deficiency syndrome, which is genetically distinct from the first two diseases described (*10*). Further studies will be necessary to confirm the distribution of the enzyme deficiency within the spectrum of humoral immunodeficiency diseases. Second, the enzyme deficiency and lymphocyte dysfunction may be etiologically related, as appears to be the case for the first two diseases (*11*). Such an etiologic relation between the enzyme deficiency and the immune dysfunction is supported by the observation that a subgroup of patients with chronic lymphocytic leukemia have a deficiency of lymphocyte ecto-5′-nucleotidase (*5, 12*). Patients with this disease may also develop a deficiency of serum immunoglobulins and recurrent infections similar to those seen in primary hypogammaglobulinemia (*13*). Finally, lymphocytes lacking 5′-nucleotidase are unable to take up AMP as a result of an inability to hydrolyze this compound to adenosine (*7*). It is possible that this decreased ability to degrade 5′-nucleotides to their catabolic products may impair B lymphocyte function and explain the occurrence of some manifestation of agammaglobulinemia. Therefore, the discovery of another disorder of the immune system associated with a specific deficiency of purine nucleotide degradation provides additional clues for the role of purine catabolism in the regulation of immune function.

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Isopod and Insect Root Borers May Benefit Florida Mangroves

Abstract. *Far from threatening the persistence and geographic extent of red mangrove* (Rhizophora mangle) *in Florida, wood-boring marine isopods may aid the plant to survive wave action by initiating branching of aerial prop roots. Evidence for a recent, sudden increase in density or range of one such isopod,* Sphaeroma terebrans, *is anecdotal and weak. Insect damage to mangrove aerial roots even before they descend to the water is at least as great as that wrought by isopods and also causes root branching. Aerial and submarine damage combine to stimulate root initiation so that, for every root produced aerially by the tree, at least 1.4 roots reach the substrate. Similar responses to herbivory, which have been reported for other plants, suggest that herbivores may both benefit and harm plants, and that their impact may be more difficult to assess in specific instances than has been realized.*

Herbivory is traditionally viewed as detrimental to plants (*1*), with victims suffering at least loss of biomass and possibly death or deformation through destruction of a growing tip or unique stem. Red mangrove (*Rhizophora mangle*) swamps of Florida's west coast, with their prominent prop roots originating from normal aerial branches often high in the trees, are said to be in grave danger from a wood-boring marine isopod, *Sphaeroma terebrans*, which attacks the roots (*2, 3*) once they descend to the water. "An ecocatastrophe of serious magnitude" is heralded: "The shoreline of the mainland and of the mangrove islands is gradually shrinking . . . *Sphaeroma* has already eliminated much of the protective outer edge of this great mangrove stand. It threatens to eliminate much more . . ." (*2*). "The isopod does not kill the tree, but sometimes, without the support of its prop roots, a red mangrove topples into the water during storms" (*3*).

A sudden, spontaneous environmental disaster of this magnitude would indeed be both a curious and a serious matter, but grounds for skepticism exist. The sole documentation for the decrease of mangrove area appears to be a 1953 photograph of Whitewater Bay, near Cape Sable, Florida, showing an isthmus and several islands that were no longer present in 1964 (*2*). But comparison of accurately drawn maps of the Florida west coast and the Keys shows that red mangrove swamps and islands are constantly in a state of flux. For example, current U.S. Coast and Geodetic Survey maps of the Florida Keys (for example, Nos. 853, 854, and 859) depict numerous islands that no longer exist, and unmapped islands are occasionally found in this area. Over a period of 113 years, the maps of a section of the Florida Keys, where *Sphaeroma terebrans* is absent or extremely rare (*2, 4*), show many changes in *Rhizophora* coverage (*5*). During 10 years of intensive monitoring in the Keys, one of us has seen several mangroves topple into the water, particularly during storms; none had extensive root damage from isopods. Therefore, the evidence that something new and catastrophic is happening to Florida mangroves is weak. Finally, it was observed as early as 1911 (*6*) that the characteristic branching of *Rhizophora* aerial roots is induced by boring, and Gill and Tomlinson (*7*) have recently documented that such branching is always caused by physical or biological damage and have described the anatomy of the branching process. This result was adumbrated by Estevez and Simon (*4*), who suggested that the production of adventitious roots from prop roots destroyed by *Sphaeroma terebrans* may accelerate mangrove island growth "provided regeneration rates exceed boring." In this report we show that regeneration rates do indeed outpace destructive boring, and provide evidence on the relative importance of different agents of damage.

