ECOLOGICAL INTERACTION OF *PANTOPHTHALMUS ROSENI* (ENDERLEIN) (DIPTERA: PANTOPHTHALMIDAE) AND THE RED OAK *QUERCUS GERMANA* SACHLTDL. ET CHAM. (FAGACEAE) IN A MEXICAN CLOUD FOREST

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RESUMEN

La interacción del barreno del encino (*Pantophthalmus roseni*) y el encino rojo (*Quercus germana*) fue estudiada en el bosque mesófilo de montaña de la Reserva de la Biosfera El Cielo, Tamaulipas, México. Se seleccionaron cuarenta individuos maduros de *Q. germana* para comparación (20 árboles sanos y 20 árboles con daño severo, $\geq$ 15 perforaciones en el fuste causadas por *P. roseni*). En árboles sanos y dañados fueron medidos los niveles de herbivoría, el porcentaje de nitrógeno foliar, la concentración total de fenoles y la producción de bellotas. La herbivoría fue significativamente mayor (*P*< 0.05) en los encinos sanos que en los dañados. El grupo de encinos sanos tuvo 1.5 veces más herbivoría foliar que el grupo de los dañados. El contenido de nitrógeno foliar en *Q. germana* (5.3%) mostró variaciones significativas en relación a las estaciones (estación lluviosa = 5.2% y estación seca = 5.1%) y entre grupos de daño, como también en la interacción de estación y grupo. El grupo de árboles dañados tuvo 1.2 y 1.5 veces más concentración de fenoles que el grupo de los sanos durante la estación lluviosa y la estación seca, respectivamente. La producción de bellotas fue significativamente más grande (*P*< 0.05) para el grupo de árboles dañados que para el grupo de los sanos. La importancia de estos resultados en la comprensión y el manejo de este insecto como una plaga forestal, así como los efectos de la herbivoría en el bosque mesófilo de montaña son discutidos.
Palabras clave: Interacción planta/insecto, herbivoría, *Quercus*, *Pantophthalmus*, bosque mesófilo de montaña, México.

ABSTRACT

The interaction of the wood driller (*Pantophthalmus roseni*) and the red oak (*Quercus germana*) in the cloud forests of the Biosphere Reserve El Cielo at Gómez Farías, Tamaulipas, Mexico was studied. Forty mature individuals of *Quercus germana* were selected for comparison (20 healthy trees, 20 with severe damage, i.e. $\geq$ 15 wood perforations caused by *P. roseni*). Healthy and damaged trees were measured for levels of herbivory, percentage of foliar nitrogen, total phenols concentration and acorn production. Herbivory was significantly greater (*P*< 0.05) in healthy than in damaged oaks. The healthy group had 1.5 times more leaf herbivory than the damaged group. Foliar nitrogen content in *Q. germana* (5.3%) showed significant variations in relation to the seasons (rainy season = 5.2% and dry season = 5.1%) and between damage groups, as well as in the interaction of season and group. The damaged trees group had 1.2 and 1.5 times more phenols concentration than the healthy group during the rainy season and dry

season, respectively. Acorn production was significant greater (*P*< 0.05) for the damaged group than the healthy group. The importance of these results in understanding and managing this insect as a forest pest, as well as, the effects of herbivory in the cloud forests are discussed.

Key words: Plant/insect interaction, herbivory, *Quercus*, *Pantophthalmus*, cloud forest, Mexico.

INTRODUCTION

The characteristics and processes of how insects damage plants have been studied in detail during the last two decades (Rockwood 1973, Crawley 1983, Marquis 1984, Dirzo 1984, Hendrix 1988, Howe 1990, Obeso 1993, Núñez-Farfán and Dirzo 1991, Escarré *et al*. 1996). There are direct causal agents associated with herbivory, that may significantly affect the richness and relative abundance of plant species, as well as affects that influence spatial heterogeneity of vegetation (Crawley 1983), and nutrient recycling in the ecosystem (Schowalter 1981).

