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Effects of the root-boring isopod *Sphaeroma peruvianum* on red mangrove forests

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ABSTRACT: Effects of *Sphaeroma peruvianum* on roots of the red mangrove *Rhizophora mangle* were measured in a forest on the Pacific coast of Costa Rica by following the presence of isopods in roots according to their historical development and intertidal height and measuring root elongation, morphological changes and root tip regeneration. Roots were classified as aerial (initiated adventitiously from branches, then growing towards the ground), lateral-G (lateral roots which originate from aerial roots after they have entered the ground) and ground (aerial roots which are established in the substrate). For each root, isopod presence or absence was noted along with burrow characteristics. Measurements were taken of root elongation, morphology and root tip regeneration. Isopod presence resulted in a 50 % decrease in aerial root growth rate (elongation). The reduction in growth rate was due to atrophy and breakage of the root tip caused by isopod boring. The stimulation of new root tip growth does not compensate for the loss of root growth. Net root production in burrowed roots was 62 % below that of unburrowed roots. The spatial distribution of burrowing isopods is not uniform. Burrows occur most frequently in aerial roots, to a lesser extent in lateral-G roots, and not at all in ground roots. Burrows are initiated close to the young growing tips of roots, and occur almost exclusively in roots having initiation points greater than 100 cm above the ground. Distribution of males and females along roots is uniform. Isopods do not remain in one burrow throughout their lifetime. Recruitment of isopods to roots is not seasonal.

INTRODUCTION

The eastern Pacific root-boring isopod *Sphaeroma peruvianum* Richardson, like its Atlantic/Caribbean congener *Sphaeroma terebrans* Spence-Bate (John 1968, 1970, Estevez & Simon 1975, Estevez 1978), bores into the growing tips of aerial roots of the red mangroves *Rhizophora mangle* L. and *R. harrisonii* Leechman once roots have reached down to the high water line. A study of *S. terebrans* in Florida, USA, suggested that isopod-inhabited roots tended to break off at the mean high water line, resulting in failure of roots to reach the ground (Rehm & Humm 1973, Rehm 1976). These authors suggested that isopods decreased productivity and stability of the mangrove community as a whole. An observed decrease of red mangroves in Whitewater Bay, Florida was attributed to the effects of *S. terebrans*.

Simberloff et al. (1978) examined mangrove-*Sphaeroma* communities in south Florida (*S. terebrans*) and Pacific Costa Rica (*S. peruvianum*), and suggested that *Sphaeroma* might stimulate new branching of aerial root tips and thus the multiplication of prop roots. Simberloff et al. (1978) concluded that damage to mangrove roots by the borers results in a multiplicative sequence of damage and branching. They hypothesized that this cycle is responsible for much of the stilt-like appearance characteristic of *Rhizophora*. Ribi (1981, 1982) pointed out that the number of root tips per parent root provides no information about growth rates because initiation of more new root tips does not necessarily mean an overall increased production.

Studies on the effects of boring isopods on red mangrove roots have resulted in conflicting conclusions because measurements were not taken of actual root growth rates and changes in root morphology in the presence and absence of isopods. This study examines the seasonal distribution and abundance of *Sphaeroma peruvianum* on different red mangrove

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root types which are classified according to their historical development. An assessment is made of the tradeoffs in the effects induced by isopods on root growth rate and net production.

METHODS

Study site and general methods. The study site was in a mangrove estuary in the Gulf of Nicoya, Costa Rica (10° 5′ N, 84° 57′ W). The site was about 2.5 km north of the Costa Rica site of Simberloff et al. (1978) at Chomes. The estuary is inhabited on its outer fringe by *Rhizophora mangle* and *R. harrisonii*, and landward by *Avicennia germinans* L. and *A. bicolor* Standley, with *Laguncularia racemosa* Gaernt and *Conocarpus erectus* L. occurring infrequently (Gocke et al. 1981). The area is characterized as a scrub mangrove forest (trees up to 5 m height), attributed to high local salinities (Cintron et al. 1978, Soto & Jimenez 1982, Jimenez & Soto 1985). During the rainy season, June through November, salinities range from 23 to 29 ppt, and precipitation from 175 to 375 mm mo^{-1} (Pool et al. 1977). In the dry season, December through May, salinities range from 27 to 32 ppt, and precipitation from 58 to 60 mm mo^{-1} (Pool et al. 1977). The Quebrada Grande Creek provides freshwater for a brief period during the rainy season, but in the dry season freshwater input to the system is minimal (Gocke et al. 1981).

