litter treatments ($p < 0.05$; Fig. 4B).

**Discussion**

This study provides evidence that litter identity can strongly influence growth of mangrove seedlings, implicating plant–litter feedbacks as a driver of seedling productivity. We found that two species of mangrove seedlings grew fastest when supplied litter from a different mangrove species, though biomass accumulation and stoichiometry were independent of changes in growth. Both red and black mangrove seedlings exhibited faster growth in each other's litter, generating an ‘away-field advantage’, (i.e. negative feedback) at least for these two species. This tendency to grow best in other species litter is opposite what would be expected considering the more commonly found ‘home-field advantage’ in litter decomposition (Gholz et al. 2000, Ayres et al. 2009). These results, taken together, seem to indicate a consistent ‘litter from another species yields faster growth’ pattern in this ecosystem. This interesting twist on a plant–soil feedback raises the question: why do mangrove seedlings benefit from the presence of organic matter from another species?

Nitrogen release alone does not seem to explain litter-driven alterations of mangrove seedling growth because total mass of N released from black and red litter was equal in both mesocosm types, despite large differences in initial [N] and decomposition rate. Black mangrove litter has higher

![Figure 3. Average mass loss from litter in black mangrove and red mangrove mesocosms. Error bars indicate SE and litter types are indicated on the x-axis. The components of the litter mixtures are indicated by combinations of single letters representing the three mangrove species: R (red mangrove), B (black mangrove), W (white mangrove). Significant differences between litter treatments are reported in the text.](image-url)
species may diminish the ‘inoculation efficiency’ of the mesocosms with root pathogens and other organisms that could decrease growth.

There has been a substantial amount of research investigating the establishment and survival of mangrove seedlings. Rabinowitz (1978) saw higher survival and growth rates of mangrove seedlings in zones dominated by a different mangrove species. Smith (1987) found that multiple mangrove species grew best in areas not dominated by conspecifics. McKee (1995b) found that transplanted black and red mangrove seedlings grew equally well in the black mangrove zone and that young red mangrove seedlings survived at the same rate as black mangrove seedlings in the red mangrove zone. These findings seem to lend support to our experimental results on seedling growth. A theoretical framework for these patterns may be found in the work of Janzen and Connell. Janzen (1970) predicted that in the tropics seedling survival should increase with distance from the parent plant. Connell (1971) hypothesized that seedling survival is higher with distance from a parent because specialist herbivores (common in the tropics) are less likely to locate the seedling. For mangrove seedlings, the importance of distance from a conspecific is likely accentuated due to the propensity of propagules and litter to ‘raft’ in the water and travel long distances. Because mangroves often exhibit strict zonation, it is likely that propagules and litter often settle in a zone dominated by a different species. Thus, perhaps seedlings are adapted to growing in the presence of litter from other species, especially for inland mangroves such as black mangroves. Though the above-mentioned patterns are interesting, zonation in mangroves is still maintained in most mangrove ecosystems. Therefore, litter movement, rather than propagule movement, may be more important in determining the productivity of seedlings and resultant mangrove stands.

Though growth was significantly altered by litter treatment, most biomass and stoichiometric parameters did not

![Figure 4. Average proportion of initial nitrogen released from litter in black mangrove (left panel) and red mangrove (right panel) mesocosms. Error bars indicate standard error and litter types are indicated on the x-axis. The components of the litter mixtures are indicated by combinations of single letters representing the three mangrove species: R (red mangrove), B (black mangrove), W (white mangrove). Positive numbers indicate N release from litter while negative values indicate N immobilization into litter. Significant differences between litter treatments are reported in the text.](image-url)
mirror these changes in growth. Other than root biomass, which was higher in red mangrove seedlings grown in black mangrove litter, there were no significant differences in shoot biomass, root:shoot, or C:N of root or shoot biomass for the seedlings grown in various litter types. There are at least three possibilities that may explain this disconnect between growth, and biomass and stoichiometry. First, due to the need to reach light, much of the available nutrients in a mangrove seedling may be allocated to stem growth. Stem elongation has been shown to respond more sensitively to altered nutrient variability than other growth parameters (Feller et al. 2009). By examining C:N and biomass of the entire shoot, perhaps we masked changes in stem biomass and C:N. Second, perhaps there are chemical signals (other than availability of nutrients) present in another species’ litter that stimulates mangrove stem elongation and therefore, tissue C:N would not be expected to change. Third, the seedlings in our study could be experiencing strong N limitation, and thus have little plasticity in C:N. Whatever the mechanism, mangrove seedlings seem able to elongate their stems at faster rates when provided certain litter types, irrespective of their total biomass or nutrient accumulation.

Litter diversity often has a large effect on litter decomposition rates (Hättenschwiler et al. 2005, Scherer-Lorenzen 2005, Chapman and Koch 2007, Jonsson and Wårdle 2008). However, these large effects may not translate to impact plant growth, particularly in systems where decomposition proceeds rapidly (Chapman and Koch 2007). In our study, only one litter mixture (i.e. white + black) impacted black mangrove seedling growth differently than expected, but this effect was pronounced. Black mangrove seedlings grew 65% faster than expected in a mix of white + black litter, matching their growth rates in red mangrove litter. White–black litter mixtures have the same lignin:N ratio as red mangrove litter (data not shown) but decompose and release N at different rates. Therefore, similar nutrient delivery by the two litter treatments is likely not driving this result. Nilsson et al. (2008) found that plants growing in litter mixtures that contained Populus tremula yielded higher than expected aboveground biomass. Because both our study and the work by Nilsson et al. (2008) have shown that mixing litter can have substantial synergistic impacts on seedling growth in two very different ecosystems, litter mixing warrants more attention in plant–soil feedback studies.

In this study, we provided answers to three questions regarding the impacts of litter identity and litter mixing on the mangrove seedling growth. First, we found that mangrove litter identity does impact seedling growth (Q1) and that mangroves grow best in litter produced by another species (Q2). Second we found that mixed litter additions can sometimes result in mangrove growth that is different, and in one case, faster than expected growth rates (Q3). That litter identity strongly alters mangrove seedling growth indicates that mangrove plant–soil feedbacks may be mediated by nutrient release during decomposition of litter or by interactions between litter and soil organisms. Coexistence of various dominant species in mangrove ecosystems may be propagated by these feedbacks via adaptations of plants to grow best in litter from other species. Though the findings presented here were generated from a mesocosm experiment, and therefore have somewhat limited application in the field, we encourage further research into plant-soil feedbacks in mangrove and other estuarine systems, where tidal movement commonly generates plant exposure to litter from various species.

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