

Bark beetle outbreaks and fire: a devastating combination for Central America's pine forests

*R.F. Billings, S.R. Clarke, V. Espino Mendoza, P. Cerdón Cabrera, B. Meléndez Figueroa,
J. Ramón Campos and G. Baeza*

Causes and impacts of bark beetle outbreaks, with emphasis on the interrelationship with fire and new prospects for integrated pest management.

The 3.8 million hectares of native pine (*Pinus* spp.) forests in Central America have long been threatened by a variety of destructive agents including hurricanes, droughts, wildfires, human activities and forest pest outbreaks. The combination of these events has in recent years had negative impacts on the region's forest resources. The climatic pattern known as El Niño in the mid-1990s produced drought conditions and increased fuels, leading to severe wildfires throughout Mexico and Central America in 1998. In October 1998, Hurricane Mitch brought high winds and excessive rain to Central America, causing floods and mudslides that ravaged local communities, forests and infrastructure, particularly in Honduras and Nicaragua.

In the following years (1999 to 2003), an unprecedented regionwide outbreak of pine bark beetles killed some 90 000 ha of pine forests. Efforts to control these outbreaks involved felling infested and adjacent healthy trees over extensive areas. Because of the magnitude of the outbreaks and lack of timber markets, most of the standing dead and felled trees were left on site, drastically increasing fuel loads. In 2003, after most bark beetle outbreaks had terminated,

treated areas became the focal point for extensive wildfires.

This article explores the causes and recent impacts of bark beetle outbreaks in Central America, including the role of fire, and describes the different approaches to bark beetle management in the countries in Central America where pine forests and pine bark beetles occur naturally: Honduras, Belize, Guatemala, Nicaragua and El Salvador.

PINE BARK BEETLES IN CENTRAL AMERICA

Pine bark beetles of the genus *Dendroctonus* (Coleoptera: Scolytidae) are the most destructive forest pests in the region wherever native pine forests occur. Twelve species of pine bark beetles native to Mexico and portions of Central America have been described. *D. frontalis* and *D. adjunctus* (the latter primarily in Guatemala) are the most destructive (Vit e *et al.*, 1975). Other species, including *D. mexicanus*, *D. vitei*, *D. approximatus*, *D. parallelicollis* and *D. valens*, are less important (Wood, 1982). Midtgaard and Thunes (2002) reported a new species of *Dendroctonus* in Central America, but the role of this new species in recent tree-

Ronald F. Billings is with the Texas Forest Service, College Station, Texas, United States.

Stephen R. Clarke is with the Forest Health Protection Unit, United States Department of Agriculture (USDA) Forest Service, Lufkin, Texas, United States.

Vicente Espino Mendoza is with the Corporaci n Hondure a de Desarrollo Forestal, Tegucigalpa, Honduras.

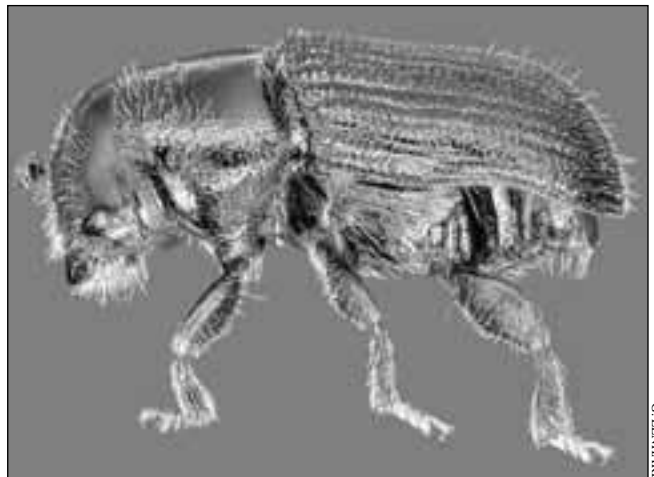
Pablo Cerd n Cabrera is with the Instituto Nacional de Bosques, Guatemala City, Guatemala.

Benjam n Mel ndez Figueroa is with the Servicio Forestal y de Fauna, San Salvador, El Salvador.

Juan Ram n Campos is with the Instituto Nacional Forestal, Managua, Nicaragua.

Gumercindo Baeza is with the Belize Forestry Department, Belmopan, Belize.

Adult southern pine beetle is only about 2-4 mm in length



G. LEWIS

killing events in the subregion remains unclear. For the purposes of this article, the recent outbreaks in Central America are principally attributed to the southern pine beetle, *D. frontalis*.

