Within-tree Distribution of Pine Bark Beetles (Coleoptera: Scolytidae) in Honduras

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ABSTRACT

The within-tree distribution of bark beetles (Coleoptera: Scolytidae) infesting Pinus oocarpa Schiede in Honduras was studied under post-epidemic conditions at elevations between 900-1700 m in 1966. Nine bark beetle species were recovered: Dendroctonus frontalis Zimmermann, Dendroctonus parallelocollis Chapuis, Dendroctonus valens LeConte, Ips bonanseai (Hopkins), Ips cribricollis (Eichhoff), Ips interstitialis (Eichhoff), Ips lecontei Swaine, Pityophthorus cacuminatus Blandford, and Pityophthorus confusus Blandford. Of these, D. frontalis was the most frequently collected species and usually the first to colonize the host trees. Ips bonanseai was the most common Ips species collected, while I. lecontei was the rarest. Overall, Dendroctonus species tended to attack the trunk region, Ips species dominated in the upper crown and larger branches, and Pityophthorus species were most numerous in the smaller branches and shoots. The bluestain fungus associated with D. frontalis galleries was identified as Ceratocystic minor (Hedgecock) Hunt.

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INTRODUCTION

*Pinus oocarpa* Schiede is one of the most widespread Latin American pines, ranging from Mexico southward through Guatemala, Belize, Honduras, El Salvador, and northwestern Nicaragua (Critchfield and Little, 1966; Schwerdtfeger, 1953). In Honduras, *P. oocarpa* is the major source of pine harvested for exportation and domestic use, although two other species are widely used: *Pinus caribaea* Morelet and *Pinus pseudostrobus* Lindl. The bulk of exported pine is taken from the highland pine and pine/oak (*Quercus*) associations, which cover much of western Honduras and range in altitude between 600-1700 m (Billings, 1982; Coyne and Critchfield, 1974; FAO, 1968; Molina, 1964).

The southern pine beetle, *Dendroctonus frontalis* Zimmermann, is considered the principal bark beetle (Coleoptera: Scolytidae) pest of *P. oocarpa* in Honduras. During 1962-1965, more than 2 million ha of pine forest were infested by *D. frontalis* and other associated bark beetles, with timber volume losses estimated at over 55 million m$^3$. This, the largest recorded *D. frontalis* outbreak, originated in the Department of Olancho and spread throughout the pine-growing regions of Honduras with exception of the lowland pine savannah, and subsided due to natural causes (Beal et al., 1964; Billings, 1982; Fox et al., 1964; Hernández, 1975; Ketcham and Bennett, 1964). Most of the infested *P. oocarpa* stands were located along mountain ridges and steep slopes where soils were shallow, nutrient depleted, and eroded (Beal et al., 1964; FAO, 1968; Ketcham and Bennett, 1964). Because of the nearly annual fires, these stands consisted of widely spaced, basally scarred trees with little or no regeneration. The trees were slow growing and often over 100 years of age. In addition to the 1962-1965 epidemic, scattered bark beetle outbreaks have occurred in Honduras during 1939, 1970, 1973, 1978, and 1982-1986 (Beal et al., 1964; Billings, 1982; R. F. Billings, personal communication).

Several species of *Dendroctonus* and *Ips* bark beetles occur in Central America (Clark, 1974; Lanier, 1987; Lanier et al., 1988; Mankins, 1980; Perry, 1951; Renwick et al., 1975; Rose, 1966; Schedl, 1955; Schwerdtfeger, 1953, 1955, 1956, 1959; Vite et al., 1974, 1975; Wood, 1982; Yates, 1972a, 1972b). Although some taxonomic debate still occurs, the
Dendroctonus species are believed to include D. approximatus Dietz (reported from Guatemala and Honduras), D. adjunctus Blandford (Guatemala), D. frontalis (Honduras), D. mexicanus Hopkins (Honduras) (but see Lanier et al., 1988), D. parallelocollis Chapuis (Guatemala and Honduras), D. valens LeConte (Guatemala and Honduras), and D. vitei Wood (Guatemala). The Central American Ips species include I. bonanseai (Hopkins) (Guatemala and Honduras), I. cribricollis (Eichhoff) (Guatemala, Belize, Honduras, and Nicaragua) (recognized at times as a synonym of I. grandicollis (Hopping, 1965; Lanier, 1970, 1988; Wood, 1977, 1982)), I. grandicollis (Eichhoff) (Honduras), I. integer (Eichhoff) (Guatemala), I. interstitialis (Guatemala, Belize, Honduras, and Nicaragua) (recognized as a synonym of I. calligraphus (Germar) by Wood (1982), (see also Lanier, 1972)), I. lecontei Swaine (Guatemala and Honduras), and I. mexicanus (Hopkins) (Guatemala).

