

Insect folivore damage in *Nothofagus* Blume trees of central Chile and its association with bottom-up plant community attributes

SCOTT H. ALTMANN[✉]

Grupo de Investigación Ecológica, Providencia, Santiago, Chile.

ABSTRACT. The study of insect folivore damage in South American *Nothofagus* spp. is important for monitoring the health of these trees and for basic research, although empirical information is scarce. Previous evidence on *N. macrocarpa* (A.DC.) F.M. Vásquez and R.A. Rodr, and *N. glauca* (Phil.) Krasser trees of central Chile suggested that insect folivore damage in these species can be intense and here I explored damage levels of the two species and their relationship with bottom-up community attributes such as plant architecture, light availability and host age. Foliage samples were collected at five field sites at the end of the 2007-2008 productive season in trees of *N. macrocarpa* and *N. glauca* and damage was measured based on lamina removal (complete absence of lamina) and lamina necrosis, and then analyzed statistically in terms of lamina removal and folivore damage (lamina removal and necrosis). Data for *N. macrocarpa* were divided into two groups based on field site elevation (high and low) whereas data for *N. glauca* corresponded strictly to low elevation sites. *N. macrocarpa* of lower elevation sites (low) had greater lamina removal and folivore damage than *N. glauca* and greater folivore damage than in individuals of *N. macrocarpa* (high). *N. macrocarpa* (low) associated with a lower aerial vegetative cover (and presumably more exposed to sun light) had greater lamina removal than individuals associated with a greater aerial vegetative cover (and presumably less exposed to sun light). *Nothofagus glauca* foliage with greater sun exposure showed greater lamina removal than that corresponding to lower sun exposure, and this pattern was marginally similar for *N. macrocarpa* (low). Lamina removal of *N. macrocarpa* (low) was positively correlated with leaf thinness (leaf length-width ratio) at the branch level. Finally, *N. macrocarpa* (low) juvenile trees had greater lamina removal than more mature trees.

[Keywords: *Nothofagus macrocarpa*, *N. glauca*, plant-insect herbivore interaction, foliage production, plant architecture, light availability, leaf "thinness"]

RESUMEN. Folivoría por insectos en árboles de *Nothofagus* Blume de Chile central y su relación con atributos de la comunidad vegetal (bottom-up): El estudio del daño por folivoría de insectos en *Nothofagus* spp. es importante para monitorear la salud de estos árboles aunque la información empírica es escasa. Evidencias previas sobre árboles de *Nothofagus macrocarpa* (A. DC.) F.M. Vásquez y R.A. Rodr, y *Nothofagus glauca* (Phil.) Krasser de Chile central sugirieron que el daño por este tipo de folivoría puede ser intenso en estas especies. En este trabajo exploré los niveles de daño sobre estas dos especies y su relación con atributos de la comunidad vegetal (bottom-up) tales como la arquitectura de la planta, disponibilidad de luz y edad del huésped. Se recolectaron muestras de follaje en cinco sitios de campo al final de la época productiva 2007-2008 en árboles de *N. macrocarpa* y *N. glauca* y el daño fue estimado a partir de la remoción de lámina (ausencia completa de la lámina) y necrosis de lámina y posteriormente analizado estadísticamente en términos de remoción de lámina y daño de folivoría (remoción y necrosis de lámina). Los datos para *N. macrocarpa* fueron divididos en dos grupos basados sobre la elevación de los sitios de campo (alta y baja), mientras los datos para *N. glauca* correspondieron estrictamente a sitios de baja elevación. *Nothofagus macrocarpa* de sitios de baja elevación tuvieron una remoción de lámina y daño de folivoría mayor que *N. glauca* y un mayor daño de folivoría que en los individuos de *N. macrocarpa* (alta). Los individuos de *N.*

✉ Grupo de Investigación Ecológica, Casilla de correo 16316 (Providencia), Santiago, Chile. scottaltmann@vtr.net

