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Interspecific Variation in Rates of Trunk Wound Closure in a Panamanian Lowland Forest[1]

Manuel R. Guariguata[2]

Center for International Forestry Research (CIFOR), P.O. Box 6596 JKPWB, Jakarta, Indonesia

and

Gregory S. Gilbert

Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Panamá

ABSTRACT

We evaluated the ability to close wounds inflicted with a drill to the trunks of seven common tree species from Barro Colorado Nature Monument, Panamá. We predicted that species lacking wood antimicrobial activity would rapidly close wounds to prevent pathogen entrance, while those species with wood antimicrobial defenses need not necessarily exhibit fast wound closure. The species studied were *Alseis blackiana, Gustavia superba, Miconia argentea, Poulsenia armata, Protium panamense, P. tenuifolium,* and *Tetragastris panamensis.* Callus, resins, and latex were all involved in wound closure, but mechanisms varied among species: after 3 months, the only pioneer species, *Miconia,* had minimal diameter closure; *Alseis* showed intermediate closure only by callus; and the other five species (which did not differ) had almost completely plugged their wounds by means of combined callus and resin production (*Tetragastris* and both species of *Protium*), latex (*Poulsenia*), or callus and woody flakes (*Gustavia*). Our initial prediction was supported for *Gustavia* and *Poulsenia* (*i.e.,* rapid wound closure and no wood antimicrobial activity) but not for *Tetragastris* and *Protium* (that showed both rapid wound closure and strong wood antimicrobial activity); *Miconia* showed slow wound closure and no wood antimicrobial activity. Only for *Alseis,* was wound closure rate proportional to stem diameter growth.

RESUMEN

En el presente estudio evaluamos la capacidad de cicatrización en heridas producidas con un taladro en el tronco de siete especies de árboles en el Monumento Natural Barro Colorado, Panamá. Nuestra predicción inicial fue de que aquellas especies con poca actividad antimicrobiana en la madera cerrarían sus heridas más rápido para evitar infección, con respecto a otras especies con presencia (constitutiva) de defensas químicas en su madera. Las especies fueron: *Alseis blackiana, Gustavia superba, Miconia argentea, Poulsenia armata, Protium panamense, P. tenuifolium,* y *Tetragastris panamensis.* Los mecanismos de cicatrización variaron de acuerdo a las especies: luego de 3 meses, la única especie pionera en nuestro estudio, *Miconia,* mostró mínima capacidad de cicatrización; *Alseis* presentó capacidad intermedia con producción de callo; y las otras cinco especies habían cerrado las heridas casi completamente ya sea por producción combinada de callo y resina (*Tetragastris* y ambas especies de *Protium*), producción de látex (*Poulsenia*), y producción de callo y hojuelas leñosas (*Gustavia*). Nuestra predicción inicial se cumplió en *Gustavia* y *Poulsenia* (rápida cicatrización y ninguna actividad antimicrobiana en la madera) pero no en *Tetragastris* y *Protium* (rápida cicatrización y fuerte actividad antimicrobiana en la madera); *Miconia* mostró baja capacidad de cicatrización y ninguna actividad antimicrobiana. Unicamente en *Alseis,* la tasa de cicatrización se correlacionó con el crecimiento radial del tronco.

Key words: antibacterial activity; antifungal activity; callus; latex; Panamá; resin; tree damage; Tropical Moist Forest; trunk wound closure.

IN TROPICAL WET FORESTS, STUDIES OF TREE RESPONSES TO STEM DAMAGE have mostly focused on resprouting after crown and branch loss (*e.g.,* Putz & Brokaw 1989, Walker 1991), whereas there are few data on recovery from trunk injuries that occur through animal activity, branch shedding, or by falling neighbors (Shigo 1977). Bark and cambium wounding can have important consequences for tree population dynamics since they create openings for pathogen invasion that may lead to stem decay (*e.g.,* Basham 1978, Anderson *et al.* 1979, Shigo 1984).

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[2] Address for correspondence: CATIE, Unidad de Manejo de Bosques Naturales, Apartado 7170, Turrialba, Costa Rica.