With the possible exception of *D. adjunctus* in the Altiplano region of northwestern Guatemala (Vité, 1980), *D. frontalis* has been credited with the greatest losses of pine forests in Central America in the past 40 years (Vité *et al.*, 1975; Billings and Schmidtke, 2002). The southern pine beetle is also the most destructive insect pest of pine forests in the southern United States and in parts of Mexico (Payne, 1980). The female lays eggs along “S”-shaped galleries constructed in the inner bark/sapwood interface. The larvae feed in the inner bark and pupate in chambers near the bark surface. Upon completing development, the new adults chew their way out of the bark and fly in search of new trees to attack. Although the beetles do not bore into the wood, they introduce a blue-stain fungus which penetrates into

Typical “S”-shaped egg galleries of southern pine beetle in *Pinus caribaea* (Jalapa, Nicaragua)



R. F. BILLINGS

the wood, quickly reducing the marketability of the trees.

Initial attacks generally are on weakened trees. However, it is the ability of *D. frontalis* to kill otherwise healthy trees that contributes to its pest status. Once the insects initiate an attack on the tree bole, they release aggregation pheromones, which attract both sexes. Thousands of adult beetles may respond to these pheromones and resin odours, and their concentrated attack overcomes the tree's defence system (resin production). When aggregation pheromones are present, emerging beetles often attack trees on the periphery of the infestation, causing the infestation to expand rapidly and increasing tree mortality (Hedden and Billings, 1979; Payne, 1980).

Other attributes that contribute to the destructive potential of *D. frontalis* include: a rapid life cycle with up to ten overlapping generations per year in Central America; the ability of females to establish multiple broods (Payne, 1980); the ability to infest and kill pine hosts of all ages beyond five years as infestations expand, regardless of the tree's physiological condition (Lorio, 1980); and infestation cycles that reach peak levels every six to nine years in certain portions of its range.

An integrated pest management (IPM)

programme is the preferred approach for mitigating losses. Prevention measures, such as thinning to reduce stand density, removing damaged and weakened trees and harvesting before trees become overmature, are primary components. Once outbreaks occur, attention shifts to the prompt detection and suppression of individual infestations, which can substantially reduce resource loss (Clarke and Billings, 2003). Direct control methods include salvage removal, cut-and-leave, the use of chemical insecticide sprays and piling and burning of infested trees (Swain and Remion, 1981). Cut-and-leave, used solely for *D. frontalis*, consists of felling all trees with fresh attacks or bark beetle broods plus a buffer strip of adjacent uninfested trees and leaving them on site. This procedure reduces beetle survival within infested trees and, by disrupting pheromone production, prevents small infestations from growing large.

Until recently, only one bark beetle IPM programme had been initiated in Central America. In 1984, the national forestry corporation (Corporación Hondureña de Desarrollo Forestal, COHDEFOR) implemented a comprehensive *D. frontalis* management programme in Honduras with financial support from international organizations

Prevention measures against bark beetle outbreaks include removing damaged and weakened trees; oxen are often used to skid logs to the nearest road (Siguatepeque, Honduras)



R. F. BILLINGS

(Billings, 1982, 2001b). This programme consists of a national pest coordinator and forest protection coordinators in each forest region to respond to both fires and bark beetle outbreaks. A permanent record-keeping system to track *D. frontalis* detection and control information, the first in Central America, has been maintained since 1982. When salvage removal is not feasible, cut-and-leave has been commonly and effectively applied for southern pine beetle control in Honduras (Billings and Schmidtke, 2002). From 1984 through 1993, a total of 6 233 *D. frontalis* infestations were detected in Honduras and 73 percent were controlled, primarily through cut-and-leave or cut-and-remove. The average size of controlled spots was 2.1 ha per infestation, compared with more than 15 ha per infestation in 1983 before the use of cut-and-leave became widespread (Billings, 2001b).