Recibido: 2 de julio de 2010; Fin de arbitraje: 25 de octubre de 2010; Revisión recibida: 27 de diciembre de 2010; Aceptado: 3 de marzo de 2011

macrocarpa (baja) asociados con una menor cobertura aérea vegetativa (y presumiblemente más expuestos a la luz solar) tuvieron una mayor remoción de lámina que los individuos asociados con una mayor cobertura aérea vegetativa (y supuestamente menos expuestos a luz solar). El follaje de *N. glauca* con mayor exposición al sol mostró una mayor remoción de lámina que el correspondiente a una menor exposición al sol, y este patrón fue marginalmente similar para *N. macrocarpa* (baja). La remoción de lámina de *N. macrocarpa* (baja) se correlacionó de forma positiva con la relación largo:ancho de la hoja a nivel de rama. Finalmente, los árboles juveniles de *N. macrocarpa* (baja) tuvieron una mayor remoción de lámina que árboles más maduros.

[Palabras clave: *Nothofagus macrocarpa*, *N. glauca*, interacción planta-insecto herbívoro, producción de follaje, arquitectura de la planta, disponibilidad de luz, delgadez de hoja]

INTRODUCTION

Southern beeches (Fagales: Nothofagaceae) include around 34 taxa distributed in Argentina, Chile, New Zealand, Australia, New Caledonia and New Guinea and are considered important in the context of biogeographical patterns from continental drift (Tanai 1986). For South America, 10 taxa have been determined for *Nothofagus* all of which function as dominant or co-dominant species within southern cone mediterranean and cool temperate forests. Their distribution along the Andean mountain chain extends latitudinally from 32°-56°S, spanning the countries of Argentina and Chile (Rodríguez & Quezada 2003). Endemic to Chile, *N. macrocarpa* and *N. glauca* are the northernmost distributed species of the genus on the continent and can be found along the central and coastal Andes mountain chain. *N. macrocarpa* extends from 32°-34° S at elevations between 800-2200 m above sea level (m.a.s.l.) and forms the upper canopy of the Deciduous Forest of Santiago. *N. glauca* has a greater range, extending from 34-37° S where it occupies elevations of <1200 m.a.s.l. and forms the upper canopy of the Maulino Deciduous Forest (Gajardo 1994; Donoso 1993; Rodríguez & Quezada 2003). Economically, the two species have been exploited for their high quality wood for construction, furniture and charcoal, among other uses (Donoso 1993) and more recently for tourism since they are central to some of the country's national parks and reserves.

Given the importance of southern beeches at a global scale, it is noteworthy that few investigations address insect folivore damage levels in these trees and the mechanisms responsible for that damage. Baseline data on

damage levels in *Nothofagus* spp. are important for monitoring the health of these trees, and information on the mechanisms responsible for insect folivore damage is important from a basic research perspective. For the South American species *N. macrocarpa* and *N. glauca* there is only one study where insect folivore damage levels were estimated for the productive season (Russell et al. 2000). In Chile, severe damage (Baldini & Pancel 2000) and seasonally early defoliation (Lanfranco et al. 2001) have been reported for *Nothofagus* spp., although the causal factors for these events are unknown. The relatively high insect damage for the 1999-2000 productive season in *N. pumilio* (Poepp. et Endl.) Krasser foliage of northern Patagonia was attributed to weather-related events (Mazía et al. 2009). Likewise, it is uncertain whether certain *Nothofagus* spp. are more susceptible to insect folivore damage than others and the factors related to these differences.

Bottom-up factors are indicative of the heterogeneity of vegetative communities and are considered to be central drivers of the spatial and temporal distribution of insect herbivores and their natural enemies (Tahvanainen & Root 1972; Root 1973; Lawton 1983; Hunter & Price 1992). Insect folivory in plants has been shown to be related to bottom-up attributes of local plant production (Root 1973; Norghauer et al. 2008; Pearson et al. 2003; Rhoads & English-Loeb 2003), light availability (Lincoln & Mooney 1984; Collinge & Louda 1988; Muth et al. 2008), plant species composition (Tahvanainen & Root 1972; Root 1973) and plant architecture (MacKay & Jones 1989; Campitelli et al. 2008; Sinclair & Hughes 2008). For South American *Nothofagus* spp., past research has addressed foliage chemical properties (Russell et al. 2000; Russell et al.

