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FACULTATIVE MUTUALISM BETWEEN RED MANGROVES AND ROOT-FOULING SPONGES IN BELIZEAN MANGAL[1]

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Abstract. We report results of transplant experiments that examined direct interactions between red mangrove (*Rhizophora mangle*) roots and two common root-fouling sponges (*Tedania ignis* and *Haliclona implexiformis*) on carbonate-based, oligotrophic mangrove cays in Belize, Central America. On these cays, subtidal prop roots of mangroves at water's edge often extend 1–2 m below lowest low water before anchoring in the substrate and host a community of algal and invertebrate epibionts dominated by massive sponges. Live sponges transplanted onto otherwise bare roots increased root growth rate two- to fourfold relative to controls. Roots fouled naturally by these and other massive sponges produce adventitious fine rootlets that ramify throughout sponge tissue; these rootlets structurally resemble underground rootlets that function in nutrient uptake. Sponges transplanted onto bare mangrove roots induced rootlet proliferation within 4 wk. Only live sponges elicited this response, indicating that adventitious rootlet production is not simply a by-product of anoxia or darkness. Sponges transplanted onto bare roots grew 1.4–10 times faster than did sponges grown on polyvinyl chloride (PVC) tubes at identical depths and locations. Relative abundances of ^{15}N (expressed as $\delta^{15}N‰$) and ^{13}C ($\delta^{13}C‰$) in *Tedania, Haliclona,* an additional sponge, *Ulosa ruetzleri,* and rootlets, roots, stems, twigs, and leaves of mangrove hosts suggest that mangrove roots obtain dissolved inorganic nitrogen from sponges, and that sponges obtain carbon from mangrove roots. No transfer of N or C was observed in similar analyses of roots fouled by the red alga *Acanthophora spicifera.* We conclude that where they co-occur, massive sponges and mangroves are facultative mutualists. In mangrove forests, as in other marginal habitats, facilitations may enable increased growth and production of component species.

Key words: Belize; ecosystem dynamics; facilitations; Haliclona implexiformis; *mangroves; mutualisms; plant–animal interactions; Porifera;* Rhizophora mangle; Tedania ignis.

INTRODUCTION

Positive interactions among species are predicted to be most prevalent and to play a significant role in controlling community structure and ecosystem dynamics in species-poor, marginal, or stressed habitats (reviewed by Bertness and Callaway 1994). In such habitats, groups of species can positively affect each other's growth and production, either directly (e.g., Bertness 1984, McKinney et al. 1990, Carlsson and Callaghan 1991, Bertness and Hacker 1994) or as intermediaries controlling nutrient transfer between apparent competitors (e.g., Newman and Ritz 1986). In addition, dominant species in marginal habitats can buffer associates from limiting stresses, such as low levels of nutrients, soil oxygen, or soil moisture (e.g., Williams 1990, Frank and McNaughton 1991, Smith et al. 1991, Callaway 1992, Tilman and Downing 1994). Because species-poor ecosystems often are characterized by relatively low spatial heterogeneity, these ecosystems also can provide experimentally tractable environments in which to determine the importance of particular species and interspecific interactions in regulating energy and nutrient flow (Naeem et al. 1994).

Tidal ecosystems are just such model marginal environments. Temperate zone salt marshes and tropical mangrove forests are the most productive ecosystems on the planet (Lugo and Snedaker 1974, Clough 1992), yet they are characterized by comparatively low plant and animal species richness, and exhibit far less spatial heterogeneity than upland environments (e.g., Odum et al. 1982, 1984, Zedler 1982, Josselyn 1983). These land-margin ecosystems are nutrient limited (e.g., Alongi et al. 1992, Vernberg 1993), and their waterlogged, anoxic soils similarly limit plant growth and distribution (e.g., Mendelssohn et al. 1982, Naidoo 1985, Mendelssohn and McKee 1988). However, the

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historical emphasis in studies of salt marsh and mangrove ecosystems on estimates of nutrient and carbon flux on net primary production of single dominant plant species (e.g., *Spartina alterniflora* in salt marshes; *Rhizophora mangle* in mangrove forests) and detritus-based trophic webs has obscured the presence and importance of direct interactions, positive or negative, among plants and animals living in these forests (but see Bertness 1984, 1985, Smith et al. 1989, Robertson 1991, Twilley et al. 1993).

Species richness of animals is 1–2 orders of magnitude greater than plant species richness in mangrove forests (e.g., Macnae 1968, Rützler 1969, Simberloff 1976, Farnsworth and Ellison 1991, 1996*b*, Alongi and Sasekumar 1992), and recent experiments in mangroves have illustrated that associated animals can affect individual plant growth rates, population dynamics, community structure, and patterns of primary production. For example, root-boring isopods reduce root growth rate by >50% (Perry 1988, Ellison and Farnsworth 1990, 1992), although root-fouling sponges and ascidians ameliorate this negative effect indirectly by preventing isopods from colonizing fouled roots (Ellison and Farnsworth 1990). Herbivorous insects reduce seedling and sapling growth rates (Farnsworth and Ellison 1991, 1993, Feller 1995). Stem-boring cerambycid beetles girdle branches and create gaps necessary for successful seedling establishment (I. C. Feller, *personal communication*). Pre- and postdispersal predation of mangrove seedlings (propagules) by scolytid beetles and other insects (Rabinowitz 1977, Robertson et al. 1990, Farnsworth and Ellison 1996*a*) and grapsid crabs (e.g., Smith et al. 1989, McKee 1995) limit seedling recruitment and contribute to the establishment and maintenance of mangrove species zonation patterns. These effects of associated fauna on mangrove growth and production suggest that nondecomposer animal–plant interactions could significantly impact carbon flux in mangrove ecosystems, yet even the most complex mangrove carbon budgets do not account for these interactions (Robertson et al. 1992, Twilley et al. 1992).

The contribution of animals to nitrogen and phosphorus dynamics in mangrove forests likewise has been overlooked. Mangrove primary production is limited by available N and P, and it has been suggested that N is the primary limiting nutrient at the seaward margin of mangal, while P is limiting in higher intertidal zones (Boto and Wellington 1983, 1984, Boto 1992, Feller 1995). In salt marshes, the temperate analogue of tropical mangrove forests, Bertness (1984) demonstrated that inorganic nitrogen (ammonium) deposited by epibenthic mussels (*Geukensia demissa*) increased growth of marsh grasses. Although birds nesting in mangroves are a significant source of inorganic nitrogen for *Rhizophora* (Onuf et al. 1977), the importance to nutrient fluxes of invertebrates associated with mangroves has not been demonstrated previously. Based on Bertness and Callaway's (1994) review of positive interactions in marginal habitats, we hypothesized that some proportion of nutrient flux in mangrove ecosystems could be mediated by interspecific positive interactions.

In the experimental study reported here, we assessed the effects of pairwise interactions between root-fouling sponges (Porifera) on growth of red mangrove (*Rhizophora mangle*) roots, an interaction that merits attention in models of nutrient flux in mangrove ecosystems. We provide evidence from manipulative experiments and analysis of stable isotope composition ($\delta^{15}N$ and $\delta^{13}C$) that mangrove root-fouling sponges facilitate growth of mangrove roots, while mangroves facilitate sponge growth. This result adds to a growing list of documented animal–plant interactions that may have important controlling effects on mangrove community structure, and supports the hypothesis that positive interactions ought to be relatively common in stressful and marginal ecosystems.