INTERACTION BETWEEN BARK BEETLES AND FIRE

Traditionally, local residents throughout Central America have set fires in rural areas to extend the agricultural frontier with minimum labour costs or to eliminate old crop residues (Murillo, 2003). Many pine forests are burned annually to provide increased grass cover, used as forage for livestock. Low-intensity, controlled burns in stands of pines ten years of age or older will reduce competition, in turn increasing tree vigour and resistance to bark beetle attack. However, fires that are too hot or too frequent may weaken established pine trees if they do not kill them directly. Weakened pines produce less resin and are less able to defend against initial attacks from both primary (*Dendroctonus* spp.) and secondary (*Ips* spp.) bark beetles. This is particularly true for native forests of *Pinus oocarpa* and *Pinus caribaea* at elevations below 1 000 m, where *D. frontalis* is indigenous. Periodic

Southern pine beetle infestation in Honduras controlled by cut-and-leave – a control method that creates a large fuel load which can lead to wildfires



R. E. BILLINGS

burning also kills most pine seedlings less than five years of age, effectively preventing the continual in-growth of young seedlings required to obtain stand age diversity. Thus, *P. caribaea* and *P. oocarpa* forests in Central America are typically composed of even-aged stands, which are very susceptible to *D. frontalis* attack (Hicks, 1980; Lorio, 1980).

Fire has become a widely used component of bark beetle control, as sites treated with cut-and-leave may be burned to increase beetle mortality. Fires set following bark beetle treatments kill established regeneration. These sites are often converted to agricultural uses or homesteads, contributing to deforestation.

Bark beetle outbreaks also influence wildfire frequency and intensity, as many trees killed by beetles are often left standing or felled and left on site. This abundance of fuel, in turn, increases the threat of wildfires during the annual dry season (December to May). Disgruntled landowners or local residents may also set fire to treated areas in reprisal for having their pines cut down by government control crews.

RECENT BARK BEETLE ACTIVITY IN CENTRAL AMERICA

Honduras

Honduras has an estimated 5.4 million hectares of forest lands, covering more

than half the country. Of this land, 3 million hectares are suited to pine forests (principally *P. oocarpa* and *P. caribaea*), but about one-third has been denuded by poor harvesting practices, shifting agriculture and cattle grazing (Sharma, 1992).

From 1962 to 1965, more than 2 million hectares were affected by *D. frontalis* in Honduras. In 1964, it was estimated that the outbreak was spreading at a rate of 150 000 ha per month (Hernández Paz, 1975). This remains the most devastating recorded epidemic of southern pine beetle throughout its range. The next outbreak began in 1982 in naturally regenerated pine stands that developed following the 1960s outbreak, and the IPM programme described above was implemented.

Despite the progress in bark beetle management, a severe *D. frontalis* outbreak developed from 2000 to 2003, when 11 650 infestations were detected. The total area affected was the greatest since 1983, amounting to 1 743 ha in 2000, 9 078 ha in 2001 and 13 511 ha in 2002. Infestations occurred almost exclusively in young, dense stands 18 to 25 years in age, with basal areas averaging more than 35 m² per hectare. The pines had been weakened by overcrowding, recent fires, resin extraction wounds and a prolonged drought. Insuf-



S.R. CLARKE

Pine forests affected by fires and bark beetles are often converted to agriculture (Honduras)

efficient funding prevented the government forestry agency from responding appropriately, but this outbreak has now been addressed in most regions of the country by means of cut-and-leave and cut-and-remove operations. In 2003, losses were reduced to 2 457 ha. Recently, Honduras has prepared a National Strategy of Forest Protection which covers both bark beetles and fire at the local and national levels.

Belize

The situation in Belize differs greatly from that of its neighbours. Unique to Belize are a low population density (approximately 10 persons per square kilometre), few pine forests, largely public landownership, single-agency management (Forestry Department) and the British legacy which created an extensive infrastructure for pine forest management. Until recently, fires, although occurring regularly in some areas, were not considered a major threat to the ecology or socio-economic landscape of the country (Billings and Schmidtke, 2002). The recent bark beetle outbreak, the first in 50 years in Belize, changed this scenario.

From early 2000 to late 2001, over 25 000 ha of mature pine stands (*P. caribaea* and *Pinus patula* var. *tecumumani*) suffered nearly 100 percent mortality from an outbreak of *D. frontalis* (and/or the new species). The devastated area represents about 60 percent of the entire Mountain Pine Ridge Forest Reserve and about 80 percent of the pine ecosystem within the reserve. In 2001, the outbreak spread to the *P. caribaea* stands along the southern coastal savannahs near the town of Independence, affecting about 30 percent of these stands. By March 2002 the beetle outbreak had largely subsided.