TABLE 1. *Sample sizes and DBH range from individuals of the study species that were artificially wounded in Barro Colorado Nature Monument, Panamá. Nomenclature follows Croat (1978).*

Species	Family	Adult stature[a]	N	median DBH (cm)	DBH range (cm)
Alseis blackiana	Rubiaceae	C	24	15.6	10.0-27.0
Gustavia superba	Lecythidaceae	M	25	12.2	9.9–19.0
Miconia argentea	Melastomataceae	M	10	13.9	11.0–20.6
Poulsenia armata	Moraceae	C	9	19.3	9.4–25.0
Protium panamense	Burseraceae	M	10	15.3	8.0–24.7
Protium tenuifolium	Burseraceae	M	9	18.3	14.0–25.7
Tetragastris panamensis	Burseraceae	C	22	17.4	9.2–43.7

[a] C = canopy; M = midcanopy (data from Welden *et al.* 1991).

In this paper we describe interspecific variation in the ability to close artificially created trunk wounds on seven tree species from Barro Colorado Nature Monument (BCNM), Panamá. Previous observations suggest that trunk wounding can be locally important in BCNM where, for example, white-collared peccaries (*Tayassu tajacu*) remove the bark and girdle the base from adult trees of *Hyeronima laxiflora* (Euphorbiaceae; Foster 1982) and of *Rheedia acuminata* (Guttiferae; R. Condit, pers. comm.). Other mammals, such as agoutis (*Dasyprocta punctata*) gnaw on stems of juvenile *Beilschmiedia pendula* (Lauraceae; G. Gilbert, pers. obs.), and stingless bees maintain open wounds in the bark from trees of *Symphonia globulifera* (Guttiferae) from which they collect latex (Roubik 1989). Additional evidence from the BCNM suggests that pathogens may exert strong pressure in structuring juvenile (Augspurger 1983) and adult tree populations (Gilbert *et al.* 1994).

Although there are numerous studies on wound-healing processes and defenses against pathogen infection in temperate trees (*e.g.*, Wargo 1977, Shortle & Cowling 1978, Shigo 1984, Weber & Brasier 1984, Houston 1992, Filip *et al.* 1992), host responses against potential infection through bark and cambium damage are understudied in tropical forests. Trees may reduce the probability of microbial infection of trunk wounds by physically closing them (producing callus tissue or secreting wood exudates) or by producing wood chemical defenses, or both (Shigo 1984, Neely 1988, Mireku & Wilkes 1989). Here, we predicted that those species lacking strong antifungal and antibacterial activity in their wood would quickly close wounds through physical means to prevent pathogen invasion, whereas those with constitutive antimicrobial activity need not exhibit rapid wound closure to be effectively protected from potential infection.

STUDY SITE AND METHODS

Barro Colorado Nature Monument is a 5400-ha lowland forest reserve in lowland Panamá (Tropical Moist Forest *sensu* Holdridge *et al.* 1975), comprised of Barro Colorado Island (BCI) and adjacent mainland sectors. Annual rainfall on BCI averages 2600 mm, with a pronounced dry season from January through April during which only 10 percent of the yearly total is received (Windsor 1990). The study species are common trees of the local flora and differ in their regeneration patterns. *Miconia argentea* is a light-demanding pioneer on BCI (Brokaw 1987) and is also widespread in human-disturbed areas. *Gustavia superba* is likewise common in secondary forests, although its seedlings appear to persist under closed canopy through repeated dieback and resprouting (M. Guariguata and K. Harms, unpublished data). The remaining study species (*Alseis blackiana, Protium panamense, P. tenuifolium, Tetragastris panamensis,* and *Poulsenia armata*) are abundant in the old-growth forest of BCI (Hubbell & Foster 1990) and show high sapling survivorship in the understory (Welden *et al.* 1991).

We marked individuals (≥8 cm DBH) of the study species located in the vicinity of trails on Gigante Peninsula (south of BCI), an area dominated by 40-50 yr-old secondary forest where vegetation manipulation is allowed. The unequal sample sizes among individuals (Table 1) reflects their relative abundance over 2–3 km of trails visited. On 12 December 1992 (late rainy season), we created wounds approximately 7 mm diameter × 20 mm deep perpendicular to the trunk's longitudinal axis at 1.3 m height in each selected tree, using an electric drill. We also measured tree DBH. We used surface-sterilized (in 70% ethanol) plastic calipers to measure the minimum diameter of the wounds to the nearest 0.1 mm (at trunk surface), three times

at 1-month intervals; we did not quantify closure at depth. During each census, qualitative observations were made for every individual on mode of external wound closure (*i.e.,* resin, latex, callus). Each tree was examined again in late September–early October 1994 (approximately 22 mo after wounding), and wounds and trunk DBH were remeasured.