Study Site and Study Species

The field experiments described here were conducted at Twin Cays (16°48′ N, 88°05′ W; referred to as Water Range by Stoddart et al. 1982), an ≈1-km^2 group of mangrove cays 4 km west of the Carrie Bow Cay marine station (Fig. 1; Rützler and Macintyre 1982). Tides in Belize are microtidal; mean tidal amplitude at Carrie Bow Cay is ≈30 cm (Kjerfve et al. 1982), mean annual temperature is 25°C, and mean annual rainfall is ≈1500 mm (Hartshorn et al. 1984, Hagerman and Smith 1993). *Rhizophora mangle* is the dominant mangrove species at Twin Cays, occurring from lowest low water (LLW) to the highest points on the islands (<1 m above mean sea level). The mangrove forest at Twin Cays is classified as a "fringing mangrove forest" (sensu Lugo and Snedaker 1974) or a "mangrove forest fringing oligotrophic waters of carbonate platforms" (sensu Twilley 1995).

All mangroves, including *Rhizophora mangle,* produce aerial roots that function primarily in gas exchange (Scholander et al. 1955, Gill and Tomlinson 1969, 1971, 1977, Tomlinson 1986). In *Rhizophora,* aerial "cable" roots originate from lateral meristems of the trunk and branches. These cable roots grow 0.5–1.5 mm/d toward the ground, and their diameter (normally 10–20 mm) changes little during this elongation phase (Gill and Tomlinson 1977). When the root tip reaches the ground, a series of pronounced morphological changes occur: the root tip loses its pigmentation, the cable root begins to thicken and lignify (secondary cambial growth), and numerous adventitious and fine rootlets begin to grow from the root tip into the substrate (Gill and Tomlinson 1977). These rootlets anchor the plant and take up nutrients from benthic sediments.

At the seaward edge of a mangrove forest, cable roots normally grow through water before reaching solid ground. Because of the relatively low tidal amplitude

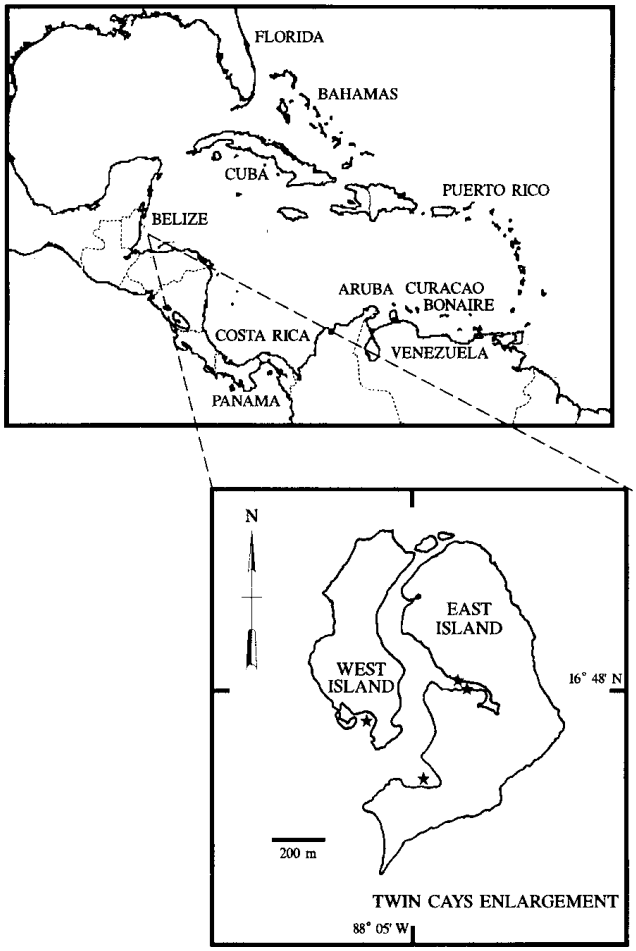

FIG. 1. Map of the Caribbean region illustrating localities from which sponges have been reported on mangrove roots. The four areas where sponge addition experiments were performed are indicated by stars on the Twin Cays enlargement. Sites are (clockwise from left): Twin Bays; Lair Channel North; Lair Channel South; Boston Bay. The two islands are separated by the Main Channel, where we examined the growth of sponges on different substrates.

(<1 m) in the Caribbean basin, the cable roots of red mangroves growing at the water's edge are continuously submerged (Fig. 2). These cable roots often are the only local hard substrate in an otherwise soft-bottom habitat; consequently, a diverse fouling community often develops on these subtidal roots (e.g., Rützler 1969, Farnsworth and Ellison 1996*b*). While many of the root-fouling organisms are epibenthic, others, such as isopods and shipworms excavate galleries into the cable roots, allowing marine fungi and other decomposers to colonize and degrade the root (e.g., Kohlmeyer 1984, Hyde and Jones 1988). Roots that grow quickly through the water and anchor into the substrate can avoid this attack, as the secondary lignification that occurs after anchoring limits direct herbivory on roots (Ellison and Farnsworth 1992).

Percent cover of epibionts on mangrove roots at Twin Cays is normally >90% (Farnsworth and Ellison 1996*b*). There, massive sponges (Porifera with lobes, "fingers," or other tertiary structures that extend above the substrate into the water column) dominate this fouling community both in terms of numbers of roots occupied (≈35%) and percent of space (≈30%) covered on a single root (Ellison and Farnsworth 1992, Farnsworth and Ellison 1996*b*). Similar, primarily qualitative patterns have been noted for mangrove–root epibiont community structure elsewhere in the Caribbean (Rützler 1969, Sutherland 1980, Alcolado 1986, Alvarez I. 1989, de Weerdt et al. 1991, Bingham 1992, Garrity and Levings 1992, Thomas et al. 1992, Levings et al. 1994). Successful colonization of roots appears to be controlled primarily by larval supply (Farnsworth and Ellison 1996*b*). Short-term (intraseasonal) abundance of epibionts on roots likely is determined by interspecific competitive interactions and predation, while longer-term abundance is limited by seasonal environmental changes, notably freshwater inputs during winter rains (A. M. Ellison and E. J. Farnsworth, *unpublished data*).

In these experiments, we focused on the effects of two species of massive sponges on growth of *Rhizophora* roots: *Tedania ignis* (Tedaniidae) and *Haliclona*

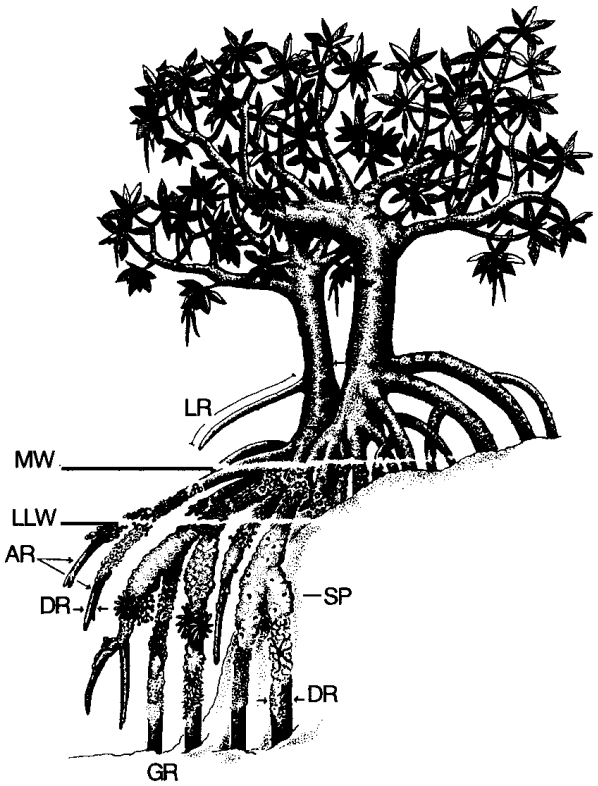

FIG. 2. Illustration of a fringing red mangrove tree at Twin Cays, showing relationship of cable roots to mean water (MW) and lowest low water (LLW) tidal levels. Aerial roots (AR) originate from the main stem well above the ground surface, and can grow through the water before anchoring (grounding) in the substrate (GR). Such roots are fouled by a number of marine epibionts (SP: sponge). Length (LR) of cable roots was measured from point of origin on the main stem to root tip, while root diameter (DR) was measured 10 cm basipetal of the root tip. Illustration by Elizabeth J. Farnsworth.