The Punta Morales region is exposed to mixed diurnal tides which range from −0.4 to 3.3 m from the mean lower low water. This tidal flux results in submergence of red mangrove trees to the canopy level (about 2 m above the ground) during most high tides to complete exposure of tree roots during low tides.

Rhizophora mangle has aerial roots which are initiated adventitiously from branches and grow geotropically, eventually penetrating the substrate. If no injury occurs to aerial roots, they remain unbranched until entering the ground (Gill & Tomlinson 1977, this study). An injury to an aerial root can result in the production of up to 5 new root tips. After aerial roots enter the ground, the above-ground portion thickens and can generate new laterals even in the absence of injury.

In this study, red mangrove roots were classified as aerial, ground and lateral-ground (lateral-G). Ground roots are aerial roots that have become established in the substrate, and are older and thicker than aerial roots. Lateral-G designates lateral roots which originated from aerial roots after they have entered the ground. These laterals are at first entirely aerial, but ultimately turn down and also enter the ground. Thus, they are younger than the ground roots to which they join, but are otherwise comparable in diameter and fleshy exterior to the aerial roots.

Isopod abundance and distribution. Aerial and lateral-G roots were collected during the dry (February) and rainy (July) seasons of 1984 in twenty 2 × 3 m (depth into forest by width along forest, respectively) random quadrats along the outer margin of a fringing red mangrove stand. Prior to cutting off each root, the intertidal height and the distance from ground to root initiation point and root tip were recorded. Roots were sawed off at their initiation points, marked with numbers, placed separately into plastic bags, and taken to the laboratory for analysis.

Ground roots were sampled differently from aerial and lateral-G roots because of higher densities. Fifty random 50 × 50 cm quadrats were placed along the outer mangrove fringe during the dry and rainy seasons. Ground roots within each quadrat were closely inspected (but not removed) for isopod burrow openings. Isopods were not observed on ground roots within the 50 quadrats nor on numerous roots visually surveyed by random inspections in the field.

All isopod burrows on the sample roots were opened with a small chisel. Four aspects of each burrow were measured: (1) distance from burrow opening to root tip; (2) burrow direction (away from or towards the root tip); (3) diameter, and (4) total length. Distributions of occupied and unoccupied burrows were also recorded. Isopods in burrows were removed, sexed, measured (total body length), and their position in the root recorded.

Isopod recruitment and root growth. All unbranching aerial roots in a 200 m^2 area along the margin of the mangrove forest were tagged and numbered with forestry flagging. A total of 126 aerial roots occurred in this area. The length, distance from root tip to ground, and distance from root origin to ground were measured. Root tip atrophy, breakage, and regeneration were noted. As root tips regenerated, the length and diameter of each tip was measured. All isopod burrow openings on these roots were mapped and measured (diameter of opening, and distance from opening to root tip and to ground). All measurements were repeated nearly monthly during the dry and wet seasons to monitor root growth rate, development with and without isopods present, and isopod recruitment (initiation of new burrows). Because burrows are always initiated close to the growing tip, growth rates of roots can be used to estimate ages of isopod burrows. During a 77 d period from February 20 to May 4, 1984, 55 of these 126 roots were monitored weekly for isopod recruitment in relationship to change in root elongation. Root tips where atrophy, breakage or branching occurred were excluded from the calculation.