To assay for constitutive chemical antimicrobial activity in the wood, healthy branch samples were collected from individuals not included in the wounding experiment for each of the seven tree species studied. We focused here on constitutive production of antimicrobial compounds, as they are probably the first and most general chemical barrier to infection by microbes, and to avoid potential complications with chemicals produced by microorganisms themselves, that may invade wounds prior to chemical sampling. Approximately 1.5-g fresh weight of material was chopped with a razor blade, placed in a test tube with methanol (ten times the fresh weight of the wood), and macerated with a polytron mixer for 2 min to produce a uniform slurry. Samples were then centrifuged for 25 min in a table-top centrifuge to remove solid material, and the liquid fraction was decanted and then lyophilized. The resulting sample was resuspended in methanol.

To test for antibacterial activity, the methanol extracts were pipetted into wells of a Biolog MT test plate (Biolog Inc., Hayward, CA). Each wood extract was tested at three concentrations (1, 2, and 3 times the concentration in the original samples) with two replicates. Biolog plates contain a tetrazolium dye indicator that turns purplish in the presence of bacterial metabolic activity in the wells (Bochner 1989). Methanol from all samples was allowed to evaporate. Wells were then inoculated with washed and resuspended cells (in half-strength Trypticase® Soy Broth, BBL Inc.) of a 24-hr culture of the bacterium *Bacillus mycoides.* This strain of *B. mycoides* was isolated from cankered stems of seedlings of *Ocotea whitei* (Lauraceae) on BCI, but apparently did not cause the canker. The controls were methanol plus bacteria and extracts without bacteria. Plates were incubated at 28°C and scored visually (0 = no color reaction; 1 = weak color reaction; 2 = strong color reaction) after 2 hr and 24 hr.

We used a similar bioassay to assess the effects of wood extracts on the growth of five strains of plant-associated fungi and one laboratory contaminant, all from BCI. The first five fungal strains are all associated with necrosis on leaves and are used in a larger study on plant-produced antifungal compounds; they are not necessarily involved with wood decay but we have found them to serve as good indicators of antifungal activity. Included were *Colletotrichum gleiosporoides* G0129 from *Licania platypus* (Chrysobalanaceae), an unknown sterile mycelium G0109 isolated from *Cupania rufescens* (Sapindaceae), *Fusarium* sp. G0132 from unidentified leaf litter, *Pestalotiopsis* sp. G0092 from *Ocotea oblonga* (Lauraceae), an unknown sterile mycelium G0134 from *Ouratea lucens* (Ochnaceae), and *Penicillium* sp. PENI isolated as a laboratory contaminant. For each fungus, three replicates of each extract, plus methanol negative control, were placed in a 96-well microtitre tissue culture plates (Falcon Microtest III) at three times the original concentration. The fungicide Benlate was included as a positive control. Fungi were grown in unshaken liquid culture (2% Malt Extract Broth: MEB) for three d at room temperature. The broth was decanted, replaced with fresh MEB, and the culture was macerated to smoothness in a polytron mixer for 30 sec at 30,000 rpm. The fungal suspension was then inoculated into the appropriate wells, incubated at ambient laboratory conditions (22°–23°C), and scored for growth after nine d with the aid of a bottom-lighted stereoscope, Each well was scored as follows: 0 = no growth beyond initial inoculum; 1 = minimal growth; 2 = growth covers part of well; 3 = well filled with fungal mycelium.

RESULTS

The species studied differed in their ability to close the artificial trunk wounds (Fig. 1). After 3 mo, internal wound diameters were statistically different among species (ANOVA, $F_{6,102} = 19.3$; $P < 0.001$). *Miconia* showed minimal closure, *Alseis* showed an intermediate response, and the remaining five species had almost completely closed their wounds. There were no differences in internal wound diameter among the later five species. Because wounded individuals of all species showed dissimilar DBH distributions (Table 1), we included tree diameter as a covariate when testing for among-species differences in wound closure rates after 45 d and 99 d (expressed as [initial wound diameter- wound diameter at census]/[initial wound diameter]); the covariate effect was not statistically significant (ANCOVA, $F_{1,102} = 0.1$ and 0.3 for both censuses, respectively; $P > 0.5$ in both cases). This suggests that initial tree size did not appear to influence closure rates over the 3 mo interval.