implexiformis (Chalinidae) (nomenclature follows Wiedenmayer 1977, de Weerdt et al. 1991). At Twin Cays, *Tedania* and *Haliclona* are the most common (in terms of number of roots occupied) and abundant (in terms of percent cover) sponge species that occur on submerged mangrove roots (Farnsworth and Ellison 1996*b*).

Methods

Effects of sponges on root growth: addition experiments

Our previous experiments had demonstrated that removing sponges from mangrove roots resulted in a 55% decrease in root growth rate as isopods (primarily *Phycolimnoria clarkae* [Limnoriidae]) attacked roots lacking sponge cover (Ellison and Farnsworth 1990). In order to determine if sponges had direct effects on root growth in addition to these indirect effects, we transplanted living and artificial sponges onto newly submerged, bare, unattacked roots. In August 1991, at each of four sites within Twin Cays (Fig. 1), 24 hanging roots were selected for manipulation and marked with permanent numbered plastic bands (National Band and Tag Company, Newport, Kentucky, USA). Water depth (at low tide) below mangrove roots at these four sites ranged from 0.5 to 1.5 m, and at least the terminal 15 cm of each root was below LLW. In each location, roots were randomly assigned to one of four treatments: control (no manipulation); foam (artificial sponges); *Haliclona implexiformis* transplants; *Tedania ignis* transplants. For the foam treatment, roots were lifted gently out of the water and coated with an ≈2 cm thick jacket of liquid polyurethane insulating foam (Macklanburg-Duncan, Oklahoma City, Oklahoma, USA) to create a seamless, inert, massive sponge-like encrustation on the root. We established living sponge transplants by cutting small pieces (≈50 mL volume by displacement) from nearby sponges and tying them onto bare roots with plastic cable ties. Fragmentation is the normal mode of asexual reproduction in many Caribbean sponges (e.g., Wulff 1985, 1991), and we observed no ill effects of this technique on growth of the transplanted sponges. Living sponge transplants normally attached to the roots within 72 h, as new pinacoderm (basal attachment epithelial tissue; Bergquist 1978) grows over the root surface. The few sponge transplants that died within the 1st wk of the experiment were replaced. Root growth rates were determined from measurements of root length (±1 mm) and diameter (±0.1 mm, measured 10 cm from point of attachment; Fig. 2) taken on 13 August 1991 (the day before all transplants were done), 30 December 1991, 18 March, 1 June, and 15 July 1992. Root volume was estimated at each sampling date by considering the root as a cylinder; estimated volume = $\pi \times (\text{diameter}/2)^2 \times \text{length}$. This experiment was treated as a randomized block design, where each of the four sites was treated as a "block." Untransformed growth rate data (in millimetres per day for length and diameter; cubic millimetres per day for volume) were analyzed using analysis of variance (SYSTAT release 5.03; Wilkinson et al. 1992). A priori pairwise contrasts (*Tedania* vs. foam; *Tedania* vs. control; *Haliclona* vs. foam; *Haliclona* vs. control; foam vs. control) were used to assess treatment effects.

Relationship between sponges and adventitious root production

While inspecting the roots used in the transplant experiments, we observed adventitious fine rootlets produced from the cable root well above the ground surface, and ramifying throughout the sponge transplants. Such rootlets are known to function in nutrient uptake in mangroves, but are found rarely above ground (Gill and Tomlinson 1977, Ellmore et al. 1983). We tabulated the frequency of rootlet production among our four transplant groups to determine if rootlet production was associated significantly with treatment. In order to ascertain whether or not rootlets occurred on other fouled roots at Twin Cays (not just those covered with massive sponges), we inspected an additional 150 haphazardly selected subtidal mangrove roots that were covered by a diversity of epibiont taxa. These sampled roots were growing in the same four sites where we conducted the sponge transplant experiments. Roots examined each had at least 50% cover of a single common epibenthic species. These epibionts represented the common higher taxonomic groups (cyanobacteria [one sp.], algae [two spp.], sponges [eight spp.], ascidians [three spp.], cnidaria [one sp.]) that occurred most frequently on submerged roots (Farnsworth and Ellison 1996*b*), and which form dense tissue masses on roots. We removed the epibionts from 10 replicate roots per epibenthic species and observed the presence or absence of adventitious rootlets on each root. Strength of association between epibionts and rootlet production was assessed using a *G*-test.

Growth of sponges on different substrates

To characterize the reciprocal half of the sponge–root interaction, we sought to determine whether carbon derived from mangrove roots could "leak" into sponges, enhancing sponge growth rate on roots relative to nonliving substrate. To examine this potential interaction, in June 1992 we grew *Tedania* and *Haliclona* on otherwise bare roots (10 replicates per species), and on 20 cm long 1.25 cm diameter polyvinyl chloride (PVC) tubes (10 replicates per species) on the western side of the Main Channel separating the east and west islands of Twin Cays (Fig. 1). Cut mangrove roots were not used for this experiment, because they rot rapidly in seawater. PVC tubes were "seasoned" in seawater for 2 wk prior to use to minimize degassing during the experiment and to allow for the development of a bacterial film that could facilitate attachment of

sponges. We have observed (E. J. Farnsworth and A. M. Ellison, *unpublished data*) sponge larvae colonizing unseasoned PVC tubes that have been immersed for <2 wk, and we are confident that there were no effects of PVC on sponge growth. A 28-g fishing weight was suspended from the bottom of each PVC tube to prevent it from floating. The PVC tube was then suspended in the water by tying it to a mangrove branch within 0.5 m of a paired living root with a sponge transplant. Sponge fragments were transplanted (as in the sponge-root growth addition experiments) onto the roots and PVC tubes, and all transplants attached to both roots and PVC tubes within 3 d. Prior to transplantation, the volume of each sponge fragment was estimated based on its displacement of seawater in a graduated cylinder (±1 mL). After 1 mo, we completely removed all sponge transplants from the roots and tubes, remeasured their volume, and calculated their relative change in volume ($[\text{volume}_{\text{final}} - \text{volume}_{\text{initial}}]/\text{volume}_{\text{initial}}$). These data were analyzed using a Mann–Whitney *U* test (*Tedania* on roots vs. *Tedania* on PVC; *Haliclona* on roots vs. *Haliclona* on PVC), since standard transformations did not eliminate heteroscedasticity in the data.