In the Department of San Francisco Morazán, Honduras, Clark (1974) collected 30 species of insects from standing and felled P. oocarpa trees that were infested with D. frontalis; however, no within-tree distributional data were given. Overall, 14 of the species were bark-beetle predators, 7 were bark-beetle parasites, and 6 were other species of bark beetles. In addition to D. frontalis, the other bark beetles were D. valens, I. cribricollis, I. interstitialis (published as I. calligraphus), I. lecontei, Orthotomicus sp. (probably a misidentification with no species of this genus occurring in Honduras; S. L. Wood, personal communication), and Pityophthorus sp. (Clark, 1974). In addition to the insect associates of D. frontalis in Honduras, several species of mites (Acarina) have also been identified (Moser et al., 1974). Some of the identified mites are known to be natural enemies of D. frontalis in Louisiana (USA) while others are known to feed on and/or transmit spores of the pine-pathogenic bluestain fungus Ceratocystis minor (Hedgecock) Hunt.

Information on the within-tree distribution of bark beetles is useful in the development of sampling methods for selected scolytids. It also can provide insight into the degree of competition between different bark beetle species. Increased competition and displacement of D. frontalis by certain Ips species has been associated with the decline of D. frontalis outbreak populations both in Mexico (Rose, 1966) and North Carolina.
The primary objective of this study was to determine the within-tree distribution of the bark beetles that infest *P. oocarpa* trees in Honduras. A secondary objective was to identify the bluestain fungus associated with the primary *Dendroctonus* species recovered. A list of the mites collected from *D. frontalis* galleries during this study has been published separately (Moser *et al.*, 1974).

**METHODS AND MATERIALS**

The study locale was near Tegucigalpa, Honduras. A few sample trees were located ca. 5 km east of Lepaterique, but most were located near Zamorano on the slopes of Mt. Uyuca at elevations between 900-1700 m. Sampling was confined to *P. oocarpa*, although *P. pseudostrobus* also was present at some of the higher elevations. Field aspects of this study were conducted by the senior author from 15 February to 24 March 1966, at least 6-9 months after the collapse of the massive 1962-1965 *D. frontalis* outbreak. Bark beetle populations were at endemic levels and trees infested by *Dendroctonus* or *Ips* species were difficult to locate. In all, 21 trees containing live parent adults or brood of scolytid bark beetles were selected for sampling.

One or two trees were sampled daily, with paired samples (each 21 cm long) cut at eight fixed locations per tree: (1) *stump* = trunk within 60 cm of the ground; (2) *breast height* = trunk near 1.4 m above ground; (3) *midbole* = trunk midway between ground and first live branch; (4) *crown base* = trunk at first live branch; (5) *midcrown* = trunk midway in the crown; (6) *mid-clear-branch* = midpoint of two major, midcrown branches between the trunk and first whorl of foliage-bearing branches; (7) *mid-shoot-branch* = midpoint of two major, midcrown branches between first whorl of foliage-bearing branches and the tip of the major branch; and (8) *shoot* = clear basal portion of apical shoot on each of two major, midcrown branches (Fig. 1). Data recorded per tree at the time of felling included date, location, elevation, diameter outside bark at breast height, total tree height, crown height, age based on
count of annual growth rings near ground level, foliage color, and absence or presence of blue-stained wood on one or more cut surfaces of the tree bole samples. Percent live crown ratio (LCR) was calculated as follows: per cent \( \text{LCR} = \left( \frac{\text{crown height}}{\text{total tree height}} \right) \times 100 \).