The study species showed various mechanisms

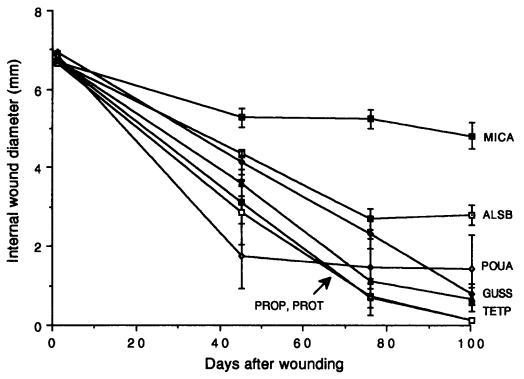

FIGURE 1. Inner diameter closure of artificial trunk wounds in trees of *Alseis blackiana* (ALSB), *Gustavia superba* (GUSS), *Miconia argentea* (MICA), *Poulsenia armata* (POUA), *Protium panamense* (PROP), *Protium tenuifolium* (PROT), and *Tetragastris panamensis* (TETP) on Barro Colorado Nature Monument, Panamá. Sample sizes as in Table 1. Data points are means ± 1 SE. A-posteriori comparisons (Fisher's Protected LSD, α = 0.05) of mean diameters at 100 d followed: MICA > ALSB > POUA = GUSS = PROP = PROT = TETP.

for trunk wound closure (Table 2). *Alseis, Gustavia, Tetragastris,* and both species of *Protium* all formed callus tissue inside the wound margins; for *Protium* and *Tetragastris,* but not for the other species, wound closure was augmented by production of resins that solidified in the wounds. *Poulsenia* formed no obvious callus tissue but relied entirely on latex production that appeared to mix with small particles of wood that dried to create a plug that filled the wound. Wound plugging by means of woody flakes was also prominent for *Gustavia. Alseis* was the only species that relied entirely on producing an internal ring of callus to close wounds. *Miconia* formed neither callus nor resins; the wound inner margins seemed to dry out, but changes in wound diameter were minimal.

After 22 mo, eight of the ten individuals of *Miconia* had completely closed their wounds. Another individual of *Miconia* had died due to stem snapping at about 2.5 m from the ground. The trunk was badly rotten and termite infested, but the area around the artificial trunk wound was no more decomposed than the rest of the trunk, and we can not speculate whether the wound was the site of pathogen infection. The remaining individual of *Miconia* maintained its wound open, and it was the only one for which negative trunk diameter growth was recorded (a loss of 0.1 cm). Presumably this tree was senescent or otherwise under physiological stress. One *Tetragastris* individual, located far from trails, could no longer be found.

We found a positive correlation between wound closure rate at 45 d and diameter growth over 22 mo (Pearson's r = 0.28; N = 108; P = 0.003). However, the correlation coefficient was low, and visual inspection of the data points suggested that *Poulsenia* exerted a strong influence on the correlation (Fig. 2). When *Poulsenia* was excluded from the analysis, the correlation was not significant (Pearson's r = 0.09; N = 99; P = 0.34). For each of the species individually, only *Alseis* had a significant relationship between diameter growth and wound closure rate (Pearson's r = 0.49; N = 24; P = 0.016).

Wood extracts from *Miconia, Poulsenia,* and *Gustavia* showed no inhibition of bacterial growth when compared to the methanol control (score = 2 in all wells). In contrast, *Tetragastris* permitted almost no growth at any concentration (means score 0.5 at 1x concentration, score = 0 at higher concentrations), while both *Protium* species and *Alseis* showed strong inhibition (all scores of 0 or 1) for 2X and 3X concentrations. Thus the three Burseraceae (*Protium, Tetragastris*) appear to have strong antibacterial compounds in their wood (all produce strongly aromatic resin), as does *Alseis*. Surprisingly,

TABLE 2. *Summary of qualitative trunk wound responses 3 mo after wounding and antimicrobial activities observed in the study species from Barro Colorado Nature Monument, Panamá. Species are arranged from those with lowest* (Miconia) *to fastest wound closure capacity.*