Stable isotope analysis

Stable isotope analyses have been used extensively to trace carbon and nitrogen movement among and between many ecosystems (e.g., Peterson et al. 1985, Peterson and Fry 1987, Rundel et al. 1988), including mangrove forests and adjacent seagrasses (e.g., Fry and Sherr 1984, Torgensen and Chivas 1985, Fry et al. 1987, Rezende et al. 1990, Hemminga et al. 1994, 1995). Organisms that derive nitrogen from organic materials and decomposition are enriched in ^{15}N relative to ^{14}N (referred to as $\delta^{15}N$), while organisms that obtain most of their nitrogen from biological fixation of atmospheric nitrogen have $\delta^{15}N \approx 0‰$. As C_3 species, mangroves show a relatively strong depletion of ^{13}C; their normal ratio of $^{13}C/^{12}C$ (referred to as $\delta^{13}C$) ≈ -27 to $-30‰$. The $\delta^{13}C$ value of consumers' tissues will reflect the $\delta^{13}C$ value of their source carbon (Peterson and Fry 1987); relatively low (large negative) values of $\delta^{13}C$ in animals living in a mangrove ecosystem indicate that some of their carbon intake is derived from mangrove trees (Ambler et al. 1994), while relatively high (small negative) $\delta^{13}C$ values would reflect a diet low in mangrove carbon.

To determine potential amounts of nitrogen transferred from sponges to roots through adventitious roots, and carbon leaking from rootlets into sponges, we examined the natural isotopic composition of N and C ($\delta^{15}N$ and $\delta^{13}C$ values) of root-fouling sponges, their associated fine rootlets, the roots they fouled, and branches, twigs, and leaves of the associated trees. Samples of root-fouling sponges and plant tissue for stable isotope analysis were collected from Twin Bays (Fig. 1). Six 50-mL samples each of *Tedania* and *Haliclona* were gently removed from cable roots (each sponge species from a different tree). Of these, three samples of each sponge species were collected from roots with fine rootlets penetrating the sponge, and three samples of each sponge species were collected from roots that had not yet produced fine rootlets. We then removed and saved all the fine rootlets from within the sponge; cut 2-cm sections of the belowwater and abovewater portion of the cable root on which the sponges were growing; and similarly sized samples of a randomly chosen branch on that tree, its terminal twig, and all leaves on that twig. The sponge sampling thus included 12 trees: 6 for each sponge species, of which 3 had fine rootlets and 3 did not. For comparative purposes, we also collected similar samples from plants with roots covered with the encrusting (rarely massive) sponge, *Ulosa ruetzleri* (Mycalidae), into which rootlets are produced only occasionally, and from plants with roots fouled by the red alga *Acanthophora spicifera,* into which rootlets are never produced. The alga also provided a control for our measurements of ^{13}C and ^{15}N, which are known to be very different in algae relative to both angiosperms and heterotrophs. Epibiont and mangrove tissue samples from these trees were collected in the same way as those on which *Tedania* and *Haliclona* were growing.

All samples were individually packaged and labelled, air-dried for 7 d in Belize (≈30°C), and then oven-dried in Louisiana (70°C) to constant mass. Dried samples were ground in a Wiley mill with 80-mesh stainless steel screen, and stored in a vacuum desiccator. Samples were treated with 1 mol/L HCl and dried at 60°C for 48 h to remove contamination from carbonate deposits. Sample material for total carbon and nitrogen determinations were combusted at >900°C in a LECO elemental analyzer (LECO Corporation, St. Joseph, Michigan). The isotopic compositions of C and N were determined with an isotopic ratio mass spectrometer at the Woods Hole Ecosystems Center's stable isotope laboratory, from samples cryogenically purified in a custom-built stainless steel manifold (Fry et al. 1992).

We compared the rate of diminution in the $\delta^{15}N$ signal between roots with rootlets penetrating the sponges and roots without rootlets using nonlinear regression. Because samples on different trees were taken from different positions relative to the sponge, we assigned dummy values to sampling location (sponge = 0, rootlets = 1, . . . , leaf = 6); these values were used as independent variables in the nonlinear regression. We then fit the following equation separately to each set of data points:

$$\delta^{15}N = a \times \exp(b\sqrt{\text{location}}),$$

where a and b were estimated parameters. The parameter b is the shape parameter for the curve; a large negative value for b indicates a rapid diminution of $\delta^{15}N$, while a less negative value for b indicates slower

TABLE 1. ANOVA table summarizing effects of transplant type on root growth rate, and results of planned pairwise contrasts between treatments. Location was considered as a block effect in the design. In the matrix of pairwise contrasts between treatments, the location × transplant mean square was used as the error term. $N = 4$ locations and 24 roots per transplant treatment at each location.

Source	SS	df	MS	F	P
Location	0.689	3	0.230	1.014	0.393
Transplant†	2.943	3	0.981	4.334	0.008
Location × Transplant	1.044	9	0.116	0.512	0.859
Error	12.674	56	0.226		

† A priori contrasts: foam vs. *Tedania*, $P = 0.105$; foam vs. *Haliclona*, $P = 0.284$; control vs. *Tedania*, $P = 0.002$; control vs. *Haliclona*, $P = 0.003$; control vs. foam, $P = 0.014$.

diminution of the $\delta^{15}N$ signal. To determine if trees with and without rootlets differed in $\delta^{15}N$ diminution rate, we contrasted our separate nonlinear models to a common model fit to all the data points:

$$\delta^{15}N = a \times \exp[(b + cX)\sqrt{\text{location}}],$$

where X identifies whether or not the observation came from a tree with rootlets ($X = 0$ if no rootlets, $X = 1$ if rootlets), and a, b, and c were estimated parameters. We then used an F-test to compare the residual sums of squares (RSS) of the common model to the sum of the RSS of the two models fit separately to trees with and without rootlets (Draper and Smith 1981).

RESULTS

Transplant experiments

Transplanting live sponges onto otherwise bare roots significantly increased root elongation rate relative to bare root controls (Table 1; Fig. 3). Changes in estimated root volume showed identical qualitative and statistical patterns (mean ± 1 SD, *Tedania*: 797 ± 182 mm^3/d; *Haliclona*: 522 ± 95 mm^3/d; foam: 410 ± 74 mm^3/d; control: 355 ± 87 mm^3/d). There were no differences ($P > 0.2$, all a priori contrasts) among treatments in root diameters at the beginning (15.1 ± 0.35 mm, $N = 96$) or end (21.7 ± 0.74 mm; $N = 72$) of the experiment, and no differences among treatments in daily change in root diameter (overall mean = 0.02 ± 0.002 mm/d). Hence, we conclude that the elongation response was not an etiolation response; rather, change in cable root length was a good measure of change in root biomass (which is directly proportional to cable root volume, and well correlated with cable root length: root dry mass = $[0.007 \times \text{cable root length} + 0.616]^3$; $r = 0.94$; $P < 0.001$ [Ellison and Farnsworth 1996]). Changes in root length also are correlated significantly with leaf production, shoot extension, and total aboveground production in saplings (leaf production: $r = 0.83$, $P < 0.001$; shoot growth: $r = 0.82$, $P = 0.001$; total annual aboveground biomass: $r = 0.79$, $P = 0.002$; data from Ellison and Farnsworth 1996), although no comparable data exist for mature trees.