We examined *Rhizophora* roots above or below (or both) the high-tide level at eight Florida sites and one in Costa Rica (Table 1); included was Rookery Bay, the "endangered" location described by Gore (*3*), which is very near the Ten Thousand Islands, said to have "extremely severe" damage (*2*). A root tip killed by isopod boring is easy to detect because necrosis quickly spreads from the bored area to engulf the growing tip in a mass of brown, deformed tissue. Subsequent new growth distal to such a mass is never observed. Among root tips (below high-tide level) suffering attack by *Sphaeroma*, destruction in west Florida ranged from 59 percent (of 304 tips) at Rookery Bay down to 34 percent (of 320) at Lemon Bay. Even higher percentages of damage (60 to 65 percent) have been reported for Cockroach Bay (*4*). The Costa Rican site, Chomes (near Puntarenas), an old, healthy tidal creek swamp in no apparent danger of toppling over, suffered 73 percent root mortality (of 209 tips) below high-tide level from *Sphaeroma* boring. The Keys sites, as well as others not included in our study, suffer no *Sphaeroma* attacks but have almost as much submarine root mortality from a different isopod, *Limnoria* n. sp. near sublittoral. For example, 43 of 208 root tips (21 percent) were destroyed at the Mud Keys site. *Limnoria* makes small cryptic holes at the very bottom of a root, whereas *Sphaeroma* bores large conspicuous ones (*8*). For clusters of roots originating from an individual tip that has descended from its aerial point of origin to the high-tide level, in contrast to the single tips discussed above, isopod damage ranges from 69 to 86 percent at the Florida west coast (*Sphaeroma*) locations to 23 percent at the Mud Keys (*Limnoria*) site. These data include unbranched (and undamaged) roots as one-root clusters, and virtually every branched cluster was seen to have isopod damage at least at its branch points, confirming that branching is induced by damage (*7*).

Table 1. Red mangrove study site locations. Sites 1 to 5 are on Florida's southwest coast; sites 6 and 7 are in the Florida Keys.

Site No.	Location
1	South Rookery Bay
2	Unnamed island, south Rookery Bay
3	Bodiford Island, near Pine Island
4	Clam Key, near Pine Island
5	Southeast Lemon Bay
6	Mud Keys
7	Bill Find's Key
8	Matheson Hammock, Miami
9	Chomes, near Puntarenas

There is no evidence that this high level of root damage by isopods threatens the existence or extent of the mangroves at any of these sites. For one thing, both isopod species are found almost exclusively along the periphery of *Rhizophora* stands. Estevez and Simon (*4*) record *Sphaeroma* only in the outer 2 m at Cockroach Bay, and we found both species restricted to this fringe at all sites. Along much of the Florida west coast the substrate under this fringe is covered with Eastern oysters (*Crassostrea virginica*) which form an impenetrable barrier. Typically, the roots in such a situation are abraded (which may induce branching) and ultimately die and rot, even those lacking isopods. Further, in these same sites the roots, with or without isopods, are quickly covered with coon oysters (*Ostrea frons*) and ivory barnacles (*Balanus eburneus*) and are thus killed (*9*). On other west Florida sites, and especially in the lower Florida Keys, many islands are surrounded by a hard-bottomed (coral lightly covered with silt) moat about 1 m deeper than the outer substrate. This hard bottom is quite impenetrable to the roots; a longer time is required for them to reach it. Once again, abrasion and subsequent branching are common; moreover, the longer it takes for roots to reach the substrate, the more likely it will be that they will be covered by oysters and barnacles on the Florida west coast and by barnacles, the coral *Porites porites*, the red alga *Bostrychia montagnei*, and several sponges in the Keys. Such overgrowth often kills the roots.

A second factor that mitigates the danger from isopod attack to *Rhizophora* is damage-induced branching. The overgrowing organisms and shallowness of the intertidal region in Florida obscure this process; but at Chomes, the site with the heaviest *Sphaeroma* infestation, the high-tide level is 2 m above the substrate, overgrowth is sparse, and damage and branching are easily observed. From 79 roots that descended to the water, isopod boring produced 152 root tips, of which 91 were alive (had green tips with normal anatomy) at time of census; several were at the end of two or even three levels of branching. So on the average, for every root tip reaching the water, isopod damage causes at least 1.15 root tips to reach the substrate. We say "at least" since many of the tips were still above ground and therefore would still be expected to undergo one or more additional episodes of attack and branching, each episode yielding a net increase in viable root tips.

Finally, the isopods and rare shipworms (*Teredo* sp.) that attack the roots below the water are no more damaging than the array of insects that destroys them above the water and also causes branching. Most numerous among these are the scolytid beetle *Poecilips rhizophorae* (which occasionally bores and survives at locations submerged much of the day) and the olethreutid moth caterpillar *Ecdytolopha* sp. However, a suite of other insects are frequently encountered, including the cerambycid beetle larva *Styloleptus biustus*, scale insects of the genera *Dysmicoccus* and *Pseudococcus*, the trogossitid bettle larva *Tem-*