Net root production was determined by converting root growth rate as measured by root elongation (cm mo^{-1}), to g dry wt added $root^{-1}$ mo^{-1} Root lengths were standardized to dry weight by using the roots collected from the quadrat-based field study described above. Roots were measured, weighed, dried for 72 h at 27 °C or to a constant weight, and weighed again to obtain dry weight. Linear regression analysis established the relationship between root length and dry weight of aerial roots (log y = log −0.64 + 1.1 log(x); F = 481.0; p ≤ 0.001) and lateral-G roots (log −0.48 + 0.02(x); F = 785.4; p ≤ 0.001) where y = dry root weight (g) and x = root length (cm) (Sokal & Rohlf 1981).

Table 1. *Rhizophora mangle*. Frequency of isopod *Sphaeroma peruvianum* burrows (number of roots with isopods compared to total number of roots) in the dry (February) and wet (July) seasons in aerial, lateral-G and ground roots of the red mangrove

Root type	Dry season	Wet season
Aerial	76 % (38/50)	61 % (27/44)
Lateral-G	27 % (13/48)	12 % (5/40)
Ground	0 % (0/200)	0 % (0/200)

RESULTS

Isopod abundance and distribution

Isopod burrows were not distributed uniformly on all 3 root types. Burrows occurred most frequently on aerial roots (61 to 76 %), to a lesser extent on lateral-G roots (12 to 27 %), and were absent from ground roots (Table 1). Isopods burrowed almost exclusively into aerial and lateral-G roots with initiation points more than 100 cm above the ground (Fig. 1a,b). All aerial roots by definition (in this study) originate from the canopy, and thus have initiation points more than 100 cm above the ground. About 50 % of all lateral-G roots originate 100 cm or more above the ground; the others have initiation points less than 100 cm above the ground. Lateral-G roots with initiation points less than 100 cm above the ground were rarely occupied by isopods (4 out of 45 roots examined, 9 %; Fig. 1a,b).

Isopods initiated burrows close to the young growing tips of the aerial roots; burrow entrances averaged 7.6 cm ± 1.4 standard error (SE; n = 33) above the root tip. Burrows were excavated along the longitudinal axis of the root, predominantly in an upward direction