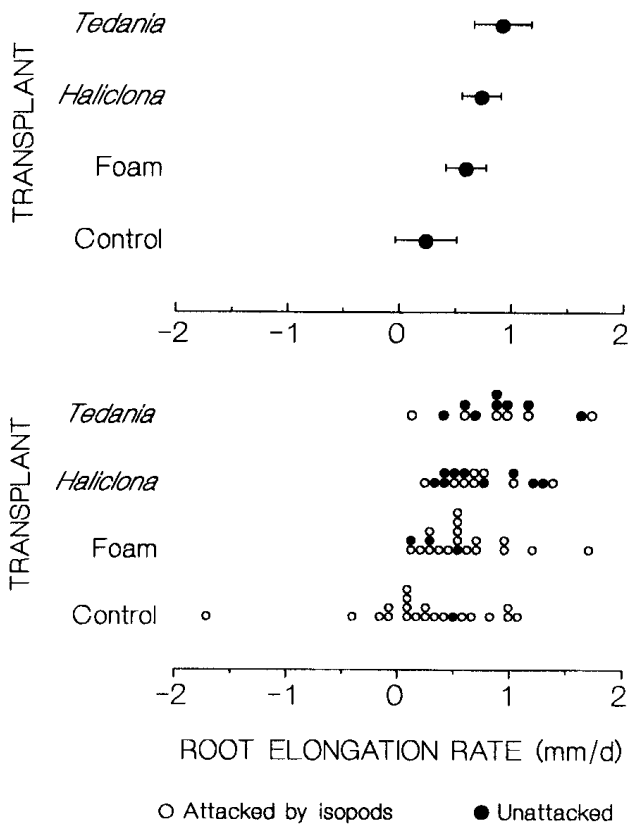

FIG. 3. Effects of epibiont transplants on root elongation rate and isopod colonization. Top: mean elongation rates (with 95% confidence intervals about the mean) of roots with no sponges, artificial sponges, or living sponges. See Table 1 for statistics and sample sizes. Bottom: a dit plot showing all data from the same transplant experiment illustrating the joint effects of the manipulations on isopod colonization and root growth.

While roots elongated and sponges grew concurrently, inert foam did not grow along with the root. Hence, as time increased, there was an increasing amount of tissue on control and foam-covered roots exposed to isopod colonization. When isopods did attack foam-covered roots, they burrowed into the root tip that had elongated beyond the foam jacket, not through the foam itself. Thus, comparing the growth rates across treatments of subsets of roots attacked by, or unattacked by isopods, allowed us to distinguish between changes in growth rates due to isopod attack and changes in root growth rate due directly to sponges.

Consistent with our previously published study of indirect effects of sponges on mangrove root growth (Ellison and Farnsworth 1990), limnoriid isopods (*Phycolimnoria clarkae*) attacked significantly fewer roots covered with living sponges than either control or foam-covered roots ($\chi^2 = 19.345$, df = 3, $P < 0.001$, G test; Fig. 3). Of roots unattacked by isopods, roots covered by live sponges grew 2–3 times faster (mean ± 1 SD, *Tedania*: 0.92 ± 0.14 mm/d; *Haliclona*: 0.73 ± 0.12 mm/d) than bare root controls (0.49 mm/d) or foam-covered roots (0.35 ± 0.10 mm/d). Since only one control root was unattacked, and only three foam

TABLE 2. Observed association between epibionts and adventitious fine rootlets is shown. The number of roots producing adventitious fine rootlets into each species is given in lightface type. The total number of roots producing fine rootlets into members of each higher taxon is given in boldface type.

Taxon	With rootlets	Without rootlets
Cyanobacteria	**0**	**10**
Scytonema polycystum	0	10
Algae	**1**	**19**
Caulerpa racemosa	1	9
Lithophyllum sp.	0	10
Tunicata	**2**	**28**
Didemnum concyhliatum	2	8
Diplosoma glandulosum	0	10
Perophora formosana	0	10
Porifera	**33**	**47**
Amphimedon viridis	0	10
Geodia papyracea	1	9
Haliclona curacaoensis	0	10
Haliclona implexiformis	8	2
Lissodendoryx sp.	8	2
Mycale magnirhaphidifera	0	10
Tedania ignis	9	1
Ulosa ruetzleri	7	3
Cnidaria	**0**	**10**
Aiptasia pallida	0	10

roots were unattacked, statistical analyses of these contrasts were not possible. Considering only those roots in the four treatments that were attacked by isopods (normally one isopod per root), there was still a significant treatment effect on root growth rate ($F = 4.113$, MS = 1.058, $P = 0.011$, ANOVA; Fig. 3); attacked roots with sponge transplants grew significantly faster than either control roots or foam-covered roots (*Tedania* vs. control: $P = 0.006$; *Haliclona* vs. control: $P = 0.023$; *Tedania* vs. foam: $P = 0.007$; *Haliclona* vs. foam: $P = 0.027$), while control and foam-covered roots that were attacked by isopods grew at equivalent rates ($P = 0.077$). Thus, live sponges ameliorate negative effects on growth of isopods and had significant direct positive effects on root growth.

Relationship between sponges and adventitious root production

Adventitious rootlets were produced commonly by cable roots fouled by massive sponges and rarely by roots fouled by other common epibionts ($\chi^2 = 59.88$, df = 4, $P < 0.001$, G test; Table 2). These rootlets proliferated throughout the sponge body and had similar structure to belowground nutrient-absorbing rootlets (Gill and Tomlinson 1977, Ellmore et al. 1983). Adventitious rootlets were produced by 58% of the roots with live transplants, but by none of the roots with foam or bare roots ($\chi^2 = 28.356$, df = 3, $P < 0.001$, G test). In two cases, *Haliclona* colonized exposed tips of foam-covered roots, and these roots also developed fine rootlets. Fig. 4 illustrates rootlet proliferation into a *Haliclona* transplant, and morphological differences between these rootlets and aboveground lateral cable roots. Like belowground fine rootlets (Fig. 4D), sponge-rootlets have an unpigmented periderm, a well-developed cortex, and a less-pronounced stele. In contrast, lateral cable roots have a highly pigmented periderm, a narrower cortex, and a pronounced stele.

Growth of sponges on different substrates

Haliclona transplants on mangrove roots grew significantly faster than sponges transplanted onto PVC tubes (Fig. 5; Mann-Whitney $U = 2.50$, $P = 0.001$). After 1 mo, *Haliclona* transplanted onto mangrove roots had increased in volume by 51 ± 24.1% (mean ± 1 SD) ($N = 9$ surviving transplants of the original 10), while *Haliclona* on PVC tubes increased in volume by only 6 ± 11.4% ($N = 9$). *Tedania* also grew more rapidly on mangrove roots (52 ± 35.3%, $N = 7$) than on PVC tubes (34 ± 19.3%, $N = 9$), but this difference was not significant ($U = 25.0$, $P = 0.486$) because of the high variance in observed growth rates (Fig. 5). Although this experiment only ran for 1 mo, fine rootlet initiation was observed in three of the surviving *Haliclona* transplants and two of the *Tedania* transplants.