Chemical variation often occurs in plants as a response to herbivore damage (Mattson and Levieux 1988, Howe and Westley 1988, Karban and Baldwin 1997). In addition to induced defenses, constitutive plant defense mechanisms have also evolved to provide protection against herbivores (Raupp and Denno 1983). It is probable that damage caused by *P. roseni* in *Q. germana* could produce changes in the secondary chemistry and in the amount of nutrients available to herbivores. These chemical changes could also influence the abundance and species composition of herbivores on the plant. Plants may also produce more tissues in order to compensate for loss of tissues after defoliation (Crawley 1983, Hendrix 1988). However, the degree and nature of responses are variable and not all species respond in the same way (Belsky 1986, Obeso 1993).

A unique insect herbivore has been found to feed on oak in the cloud forests of northeastern Mexico. This insect is the dipteran «oak driller» *Pantophthalmus roseni* (Enderlein) (Diptera: Pantophthalmidae) and causes damage to oaks (*Quercus spp.)* by drilling into trunks, excavating galleries deep within trees and feeding on the xylem. *Pantophthalmus roseni* is considered as a pest in this ecosystem in Gómez Farías, state of Tamaulipas, in the El Cielo Biosphere Reserve (Reyes-Castillo 1985, Flores and Sánchez-Ramos 1989, Sánchez-Ramos *et al*. 1993). Currently, it is known that the cloud forests from Tamaulipas are the most northern record in the American Continent for this insect (Sánchez-Ramos *et al*. 1993).

Since this insect was first registered from the cloud forests in Gómez Farías, Tamaulipas (Reyes-Castillo 1985), more recent reports (Flores and Sánchez-Ramos 1989, Sánchez-Ramos *et al*. 1993, Niño *et al*. 2005) showed that oaks are the most attacked and damaged plants by *P. roseni* in these forests (Sánchez-Ramos *et al.* 1993). Damage caused by this insect consists of a perforation hole from which forms a central gallery in the xylem with secondary tunnels which can extend in various directions from the central gallery. The insect lives in a humid chamber inside the heartwood that causes a staining of adjacent wood with a reddish-dull color (personal observation). Externally the damage can be seen as intense exudates with a dark

coloration, and fermentation by fungi and bacteria occurring on the outside of the tree (Reyes-Castillo 1985, Flores and Sánchez-Ramos 1989).

Pantophthalmus roseni reproduces and develops in trees of the cloud forest located between 1,100 to 1,200 m asl. The fly lives in the trunks of different species of oak trees (*Quercus* spp.) characteristics of the canopy (18-30 m of height). The emergence period of adults begins towards the end of spring and ends at the beginning of the autumn. Adults have a maximum longevity of 20 days. The females' oviposita groups of eggs formed by 2 to 35 eggs between the cracks and fissures of the bark of live trees. The larva emerges, perforates the bark and xylem, initiating the permanent excavation of one gallery, where it develops through all stages of the larva and pupa. The egg development to adult is completed in a period of approximately two years.

The red oak (*Quercus germana*) is a dominant species that occupies the second place of ecological importance in the trees of the cloud forests of Gómez Farías, Tamaulipas (Sánchez-Ramos 2002). This species has moderate seedling survival and acorn production, with the later presenting very irregular yearly cycles. Trees and seedlings are randomly distributed in the Gómez Farías forests (Puig *et al.* 1987, Puig 2005).

The first record of *P. roseni* in the cloud forests from Gómez Farías (Reyes-Castillo 1985) generated interest in conducting more systematic and biological studies. It is reported that *P. roseni* does not directly kill trees, but when severally affected can cause a decline in the foliage of the tree crown. However, it is not known how normal, moderate infestation levels of *P. roseni* affect the physiological conditions and reproductive ecology of oak trees. It is also unknown if there are indirect effects induced by *P. roseni* feeding that affects other organisms associated with oaks, especially the herbivores.

During our study, we address the following questions: How does defoliation (herbivory) rates occurs compare between trees damaged by *P. roseni* and healthy trees? How are these changes reflected in the changes in secondary chemistry (*i.e.* total phenols concentration and foliar nitrogen)? Are there considerable physiological variations or fitness changes (as reflected in acorn production) between damaged and healthy oak trees?