One set of samples from each tree was processed soon after collection. All adult and immature bark beetle specimens were dissected from the outer and inner bark with a knife, sorted to probable genus, counted, and stored in 70\% ethanol. Bluestain fungus isolations were made from these field samples by aseptically removing stained chips of sapwood underlying \( D. \) frontalis galleries, implanting the chips in potato dextrose agar (P. D. A.) medium in Petri dishes, incubating for 3 days at 28-30°C, and reisolating to P.D.A. in shipping tubes. The second set of samples from each tree was held for an average of 10 days at \( \text{ca.} 27^\circ \text{C} \) before removing the bark beetles; all collection data were combined for each pair of bolts for a given sampling location. The mean diameter inside bark of all samples was recorded to the nearest centimeter and tracings of isolated
beetle galleries were made on sheets of cellulose acetate to assist in identification.

In 1966, *Ips* species were identified by G. R. Hopping of the Canadian Forestry Service, *Dendroctonus* and *Pityophthorus* species by S. L. Wood of Brigham Young University, Provo, Utah, USA, and the bluestain fungus by M. A. Rosinski of the University of Iowa, Iowa City, Iowa, USA. In 1987, many bark beetle specimens were reexamined by G. N. Lanier of the State University of New York, Syracuse, New York, USA, and S. L. Wood. Scolytid specimens were deposited in the Florida State Collection of Arthropods, Gainesville, Florida, USA.

RESULTS

Tree and beetle summary data for the 21 infested *P. oocarpa* trees are presented in Table 1. Overall, the sampled trees were 9-30 m in height, 9-51 cm in diameter at breast height, 14-58 years old, and felled between elevations of 900-1700 m.

The foliage color of the sampled trees varied from totally green to totally red (Table 1), suggesting that some trees were more recently attacked than others. Other evidence suggesting differences in the timing of attack is that xylem discoloration due to blue-stain fungi (*Ceratocystis* spp.) was observed in about half the trees with some green foliage, but in all trees with red foliage (Table 1). Thus, further colonization by the same or other bark beetle species would probably have occurred on several trees, especially on those that had been only partially attacked (e.g., No. 1, 5, 6, 9, and 19; Table 1).

Three *Dendroctonus* (*D. frontalis, D. parallelocollis*, and *D. valens*), four *Ips* (*I. bonanseai, I. cribricollis, I. interstitialis*, and *I. lecontei*), and two *Pityophthorus* species (*P. cacuminatus Blandford and P. confusus Blandford*) were collected. Species diversity was richest (7 species) in the bole samples within the crown region (locations 4 and 5), whereas diversity was poorest in the stump (3 species) and shoot (2 species) locations (Fig. 2).

*Dendroctonus frontalis* was the most frequently encountered bark beetle in this study, being found in 16 of the 21
Table 1. Summary tree and insect data for bark beetles infesting *Pinus oocarpa* in Honduras (February-March 1966).