The extensive loss of pine resources in Belize to this unprecedented outbreak of pine bark beetles can be attributed to several factors: an abundance of dense, susceptible pine stands, particularly in the Mountain Pine Ridge Forest Reserve; failure to recognize and respond to the beetle outbreak in its early stages, with no monitoring system and with control measures begun only after more than 15 000 ha had become infested; and a severe reduction in forestry personnel in 1995, from 120 forestry personnel

to just eight permanent forest officers and 36 others, including forest guards (Billings and Schmidtke, 2002). The dead trees have greatly increased the potential for devastating wildfires in the reserve. Unfortunately, forest fire control remains embryonic in Belize, in spite of increasing fire frequency and severity as farmers migrate from neighbouring countries in search of fertile, untitled land (Murillo, 2003).

Guatemala

Guatemala has 2.9 million hectares of forest cover of which 602 000 ha are natural pine forests of various species. Wildfires are a common occurrence, particularly in the lowland pine forests of *P. caribaea* and mid-elevation forests of *P. oocarpa*. Guatemala has developed a National Forest Fire Prevention and Control System, one of the most coordinated and effective fire control programmes in Central America (Billings and Schmidtke, 2002).

Historically, bark beetles have received much less attention than fire in Guatemala. The most severe bark beetle problems have occurred in the Altiplano region and have involved *Dendroctonus adjunctus* rather than *D. frontalis*. The principal pine host has been *Pinus hartwegii* (= *Pinus rudis*).

An estimated 100 000 ha of *P. hartwegii* were killed by *D. adjunctus* from 1975 to 1980 (Vité, 1980). As a result of higher rainfall, fire is less important as a predisposing factor for bark beetle attacks in the Altiplano region than it is in the lower-elevation forests of *P. caribaea* and *P. oocarpa*.

In 2000 and 2001, the pine forests in

the Petén region of Guatemala suffered a severe bark beetle outbreak, presumably of *D. frontalis*. Nearly 3 000 ha or 40 percent of the existing 7 500 ha of *Pinus caribaea* forests were killed. The government forestry and park departments were slow to respond to the rapidly developing outbreak and many infestations were larger than 10 ha prior

to initiation of control action. Control methods included salvage, chemical control and cut-and-leave (Billings and Schmidtke, 2002).

Nicaragua

Nicaragua has 3.3 million hectares of forest cover (almost all classified as natural forest), mostly tropical hardwoods or

Global data on insects and diseases affecting forest ecosystems

In recent years, insect pest and disease outbreaks have escalated worldwide, causing extensive damage to forest ecosystems. Yet too little information has been collected on the extent and severity of outbreaks and on the environmental and economic damage they cause. Information from developing countries and countries with economies in transition is particularly weak.

FAO, with the cooperation of experts from member countries, is making an effort to monitor the impact of insect pests and disease outbreaks on forests through the collection of global statistics. This information will assist governments and forest managers in policy-making and forest management planning. Annual data on the area affected in a given country will also enable comparison of the percentages of national forest cover lost to pest and disease problems over a period of time.

So far, FAO has gathered information from 77 countries through field project reports (275 from 75 countries) and a pilot questionnaire

sent to selected technical experts in 2002. However, the data are still quite incomplete. Quantitative data on the estimated area affected by insect pests and diseases are available for only 42 countries. Information on host and insect or disease is often lacking. Adequate annual time series are available for very few countries. For most countries only sporadic or single outbreaks are registered. Many countries have provided single cumulative figures regarding the area affected over many years.

To fill in the gaps, a new questionnaire has been designed and formatted to make it easier for country experts to provide more complete information. Information requested has been stratified in two levels. In the first level, countries will be requested to provide a simple estimation of the area affected, the insect or disease name and the type of trees affected. In the second level, countries will be asked to provide detailed information on each outbreak reported (exact location and timing, forest type and trees affected, pest causes and effects, economic and environmental impacts and control strategies applied). Countries will be asked to specify clearly the source of the data, the level of approximation and the methodology applied every year to calculate the area affected by insect pests and diseases.

It is hoped that the new questionnaire will provide additional in-depth information to supplement global statistics on the status and

trends of forests and forestry to be published in FAO's Global Forest Resources Assessment Update 2005 (FRA 2005), currently under way. The new questionnaire complies with the FRA 2005 principles of transparency and traceability, and the stratified format should facilitate the work of the respondent. Information obtained through the questionnaire will be supplemented by extensive literature searches. In addition, parallel databases on experts and institutions involved with forest health will be regularly updated.

For further information, please consult FAO's forest health Web site (www.fao.org/forestry/pests) or send an e-mail to: Gillian.Allard@fao.org

mangroves. Only 318 000 ha are classified as pine forests, located primarily in the Department of Nueva Segovia along the border with Honduras. Several government agencies are involved in the protection of managed forests and protected areas (Billings and Schmidtke, 2002). The country's armed forces have joined in the annual fight against fires (Murillo, 2003).