Species	Callus formation	Latex or resin	Antifungal activity	Antibacterial activity
Miconia argentea	no	no	no	no
Alseis blackiana	yes	no	weak	yes
Gustavia superba	yes	no	no	no
Poulsenia armata	no	latex	no	no
Protium panamense	yes	resin	no	yes
Protium tenuifolium	yes	resin	no	yes
Tetragastris panamensis	yes	resin	weak	yes

TABLE 3. *Two-way ANOVA of antifungal bioassay from wood extracts of the study species. Included were the six species of fungi described in the text (fungus), and the seven wood extracts plus Benlate and broth controls (extracts).*

Factor	df	MS	*F*	*P*
Fungus	5	16.20	62.49	0.0001
Extract	8	1.44	5.55	0.0001
Fungus × Extract	40	0.75	2.88	0.0001
Error	108	0.26		

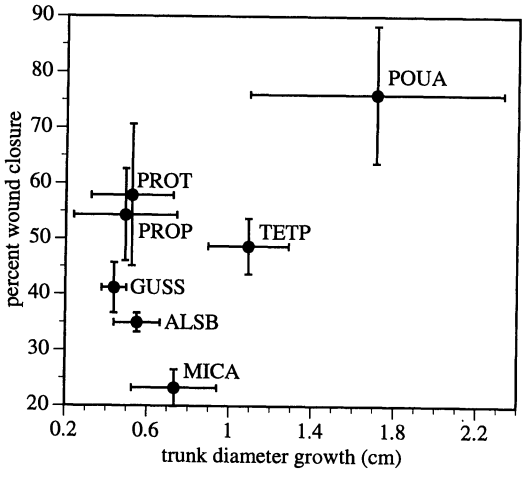

FIGURE 2. Relationship between trunk diameter growth and percent of trunk wound closure in the seven study species. Diameter growth was the absolute increase measured over 22 mo, and percent wound closure corresponds to 45 d after wounding. Data points are means ± 1 SE. Species abbreviations as in Fig. 1, and sample sizes as in Table 1 (minus one each for MICA and TETP, as described in the text).

Poulsenia, which produced copious white latex to plug the wounds showed no antibacterial activity. The results from the antibacterial assay were identical at the two- and 24-hr readings.

Data from the antifungal assay were analyzed by two-way ANOVA with factors being the six fungi and the seven wood extracts plus (Benlate and methanol) controls. There were highly significant main effects for both fungal species and extract, as well as a highly significant interaction term (Table 3). One-way ANOVA for effect of extracts was then performed for each fungal strain independently. Only four strains had significant *P*-statistics ($P < 0.05$). Fisher's protected Least Significant Difference at $\alpha = 0.05$ was used to compare means across extracts for these four fungi (Table 4). In general, extracts from wood either stimulated fungal growth or had no effect, and inhibitory effects were rare. Only for the *Fusarium* sp. isolated from leaf litter, did extracts of *Tetragastris* and *Alseis* have a significantly inhibitory effect when compared to the methanol control. Although the fungicide Benlate usually permitted less fungal growth than the methanol controls, the difference was never statistically significant.

TABLE 4. *One way ANOVA and means comparisons for effects of wood extracts* (N = 3) *of the study species on each of four fungal strains. Values shown are mean ratings of fungal growth in wells, where 0 = no growth and 3 = well filled with mycelium. Means followed by different letters within a fungal species are significantly different (Fisher's Protected LSD, α = 0.05). Species abbreviations as in Fig. 1. MeOH = Methanol.*

a) Fungal strain G0092 ($F_{8,18} = 7.87$; $P < 0.0001$)

Benlate	PROP	MeOH	POUA	ALSB	GUSS	MICA	PROT	TETP
2.0a	2.0a	2.33ab	2.67bc	3.00c	3.00c	3.00c	3.00c	3.00c

b) Fungal strain G0132 ($F_{8,18} = 15.08$; $P < 0.0001$)

TETP	ALSB	Benlate	MeOH	POUA	MICA	GUSS	PROP	PROT
1.00a	1.33ab	1.67bc	2.00cd	2.00cd	2.33d	3.00e	3.00e	3.00e

c) Fungal strain G0134 ($F_{8,18} = 3.00$; $P < 0.025$)

Benlate	MeOH	POUA	TETP	ALSB	MICA	GUSS	PROP	PROT
2.33a	2.33a	2.33a	3.00b	3.00b	3.00b	3.00b	3.00b	3.00b

d) Fungal strain PENI ($F_{8,18} = 4.88$; $P < 0.003$)