Stable isotope analyses

$\delta^{15}N$ values for the three sponge species ranged from 4.5 to 7.5‰, consistent with these species being heterotrophic filter-feeders (Fry et al. 1987; Fig. 6). The relative abundance of ^{15}N declined along the root with increasing distance from the sponge (Fig. 6), indicating that the importance of inorganic nitrogen relative to fixed atmospheric nitrogen ($\delta^{15}N \approx 0$‰) in plant tissues diminished with distance from the sponge. We observed that values of $\delta^{15}N$ were higher in cable root sections when rootlets were present than when rootlets were absent for roots fouled by all sponge species (Fig. 6). Diminution rate (the coefficient b in the nonlinear regression model described in *Methods*: *Stable isotope analysis*) of $\delta^{15}N$ in roots was significantly slower when rootlets were present than when rootlets were absent (Table 3; Fig. 6), indicating that inorganic nitrogen was being transferred from these sponges into rootlets and cable roots. Fitting separate nonlinear models to $\delta^{15}N$ data from trees with and without rootlets explained significantly more of the variance in the data than a common nonlinear regression model (*Haliclona*: $F_{1,36} = 161.893$, $P < 0.0001$; *Tedania*: $F_{1,35} = 50.479$, $P < 0.0001$; *Ulosa*: $F_{1,36} = 42.120$, $P < 0.0001$). By way of comparison, the $\delta^{15}N$ value of the red alga *Acanthophora* ranged from 2.9 to 4.1‰, and the shape parameter b was similar to that found for sponge-covered roots that lacked rootlets (Table 3; Fig. 6).

$\delta^{13}C$ values for all plant tissues (Table 4) were within the range expected for a C_3 plant like *Rhizophora* (−25 to 29‰). $\delta^{13}C$ values for sponges with associated root-

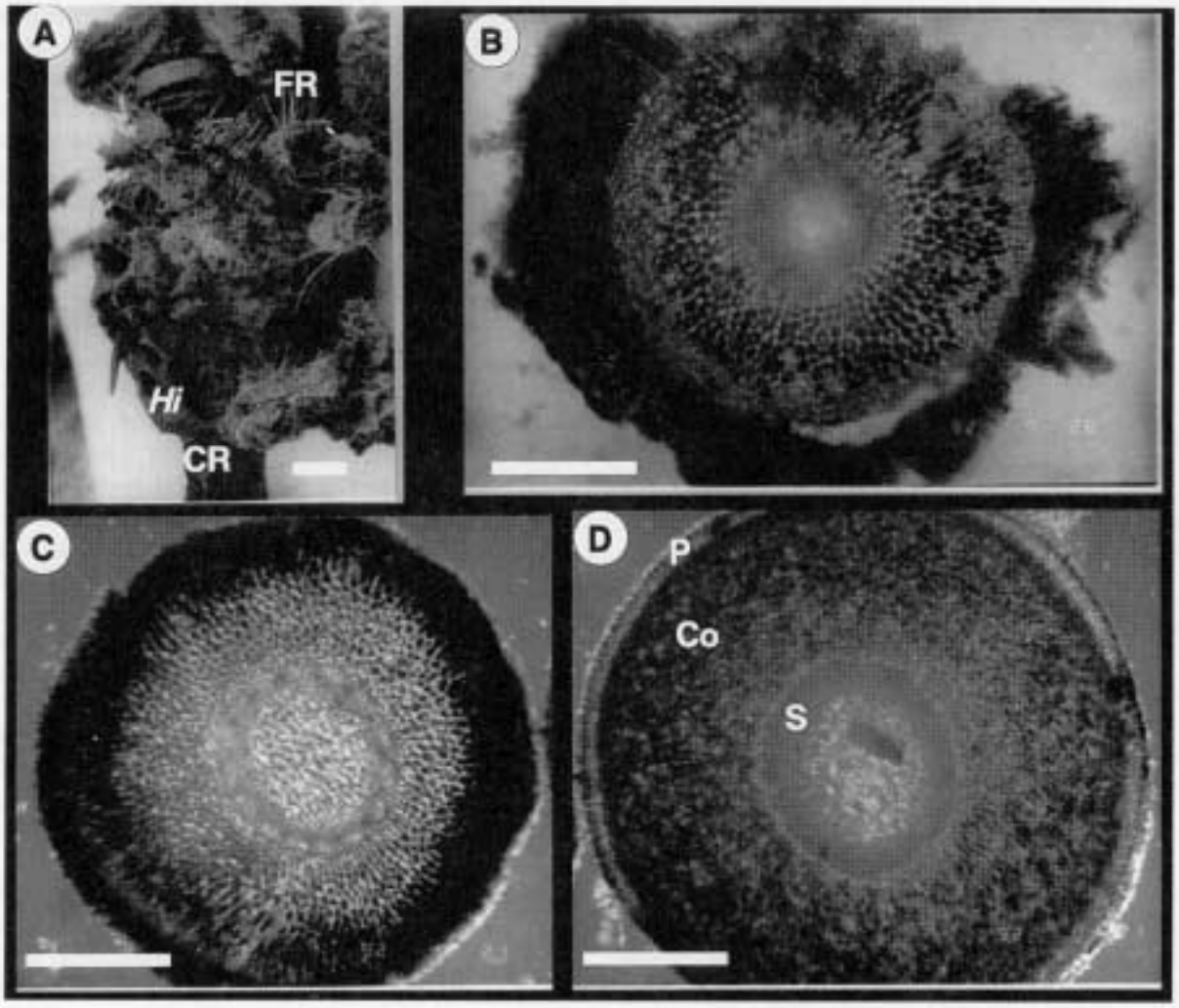

FIG. 4. Morphology of *Rhizophora* rootlets. (A) *Haliclona implexiformis* (*Hi*) transplant with sponge partially removed from cable root (CR) to show fine rootlets (FR). Scale bar = 10 mm. (B) Cross-section of a rootlet from within the sponge. (C) Cross section of the tip of an aboveground lateral (nonsponge) root. (D) Cross section of an underground rootlet, showing the characteristic loss of pigmentation and well-developed aerenchyma in these rootlets (Ellmore et al. 1983). Note that the periderm (P) is less pigmented, the stele (S) less pronounced, and the aerenchyma within the cortex (Co) more developed in (B) than in (C). (B–D) are fresh sections cut with a razor blade and photographed with unfiltered light. Scale bar = 0.25 mm.

lets were significantly more negative (1–3‰) than $\delta^{13}C$ values for sponges without rootlets (Table 4), indicating that some plant-derived carbon was incorporated into the sponge tissue.

DISCUSSION

Biotic interactions in general have received little attention in studies of mangrove population and community dynamics (reviewed by Smith 1992). A few studies have demonstrated the importance of plant–plant competition (Ball 1980, Smith 1992, Ellison and Farnsworth 1993) and herbivory/predation (Smith et al. 1989, Robertson et al. 1990, Farnsworth and Ellison 1991, Smith 1992) on seedling recruitment and stand structure (species zonation), but facilitative interactions only recently have been explored in Belizean (El-

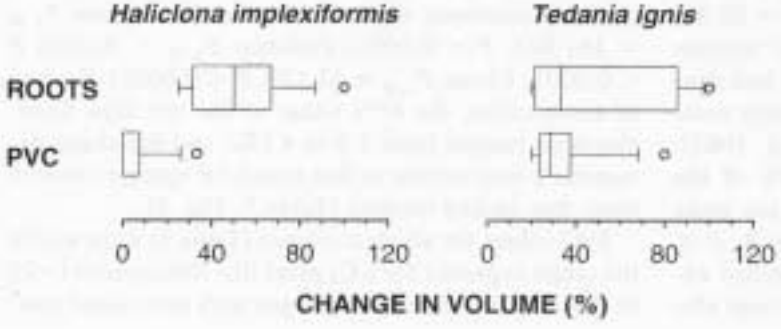

FIG. 5. Growth (change in volume by displacement) of *Haliclona implexiformis* (left) and *Tedania ignis* (right) on live mangrove roots (top) and PVC tubes (bottom). Box plots illustrate medians (center vertical lines), upper and lower quartiles (box edges), upper and lower deciles (horizontal lines), and outlier points (open circles). $N = 9$ per treatment, except for *Tedania* on living roots ($N = 7$).