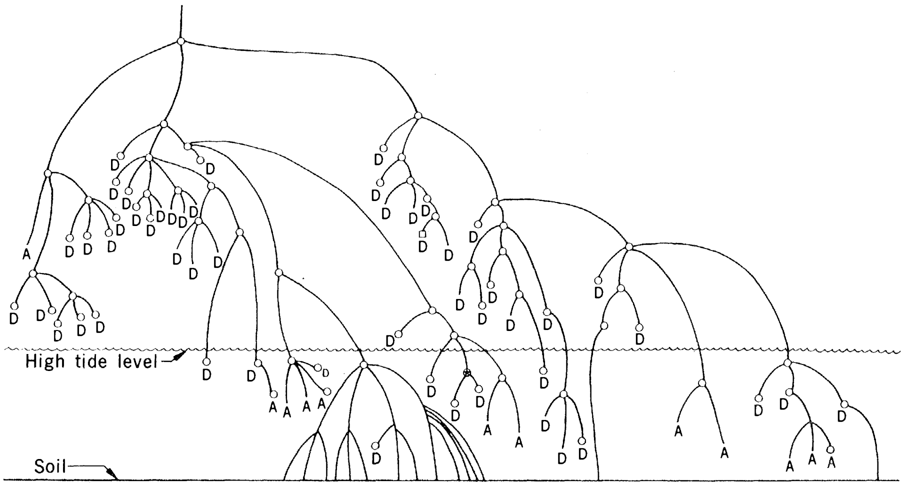

Fig. 1. Branching pattern for a single *Rhizophora mangle* root from Clam Key, Florida. *A*, alive; *D*, dead; □, bored by *Ecdytolopha* sp.; ○ (above water), bored by unknown insect; ○ (below water), bored by *Sphaeroma terebrans*; and ★, bored by *Teredo* sp.

nochila hubbardi, and the thrips *Neothrips* n. sp. Other wood borers, especially anobiid and buprestid beetle larvae and *Nemapogon* (Tineidae) moth caterpillars, are often found in aerial roots but appear to attack only those that are already dead. The net effect of these borers above the water is similar to that of the isopods below, but even more striking. Of 75 root clusters originating from a single root above the high-tide level at sites 3, 4, 7, and 8, at least 94 percent had root tips killed by insects. Most of the branching could be traced to boring by insects, in spite of the ephemeral nature of remains of such damage, and we concur with Gill and Tomlinson (*7*) that most, if not all, *Rhizophora* root branching is due to damage, except for prop roots initiated on a root which has already reached the substrate. Of 80 roots observed from their origins on branches at sites 3, 4, 7, and 8, 90 percent branched at least once, and the average number of levels of branching for these roots was 3.5. These branching episodes yielded 734 root tips, of which 112 were alive and were either in the air or had reached the water at time of census. That is, for every root that the trees produce, at least 1.40 roots reach the water because of branching induced by insect damage. The comparable statistic for a sample of 40 roots at Chomes was at least 0.93.

The net effect of aerial and marine damage to mangrove roots is thus a multiplicative sequence of damage, branching, damage, branching, and so forth. This cycle is responsible for much of the striking, stiltlike appearance characteristic of *Rhizophora* and must, if anything, secure the tree against toppling by increasing the number and spread of its anchored roots. A single root, from a tree at Clam Key on the Florida west coast, that exemplifies this process is shown in Fig. 1. The greatest number of branching levels is seven (at least six induced by boring), and from the single root originating from a branch, 15 roots have already become implanted in the soil. Six of these are the direct result of damage (a minimum of five levels), and the remaining nine were produced without boring from the six after they had rooted. One root is still alive and not yet in the water, while 11 others are alive in the water but have not yet reached the substrate. All boring in the water was by *Sphaeroma* (except possibly for one shipworm), and, while only one of the aerial borers (an *Ecdytolopha* caterpillar) was collected, insect frass was found at all other aerial branch points. Only one episode of branching was observed (in the water) where evidence of boring could not be found, whereas 54 aerial and 22 marine borers were detected. Had none of this happened, there would have been only the original root plus at most four or five that might have been produced directly from the first after it had implanted.

The net effect of boring must be the product of the aerial and underwater effects. At Chomes, for every root produced, more than 1.08 (that is 0.93×1.15) roots implant in the substrate. For Florida the below-water multiplicand is unknown but appears to be greater than 1; for the Clam Key example, 12 roots reached the water, resulting in 17 which are either rooted or still alive in the water. The aerial multiplicand is at least 1.40, compared to only 0.93 for Chomes, so that the product is likely at least 1.40, and the borers increase the number of successful roots.

All this is not to say that the Darwinian fitness of *Rhizophora*, the product of its survival and reproduction, is increased by boring. One would have to show that the increased metabolism allocated to producing all these damage-induced roots is not overweighed by a concomitant decreased production of propagules. Further, although our data do not suffice to test this possibility, it may be that in areas with low isopod densities their net effect is to increase root production through induction of branching, while at higher densities rate of root destruction exceeds that of root production. But at least it is clear that the herbivory is not trivially detrimental to the plant, a result in accord with several other recent results. Boring by *Poecilips rhizophorae* into viviparous mangrove propagules increases root production above the excavated region (*10*), and similar observations are reported for roots of other plants (*11*) as well as for other plant parts (*12*). Although such plant responses to both specific and nonspecific damage have not been widely discussed (*13*), they must always be kept in mind when one assesses the impact of herbivores on plants.

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