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The effect of wood-boring beetles on the radial growth of *Prosopis flexuosa* DC. in the arid Chaco of Argentina

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ABSTRACT

Traditionally, the effect of wood-boring insects has been related to mechanical damage, which in severe infestations results in breakage of branches and trunks. In contrast, few studies have evaluated the physiological effects of wood-borers on the radial growth of trees. *Prosopis flexuosa* is the main resource for rural inhabitants in the arid Chaco of Argentina and the cerambycid *Torneutes pallidipennis* is the principal cause of insect damage in these forests. The presence of annual growth rings in *P. flexuosa* allowed us to use dendrochronological methods to assess the effect of *T. pallidipennis* on radial tree growth. *P. flexuosa* with external infestation symptoms were sampled in Chancaní (Córdoba), central Argentina. Cores from "healthy" and "infested" branches were taken and processed following standard methods in dendrochronology. Generalized Linear Models were applied to compare the growth of healthy and affected tree-ring growth series. Our results showed a growth reduction in branches with cerambycid infestation. These data strongly suggest that the biological cycles of this heartwood-borer affect the growth and normal development of trees, in addition to "mechanical" effects previously proposed. Insects may produce weakening of the host plants and a pronounced reduction in radial tree growth in the most severe cases.

1. Introduction

The structure and dynamics of a forest result from the combined effect of abiotic and biotic factors. In addition to climate variations, soil properties, natural and human-induced disturbances, biological interactions determine the rates of establishment, growth and mortality of the different components in a community. However, the importance of each factor in controlling population dynamics varies between factors and between biomes (Archer, 1994). Disturbances originating from biotic interactions may be less conspicuous, but no less important (Feller, 2002).

Defoliating and phloem-boring insects are widely recognized agents of ecosystem disturbance that can have an impact on forest production and nutrient cycling, and their outbreak events can create large-scale disturbances (Coulson and Witter, 1990; Stephen et al., 2001). In temperate forests, primary consumption by wood-boring insects can cause structural and functional disruption of primary and secondary tree growth (Barbosa and Wagner, 1989; Echaves et al., 1998). Wood-borers also play important ecological roles in nutrient cycling and succession both in temperate and tropical ecosystems (Feller, 2002; Schowalter, 1981).

Plant production in an ecosystem determines the energy available to consumers and decomposers (Whitford, 2002). Although the effects of decomposers on primary production are probably not as prominent in desert as in temperate systems, they are certainly not negligible. A considerable greater proportion of the litter, wood and standing dead material in arid communities disappears by weathering and herbivore activity than by microbial decomposition (Noy-Meir, 1974). Even solar radiation plays an important role on litter decomposition in arid environments (Austin and Vivanco, 2006; Day et al., 2007). Therefore, moisture limitation on microbial activity in arid ecosystems may assign an especially important role for macrodecomposition by detritivorous arthropods, before and between stages of microbial and fungal decomposition (Noy-Meir, 1974).

Cerambycid beetles are significant in the decomposition of wood in arid and semiarid ecosystems. According to Hovore and

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Penrose (1982), over 70% of dead *Leucaena*, *Celtis* and *Acacia* mass was consumed by cerambycid larvae in Southern Texas (USA). Based on the large number of cerambycid species found in the Chihuahuan desert in New Mexico, MacKay et al. (1987) suggested that cerambycids are important to the functioning of desert ecosystems as active agents in the accumulation, decomposition and nutrient recycling of woody plants. Within the Argentinean phytogeographic provinces of Monte, Chaco and Espinal, 74 species of cerambycids were recorded in *Mimosaceae* trees and shrubs (Di Iorio, 1996, 1998; Fiorentino and Diodato, 1997).

The mesquite *Prosopis flexuosa* DC. (Fabaceae: Mimosoideae) is a major component of the arid Chaco woodlands. This species has historically provided food, timber and fuel for local populations and thereby plays an important social and economic role (Karlin et al., 1992; Villagra et al., 2005). Additionally, this woody species has high potential for the development of dendroclimatic and dendroecological studies of these arid and semiarid systems (Giantomasi et al., 2009; Villalba and Boninsegna, 1989; Villalba et al., 2000).