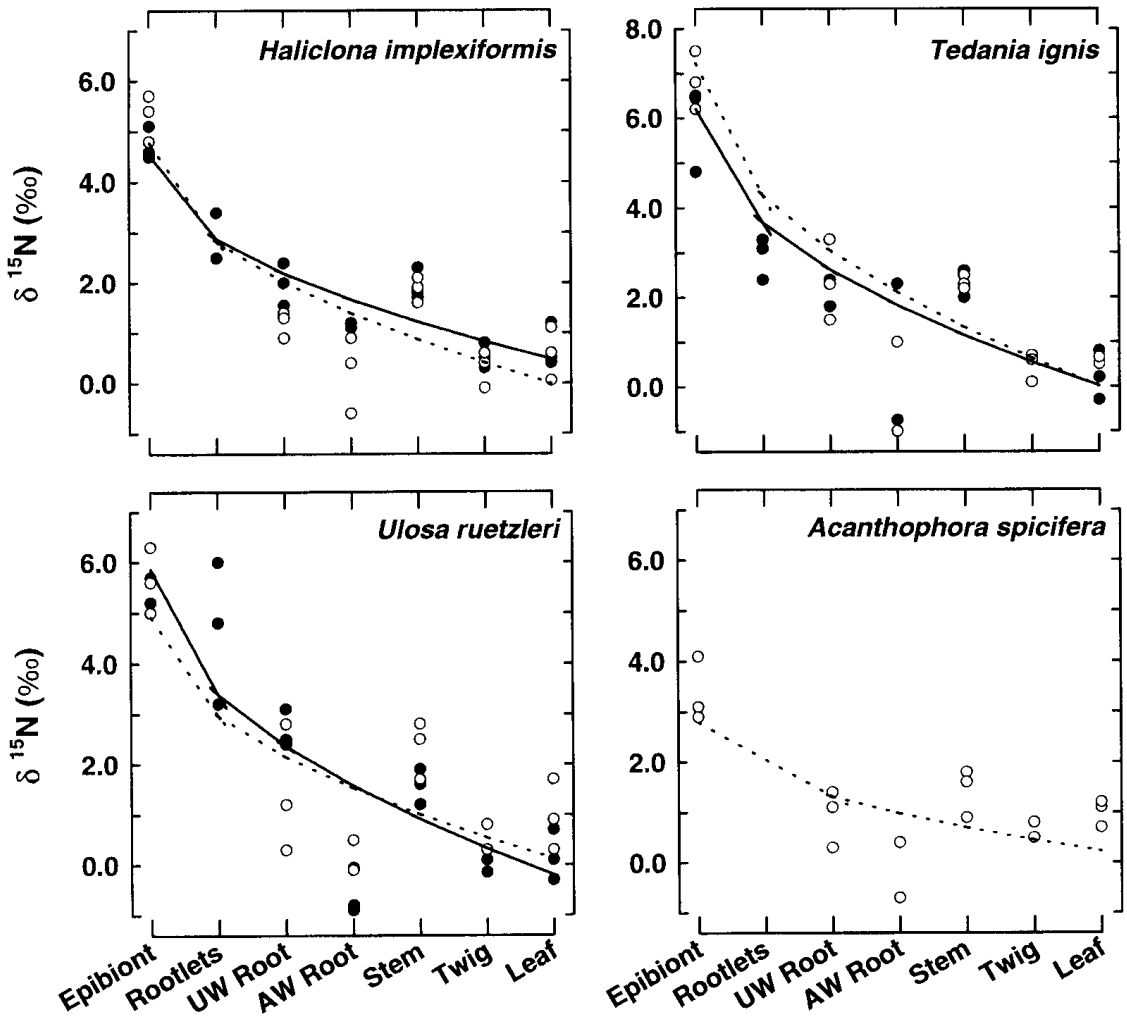

FIG. 6. Values of $\delta^{15}N$ (‰) in epibionts, and associated root and shoot tissues. Each panel illustrates $\delta^{15}N$ for one species of epibiont. Solid symbols and solid lines are data from roots with adventitious fine rootlets within the associated sponges; open symbols and dotted lines are data from roots with associated sponges or algae but lacking adventitious fine rootlets. Lines are derived from nonlinear regressions described in Table 3.

lison and Farnsworth 1990, 1992) and Australian mangal (Smith et al. 1991). Similarly, the abundance of benthic and epibenthic invertebrates in Caribbean (Rützler 1969, Farnsworth and Ellison 1996*b*) and Indo-Pacific mangal (Macnae 1968, Alongi and Sasekumar 1992) have yet to be included in comprehensive conceptual or quantitative models focusing on the fate of carbon and nutrients in mangrove ecosystems (e.g., Alongi et al. 1992, Robertson et al. 1992). The general absence of animal–plant interactions in mangrove carbon and nutrient budgets may reflect the fact that the majority of early studies (e.g., Pool et al. 1977, Twilley 1985, Twilley et al. 1986) were done in a small set of mangrove habitats where the abundance of animals was relatively low due to high sedimentation rates and other prevailing geomorphological conditions. Current available evidence, derived from a broader range of mangrove forest types, indicates that invertebrates can significantly affect plant growth and productivity in the Caribbean (Ellison and Farnsworth 1990, 1992, 1993, Farnsworth and Ellison 1991, 1993, Feller 1995) the eastern Pacific (Perry 1988), and Australia (Robertson et al. 1990, Smith et al. 1991).

TABLE 3. Estimated shape parameter (*b*) for the nonlinear regressions (Fig. 6) of $\delta^{15}N$ on sampled location within a plant.

Epibiont	Rootlets	*b*	SE	r^2	*P*
Haliclona	No	−0.983	0.134	0.919	<0.001
	Yes	−0.673	0.059	0.958	<0.001
Tedania	No	−0.979	0.159	0.883	<0.001
	Yes	−0.909	0.138	0.875	0.001
Ulosa	No	−0.982	0.238	0.789	0.082
	Yes	−0.806	0.142	0.810	<0.001
Acanthophora	No	−0.940	0.319	0.669	0.226

The results presented in this paper demonstrate that two common massive sponges directly and significantly enhance growth rate of red mangrove roots (Table 1; Fig. 3). The mechanism for this facilitation appears to be transfer of inorganic nitrogen from sponges to roots via adventitious fine rootlets (Figs. 4 and 6).

TABLE 4. Values of $\delta^{13}C$ (‰) for epibionts and associated plant tissues. Values given are means ± 1 SD. $N = 3$ for all values.

	Haliclona			*Tedania*		
	Rootlets		No rootlets	Rootlets		No rootlets
Epibiont	−14.7 ± 0.47	*	−14.0 ± 0.00	−14.2 ± 0.15	*	−14.1 ± 0.06
Rootlet	−25.1 ± 0.38		...	−24.6 ± 1.76		...
Cable root below water	−25.5 ± 0.56	NS	−25.9 ± 0.63	−26.0 ± −1.04	NS	−25.5 ± 0.56
Cable root above water	−26.5 ± 0.76	NS	−27.0 ± 0.95	−27.0 ± 1.13	NS	−27.8 ± 0.20
Branch	−29.1 ± 1.34	NS	−28.7 ± 0.50	−29.2 ± 1.32	NS	−28.5 ± 0.83
Twig	−29.0 ± 1.10	NS	−28.7 ± 0.25	−29.1 ± 1.39	NS	−28.6 ± 0.87
Leaf	−29.1 ± 1.29	NS	−28.8 ± 0.30	−28.8 ± 1.27	NS	−28.6 ± 1.01

* Indicates significant differences between $\delta^{13}C$ values from plants with and without rootlets (from trees with fouling sponges) ($P < 0.05$, Mann-Whitney U test).

