Fine root respiration in the mangrove *Rhizophora mangle* over variation in forest stature and nutrient availability

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**Summary** Root respiration uses a significant proportion of photosynthetically fixed carbon (C) and is a globally important source of C liberated from soils. Mangroves, which are an important and productive forest resource in many tropical and subtropical countries, sustain a high ratio of root to shoot biomass which may indicate that root respiration is a particularly important component in mangrove forest carbon budgets. Mangroves are often exposed to nutrient pollution from coastal waters. Here we assessed the magnitude of fine root respiration in mangrove forests in Belize and investigated how root respiration is influenced by nutrient additions.

Respiration rates of excised fine roots of the mangrove, *Rhizophora mangle* L., were low (4.01 ± 0.16 nmol CO₂ g⁻¹ s⁻¹) compared to those measured in temperate tree species at similar temperatures. In an experiment where trees were fertilized with nitrogen (N) or phosphorus (P) in low productivity dwarf forests (1–2 m height) and more productive, taller (4–7 m height) seaward fringing forests, respiration of fine roots did not vary consistently with fertilization treatments or with forest stature. Fine roots of taller fringe trees had higher concentrations of both N and P compared to dwarf trees. Fertilization with P enhanced fine root P concentrations in both dwarf and fringed trees, but root N concentrations compared to controls. Fertilization with N had no effect on root N or P concentrations. Unlike photosynthetic C gain and growth, which is strongly limited by P availability in dwarf forests at this site, fine root respiration (expressed on a mass basis) was variable, but showed no significant enhancement with nutrient additions. Variation in fine root production and standing biomass are, therefore, likely to be more important factors determining C efflux from mangrove sediments than variations in fine root respiration per unit mass.

**Keywords:** Belize, fertilization, nitrogen, phosphorus

**Introduction**

Root respiration uses a significant proportion of photosynthetically fixed carbon (C) (Boone et al. 1998), and is a globally important source of C liberated from forest soils (Raich and Schlesinger 1992, Ruess et al. 2003). Mangrove forests cover large areas of the coastal zone in the subtropics and tropics, where they may comprise significant components of regional C budgets (Alongi 2002). They are characterized by conspicuous aboveground roots and, in many regions, by peat substrates that are composed almost entirely of fine roots (McKee 2001, Middleton and McKee 2001). Mangrove sediments are rich in C and have high rates of C accumulation per unit area (mean value of 210 g C m⁻² year⁻¹; Chmura et al. 2003), much of which is derived from fine roots (McKee 2001, Middleton and McKee 2001). The high biomass allocation to aboveground- and coarse belowground roots with abundant aerenchyma ensures an adequate supply of oxygen for fine root metabolism in anaerobic sediments (McKee 1996), whereas high C allocation to fine roots is thought to facilitate nutrient uptake in nutrient limited settings (McKee 1996, 2001). Although aboveground C stocks and rate of C fixation in mangrove forests are relatively well documented (Twilley et al. 1992, Twilley 1995, Clough 1998), and estimated to be globally significant (Ewel et al. 1998), belowground C stocks and rates of C turnover are poorly known (e.g., Ong et al. 1995).

Respiration rates of fine roots in temperate ecosystems are known to vary over sites and tree species, and are strongly influenced by root temperature and tissue nitrogen (N) concentration (Pregitzer et al. 1998, Reich et al. 1998, Burton et al. 2002). Nitrogen concentrations of fine roots are correlated with N uptake rates and assimilation (Pregitzer et al. 1998, Reich et al. 1998). Mangrove forests are subject to nutrient enrichment due to agricultural and urban pollution of estuaries (Valiela et al. 2001), which is likely to affect nutrient uptake, fine root nutrient content and, hence, fine root respiration. Effects of nutrient enrichment on fine root respiration may, in turn, affect C cycling and ecosystem function (Rivera-Monroy et al. 2004).

In aboveground tissues, enhanced growth rates (e.g., Onuf et al. 1977, Feller 1995, Lovelock et al. 2004) and rates of photosynthetic C gain have been observed in mangroves fertilized with both N and phosphorus (P) (Lovelock and Feller 2003, Lovelock et al. 2006), but less is known about responses...
of belowground tissues to nutrient enrichment.