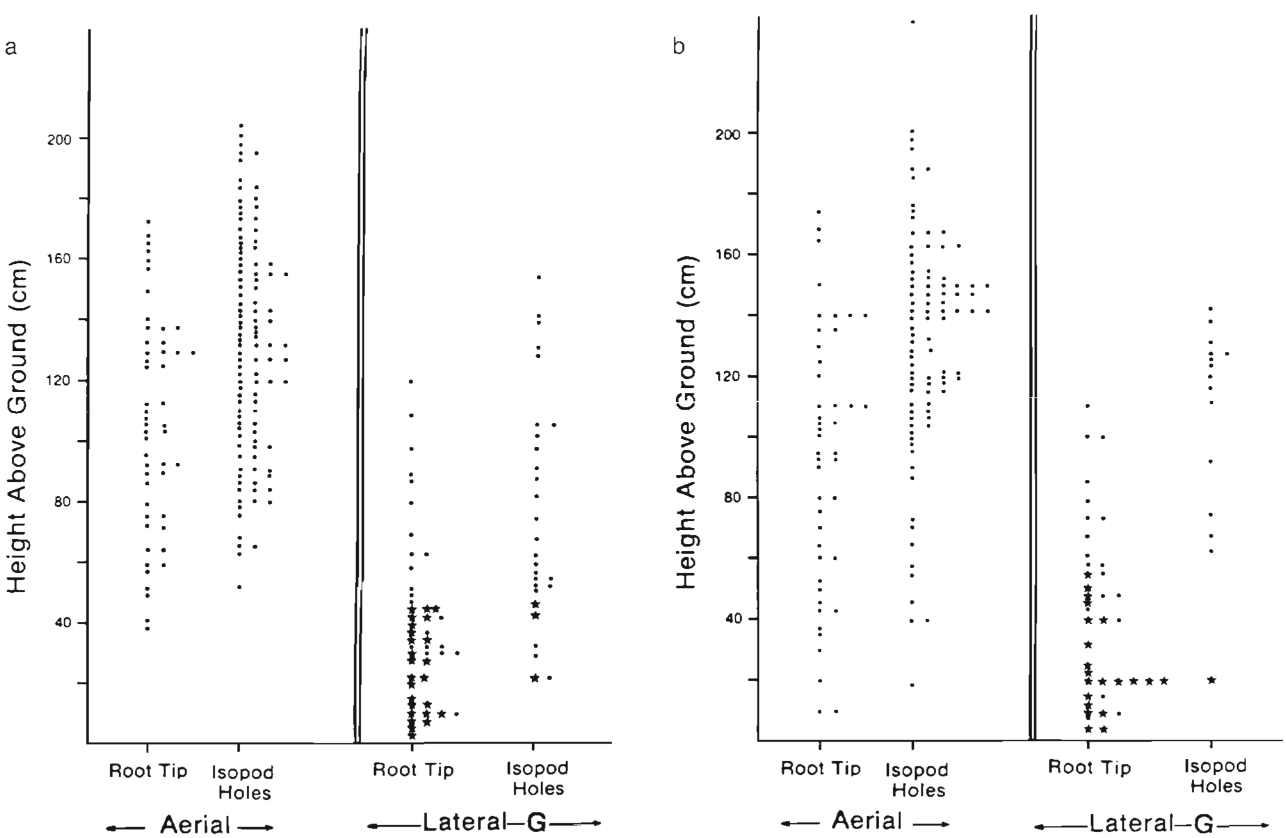

Fig. 1. *Rhizophora mangle*. Distribution of root tips compared to *Sphaeroma peruvianum* burrow holes on aerial and lateral-G roots: (a) dry season; (b) wet season. (★) Roots with initiation points less than 100 cm from the ground; (•) roots with initiation points more than 100 cm from the ground

away from the root tip (observations on 35 out of 38 roots). Burrow diameters averaged 5.2 mm ± 0.2 SE (n = 39), and mean lengths averaged 28.0 mm ± 1.8 SE (n = 42).

The distance between the burrow opening and the root tip increased with the downward growth of the aerial root, yet the distance between the burrow opening and the ground remained constant. Isopods were present in burrows located up to 75 cm from the root tip (Fig. 2). If isopods remain in one burrow during their lifetime, larger individuals should occur at greater distances from the root tip, and burrow vacancy should increase with distance from the root tip. However, the frequency of empty burrows did not increase with greater distance away from the root tip (χ^2 = 1.92, p > 0.50; Fig. 2), and isopod body length did not change

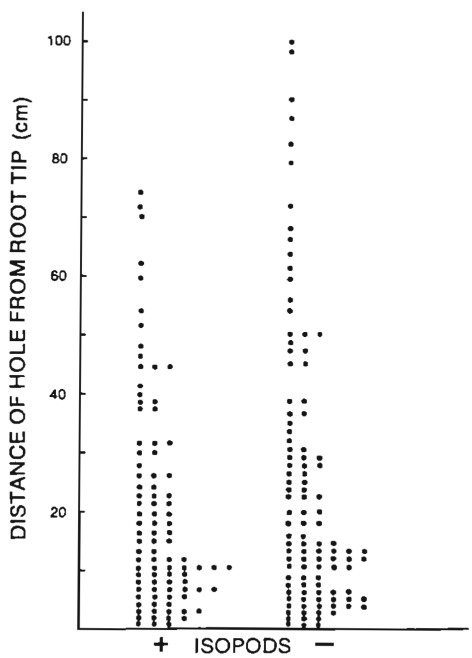

Fig. 2. *Rhizophora mangle*. Distribution of the distance from *Sphaeroma peruvianum* burrow holes to root tips where isopods are present (+) or absent (−) in burrows

significantly with distance from the root tip (linear regression: females, y = 8.55 + −0.004(x), F = 0.09, p > 0.75; males, y = 7.13 + −0.01(x), F = 0.83, p > 0.50, where y = body length (mm) and x = distance of hole from root tip (cm)).