Benlate	MeOH	MICA	POUA	PROP	ALSB	GUSS	PROT	TETP
1.33a	2.00ab	2.00ab	2.33bc	2.33bc	3.00c	3.00c	3.00c	3.00c

DISCUSSION

We found mixed support for our initial prediction that species with little antimicrobial activity in their wood extracts would show rapid wound closure, while those species with strong antimicrobial properties rely less on fast wound healing. For example, we measured fast wound closure for *Gustavia* and *Poulsenia,* but very slow closure for *Miconia,* even though these three species showed no detectable antimicrobial activity in their wood extracts. On the other side, wound healing was rapid for *Tetragastris* which was coupled with a strong antimicrobial activity. The species that produce latex or resins were able to close most quickly the wounds with secretions. But *Gustavia* was the exception; we did not observe wood exudates for this species but instead rapid wound plugging by woody flakes and callus.

Neely (1983, 1988) reported that high rates of wound closure were positively correlated with radial tree growth in temperate-zone trees. Neely's study species, however, relied exclusively on callus production as an external repair mechanism (see also Martin and Sydnor 1987). This is consistent with our findings for *Alseis,* the only species that showed a significant relationship between radial stem growth and wound closure rate, and that depended entirely on production of callus to close wounds. It is possible that a similar pattern occurs among our other study species, had we been able to confidently measure callus growth alone in the presence of wood exudates; this might be a reason why we did not detect a correlation. Our results suggest, however, that latexes and resins have the potential to function as physical barriers to potential pathogen infection as much as callus production, and that rapid wound closure by wood exudates may be independent of tree vigor among our study species.

Individuals of *Miconia,* our only pioneer species, showed no apparent wound response in the first 100 d and wood extracts had no detectable antimicrobial activity. We speculate that because of its intrinsically short life-span due to limitations imposed by biophysical and successional changes, this pioneer species, and others like it, might benefit more from additional resource investment into early growth than from "expensive" wound healing mechanisms. The measured stem growth rates of *Miconia* were comparable to most of the other study species (Fig. 2), that in turn showed much faster wound closure. It is also possible, however, that our *Miconia* individuals showed a poor healing response due to senescence.

Although the potential effect of microhabitat differences on the capacity of wound closure was not directly examined in this study, wounded *Poulsenia* (a slope-specialist, moisture-loving species; Hubbell and Foster 1990) appeared to be sensitive to topographic differences in their ability to respond to trunk wounding. Two *Poulsenia* individuals located on a ridge (microsites that are usually drier than slopes in the BCNM; Becker *et al.* 1988) showed a reduced capacity to close wounds when compared to their conspecifics growing along slopes. All other individuals ($N = 7$) had completely closed their wounds after 75 d. If these two ridge-dwelling individuals were removed from the analysis in Figure 1, the mean final diameter in *Poulsenia* wounds would have been 0.0 mm (SE = 0.0) instead of 1.3 mm (SE = 0.87).

The overall lack of antifungal activity in the wood extracts, while four species showed substantial antibacterial activity, is interesting because the vast majority of tree pathogens are fungi, with only a few bacteria causing significant damage to trees (Manion 1981). Of course, the variation in responses among fungal strains in this study may suggest that chemical defenses in tropical trees may have evolved according to specific fungal pathogens, rather than as defenses against fungal attack in general, and that assays with other fungi may have provided stronger evidence for antifungal components.

It should be noted that our observations are limited both to describing external signs of wound closure, and to evaluate constitutive production of wood antibacterial and antifungal chemicals in healthy wood. A suite of chemical and anatomical changes that occur internally after trunk wounding have been described for many temperate tree species (see review in Shigo 1984), all of which have been proposed as mechanisms to halt the spread of wood pathogens. It is possible that those responses occur in tropical trees as well, and that such internal mechanisms may vary to a greater or lesser extent among the study species than those observed to occur externally. Our observations indicate that external wound healing mechanisms are not necessarily a trade-off between physical and chemical attributes in our study species. Analysis of additional species, particularly of fast-growing pioneers, would help clarify whether strong wound responses are associated with life history strategies. Future research on the specificity of trunk defenses against particular pathogens could be rewarding and lead to a better understanding of tropical forest tree dynamics.