Nicaragua has suffered significantly from natural disasters over the past several years. From 1998 to January 2002, *D. frontalis* killed over 30 000 ha of Nicaragua's pine forest (*P. caribaea* and *P. oocarpa*). In May 2001 an organized control effort was initiated, with emergency funds and technical assistance provided by the United States Department of Agriculture and subsequently by the Nicaraguan Government. Potential losses were reduced by application of extensive buffer strips to slow the spread of great infestations plus the use of cut-and-leave to treat smaller infestations as they were detected (Billings, 2001a). Although the outbreak ended in Nicaragua in December 2001, it continued at very high levels in adjacent forests in Honduras throughout 2002 because of the delay in this country's control efforts.

Access to infestations in Nicaragua was complicated by the presence of anti-personnel mines along the Nicaragua/Honduras border left from the 1980s conflict. Because local and export markets for beetle-killed trees were largely saturated, most beetle-affected trees and those felled in buffer strips were left on site. This greatly increased the risk of wildfires throughout the outbreak area. Indeed, in April 2003, devastating wildfires erupted in the treated region, spreading over 8 000 ha. The fires eliminated much of the natural pine regeneration that had developed since the beetle outbreak was controlled in 2001. In response to

recent disasters, a new forest law has been enacted and a national strategic plan for fires and bark beetles has been prepared and is being implemented.

El Salvador

Severe deforestation has left El Salvador with the least forest cover remaining (121 000 ha of which 25 000 ha are natural pine forests) among the seven countries of Central America. The country also has one of the highest population densities (almost 300 persons per square kilometre). A few intact forest systems remain, primarily pine-oak (*Quercus* spp.) associations at higher elevations along the border with Guatemala and Honduras, and tropical broadleaf forests near the top of high volcanic peaks. Both insect outbreaks and fires threaten these forests (Billings and Schmidtke, 2002). Responsibilities concerning fire and forest pest management are divided within a complex bureaucracy.

A direct relationship between wildfires and southern pine beetle attacks has been observed in El Salvador. For example, a wildfire burned 80 ha of 25- to 35-year-old *P. oocarpa* in the Department of Santa Ana (1 450 m elevation) in April 2003. In January 2004, two infestations of *D. frontalis* were detected in the burned area and none in adjacent unburned forests. Historically, financial support for forest protection has been devoted to training firefighting crews and controlling fires in El Salvador. Recently, a national strategy for bark beetles was developed, but funds needed for its full implementation are lacking.

SUBREGIONAL RESPONSE AND OUTLOOK

The frequent and often indiscriminate use of fire by small farmers in pine-forested areas, combined with lack of thinning to reduce high stand densities, continues to predispose forests to bark

beetle outbreaks. Bark beetle problems are usually associated with poor forest management. Several steps are necessary to mitigate the impacts of future bark beetle/fire events:

- development of long-term bark beetle management plans, with an emphasis on prevention;
- increased training opportunities and effectiveness;
- involvement of communities and other agencies in detection and prompt suppression of those infestations that merit treatment;
- development of a bark beetle hazard rating system for forests;
- increased communication concerning bark beetle activity and management between and within countries;
- initiation of a research programme on pine bark beetles in Central America.

New measures are being taken to address these needs on a subregional basis. National forest pest and fire coordinators have been established in each Central American country (see Billings and Schmidtke, 2002). These specialists maintain communication by serving on newly created regional councils. In August 2002, the national fire and forest pest coordinators met in Siquatepeque, Honduras to define common problems and to prepare a regional strategy for fire and pest management. The strategy for fire and bark beetles has received approval and support from the Central American Commission on Environment and Development, consisting of the ministers of agriculture from the seven Central American countries. The IPM programme developed in Honduras is serving as the model for similar programmes in other countries of Central America. The Instituto Nacional de Bosques in Guatemala prepared a pamphlet to inform communities about bark beetle prevention, detection and

suppression, and it is being adapted for use in the other countries. A recent FAO technical cooperation project has provided training for the pest coordinators and increased awareness of bark beetle prevention and control measures in each country in the subregion (Rodríguez, 2003).