Isopod recruitment

Isopod recruitment to aerial roots, as measured by mean number of holes per root and percent inhabitation or vacancy of roots, was not seasonal. During the dry season (February) 76 % of the aerial roots had isopod holes, with an average of 2.9 ± 0.48 SE holes per root (n = 107) and a 68 % burrow vacancy (n = 50). During the wet season (July) 61 % of the aerial roots had holes, with an average of 3.7 ± 0.65 SE holes per root (n = 98), and a 62 % burrow vacancy (n = 44). New recruitment to roots did not differ significantly during the dry season (47 %, n = 34) compared to the wet season (54 %, n = 52, χ^2 = 0.15, p > 0.50).

The frequency of recruitment to roots with and without isopods present was similar. Over 77 d, aerial roots originally with isopods present had a 36 % increase while aerial roots without isopods had a 32 % increase in number of burrow holes (Table 2).

Table 2. *Sphaeroma peruvianum*. Isopod recruitment during 77 d to red mangrove aerial roots that originally had isopods present (+) or absent (−). Percent recruitment is expressed as number of new isopod holes compared to the original number of holes in roots

Roots	N	Day 0 Total no. holes	Day 0 Mean no. holes/root (± SE)	Day 77 Total no. holes	Day 77 Mean no. holes/root (± SE)
+ Isopods	39	77	2.0 (0.31)	105	2.7 (0.28)
− Isopods	16	0	0.0	32	2.0 (0.24)

Recruitment: + isopods = 36 % (28/77), χ^2 = 0.48, p ≤ 0.10
− isopods = 32 % (32/0)

Effects of isopods on root growth

Roots without isopods grew almost 50 % faster than roots with isopods (increase in root length without isopods, mean = 26.7 cm ± 4.2 SE, n = 16; with isopods, mean = 15.0 cm ± 1.3, n = 39; Student's *t*-test, where *t* = 5.0, p ≤ 0.001). Isopod presence in aerial roots resulted in a significantly higher degree of root tip atrophy and breakage, compared to roots without isopods (61 % versus 3 %, χ^2 = 13.2, p ≤ 0.001; Table 3). Of 62 aerial roots examined, 33 (53 %) were burrowed

Table 3. *Rhizophora mangle*. Frequency of red mangrove aerial roots with broken or atrophied tips that had regenerating tips in the absence (− isopods) and presence (+ isopods) of the isopod *Sphaeroma peruvianum*

	Root tips examined	Broken tips	Tips regenerated	Total no. new root tips
+ Isopods	33	20 (61 %)	15 (75 %)	27 (35 %)
− Isopods	29	1 (3 %)	1	4
Total	62	21		

Table 4. *Rhizophora mangle.* Net production in aerial roots calculated from growth rate and biomass measurements (see text) during 5.3 mo from February to July in the absence of *Sphaeroma peruvianum,* and where roots were burrowed by isopods. x: mean aerial root productivity; SE: standard error; n: number of roots

	Aerial root productivity (g mo^{-1} $root^{-1}$)			Reduction in productivity (%)
	n	x	± SE	
Without isopods present	18	13.0	1.4	0
With isopods present				
A. Slowed root elongation in whole root	6	6.9	0.67	47
B. Slowed root elongation in roots with broken tips	20	3.1	0.39	76
C. Slowed root elongation with broken tips which regenerate	50	4.9	0.60	62

by isopods; 20 of these (61 %) had broken or atrophied growing tips. Fifteen (75 %) of these damaged roots had newly regenerated root tips, usually 2 to 4 new tips per root, for a total of 27 new root tips for 20 damaged plants. This is an increase in root number due to isopod burrowing of 35 % (7/20; Table 3).

The presence of isopods resulted in a decrease in net production by 47 % without root tip atrophy or breakage, and by 76 % with root tip atrophy or breakage (Table 4). Roots that were burrowed by isopods, with broken or atrophied tips, and with root tips that were regenerating had an average of 62 % less net production than unburrowed roots.