Similar transfer of nutrients from epiphytes to their host plants through aboveground adventitious roots has been observed in temperate and tropical upland forests worldwide (Nadkarni 1981, 1994; reviewed recently by Davies and Hartmann 1988). In other marginal, nutrient-poor habitats there are parallel examples of interspecific interactions facilitating nutrient uptake. For example, bacterial N fixation has been observed to increase plant growth in seagrass beds (e.g., Capone et al. 1977) and affect successional processes on newly colonized lava flows (Vitousek et al. 1987, Vitousek and Walker 1989). Sheridan (1991, 1992) has measured significant N fixation by cyanobacteria growing epiphytically on roots and trunks of the mangrove *Avicennia germinans,* but whether or not this fixed nitrogen is used by the tree is unknown. Ectomycorrhizae increase rates of litter decomposition and thereby increase available nutrients for trees growing in nutrient-poor habitats (e.g., Malloch et al. 1980). Analogously, mussels facilitate plant growth in New England salt marshes through deposition of ammonium-rich waste products (Bertness 1984).

Nadkarni (1994) demonstrated experimentally that epiphytes intercepting and retaining nutrients triggered formation of aboveground adventitious roots (AARs) in *Senecio cooperi.* Production of AARs in other terrestrial plants has been attributed to low oxygen levels and/or hormonal changes brought on by permanent or seasonal flooding (e.g., Haissig 1974, Gill 1975, Pereira and Kozlowski 1977, Kozlowski 1984, Davies and Hartmann 1988). However, mangroves, which live in anoxic, flooded conditions, do not routinely make AARs; the aerial roots characteristic of mangroves are morphologically distinct from underground roots and rootlets (Gill and Tomlinson 1969, 1971, 1977).

The rootlets we observed in sponges (Fig. 4), like AARs in terrestrial forests, closely resemble subterranean rootlets (Nadkarni 1981). Our transplant experiments indicated that we could reliably induce fine rootlet production by placing live sponges onto roots, but that rootlet induction was not observed under the dark, anoxic foam controls. This result, together with the observation that rootlets rarely are associated with other epibiont taxa (Table 2), implies that it is the sponge itself, nutrients flowing from the sponge, or plant hormone analogues present in sponge tissue that cause rootlet formation on submerged aerial roots of *Rhizophora mangle.*

The significantly slower diminution rate of $\delta^{15}N$ in roots with rootlets penetrating sponges, relative to roots lacking fine rootlets, indicates that these rootlets do function in nutrient uptake (Table 3; Fig. 6). This provides inferential support for the notion that some inorganic nitrogen is transferred from sponges to rootlets and adjacent cable roots. It has been estimated that nearly 18% of the nitrogen input into mangrove forests is derived from biological nitrogen fixation (Alongi et al. 1992); hence most mangrove tissues would be expected to have a relatively low $\delta^{15}N$ value (→0‰). Relatively low values of $\delta^{15}N$ observed in all aboveground plant tissues provide additional support for the overall importance of nitrogen fixation (presumably on the soil or tree surface, or within the benthic sediments: Mann and Steinke 1989, Sheridan 1991, 1992, Alongi et al. 1992, Nedwell et al. 1994) to the total plant's nitrogen budget. Nitrogen fixation likely contributes much more to whole plant growth than does ammonium transferred to roots by sponges. However, determining the relative importance of sponges, nitrogen-fixers, and other nitrogen sources to the overall nitrogen budget of this mangal will require additional detailed data on fluxes of nitrogen attributable to soil bacteria, litter decomposition, and birds, among others.

Sponges also grow better on living roots than they do on plastic substrate at identical depths. Sponges growing on mangrove roots with rootlets have an ≈1–3% lower $\delta^{13}C$ value than sponges growing on roots without rootlets (Table 4). This implies that there is some transfer of plant carbon into these sponges. While other micronutrients important to sponge metabolism also may leak from roots, we lack information on the chemistry of root exudates and nutritional requirements of sponges. Thus, we did not try to measure substances other than carbon that could be transferred from roots to sponges. Although there are no other data on leakage of carbon or micronutrients by mangrove roots (or other noncrop plants), the rhizosphere is thought to be a source of carbon in mangrove ecosystems (Robertson

TABLE 4. Continued.

Ulosa			*Acanthophora*
Rootlets		No rootlets	No rootlets
−15.5 ± 0.21	*	−15.2 ± 0.21	−15.3 ± 0.88
−25.3 ± 0.46		...	...
−25.6 ± 0.12	NS	−25.6 ± 0.61	−26.4 ± 1.32
−26.1 ± 0.33	NS	−26.0 ± 0.17	−26.1 ± 0.56
−28.9 ± 1.63	NS	−28.8 ± 0.90	−27.9 ± 1.06
−29.3 ± 1.58	NS	−28.7 ± 1.29	−27.7 ± 0.46
−29.4 ± 2.09	NS	−28.8 ± 1.25	−27.1 ± 0.61

et al. 1992). The relative decrease in $\delta^{13}C$ seen in sponges associated with rootlets is within the range expected if, as has been found for crop plants, ≈5% of plant-derived carbon is lost through rootlets (Martin 1977, McCulley and Canny 1985, Goss 1991). Further work on carbon fluxes in these mangrove cays that focuses on ecosystem processes other than litter export is needed to determine the relative importance of this and other animal–plant interactions in the overall carbon budget of this ecosystem.

Based on the results presented here, we conclude that mangroves and these abundant massive sponges are facultative mutualists. Mangroves provide the only habitat (hard substrate) for sponges in this ecosystem, and passively leak carbon from their roots that is assimilated by sponges. In addition to protecting roots from isopod attack that substantially reduces root growth rate (Ellison and Farnsworth 1990), sponges directly enhance cable root growth by inducing adventitious rootlet formation and by transfer of ammonium through these rootlets into cable roots. Demonstration that sponges facilitate mangrove tree growth, as opposed to only root growth, requires evidence of a strong relationship between cable root growth and whole tree growth. This relationship has been documented only for *R. mangle* saplings on Belizean mangrove cays (Ellison and Farnsworth 1996). In that study, we found strong correlations ($P \leq 0.001$) among cable root growth rate and leaf production, shoot extension, and annual aboveground net primary production. While we recognize that ontogenetic differences in patterns of growth and reproduction exist between saplings and mature trees (Farnsworth and Ellison 1996*c*), we are confident that the average twofold increase in cable root growth observed when sponges are present on roots would translate into a measurable growth response by the fringing trees themselves. Additional study of whole-plant responses to sponge–mangrove interactions is needed to test the validity of this assertion.

The occurrence of similar facilitative interactions between plants and animals in mangal, especially in the Indo-Pacific where mangrove species richness is highest, remains unknown. Further comparative studies in mangroves around the globe could also test the hypothesis of Bertness and Callaway (1994) that facilitations should be common in marginal, stressed, or species-poor ecosystems. New conceptual models are required that explicitly account for animals, the dominant component of species diversity in mangal.

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