During the last decades, *Prosopis* woodlands have experienced a noticeable decay due to human overexploitation and the action of wood-boring insects. In the central region of Argentina, infestation intensity by cerambycids may reach 60–80% in *Prosopis* spp. (Fiorentino and Diodato de Medina, 1995, 1988; Mazzuferi and Coirini, 1989) with the wood-borer *Torneutes pallidipennis* Reich (Coleoptera: Cerambycidae) as the major infestation agent.

Several publications point out inverse relationships between insect infestation and radial tree growth. In a pioneer work, Morrow and LaMarche (1978) found that primary productivity in *Eucaliptus* species was strongly suppressed by folivorous insects, and that this suppression occurred over long periods of time. Echaves et al. (1998) also established that the periodic growth rate and sapwood thickness (considered as a vigor factor) of black locust *Robinia pseudoacacia* L. (Fabaceae), was inversely correlated with the number of *Megacyllene robiniae* (Coleoptera: Cerambycidae) borer tunnels.

Radial growth losses associated with insect activities have been documented for defoliating and bark-boring beetles of temperate forests in the Northern Hemisphere, though little is known concerning the impact on tree growth by wood-boring insects in arid systems.

Larvae of the wood-borer *T. pallidipennis*, feed mainly on hardwood in living trees, but make subcortical tunnels by burrowing through sapwood, phloem and bark. By affecting the physiologically active tissues of the tree, subcortical tunnels can produce weakness in the plant and therefore this disturbance should be reflected in the growth pattern of trees.

To assess the damage magnitude of *T. pallidipennis*, we evaluated the effect that infestations produced on *P. flexuosa* woody growth in arid Chaco forests. As the response of the tree to infestation may not be linear, we fitted Generalized Linear Models to tree-ring series. Our goal was to develop the first assessment of changes in radial growth of trees by a wood-boring insect in arid ecosystems.

2. Material and methods

2.1. Study area

The work was carried out in the Chancaní Reserve (31°25′S, 65°26′W), province of Córdoba, Argentina. The area includes remnants of the original arid Chaco forest (Fig. 1). Arid Chaco in Argentina occupies the southwestern portion of the American Gran Chaco, between 64°30′–67°30′W and 28°30′–33°00′S. Arid Chaco is practically surrounded by hills which acting as topographic barriers, strongly restrict rainfall (Torrella and Adámoli, 2006). The climate is subtropical dry, with annual precipitation ranging 500 mm in the east to 300 mm on the western boundary. Eighty percent of the rainfall is during summer season (November to February) and other months are dry. Summer temperatures are high, with a mean of 26 °C in January, and an absolute maximum of 45 °C. In contrast to these very hot summers, winters are temperate with mean July temperatures of 12 °C. Soils are formed from the eolian Quaternary sediments characteristic of the Chaco plains and are sandy-loams, with low organic matter content (Karlin et al., 1992). Among Chaco forests, arid Chaco is the driest and least productive region.

Vegetation consists of a scanty xerophilous tree layer, 7–12 m tall. The most abundant species are evergreen *Aspidosperma quebracho-blanco* and *Prosopis* spp. followed by *Zyzyphus mistol*, *Celtis tala*. Due to logging activities and overgrazing, huge areas of the original vegetation have been replaced by degraded structure called “fachinal”, which is dense shrubland with few trees. Here, predominant shrubs are *Larrea divaricata*, *Capparis atamisquea*, *Cassia aphylla* and *Celtis pubescens* (Karlin et al., 1992).