METHODOLOGY

Study zone: The mountain cloud forests from the Gómez Farías region are located in the southeast of the state of Tamaulipas, in north eastern Mexico in what is known as the Biosphere Reserve El Cielo in the Sierra Madre Oriental (22° 55' 30", 23° 25' 50"N and 99° 05' 50", 99° 26' 30"W). Altitudinal ranges in Rancho El Cielo are from 1,130 to 1,400 m. The cloud forests are distributed in only 200 km² of the reserve (Puig and Bracho 1987). The mountains have a divergent structure in the Sierra Madre Oriental formed by several hills in a north-south direction, showing deep slopes and altitudes vary from 300 to 2,100 m in less than 7 km (Rzedowski 1992).

In this cloud forests, mean annual temperatures range 19.4°C and the mean rainfall is from 2,000 to 2,500 mm, with clouds present all year long. According to the Köppen classification

system modified by García (1981) the climate in this location is humid-temperate (Cfa). Soils are lithosols and rendzins, topography is carstical, presenting deep valley depressions that give place to the formation of a number of microclimates in this zone.

Floristic elements from the cloud forests have been described previously (Puig *et al*. 1987). These forests are composed mainly of four sublayers as: the mixed oak forests in the tree layer with 12-25 m in height and some characteristic species in these forests are: *Acer skutchii*, *Cercis canadensis* var. *mexicana*, *Clethra pringlei*, *Liquidambar styraciflua*, *Magnolia tamaulipana*, *Podocarpus reichei*, *Quercus sartorii* and *Quercus germana*. There are some other important floristic elements in these forests that have a rather small distribution in Mexico and a small relative dominance in these forests. Some of the characteristic species are: *Carya ovata* var. *mexicana*, *Fagus mexicana, Abies vejarii, A. religiosa, Juglans mollis* and *Taxus globosa*. The second layer has 6 to 12 m in height and is represented by *Meliosma oaxacana*, *Turpinia occidentalis*. A third layer is composed of trees <6 m in height such as *Eugenia capuli* and *Ternstroemia sylvatica*. The fourth is a very dense herbaceous layer abundantly composed by tree climber species and ferns.

Field collection data: Considering the level of damage caused by *P. roseni*, 20 mature damaged trees of *Q. germana* were located and selected those severe damages by *P. roseni* (i.e. ≥ 15 perforation holes, see Flores and Sánchez-Ramos 1989). In addition, another 20 healthy trees of the same species were selected from the same habitat that did not show apparent damage. In these two groups of contrasting mature trees, the following data were recorded: Herbivory levels measured as the percentage of foliar area consumed (% FAC), percentage of foliar nitrogen, total phenols concentration (g/mg dry weight) and acorn production (kg/tree). Care was taken in order to select individual trees that showed similar overall age and structure (*e.g.* diameter, height and cover).

Measurement of foliar damage: To evaluate herbivory levels, measurements of all individuals were made during two seasons. This was made by choosing 20 leaves randomly from each tree during each season (*i.e.* 20 x 40 x 2; *n* = 1,600 leaves). Foliar samples were taken during the dry season (February) and rainy season (September) during 1996.

Herbivory was estimated using instant measurements (*cf*. Filip *et al*. 1995) corresponding to the dates mentioned above. To quantify foliar damage area, a plastic square grid (5 x 5 mm) was used to measure the foliar area occupied by the number of squares with intact and consumed foliar areas. In some instances replacement of the foliar «lamella» was made extrapolating foliar margins and using leaves of the same size and species (*cf*. Coley 1983, Dirzo 1987, Ernest 1989, Farnsworth and Ellison 1991). To determine herbivore damage, the foliar damaged area coefficient plus the total foliar area (without damage + damaged) x 100 was used.

48

Measurement of foliar nitrogen: Foliar nitrogen content was determined using the methodology by Microkjeldhal (Technicon Industrial Systems, 1977). A foliar sample (20 leaves) was taken randomly from each of the trees selected (healthy and damaged). These were analysed during each season (*i.e.* 20 samples x 2 groups x 2 seasons; $n =$ 80). Leaves were dehydrated and analysed using the kit by Technicon (1977).