<table>
<thead>
<tr>
<th>Tree data a</th>
<th>Elev.</th>
<th>Foliage</th>
<th>Most</th>
<th>Other bark beetles in same tree</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. Ht DBH LCR</td>
<td>No.</td>
<td>age (m)</td>
<td>color</td>
<td>stain</td>
</tr>
<tr>
<td>-------------</td>
<td>-----</td>
<td>---------</td>
<td>-------</td>
<td>-------</td>
</tr>
<tr>
<td>1 9 9 28 20</td>
<td>1700</td>
<td>G b</td>
<td>— c</td>
<td>DF 2</td>
</tr>
<tr>
<td>2 10 16 55 15</td>
<td>1400</td>
<td>Y +</td>
<td>DF 2</td>
<td>PA PO</td>
</tr>
<tr>
<td>3 10 12 56 15</td>
<td>1700</td>
<td>R +</td>
<td>DF 2</td>
<td>IB IC PA PO</td>
</tr>
<tr>
<td>4 11 13 37 14</td>
<td>1700</td>
<td>G —</td>
<td>DF 2</td>
<td>PO</td>
</tr>
<tr>
<td>5 11 13 57 17</td>
<td>1700</td>
<td>G -</td>
<td>DF 2</td>
<td>—</td>
</tr>
<tr>
<td>6 11 13 35 17</td>
<td>1700</td>
<td>G -</td>
<td>DF 2</td>
<td>—</td>
</tr>
<tr>
<td>7 12 16 61 14</td>
<td>1700</td>
<td>G,Y +</td>
<td>DF 2</td>
<td>DV IB II IL</td>
</tr>
<tr>
<td>8 12 26 85 15</td>
<td>1400</td>
<td>R +</td>
<td>DF 2</td>
<td>II PA</td>
</tr>
<tr>
<td>9 13 16 36 16</td>
<td>1700</td>
<td>G —</td>
<td>DF 2</td>
<td>—</td>
</tr>
<tr>
<td>10 16 23 54 18</td>
<td>1700</td>
<td>Y,R +</td>
<td>DV 1</td>
<td>DF PA PO</td>
</tr>
<tr>
<td>11 16 35 69 18</td>
<td>1400</td>
<td>Y,R +</td>
<td>DV 1</td>
<td>DF IB IC II IL P</td>
</tr>
<tr>
<td>12 17 20 44 23</td>
<td>1700</td>
<td>Y,R +</td>
<td>DF 2</td>
<td>DV IB PA PO</td>
</tr>
<tr>
<td>13 20 27 54 25</td>
<td>1200</td>
<td>Y,R +</td>
<td>IB 4</td>
<td>DV IC II PA PO</td>
</tr>
<tr>
<td>14 20 34 71 32</td>
<td>1500</td>
<td>G,Y -</td>
<td>DF 2</td>
<td>IL</td>
</tr>
<tr>
<td>15 23 36 49 36</td>
<td>1700</td>
<td>G,Y +</td>
<td>IB 4</td>
<td>DF DV PA PO</td>
</tr>
<tr>
<td>16 24 32 63 30</td>
<td>900</td>
<td>G,Y —</td>
<td>IC 5</td>
<td>PA PO</td>
</tr>
<tr>
<td>17 24 36 58 58</td>
<td>1700</td>
<td>G,Y +</td>
<td>DF 2</td>
<td>PO</td>
</tr>
<tr>
<td>18 27 34 46 22</td>
<td>1700</td>
<td>G +</td>
<td>DV 1</td>
<td>DF</td>
</tr>
<tr>
<td>19 28 39 49 33</td>
<td>1500</td>
<td>G +</td>
<td>DV 1</td>
<td>—</td>
</tr>
<tr>
<td>20 30 45 26 37</td>
<td>1100</td>
<td>Y,R +</td>
<td>IB 4</td>
<td>IC PA</td>
</tr>
<tr>
<td>21 30 51 28 58</td>
<td>1500</td>
<td>Y,R +</td>
<td>DV 1</td>
<td>IB IC IL PA PO</td>
</tr>
</tbody>
</table>

a. Ht = total tree height, DBH = tree diameter at breast height, LCR = live crown ratio.

b. Foliage color at time of felling: G = green, R = red, Y = yellow.

c. visible blue stain detected on xylem surface of at least one sample for a given tree: + = positive, — = negative.


See Fig. 1 for identity of sites (i.e., sampling locations) in which most advanced brood were observed.
Fig. 2. Relative frequency (o/o) of bark beetles infesting Pinus oocarpa trees in Honduras at eight sampling heights. For example, considering all trees from which beetles were found at sample location 1, 35o/o were attacked by DV, 55o/o by DF, and 10o/o by PO; species are DF = Dendroctonus frontalis, DV = Dendroctonus valens and Dendroctonus parallelocollis, IB = Ips bonanseil, IC = Ips cribricollis, II = Ips interstitialis, IL = Ips lecontei, PA = Pityophthorus cacuminatus, PO = Pityophthorus confusus.

trees sampled (Tables 1 & 2). It had the most advanced brood in 12 of the sampled trees (Table 1), suggesting that it was first to attack those trees. This species infested some of the smallest- as well as some of the largest-diameter trees (Table 1). It usually initiated attack along the lower trunk (location 2; Table 1), and then colonized above and below that area. Most D. frontalis were found in samples taken from the clear bole (locations 1-4, Table 2, Fig. 2); none were recovered from branch samples. When found in a given sample, it was most often the only species of bark beetle present (Table 2); its most common associate was P. confusus. Dendroctonus frontalis was the only species associated with each of the other bark beetles on at least one occasion. The blue-stain fungus associated with the D. frontalis galleries was identified as Ceratocystis minor (Hunt, 1956).