Agriculture is limited by the high evapotranspiration and low soil moisture retention, by edaphic conditions including salinity,

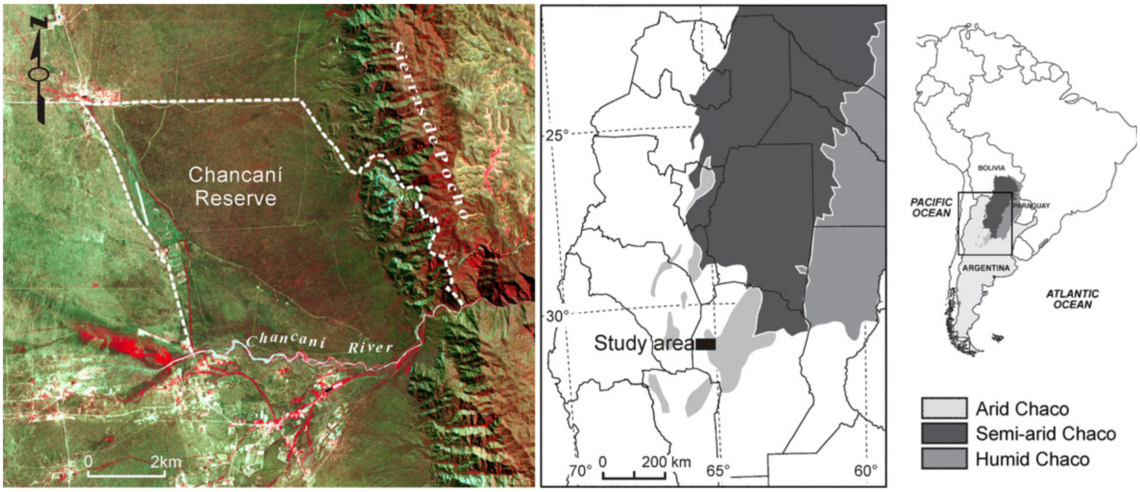

Fig. 1. Location of Chancaní Forest Reserve (framed in dashed lines, left image). The study area extends down the western slope of Sierras de Pocho (~400 m.a.s.l.; Córdoba province, Argentina) and comprises southern extension of arid Chaco forests.

soil texture and low water-table depth, and by extreme climatic conditions. The main activities of the local population are extensive livestock breeding (goat and bovine cattle) and forest exploitation for wood and charcoal production. Timber and forage resources are highly degraded due to poor management practices (Karlin et al., 1992).

2.2. *Injury by T. pallidipennis (Fig. 2)*

Infestation of *T. pallidipennis* begins on the thinner branches of the tree where the female deposits her eggs. Larvae proceed downwards until they reach thicker branches, where individuals penetrate into the hardwood; if infestation is severe, some larvae may be found at the bole. Cerambycid larvae usually have long life cycles due to the low nutritional quality of the tissues they feed on and the stable environment in which they develop (Daly et al., 1998). In the case of *T. pallidipennis*, several larvae may coexist within the same branch (Fiorentino et al., 1995) and there could be superimposition of generations (Di Iorio, 2006).

Each larva bores a small hole in the bark though which it expels wood fragments and sawdust. Active infestations can be recognized by these accumulations in the branches or on the ground below the injury. The expelling hole is linked to a *subcortical tunnel* underneath the bark, which leads into the longitudinal larval tunnel in the hardwood (Di Iorio, 1996; Fiorentino and Diodato de Medina, 1988). Subcortical galleries are easily observed since they are accompanied by bark detachment showing the larval path (Fiorentino and Diodato de Medina, 1988). As larvae grow and descend along the branch, subcortical galleries change in size and shape; in thinner branches are usually long and relatively narrow (40 × 10 mm), whereas in thicker branches galleries may be larger (150 × 30 mm) and irregular in shape (Fig. 2; Di Iorio, Personal communication). Before pupation, larvae bore an emergence tunnel and emergence hole, and may be a single or more than one per branch (Fiorentino and Diodato de Medina, 1995).

2.3. *Sample collection and processing*

For sampling we considered 15 trees where one of the two main branches was infested and the other was healthy. We verified the presence of tunnels beneath the bark. We measured the area of subcortical galleries and the total area of the whole infested branch to obtain percentages of *subcortical damage*. Allometric variables such as tree height, bole height, infested branches (IB) and healthy branches (HB) diameter, and diameter at breast height (DBH) of each tree were measured.