It is hoped that this increased technical capacity, governmental support and intercountry communication among pest and fire coordinators will lead to greater public education and prevention measures for both fire and bark beetles. When the next bark beetle outbreak occurs, detection and direct control responses should be more timely and effective, and Central America should be able to avoid a repetition of recent bark beetle/fire disasters. ♦



Bibliography

- Billings, R.F.** 1982. *Evaluation and recommendations for control of the 1982 outbreak of Dendroctonus in the pine forests of Honduras*. Lufkin, Texas, USA, United States Department of Agriculture (USDA) Office of International Cooperation and Development/United States Agency for International Development (USAID). (Unpublished report)
- Billings, R.F.** 2001a. *Evaluación de la plaga del gorgojo descortezador del pino (Dendroctonus frontalis) en los pinares de Nicaragua y recomendaciones para su control*. Lufkin, Texas, USA, Instituto Nacional Forestal, Nicaragua/USDA Foreign Agricultural Service. (Unpublished report)
- Billings, R.F.** 2001b. *Evaluación de la plaga del gorgojo descortezador del pino (Dendroctonus frontalis) en los pinares de Honduras con recomendaciones para su control*. Lufkin, Texas, USA, Corporación Hondureña de Desarrollo Forestal/USDA Foreign Agricultural Service. (Unpublished report)
- Billings, R.F. & Schmidtke, P.J.** 2002. *Central American southern pine beetle/fire management assessment*. College Station, Texas, USA, USAID. (Unpublished report)
- Clarke, S.R. & Billings, R.F.** 2003. Analysis of the southern pine beetle suppression program on the national forests in Texas in the 1990s. *Journal of Forestry*, 27(2): 122-129.
- Hedden, R.L. & Billings, R.F.** 1979. Southern pine beetle: factors influencing the growth and decline of summer infestations in east Texas. *Forest Science*, 25: 547-556.
- Hernández Paz, M.** 1975. *El gorgojo de la corteza, plaga principal de los pinares*. Publ. 1. Lufkin, Texas, USA, Corporación Hondureña de Desarrollo Forestal.
- Hicks, R.R. Jr.** 1980. Climate, site, and stand factors. In R.C. Thatcher, J.L. Searcy, J.E. Coster & G.D. Hertel, eds. *The southern pine beetle*, p. 55-68. Technical Bulletin 1631. Washington, DC, USA, USDA Forest Service, Science and Education Administration.
- Lorio, P.L. Jr.** 1980. Rating stands for susceptibility to SPB. In R.C. Thatcher, J.L. Searcy, J.E. Coster & G.D. Hertel, eds. *The southern pine beetle*, p. 153-163. Technical Bulletin 1631. Washington, DC, USA, USDA Forest Service, Science and Education Administration.
- Midtgaard, F. & Thunes, K.H.** 2002. *Pine bark beetles in the Mountain Pine Ridge Forest Reserve, Belize: description of the species and how to monitor and combat the beetle infestations*. Isadaltø, Norway, Norwegian Forestry Group, Inter-American Development Bank.
- Murillo, W.** 2003. Wildfires, the biggest cause of environment degradation in the Central American isthmus, fought with mixed results. *ISDR Informs – Latin America and the Caribbean*, 7.
- Payne, T.L.** 1980. Life history and habits. In R.C. Thatcher, J.L. Searcy, J.E. Coster & G.D. Hertel, eds. *The southern pine beetle*, p. 7-28. Technical Bulletin 1631. Washington, DC, USA, USDA Forest Service, Science and Education Administration.
- Rodríguez, J.** 2003. *Estrategia regional de sanidad forestal con énfasis en el descortezador de los pinos*. Project TCP/RLA/2803. Rome, FAO.
- Sharma, N.P.** 1992. *Managing the world's forests: looking for balance between conservation and development*. Dubuque, Iowa, USA, Kendall/Hunt Publishing Company.
- Swain, K.M. & Remion, M.C.** 1981. *Direct control methods for the southern pine beetle*. USDA Forest Service Agriculture Handbook 575. Washington, DC, USA, United States Government Printing Office.
- Vité, J.P.** 1980. Planificación del control de la plaga del *Dendroctonus* (in Guatemala). In *Planificación del control de la plaga del Dendroctonus y del aprovechamiento de la madera dañada*, p. 51-69. Project TCP/GUA/8003. Rome, FAO.
- Vité, J.P., Lühl, R., Hughes, P.R. & Renwick, J.A.A.** 1975. Pine bark beetles of the genus *Dendroctonus*: pest problems in Central America. *FAO Plant Protection Bulletin*, 23: 178-184.
- Wood, S.L.** 1982. *The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph*. Great Basin Naturalist Memoirs, No. 6. ♦