Based on examination of the male genitalia, G. N. Lanier found no D. mexicanus among our specimens. Morphologically, these two species are extremely difficult to distinguish (Lanier et al., 1988; Wood, 1982), and for several years D. mexicanus was considered a synonym of D. frontalis (Wood, 1963, 1974).
Table 2. Within-tree distributional data, associated bark beetles, and average diameter of infested host material for eight *Dendroctonus*, *Ips*, and *Pityophthorus* species collected from *Pinus oocarpa* in Honduras.

<table>
<thead>
<tr>
<th>Bark beetle species</th>
<th>No of trees in which found</th>
<th>Sampling locationb</th>
<th>Associated beetlesc</th>
<th>Diam. (cm) of infested material</th>
<th>Mean (Range)</th>
<th>Mean male body width (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DFa</td>
<td>16</td>
<td>11 11 11 8 3 0 0 0 0</td>
<td>25 5 7 1 4 2 4 18</td>
<td>16 (6-32)</td>
<td>1.4</td>
<td></td>
</tr>
<tr>
<td>DV</td>
<td>9</td>
<td>7 4 1 0 0 0 0 0 0</td>
<td>5 6 2 0 1 0 0 3</td>
<td>28 (13-45)</td>
<td>3.5</td>
<td></td>
</tr>
<tr>
<td>IB</td>
<td>7</td>
<td>0 2 4 6 6 3 1 0</td>
<td>7 2 3 5 0 2 7 8</td>
<td>17 (4-42)</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td>IC</td>
<td>5</td>
<td>0 0 0 2 4 3 4 0</td>
<td>1 0 5 4 1 2 5 3</td>
<td>11 (2-31)</td>
<td>1.4</td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>4</td>
<td>0 2 1 2 1 1 1 0</td>
<td>4 1 0 1 1 3 1</td>
<td>14 (2-28)</td>
<td>1.8</td>
<td></td>
</tr>
<tr>
<td>IL</td>
<td>4</td>
<td>0 0 0 2 2 0 0 0</td>
<td>2 0 2 2 1 1 0</td>
<td>20 (7-31)</td>
<td>1.7</td>
<td></td>
</tr>
<tr>
<td>PA</td>
<td>11</td>
<td>0 0 0 4 5 3 8 5</td>
<td>4 0 7 5 3 1 1 1</td>
<td>7 (1-25)</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>PO</td>
<td>10</td>
<td>2 6 6 2 2 1 1 1</td>
<td>13 3 8 3 1 0 1 2</td>
<td>18 (1-42)</td>
<td>0.5</td>
<td></td>
</tr>
</tbody>
</table>

a. Species are: DF = *Dendroctonus frontalis*, DV = *Dendroctonus valens* and *Dendroctonus parallelocollis*, IB = *Ips bonanseai*, IC = *Ips cribricollis*, II = *Ips interstitialis*, IL = *Ips lecontei*, PA = *Pityophthorus cacuminatus*, PO = *Pityophthorus confusus*.

b. See Fig. 1 for identity of sampling locations. Tabular values represent the number of trees in which a given bark beetle species was found by sampling location.

c. See footnote “a” above for identity of each bark beetle species. Tabular values represent the number of sample locations (paired bolts) in which each bark beetle species was either found singly or in association with another species. For example, *D. frontalis* was found singly at 25 sampling locations, with *D. valens* and/or *D. parallelocollis* at 5 locations, with *I. bonanseai* at 7 locations, etc. Total number of sampling locations was 168, i.e., 21 trees x 8 locations/tree = 168 locations.

d. Values calculated from data presented in Wood (1982); average pronotal width for *D. parallelocollis* is 2.1 mm.