In the mangrove forested islands in Belize, where our experiment was conducted, there is a marked gradient in tree height from taller (4–7 m) more productive fringing forests of Rhizophora mangle L. on the seaward side of the islands to less productive inland stands of dwarf trees, 1–2 m in height. The soils in the fringing forest are flooded by the tide daily, whereas the inland dwarf forest is perennially flooded except during unusually low tides. By means of a fertilization experiment, it was established that aboveground growth of trees in the taller fringing forests is N limited whereas growth of dwarf trees is strongly P limited (Feller et al. 2002). In this study, we aimed to test whether fine root respiration of R. mangle was sensitive to nutrient additions. We, therefore, assessed fine root respiration across the natural tree-height gradient and in settings where aboveground growth was limited by either N or P or both.

Based on the existence of correlations among plants traits (Chapin 1980), in particular between above- and belowground traits (e.g., Comas et al. 2002, Tjoelker et al. 2005), and reports linking tissue nutrient concentration and respiration rate over a range of species (Reich et al. 1998), we expected root respiration of R. mangle to reflect aboveground growth, with taller fringe trees having a higher fine root respiration rate than dwarf trees. We also anticipated that taller N-limited trees of the fringing forest would exhibit enhanced fine root respiration in response to N fertilization, whereas P-limited dwarf trees would exhibit enhanced fine root respiration rates in response to P fertilization.

Materials and methods

Site description and experimental design

The study was conducted at Twin Cays (16°50′ N, 88°6′ W), a 92-ha archipelago of mangrove islands located approximately 1.6 km inside the Belizean Barrier Reef Complex (see Feller et al. 2002, McKee et al. 2002 and references therein for a full site description). The islands are composed of peat that rests on the Pleistocene coral reef platform. They are situated approximately 12 km from the mainland and receive no terrestrial inputs of freshwater or sediments. Twin Cays is dominated by Rhizophora mangle (red mangrove) and Avicennia germinans (L.) Stearn. (black mangrove) with scattered Laguncularia racemosa (L.) Gaertn. f. (white mangrove).

There is a distinctive tree-height gradient, from a narrow (5–10 m wide) fringe zone of uniformly tall trees (4–7 m) that occur within the low intertidal zone around the margins of the islands to a zone of dwarf trees, 1–2 m in height, in the island interior. Soil surface elevation varies along this height gradient, with the transition zone, or zone intermediate between fringe and dwarf, having the highest elevation and the dwarf zone having the lowest (McKee et al. 2002). Flooding follows the variation in elevation: the fringe zone is flooded and drained > 700 times per year, while the dwarf zone is perennially flooded, except during unusually low tides. Both fringe and dwarf zones are dominated by R. mangle.

Experimental sites were established on the two largest islands of Twin Cays. There were two sites on the eastern island, one near Boa Flats to the south and the other on the Lair Channel to the north, and there was one site on the western island, near the boat dock (see Feller et al. 2002 and McKee et al. 2002 for a full site description). The dwarf trees at Boa Flats and the boat dock, but not at the Lair Channel site, were adjacent to inland ponds. Trees at the Lair Channel site were flooded less often than at the other sites.

At each site, three transects, 10 m apart, were established perpendicular to the shoreline and traversing the tree-height gradient from shoreline to island interior. Transects were subdivided into three zones based on tree height (fringe: 4–7 m; dwarf: 1–2 m; and transition: 2–4 m), and three experimental trees were selected within each zone for a total of nine trees across each transect and a total of 81 trees overall. Rhizophora mangle trees selected were each fertilized first in January 1995, and then at 6-month intervals with 300 g of N fertilizer as urea (N.P.K, 45.0,0) or P fertilizer as P2O5 (N.P.K, 0.45.0), as described in Feller (1995). Only trees from the fringing and dwarf zones were studied (54 trees, 18 each of N and P fertilized and 18 control trees). Over the 9 years between establishment of the experiment and measurement of fine root respiration in February 2004, each tree received approximately 5.5 kg of fertilizer.

Root respiration

Fine roots were harvested from the top 5 cm of sediment at the base of each experimental tree in February 2004. Roots were harvested during the mornings (between 0900 and 1100 h local time). The harvested roots were washed in seawater and a sample with roots of less than 2 mm diameter selected. The fine root sample (between 0.05 and 0.4 g dry mass) was loosely wrapped in a tissue paper moistened with sea water and placed immediately in an aluminum cuvette (5.4 cm diameter × 15 cm in length) coupled to an LI-6400 photosynthesis system (Li-Cor, Lincoln, NE) configured as an “open” system. The cuvette was immersed in sea water to keep the chamber at ambient temperature (28 °C). Humidified air (>90% RH) was drawn through both the sample and reference cuvette of the LI-6400. Roots were allowed to equilibrate with ambient air with a CO2 concentration of approximately 370 ppm for 5 min, in which time a constant CO2 exchange rate was achieved. Subsequently, CO2 exchange was logged every 30 s for 7.5 min. Respiration rate for each sample was calculated as the mean of the 15 values.