DISCUSSION

The present study resolves several issues on the effects of boring isopods on red mangrove forests (Rehm & Humm 1973, Enright 1974, Snedeaker 1974, Simberloff et al. 1978, Ribi 1981, 1982). The root-boring isopod *Sphaeroma peruvianum* induces specific responses in roots of the red mangrove: (1) a decrease in net root productivity; (2) a change in the morphological development of the roots due to regeneration of multiple sets of root tips; and (3) an increase in intertidal root tip breakage or atrophy. The degree to which these effects are manifested should depend upon the frequency of occurrence of the isopods in red mangrove forests. At the Punta Morales site, a 61 to 76 % frequency of burrows in aerial roots with an average of 2 isopods per root resulted in an overall 62 % reduction in net root production and a 1.35 regeneration ratio of new root tips per broken/damaged root tip. The loss in root production when boring isopods are present is caused primarily by a reduction in root elongation (47 %), and secondarily from loss of root biomass and delay in new growth when root tips are broken or damaged (29 %). The critical aspect of this combined loss is that root regeneration only partially compensates (15 % new root production) for the decrease (76 %) in net root production.

Simberloff et al. (1978) found a slightly lower regeneration ratio, 1.15, at their Chomes site, near the Punta Morales locality. However, they concluded that isopods induced a positive response in root production since regeneration of new tips exceeded the number of broken or damaged ones. We show that even when the root regeneration ratio is greater than 1, there is still a net loss of 62 % in net root production. Hence, the root regeneration ratio alone is not sufficient to establish whether there is a net loss or benefit to mangrove trees by the isopods.

Isopods were not selectively inhabiting weakened roots that would have otherwise grown more slowly in their absence because: (1) root elongation is reduced by about 50 % when isopods were experimentally added to lateral roots compared to roots without isopods (Perry 1988); (2) inhabitation of isopods in roots is correlated with decrease in elongation and root tip atrophy or breakage when surveying a large number of roots; and (3) isopods do not select a few roots that may be different than the majority of roots in the area. Isopods burrowed into 61 to 76 % of available roots that did not differ in appearance prior to inhabitation.

The second major response which isopods induce in red mangrove roots is to change the morphological development of the roots. Of root tips which are broken or damaged, 75 % regenerate tips, usually in sets of twos, threes or fours. This regeneration pattern results in a stilt-like morphological development of root systems. The critical factor perhaps is the number of roots entering the ground per unit time. A higher density of roots reaching and entering the ground would provide more surface area for nitrogen-fixing bacteria (Zuberer & Silver 1975, 1978) and perhaps increase stability to trees during storm periods. At Punta Morales, intertidal aerial roots without isopods grow at an average rate of 10.5 cm mo^{-1} and contact the ground in about 16 mo (based on root growth rate experiments, this study, and on an average canopy to ground height of 175 cm). Roots with isopods where root atrophy or breakage occurs 1 or 2 times during 9 mo grow at an average of 1.8 cm mo^{-1} and should require about 97 mo to reach the ground. Hence, isopod presence in aerial roots does not result in a greater number of roots entering the ground per unit time (assuming that an aerial root not inhabited by isopods will be initiated at least every 14 mo).

The magnitude of the effects induced by isopod inhabitation of mangrove roots also varies depending on root type and intertidal height, but does not substantially change on a seasonal basis. At our study site, isopod recruitment to aerial roots occurred throughout the year with little change in recruitment intensity. Isopods were just as likely to recruit to roots with existing burrows as to roots not yet inhabited by isopods. Aerial roots had the highest incidence of isopod burrows, whereas lateral-G and ground roots had a low frequency of occurrence of burrows. Ground roots are older and thicker than aerial and lateral-G roots and do not provide an appropriate surface area for burrowing (Perry 1988). Lateral-G roots initiated from ground roots can be bored by isopods depending upon their intertidal height. Lateral-G roots with initiation points less than 100 cm from the ground were rarely occupied by isopods, even though isopods are capable of burrowing into these roots within 24 h, inducing a 50 % growth rate reduction (Perry 1988). Predation probably prevents isopods from boring into low lateral-G roots, since juvenile and adult isopods are clearly capable of migrating by crawling or swimming to these roots (Perry 1988). Thus, lateral-G roots within 100 cm of the ground (without isopods) grow at a faster rate and should become established in the ground in a shorter time period than higher lateral-G roots which are susceptible to isopod boring and have a greater distance to reach the ground.

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