Wood (1982) states that both species occur in Honduras, with *D. frontalis* occurring mostly below elevations of 1,000 m and *D. mexicanus* above 700 m. However, Lanier et al. (1988) questions the occurrence of *D. mexicanus* in Central America, suggesting that the specimens indicated by Wood (1982) are actually *D. vitei*. 
With reference to *D. parallelocollis* and *D. valens*, it was not always possible to collect adults (4 of 12 occasions; although galleries and brood were observed), and therefore both species will be discussed under the name *D. valens*. Where positive identifications were made, *D. valens* was found in seven samples and *D. parallelocollis* in three; both species were found in the same bolts on two occasions. Together, they were found in nine of the sampled trees (Tables 1 & 2), with *D. valens* (positive identifications) having the most advanced brood in five trees (Table 1). All but one of the attacks by these beetles were found in the two lowermost sampling locations (1 & 2; Table 2, Fig. 2). When present, these two species were commonly found by themselves or in association with *D. frontalis* (Table 2).

*Ips bonanseai* was the most frequently collected of the *Ips* bark beetles, being recovered from 7 of the 21 trees (Table 1 & 2). This species had the most advanced brood in three trees (Table 1), making it the most aggressive of the *Ips* species encountered. Most attacks by this beetle were along the trunk in the area of the crown (locations 4 & 5; Table 2, Fig. 2). *Ips bonanseai* was seldom collected alone, but rather was commonly associated with *D. frontalis, I. cribricollis, P. cacuminatus*, and *P. confusus* (Table 2).

*Ips cribricollis* was recovered from five trees, and of those, it had the most advanced brood in one tree (Table 1 & 2). Attacks by this beetle occurred predominantly in the crown region (locations 4-7; Table 2, Fig. 2). *Ips cribricollis* was commonly found by itself or with *I. bonanseai* and *P. cacuminatus* (Table 2). Based on examination of male genitalia, G. N. Lanier found no *I. grandicollis* among our specimens; both species occur in Honduras (Lanier, 1987).

*Ips interstitialis* was collected from only four trees (Tables 1 & 2). It was found rather uniformly over the trunk and branch samples (locations 2-7; Table 2, Fig. 2). This species was most frequently associated with *D. frontalis* and *P. cacuminatus* (Table 2).

*Ips lecontei* was the rarest bark beetle in this study, being found at single locations on four different trees (Table 1 & 2); these four trees were sampled between 1400-1500 m. In Guate-
mala, *I. lecontei* had the narrowest elevational range (1500-2000 m) of any *Dendroctonus* or *Ips* species (Schwerdtfeger, 1955, 1956). It was found at only two sample locations within the crown region (4 & 5; Table 2, Fig. 2). When present, *I. lecontei* was usually associated with two or more other species of bark beetles such as *D. frontalis, I. bonanseai*, and *I. cribicollis* (Table 2).

*Pityophthorus cacuminatus* was the second most frequently collected bark beetle in this study, being found in 11 sample trees (Tables 1 & 2). It occurred at all crown locations (4-8) but predominated in the outer branch samples (locations 7 & 8; Table 2, Fig. 2). This species was most often found by itself, and next most often with *I. bonanseai* and *I. grandicollis* (Table 2).

*Pityophthorus confusus* was found in 10 trees (Tables 1 & 2), being the only species collected at all eight sampling locations (Table 2, Fig. 2). Most attacks were along the clear bole (locations 2 & 3; Table 2), where it frequently was found in association with *D. frontalis* and *I. bonanseai* (Table 2).

**DISCUSSION**

In this post-epidemic study, the *Dendroctonus* species tended to attack the trunk region, the *Ips* species were most numerous in the upper trunk and larger branches, and the *Pityophthorus* species dominated the smaller branches and shoots. Overall, this general pattern has been documented for other pine/bark beetle associations in North America (Foltz et al., 1985, Paine et al., 1981, Wagner et al., 1985), Mexico (Perry, 1951), and Central America (Schwerdtfeger, 1955, 1956, 1959; Vite et al., 1975). For certain pines (e.g., *Pinus elliottii* Engelmann and *P. caribaea*), however, *Dendroctonus* species are absent, rarely present, or are secondary to *Ips* attack (Billings, 1972; Foltz et al., 1985; Garraway, 1986; Yates, 1972b).