Measurement of phenolic content: Analysis of the total phenolic content in *Q. germana* leaves was made using the phenolic quantification technique by Folin-Ciocalteu. Besides total phenolic content, this method also measured the content of simple phenolics and hydrolyzable tannins. The sample size was equal to that used for nitrogen ($n =$ 80 samples of 1 gram). Samples were dried, mashed and later analyzed
using an ultraviolet spectrophotometer (M-230-UV) calibrated at 750 nanometers (1 nm $= 10^{-9}$ m). Readings were registered in parts per million (ppm) and results are expressed as mg/g of dry weight (Waterman and McKey 1989).
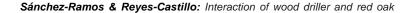
Measurement of acorn production: Acorn production (kg/tree) of *Q. germana* was quantified using four 1 m^2 traps (Puig and Bracho 1987) that were placed under the crown of five randomly selected (each of both healthy and damaged) trees. Four traps were placed equidistant below each sampled tree (*i.e.* 5 trees x 4 traps x 2 groups; $n =$ 40 m^2). Acorn collection was made in November 1996 after all the acorns had fallen. These were collected from the traps, weighed and dried in a convection stove at 80°C for 48 hours. After drying, acorns were reweighed (Puig and Bracho 1987).
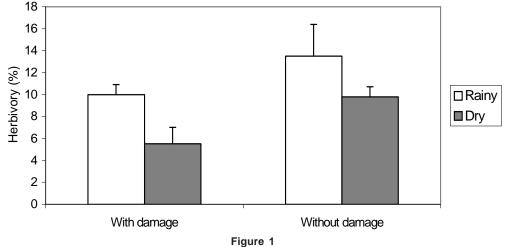
Statistical analysis: Herbivory results were analysed considering two variables: a) tree groups (healthy and damaged) and b) season of year (rainy and dry). Results (percentages) were transformed using an arcsine transformation to get normality and homocedasticity. A nested ANOVA (leaves within trees) was used to determine differences in herbivory both within and among trees. Subsequently, for comparison of foliar consumption analysed by season and groups, a repeated-measures ANOVA was carried out (Zar 1984).

Nitrogen foliar content and total phenolics compounds data also were analyzed using the repeated-measures analysis of variance (ANOVA). One nested ANOVA was conducted to test for differences in acorn production in each trap per tree and in the two treatment groups. Data are presented as the mean and the standard deviation (± 1 S.D.).

RESULTS

Foliar damage: Significant differences in foliar damage were found between damaged and healthy trees. Herbivory of *Q. germana*, expressed as the percentage of foliar area consumed (hereafter FAC) had a mean value of 9.7% ± 3.3. The FAC analysis for the damaged and healthy trees showed significant differences. Trees damaged by *P. roseni* showed less foliar damage in the two seasons (7.7% *vs.* 11.6% for damaged and healthy trees, respectively). This mean 1.5 times less herbivory.

Figure 1

Herbivory (% foliar area consumed) of *Quercus germana* comparing damaged trees and healthy trees by dipterous *Pantophthalmus roseni*. Values are expressed in means (± 1 S. D.).

The healthy group during the rainy season had 3.5% more herbivory (13.5 ± 2.9) than the damaged group (10 ± 0.9). During the dry season the healthy group also had more herbivory (1.7% more with 9.8 ± 0.8) than the damaged group (5.4% ± 1.5). These differences were statistically significant between healthy and damaged groups ($F_{(1, 76)}$ = 91.44; $P< 0.0001$), in the measures ($F_{(1, 76)}$ = 2075.2; $P< 0.0001$), in the healthy and damaged groups and seasons interaction ($F_{(1, 76)}$ = 101.27; $P< 0.0001$), as well as healthy and damaged groups and seasons and measures interaction ($F_{(1, 76)}$ = 101.27; $P< 0.0001$) (Fig. 1).