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LITERATURE CITED

ANDERSON, N. A., M. E. OSTRY, AND G. W. ANDERSON. 1979. Insect wounds as infection sites for *Hypoxylon mammatum* on trembling aspen. Phytopathology 69: 476–479.

AUGSPURGER, C. K. 1983. Seed dispersal of the tropical tree, *Platypodium elegans,* and the escape of its seedlings from fungal pathogens. Journal of Ecology 71: 759–771.

BASHAM, J. T. 1978. Early sugar maple stem discoloration and microorganism invasion in simulated wounds of felling and fire scars. Phytopathology 68: 1693–1699.

BECKER, P., P. E. RABENOLD, J. R. IDOL, AND A. P. SMITH. 1988. Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. Journal of Tropical Ecology 4: 173–184.

BOCHNER, B. R. 1989. Sleuthing out bacterial identities. Nature 339: 157–158.

BROKAW, N. V. L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. Journal of Ecology 75: 9–19.

CROAT, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California, USA.

FILIP, G. M., B. E. WICKMAN, R. R. MASON, C. A. PARKS, AND K. P. HOSMAN. 1992. Thinning and nitrogen fertilization in a grand fir stand infested with western spruce budworm. Part III: tree wound dynamics. Forest Science 38: 265–274.

FOSTER, R. B. 1982. Famine on Barro Colorado Island. *In* E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). The ecology of a tropical forest: seasonal rhythms and long-term changes, pp. 201–212. Smithsonian Institution Press, Washington, D.C., USA.

GILBERT, G. S., S. P. HUBBELL, AND R. B. FOSTER. 1994. Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. Oecologia 98: 100–108.

HOLDRIDGE, L. R., W. G. GRENKE, W. H. HATHEWAY, T. LIANG, AND J. A. TOSI, JR. 1975. Forest environments in tropical life zones. Pergamon Press, Inc., New York, USA.

HOUSTON, D. R. 1992. A host–stress–saprogen model for forest dieback–decline diseases. *In* P. D. Manion and D. Lachance (Eds.). Forest decline concepts, pp. 3–25. APS Press, St. Paul, Minnesota, USA.

HUBBELL, S. P., AND R. B. FOSTER. 1990. Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. *In* A. H. Gentry (Ed.). Four Neotropical rainforests, pp. 522–541. Yale University Press, New Haven, Connecticut, USA.

MANION, P. D. 1981. Tree Disease Concepts. Prentice-Hall, Englewood Cliffs, NJ, USA.

MARTIN, J. M., AND T. D. SYDNOR. 1987. Differences in wound closure rates in 12 tree species. HortScience 22: 442–444.

MIREKU, E., AND J. WILKES. 1989. Seasonal variation in the ability of the sapwood of *Eucalyptus maculata* to compartmentalize discolouration and decay. Forest Ecology and Management 28: 131–140.

NEELY, D. 1983. Tree trunk growth and wound closure. HortScience 18: 99–100.

———. 1988. Tree wound closure. Journal of Arboriculture 14: 148–152.

PUTZ, F. E., AND N. V. L. BROKAW. 1989. Sprouting of broken trees on Barro Colorado Island, Panama. Ecology 70: 508–512.

ROUBIK, D. W. 1989. Ecology and natural history of tropical bees. Cambridge University Press, New York.

SHIGO, A. L. 1977. Compartmentalization of decay in trees. U.S. Department of Agriculture Information Bulletin No. 405.

———. 1984. Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. Annual Review of Phytopathology 22: 189–214.

SHORTLE, W. C., AND E. B. COWLING. 1978. Development of discoloration, decay, and microorganisms following wounding of sweetgum and yellow-poplar trees. Phytopathology 68: 609–616.

WALKER, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 379–385.

WARGO, P. M. 1977. Wound closure in sugar maple: adverse effects of defoliation. Canadian Journal of Forest Research 7: 410–414.

WEBER, J. F., AND C. M. BRASIER. 1984. The transmission of Dutch elm disease: a study of the processes involved. *In* J. M. Anderson, A.D.M. Rayner, and D. Walton (Eds). Invertebrate-microbial Interactions, pp. 271–306. Cambridge University Press, Cambridge.

WELDEN, C. W., S. W. HEWETT, S. P. HUBBELL, AND R. B. FOSTER. 1991. Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. Ecology 72: 35–50.

WINDSOR, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. Smithsonian Contributions to the Earth Sciences 29.