The above pattern of species-specific host colonization has been discussed in terms of beetle size and resource partitioning (Billings, 1972; Haack et al., 1987; Paine et al., 1981; Wagner et al., 1985). Because bark (both inner and outer bark) tends to decrease in thickness from ground level upwards,
relatively large bark beetles may be physically restricted to the lower trunk. Theoretically, smaller bark beetles would be less restricted and therefore able to utilize a greater vertical extent of their host. However, in highly resinous pines such as *P. elliottii* (Hodges *et al.*, 1979), it is the largest *Dendroctonus* and *Ips* species that attack first, with colonization occurring mostly along the clear bole (Foltz *et al.*, 1985). As a result, many late-arriving bark beetle species tend to colonize the less occupied crown region. Besides being resource limited along the trunk, late-arriving bark beetles are often chemically deterred (via pheromones produced by the resident species) from colonizing already occupied areas (Borden, 1982). Such partitioning of the host probably enhances bark beetle reproductive success by minimizing interspecific competition (Alcock, 1982; Flamm *et al.*, 1987; Haack *et al.*, 1987).

Adult body width and average diameter of the host material infested are presented for each species of bark beetle collected in this study (Table 2); body width is a good indicator of gallery diameter. *Dendroctonus valens* and *D. parallelocolis*, the two largest bark beetles in this study, infested the largest diameter host material. At the other extreme, *P. confusus*, the smallest species in this study, also infested relatively large diameter host material. It tended to colonize between areas already occupied by *D. frontalis* and *I. bonanseai*. Similar behavior, apparently allows the relatively small *Ips avulsus* (Eichhoff) to have the widest (vertical) niche breath among the southern pine bark beetles in the USA (Paine *et al.*, 1981).

Bark beetle outbreaks commonly occur in forest stands that are stressed by fire, wind damage, air pollution, and drought (Dixon *et al.*, 1984; Haack and Slansky, 1987; Mattson and Haack, 1987; Wilkinson *et al.*, 1978). Many plants, including pines, become more susceptible and suitable to insects as a result of stress. In the case of drought-stressed pines, for example, susceptibility increases due to reduced oleoresin exudation pressure, whereas suitability increases due to elevated concentrations of soluble nitrogen and sugars (Mattson and Haack, 1987).

The junior author witnessed a bark beetle outbreak in Guatemala during the mid-1970's. Although several pine species were attacked, *Pinus hartwegii* Lindl. (= *P. rudis* Endlicher) was
the principal host; similarly, D. adjunctus was the principal bark beetle. *Pinus hartwegii* occurs at high elevations in Guatemala (2500-4000 m; Schwerdtfeger, 1953) where it often grows on shallow or eroded soils. Besides poor soils, many *P. hartwegii* stands suffer from fire and overgrazing (Schwerdtfeger, 1955). In addition to these stress agents, a severe drought occurred in Guatemala during the mid-1970's. In many respects, these factors are identical to the stress agents reported to have provoked the bark beetle outbreaks in Honduras (Beal *et al.*, 1964; Ketcham and Bennett, 1964).

Another drought-related bark beetle outbreak has recently (1986-87) occurred in the Dominican Republic (R. A. Haack, unpublished data). The principal bark beetle involved was *I. interstitialis*; no other species of *Ips*, nor any species of *Dendroctonus* were found. *Pinus occidentalis* Sw., which is native to the islands of Hispaniola and Cuba, was the host pine.

Because bark beetle outbreaks are often linked to environmental and man-made stresses, management practices that promote healthy and vigorous forests should be favored (Beal *et al.*, 1964; Billings, 1982; FAO, 1968; Ketcham and Bennett, 1964). Wildfire control would reduce tree injury, allow pine seedlings to establish, and eventually lead to improved soil conditions.

In the short term, however, direct control (e.g., salvage, chemical control, cut-and-leave, and pile-and-burn) of currently infested areas is often recommended (Billings, 1982; Hernández, 1975; Mankins, 1980). The type of control practice used will depend on the size, rate of expansion, and accessibility of the infestation; availability of manpower; finances; and other factors. Insecticidal control is often prohibitively costly under forest conditions, and often eliminates many of the bark beetles’ natural enemies. Some frequently observed recommendations for national forestry agencies include: (1) advanced training for key personnel in areas of evaluation, survey, and control techniques; (2) conducting detailed life-history studies of the principal bark beetles; (3) providing proper equipment and incentives to ensure timely control efforts; and (4) establishment of a permanent forest protection survey and control system at the national level (Billings, 1982; Billings *et al.*, 1973).
RESUMEN


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