Because the moistened tissue paper was found to de-gas CO2 over the course of the root respiration measurement, tissue paper controls, without fine roots, were run and the control values subtracted from root respiration values.

After the respiration measurement, the root samples were oven-dried at 60 °C. Nitrogen concentrations of the dried tissue were determined by near infrared spectrometry (NIRS, Model 5000, Foss NIRS Systems, Silver Springs, MD), the instrument being calibrated against R. mangle tissue by analysis with a CHN Analyzer (Perkin-Elmer 2400, Perkin Elmer,
Norwalk, CT) at the Smithsonian Environmental Research Center, Edgewater, MD. Tissue phosphorus concentrations were determined by inductively coupled plasma spectroscopy (ICP) by Analytical Services, Pennsylvania State University, State College, PA.

Data analysis

Effects on fine root respiration, and N and P concentrations were evaluated by a $3 \times 2$ factorial (nutrient treatment $\times$ zone) analysis of variance (ANOVA), blocked by site. Where significant main effects or interactions were identified, Fisher’s Least Significant Difference post hoc hypothesis test was used to assess pairwise differences within and among the treatments. To analyze for heteroscedasticity, probability plots of all variables and residual plots were examined.

Results

Fine root respiration was low in all treatments. The overall mean value of $4.01 \pm 0.16 \text{ nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ (Figure 1) was not significantly ($P < 0.05$) affected by site, zone or fertilization (Table 1), although respiration tended to be higher in fertilized than in control trees (particularly in the dwarf trees) and in fringe trees than dwarf trees (Figure 1). There were highly significant site $\times$ zone, site $\times$ treatment and site $\times$ zone $\times$ treatment interactions on fine root respiration (Table 1), which were largely caused by the low respiration of control dwarf trees at the Boa Flats site (data not shown).

Fine root nutrient concentrations were significantly influenced by forest zone and by the P fertilization treatment (Table 1). Dwarf forests had lower fine-root N and P concentrations than fringe forest trees (Figure 2). Fertilization with P enhanced P concentrations in fine roots in the dwarf and fringe forest trees, and resulted in significant reductions in fine root N concentrations. Within treatments, N and P were correlated (Figure 3). Regressions of N and P concentrations of fine roots for the three treatments had similar slopes (unfertilized control ($C$) = 0.049, N = 0.054, P = 0.057), but fine roots of P fertilized plants had higher P concentrations at the same N concentration (i.e., different intercepts). Despite large variation in fine root N and P (from 1–6 mg g$^{-1}$ N and 0.15–0.5 mg g$^{-1}$ P) there was no correlation between fine root respiration and fine root N or P concentration (data not shown; $r^2 = 0.04$ and 0.05, respectively).

Discussion

In this study we observed fine root respiration rates in $R$. mangle of 0.5–6 nmol CO$_2$ g$^{-1}$ s$^{-1}$, which are comparable to rates reported for $R$. mangle in hydroponic culture (3–6 nmol CO$_2$ g$^{-1}$ s$^{-1}$ at 25 °C; McKee 1996). These rates are low compared with the reported range (3–55 nmol CO$_2$ or O$_2$ g$^{-1}$ s$^{-1}$) for other angiosperm trees species (Reich et al. 1998, Burton et al. 2002, Comas et al. 2002, Tjoelker et al. 2005). Only in junipers and pines in arid, high-elevation sites in New Mexico have such low fine root respiration rates been reported (Burton et al. 2002).

Fine root N concentrations on a mass basis were low in $R$. mangle (range 1–6 g kg$^{-1}$) compared to fine roots of a range

Table 1. Summary of three-way ANOVAs performed on fine root respiration, and nitrogen and phosphorus concentrations of $Rhizophora$ mangle trees at Twin Cays, Belize, with three nutrient treatments (control; nitrogen; and phosphorus) in two zones (fringe and dwarf) blocked by site (two on the eastern island (Boa Flats and Lair Channel) and one on the western island).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>F ratio</th>
<th>P</th>
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</thead>
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<td>Fine root respiration</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>0.99</td>
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<tr>
<td>Zone</td>
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<tr>
<td>Treatment</td>
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<td>0.3302</td>
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<tr>
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<td>0.0105</td>
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<td>0.0008</td>
</tr>
<tr>
<td>Zone $\times$ Treatment</td>
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<td>0.6856</td>
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<td>Site $\times$ Zone $\times$ Treatment</td>
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<td>6.39</td>
<td>0.0006</td>
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<td></td>
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<tr>
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<td>Treatment</td>
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<td>0.9796</td>
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<tr>
<td>Fine root phosphorus</td>
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<td></td>
</tr>
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<td>0.880</td>
<td>0.4853</td>
</tr>
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</table>