Selected trees were cored with an increment borer especially designed for hardwoods (wood density > 0.7 kg/dm^3). Samples were taken both from IB and HB of each tree 0.30 m from the bole bifurcation. Samples were mounted, polished and dated following the standard dendrochronological methods (Stokes and Smiley, 1968). Tree rings were correctly dated and measured with a 0.01 mm precision. Tree-ring patterns from IB and HB were crossdated and corrected using COFECHA software (Holmes, 1983) to verify annual dating. Low-frequency variability of tree ring width series was removed using negative exponential curve or linear regression filters of 30 years, due to the relatively short length of the tree-ring series (20–40 years). This standardization process eliminates the biological tendencies of growth and most of the endogenous stand disturbances. This process enhances the damage signal present in the tree-ring series (Fritts, 1976). Standardization was conducted with ARSTAN program (Cook, 1985). The overall process produced 30 standardized tree-ring series (two per analyzed tree): one series from the healthy branch and the other from the infested one.

2.4. *Statistical analysis*

2.4.1. *Damage categorization. Tree-ring series modeling*

Damage amount was categorized into three classes, namely: Class 1: less than 1% of subcortical damage, Class 2: between 1% and 2% of damage, Class 3: more than 2% of damage (Table 1).

In order to examine whether wood-borer subcortical damage produced significant differences in the growth of *P. flexuosa*, we fitted Generalized Linear Models (GLMs; McCullagh and Nelder, 1989) to IB and HB tree-ring series, with random component Gamma and Identity link function to build the estimates. Series were analyzed by GEE models (Generalized Estimation Equations; Farhmeir and Tutz, 2001; Liang and Zeger, 1986) which evaluated differences between mean values of damage classes, under the hypothesis that damage degrees are the same. This ANOVA model includes IB and HB as repeated series, which parameters were estimated using the scaled deviance as goodness-of-fit test. Additionally, a covariance analysis was applied to IB and HB series: since both series came from a same tree, it is possible to analyze IB growth controlled by the reference HB value.

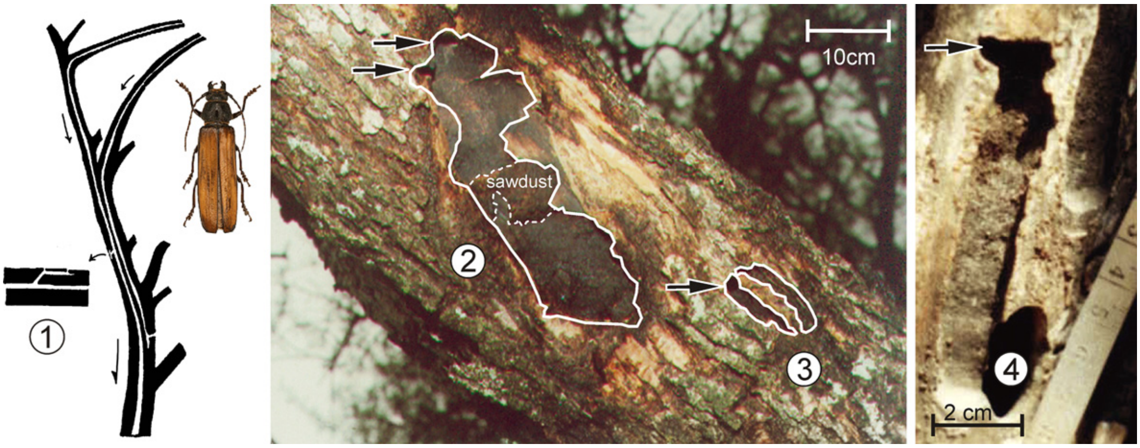

Fig. 2. Effects of larval infestation. (1) Diagram of larvae trajectory during their development, with detail of the subcortical gallery of sawdust expulsion (modified from Fiorentino and Diodato, 1997); *Torneutes pallidipennis* adult (6.5 cm long). (2) Subcortical gallery of an advanced stage larva, with accumulation of sawdust and waste material on *P. flexuosa* branch. (3) Early subcortical tunnel of another larva. (4) Adult exit hole beside a subcortical gallery of an early stage larva. Arrows indicate the larva entrance/exit to the subcortical cleaning galleries.