Foliar nitrogen: The nitrogen level in leaves of *Q. germana* had an overall mean of 5.4% ± 1.9. These values varied according to the season and treatment with the greatest difference found between seasons (5.22% and 5.14% in the rainy and dry season, respectively). These differences were statistically significant (ANOVA) for the seasons ($F_{(1, 76)}$ = 55.30; $P< 0.0001$), for the measures ($F_{(1, 76)}$ = 843.4; $P< 0.0001$), as well as for the interaction healthy and damaged groups and seasons and measures studied with ($F_{(1, 76)}$ = 4.62; $P= 0.034$). However, no statistical significant difference was found between damaged and healthy groups ($F_{(1, 76)}$ = 2.98; $P = 0.088$).

Phenolic concentrations: The total foliar phenolic concentration had a mean value of 74.5 ± 31.1 mg/g of dry weight. The group of damaged trees showed 1.2 times greater phenolic concentrations than the healthy group during the rainy season, and 1.5 times more during the dry season. Mean phenolic concentration for combined groups was 134.1 mg/g and 136.8 mg/g of dry weight, respectively, for during the rainy season and dry season (Table 1).

Table 1

Variables analyzed in two groups (healthy and damaged) of *Quercus germana*, in the cloud forest taking two seasons

Variable	Damaged group*		Healthy group B**		P
	Rainy	*Dry*	*Rainy*	*Dry*	
Herbivory (%)	10.0 ± 0.9	5.4 ± 1.5	13.5 ± 2.9	9.8 ± 0.8	0.0001
Nitrogen (%)	6.9 ± 1.2	3.3 ± 0.9	6.8 ± 0.7	4.4 ± 1.6	0.0001
Total phenols (mg/g)	102.8 ± 24.9	67.1± 24.6	84.1 ± 24.3	44.1 ± 15.2	0.0001
Acorn (kg)	-	26.1 ± 1.2	-	24.4 ± 0.8	0.0001

Note: *Trees with severe damage by *Pantophthalmus roseni* (^{3} 15 perforation holes); ** Trees without damage. The values are expressed in means (± 1 S. D.). Statistical different ($P< 0.05$), comparison made between both healthy and damaged groups.
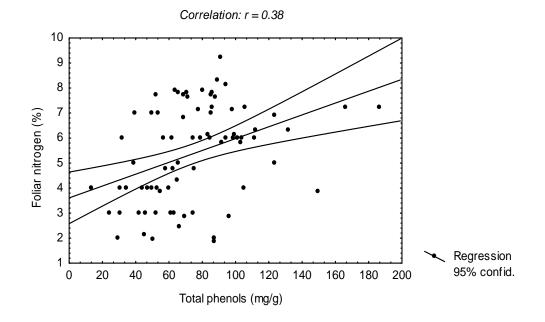

Correlation: r = 0.38

Figure 2

Correlation ($r^2= 0.14$) among foliar nitrogen (%) and total phenols (mg/g dry weight) in *Quercus germana*

Phenolic concentration was significantly different between healthy and damaged trees ($F_{(1, 76)}$ = 17.05; P< 0.0001), as well as for seasons ($F_{(1, 76)}$ = 53.14; P< 0.0001), for the measures ($F_{(1, 76)}$ = 17.05; P< 0.0001), but not for the interaction healthy and damaged trees-seasons-measures ($F_{(1, 76)}$ = 0.18; P = 0.67).

A multiple regression was carried out in order to determine the effects of total phenol concentration and foliar nitrogen content in relation to herbivory. The analysis of variance (ANOVA) from the regression showed statistical difference ($F_{(2, 77)}$ = 5.24; P= 0.007). The correlation coefficient (considering phenols and nitrogen) was r = 0.38 (14% of the variability) (Fig. 2). Considering the variables separately the correlation coefficient for total phenols was r = -0.35, and for foliar nitrogen was r = 0.26.

Acorn production: The production of acorns was significantly higher for damaged trees than healthy ones ($F_{(1, 38)}$ = 26.73; P< 0.0001). The damaged tree group showed a mean of 26.11 kg/tree ± 1.2. The healthy tree group showed a mean of 24.41 kg/tree (± 0.79).