Figure 1. Fine root respiration of $Rhizophora$ mangle trees of the seaward fringe (Fringe) and landward dwarf (Dwarf) stands either unfertilized (C) or fertilized with nitrogen (N) or phosphorus (P). Values are means ± standard errors.
of temperate forest tree species (Burton et al. 2002; range 8–20 g kg⁻¹), and were within or beyond the low end of the range (2–28 g kg⁻¹) reported for coniferous forest tree species (Gordon and Jackson 2000). Low fine root N and fine root respiration rates in *R. mangle* compared to other tree species may be related to the dominance of ammonium as a source of N in mangrove soils (Alongi 1996, McKee et al. 2002). Because ammonium is energetically inexpensive to assimilate, its use limits the respiratory costs of N uptake and assimilation.

On a unit N basis, fine root respiration of *R. mangle* averaged 20 µmol mol⁻¹ N s⁻¹ at 28 °C, corresponding to a rate of 7 µmol mol⁻¹ N s⁻¹ at 15 °C, assuming a *Q₁₀* of 2.0. This is considerably higher than rates (2.1–2.60 µmol mol⁻¹ N s⁻¹) reported for *Pinus pinaster* L. and other species after standardization to 15 °C (Vose and Ryan 2002).

We found no significant correlation between root nutrient concentration and fine root respiration despite a large range of N concentrations, which contrasts with results of interspecific comparisons (Burton et al. 2002, Tjoelker et al. 2005) and a study of variation within *Pinus radiata* L. (Ryan et al. 1996). Our result are consistent, however, with findings for *Pinus strobus* L. (Vose and Ryan 2002).

One possible reason for the absence of a correlation between fine root respiration and tissue N content is that root N is, in part, stored in metabolically inactive compounds when N availability is high (Chapin 1991). This interpretation is consistent with the reduction in N concentration of roots of trees fertilized with P (Figure 2). Growth at our experimental site is strongly P limited, particularly in dwarf trees. Thus, fertilization with P reduces N concentrations of both fine roots (Figure 3) and leaves (Feller et al. 2002, Lovelock et al. 2004), presumably because limiting P stimulated growth, allowing deployment of excess N to growing tissues.

Fine root respiration rates have been found to correlate with aboveground growth and other traits in tree seedlings over a range of species (Reich et al. 1998, Comas et al. 2002). However, in our study, although growth rates varied more than 10-fold between fertilized and control trees, we found no significant correlation between rates of fine root respiration and aboveground growth (data not shown). A similar absence of correlation was reported by Comas and Eissenstat (2004) in a study of mature individuals of 11 temperate tree species. Furthermore, within a single species (*Pinus strobus*), the strength of correlations between growth and respiration in different tissues was found to depend on the tissues considered, shoot growth, for example, being correlated with stem respiration, but not with branch or coarse root respiration (Vose and Ryan 2002).

In our study, growth of trees in the fringing forest at the island margins was enhanced by N fertilization, but photosynthetic C gain expressed on a per unit leaf area basis was not; whereas in dwarf trees in the island interior, growth and photosynthetic C gain were both strongly enhanced by additions of P (Feller et al. 2003, Cheeseman and Lovelock 2004, Lovelock et al. 2006). In another fertilization experiment in Bocas del Toro, Panama, both N and P additions stimulated shoot growth of *R. mangle*, but not photosynthetic rate (Lovelock et al.
Comparison of trait plasticity in *R. mangle* for aboveground processes showed that leaf-level physiological processes are less plastic than architectural and biomass allocation traits (Lovelock et al. 2006). Similar trends may be evident below ground, with the biomass allocation to fine roots being more variable than the physiological processes of roots themselves. Meta-analysis of variation in the strength of physiological responses to nutrient availability over a range of terrestrial species found the strength of responses to nutrient additions depended on differences in allocation to plant organs and to variation in availability of other resources and abiotic stresses (Poorter and Nagal 2000).

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