Table 1
Infestation and diameter of healthy (HB) and infested branches (IB). Each group is arranged according to the percentage of damage; Class 1: <1%, Class 2: between 1 and 2%, Class 3: >2% of subcortical damage.

Tree #	Class	Damage percentage	Branch diameter (m)	
			HB	IB
1	1 (<1%)	0.500	0.124	0.153
2		0.522	0.134	0.188
3		0.607	0.178	0.172
4		0.831	0.094	0.088
5	2 (≥1 < 2%)	1.120	0.146	0.140
6		1.300	0.111	0.127
7		1.357	0.185	0.191
8		1.500	0.214	0.197
9		1.800	0.108	0.119
10		1.960	0.185	0.204
11	3 (>2%)	2.380	0.175	0.185
12		3.110	0.090	0.080
13		4.678	0.143	0.143
14		5.130	0.090	0.086
15		5.700	0.099	0.094

Independently, we measured the influence of infestation on the growth rate of IB. A GLM (1) with random component Gamma and linear predictor corresponding to a simple linear regression model was applied to the continuous (not grouped in classes) tree-growth variable;

$$E(y) = \mu = f(\alpha + x\cdot\beta) \tag{1}$$

where y is tree growth, x is damage percentage, and β the regression coefficient, or growth rate.

2.4.2. Vigor indicators

When physiologically stressed, plants have limited growth (Giese and Benjamin, 1991) and become more susceptible to herbivores (Price, 1991). Vigor status is used to analyze plant stress and then to assess the effects of damage intensity on plant growth. Sapwood thickness as an indicator of vigor was measured in IB and HB cores with 0.01 mm accuracy. Data were compared with paired *T*-tests, controlling each tree by its damage class.

3. Results

3.1. Tree-ring statistics by damage classes

Trees were grouped into three categories according to the IB damage percentages (Table 1). Statistics of the tree-ring series are shown in Table 2. Overall, mean values of radial growth are smaller in infested branches than in healthy ones.

3.2. Tree-ring series modeling

The analysis of the models applied to tree-ring series of IB showed differences between Class 2 and 3 (Table 3). As no difference was observed between Class 1 and 2 (via independent contrast) these two classes were merged into a new category, Class 1 + 2. The new ANOVA model now has two classification levels that were contrasted (1 + 2 vs. 3).

The analysis (Table 4) indicates there were significant differences ($P = 0.0887 < \alpha = 0.10$) between the new damage categories. The estimate value for Class 1 + 2 is positive (0.0344), indicating that infestation has a negative effect on radial tree growth when moving from category 1 + 2 to category 3 (i.e. more than ca. 2% of subcortical damage).

Table 2
Statistics of tree-rings series from healthy (HB) and infested (IB) branches, grouped by the damage classes of the IB.

Statistics tree-rings (mm)	Class 1		Class 2		Class 3	
	HB	IB	HB	IB	HB	IB
Tree rings (n)	66	66	146	146	127	127
Minimum	0.28	0.28	0.11	0.21	0.21	0.08
25% percentile	0.77	0.76	0.68	0.52	0.57	0.41
Median	1.14	1.16	1.10	0.96	0.85	0.70
75% percentile	1.86	1.66	1.75	1.55	1.49	1.29
Maximum	6.19	4.58	5.36	4.20	6.70	4.88
Mean	1.580	1.336	1.349	1.192	1.202	0.983
SD	1.204	0.868	0.968	0.832	1.016	0.851
SE	0.148	0.107	0.080	0.069	0.090	0.076

SD: standard deviation, SE: standard error.

The covariance analysis was applied to verify whether there was effectively a correlation between growth and subcortical damage (Table 5). Controlling by HB we observed that there is a significant effect between damage categories and tree growth ($P = 0.0718 < \alpha = 0.10$).