DISCUSSION

Results obtained from the present study showed some ecophysiological distinct differences between healthy trees and those damaged by *P. roseni*. Damaged trees had less foliar damage (1.5 times) than healthy trees. The mean herbivory value for both groups (*i.e.* damaged = 7.7% and healthy = 11.6%) agree with previous reports of herbivory in tropical forest (2-20%) (Reichle *et al*. 1973, Odum and Ruíz-Reyes 1970, Lowman 1984, Dirzo 1987). Sixteen deciduous tropical species from Chamela, México have 1.2-72.7% (Filip *et al*. 1995) and there are medium values for two mangrove species in Belize (4.3-25.3% (Farnsworth and Ellison 1991). Higher values have been reported from tropical species with 7.0-12.5 (Dirzo 1987) but the data hereby presented are higher than those reported from temperate species with 7.5% (Coley and Aide 1991).

In a previous study, levels of herbivory for 46 representative species were measured in this ecosystem (Sánchez-Ramos 2002), using the instant herbivory method and consumption mean values for these species during the rainy season were 8.97% (± 47.9), and 2.94% (± 30.4) during the dry season. In the same study (in 1995), *Q. germana* had a mean foliar consumption of 10.04% during the rainy season and 3.03% during the dry season. The main insect causing this foliar damage was a geometrid lepidopteran that showed a marked preference and specificity for this oak species (Sánchez-Ramos *et al*. 1999).

The differences found between healthy and damaged trees may be due to the amount of secondary chemical compounds shown (phenols) which when evaluated had 1.2 higher concentrations in trees from the healthy tree group. This may be an induced chemical response to secondary compounds produced by the plant (Karban and Baldwin 1997). Fagaceae is a family that has been placed in a vast group of plants that show induced responses to insects attack. Generally, most of these plants of this family are perennials and this is contrasting to what occurs in some annuals (*e.g. Ipomoea purpurea* y *Lycopersicum esculentum*) that are poorly represented in this group (Karban and Baldwin 1997).

Although herbivory is considered to have negative effects in plants (Obeso 1993), there is evidence showing overcompensation by plants attacked by herbivores resulting in greater biomass and seed production when compared with healthy plants (McNaughton 1983, Paige and Whithman 1987, Alward and Joern 1993, Hjaltén *et al.* 1993, Paige 1994). Some studies have been analysed considering whether herbivory favours or not seed production (Obeso 1993). From 40 species studied, 7 (*i.e.* 18%) showed innocuous or sometimes positive effects in seed production after defoliation was evaluated (Obeso 1993). It is worth mentioning that in all cases, herbivory is analyzed as the removal of foliage and not as the effect of a trunk driller, as in the present study. This may have a differential response in induced defences as a result of the attack; most examples of induced resistance occurred during the same year when the attack took place (Karban and Baldwin 1997). This is the main reason why in this study evaluation was made during one year.

Karban and Baldwin (1997) recognised in the Fagaceae eight oak species *Quercus calliprinos, Q. emoryi, Q. garryana, Q. hemisphaerica, Q. nigra, Q. robur, Q. rubra* y *Q. velutina*, that show induced responses in foliage and *Q. velutina* show these responses in trunk producing resin and galls.

Differences in acorn production were found and damaged trees had 1.1 times more than healthy trees. This situation has been reported for some perennial herbs as *Ipomopsis aggregata* and *I. arizonica* (Polemoniaceae) (Paige and Whithman 1987).

An interesting and important observation from this study is that the insect *P. roseni* never kills the trees (Flores and Sánchez-Ramos 1989, Sánchez-Ramos *et al*. 1993). From the 18 oak driller insects reported for the genus *Quercus,* only *Agrilus bilineatus* can kill the tree and all the other species may show damages which might affect wood quality as in the case of *Prionoxystus robinae* causing a 15.0% reduction of quality for commercial purposes (Solomon *et al*. 1980). The consequences in oaks wood production (respect of the damage for *P. roseni*) in the cloud forest is an aspect that warrants further study.

ACKNOWLEDGEMENT

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