As the above results indicate that radial tree growth is affected by subcortical damage, we estimated the rate of growth reduction of IB by applying a simple linear regression model (1). The coefficient (slope) is negative (−0.0114) and highly significant ($P = 0.0012 < \alpha = 0.10$) (Table 6), which means that IB growth decreases by 1.14% in proportion to the percentage of damage.

3.3. Relation between infestation and sapwood

Sapwood behavior from IB and HB was evaluated through a paired *T*-test. Table 7 indicates that for infestation Class 3 there are statistically significant differences ($P = 0.022 < \alpha = 0.05$) in sapwood thickness between infested and healthy branches. Fig. 3 sketches the magnitude of change; as percentages of insect infestation grow higher sapwood thickness decreases in infested branches.

4. Discussion and conclusion

Phytophagous insects have been widely recognized to affect ecosystem processes by modifying vegetation structure and composition (Schowalter, 2000). Phytophagy can stimulate primary productivity at low-to-moderate intensities; on the other hand,

Table 3
Analysis of variance of GEE parameters, by three damage classes.

Parameter	Estimate	SE	95% Confidence limits		Z	$P > \|Z\|$
Class 1	0.0228	0.0231	−0.0224	0.0680	0.99	0.3227
Class 2	0.0421	0.0224	−0.0019	0.0861	1.88	0.0605*
Class 3	0.000	0.000	0.000	0.000	–	–

SE: standard error; $P < \alpha = 0.10$, *Significant.

Table 4
Analysis of variance of GEE parameters, by two damage classes.

Parameter	Estimate	SE	95% Confidence limits		Z	$P > \|Z\|$
Class 1 + 2	0.0344	0.0202	−0.0052	0.0740	1.70	0.0887*
Class 3	0.000	0.000	0.000	0.000	–	–

SE: standard error; $P < \alpha = 0.10$, *Significant.

Table 5
Covariance analysis with healthy branch (HB) as dependent variable. If damage classes were not controlled by HB covariate, no significant differences are detected.

Parameter	Estimate	SE	95% Confidence limits		Z	$P > \|Z\|$
Class 1 + 2	−0.8524	0.7757	−2.3728	0.6680	−1.10	0.0718*
Class 3	0.000	0.000	0.000	0.000	–	–
HB	−40.7918	8.3110	−57.0811	−24.5024	−4.91	<0.0001
Class 1 + 2 (without controlling)	−2.1683	1.3876	−4.8879	0.5514	−1.56	0.1181

SE: standard error; $P < \alpha = 0.10$, *Significant.

persistent herbivory may reduce plant's defenses and lead to a reduction in reproduction and/or growth (see Stamp, 2003). In the case of cerambycid beetles, Boring et al. (1988) found that dense forest stands in southern USA suffered a decrease in vigor and high mortality associated with attacks of *M. robiniae* borer. In this sense, investigations on *M. robiniae* are suitable to our study since it develops in live plants and feeds on hardwood.

Results from the present work in tree-rings of *P. flexuosa* indicate reduced growth in branches with evidence of infestation by the wood-boring beetle *T. pallidipennis* in the arid Chaco of Argentina. The subcortical tunnels produced by *T. pallidipennis* larvae were considered to be the most appropriate variable to correlate with radial growth. Subcortical damage ranged from 1% to almost 6% in infested braches; grouping the damage percentages into three classes facilitated the statistical comparison between trees. In order to evaluate the relationship between subcortical damage and radial growth, standardized tree-ring series from healthy and infested branches were modeled with Generalized Linear Models. The traditional dendrochronological methods used to detect insect outbreaks (e.g. Swetnam et al., 1985; Veblen et al., 1991; Weber, 1997) were not suitable to analyze the damage caused by *T. pallidipennis*, because the wood-borer infestation does not occur as "pulses" or sudden occurrences that typify defoliators or phloem borers which produce narrow rings at stand level. In our case, each tree studied had its own damage percentage.

The comparison between the modeled "healthy" and "infested" tree-ring series showed that there is a reduction in radial growth when subcortical damage produced by larvae affects over 2% the surface area of the branch. There are very few publications describing this kind of damage caused exclusively by xylem feeders. Harman and Dixon (1984) studied wound manifestations of the locust borer *M. robiniae* and determined that trees with longer infestations have reduced growth rate.

The amount of subcortical tunnels and the emergence holes (not shown), is intimately related to the number of larvae upon a tree. The long life cycle of the larva of *T. pallidipennis* produce larger damage on the same tree; and adult females tend to lay eggs on previously infested trees, increasing re-infestations rates (Di Iorio, 2006). Several studies (e.g. Walczynska, 2010; Walczynska et al., 2010) indicate that larvae living in deep wood of low nutritional value with low predation pressure extend the development time to several years. As several larvae of *T. pallidipennis* may coexist in a single tree, consecutive infestations translate into higher infestation pressure on the tree, which in turn causes the host to weaken.

Table 6
Parameters of the linear regression model for the "damage percentage" variable.

Parameter	Estimate	SE	95% Confidence limits		Test Z	$P > \|Z\|$
% damage	−0.0114	0.0035	−0.0183	−0.0045	−3.24	0.0012*

SE: standard error, $P < \alpha = 0.10$, *Significant.

Table 7
Paired *T*-test for sapwood thickness (mm) between HB and IB, grouped by damage category.

Class	n	Mean thickness (mm)		P
		HB	IB	
1 + 2	10	5.863	6.938	0.863
3	5	6.076	3.536	0.022*

$P < \alpha = 0.05$, *Significant.

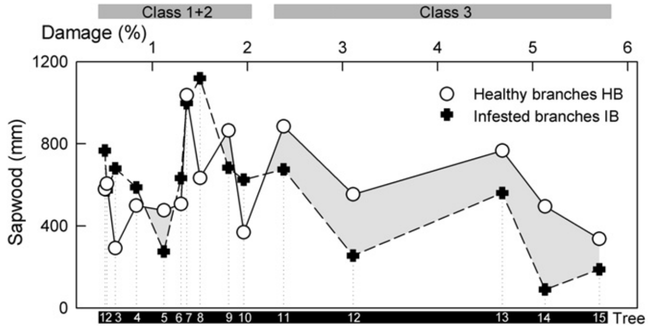

Fig. 3. Sapwood thickness of healthy (HB) and infested branches (IB) in relation to damage percentage (above). Sapwood behaves differentially in IB, reducing its thickness (shown as shaded area) when subcortical damage is over 2% (corresponding to Class 3). Trees are ordered by increasing infestation from left to right.

Plant resistance to attack has been attributed, in part, to high moisture of bark or sapwood, and most cerambycid species require host plants to be weakened in some way (Hanks, 1999) when comparing sapwood thickness between "healthy" and "infested" branches, we also found significant differences at Class 3 (>2%) of infestation. Even though *Torneutes* seems to be a primary invader, the successive subcortical galleries of larvae directly affect the active tissues of the sapwood and cambium, which transport water and nutrients and produce formation of growth rings. The stress caused by these losses leads to diminishing plant vigor, allowing re-infestations and result in reduced growth in heavily infested trees.

Few studies deal with the damage caused by intra-ligneous insects. Chapman et al. (2003) state that a less intense but more persistent insect herbivory may have an important influence on ecosystem processes. The comparison of branches within *P. flexuosa* in the present study shows that wood-borers cause damage to the plant tissues that transport nutrients and water, weakening of the plant, and decrease in radial growth. These data support the idea that the biological activities of *T. pallidipennis* (as well as similar cerambycid beetles) play an important role as primary agents of tree decay and succession facilitators in arid ecosystems.

Moreover, the intra-ligneous damage caused by larvae tunnels diminishes the economic value of *Prosopis* wood (Coirini et al., 2001; Villagra et al., 2005) which is an essential resource for the region's inhabitants. Hence, it is important to counterbalance the effects of external disturbances and insect populations in the management and recovery of these vulnerable woodlands.

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