2004; Lavandero et al. 2009), host plant height (Lavandero et al. 2009), host leaf size (Silva & Simonetti 2009), and climatic events (Mazía et al. 2009).

Insect folivore damage might be associated with local foliage production and/or light availability to host foliage (Lincoln & Mooney 1984; Collinge & Louda 1988; Norghauer et al. 2008; Pearson et al. 2003; Muth et al. 2008). The plant vigor hypothesis supposes that plants or plant parts with greater access to resources (e.g., soil nutrients) will have greater vigor (i.e., growth rate) and will be preferred by insect herbivores. It follows that a host plant within a sparsely foliated area (e.g., gap) relative to a host plant in a more densely foliated area, will face less competition (e.g., between plants) for resources and thus will be more vigorous (Coley et al. 1983; Price 1991). Light is one resource that is of great importance to the plant vigor hypothesis since it has been shown to be strongly correlated with plant growth rates. Variable insect folivore responses to foliage exposed to different light levels have been found within plant species (Lincoln & Mooney 1984; Collinge & Louda 1988) and have been attributed to foliage nutritional quality (Osier & Jennings 2007) among other factors. Conversely, the resource concentration hypothesis predicts that insect specialists will reach greater densities where host density is greatest since these areas are more likely to be discovered by them and insect fitness will be greater there (Root 1973). Since then the idea of "host density" has been extended to include other definitions of host resource availability (e.g., host foliage).

The intensity of herbivory to a plant is also affected by the composition of the surrounding vegetation (Root 1973). The associational resistance hypothesis predicts that a greater presence of non-host vegetation (e.g., non-host foliage) will result in lower insect herbivore densities (Tahvanainen & Root 1972; Andow 1991). Mechanisms to explain this pattern include the presence of physical or chemical cues from non-host plants which act to interfere in the ability of insect herbivores to find their host (Tahvanainen & Root 1972) and a greater presence of insect herbivore enemies and parasitoids associated with a

more vegetationally complex habitat (Atsatt & O'Dowd 1976; Andow 1991).

Leaf morphology is a component of plant architecture which may influence the spatial distribution and shape of resources within a plant and affect herbivorous insects (Southwood et al. 1979; Lawton 1983). Leaf morphology and leaf physical characteristics are especially important to insect herbivores since they affect leaf choice and efficiency of use by them as a resource (e.g., as food or oviposition sites) (Rivero-Lynch et al. 1996). Studies have demonstrated insect preference for leaves based on traits such as leaf area, leaf length-width ratio (Stone & Bacon 1995), leaf thickness (Sinclair & Hughes 2008), and leaf form (e.g., lobed vs. not lobed) (MacKay & Jones 1989; Campitelli et al. 2008). In central Chile, the longer and less stout (i.e., thinner) leaves of *N. macrocarpa* would be more susceptible to insect folivory than shorter and stouter leaves of *N. macrocarpa* individuals.

Here I investigated levels of damage within and between *Nothofagus* species and their relationship with a number of bottom-up factors. I specifically evaluated (1) insect folivore damage levels at the end of the productive season of *N. macrocarpa* and *N. glauca* individuals, and (2) the relationship of insect folivore damage with host and non-host plant cover, vascular plant richness, host plant foliage light availability, leaf thinness, and chronological age.

METHODS

Study area

Five field sites were sampled along the coastal Andean mountain chain of central Chile administratively located within the Libertador Bernardo O'Higgins Region and the Metropolitan Region within 150 km south of the city of Santiago (Figure 1). This area corresponds to the southern range of *N. macrocarpa* (32°-34° S) and the northern range of *N. glauca* (34-37° S) (Donoso 1993; Hechenleitner et al. 2005). All field sites were separated by at least 10 km and site altitude

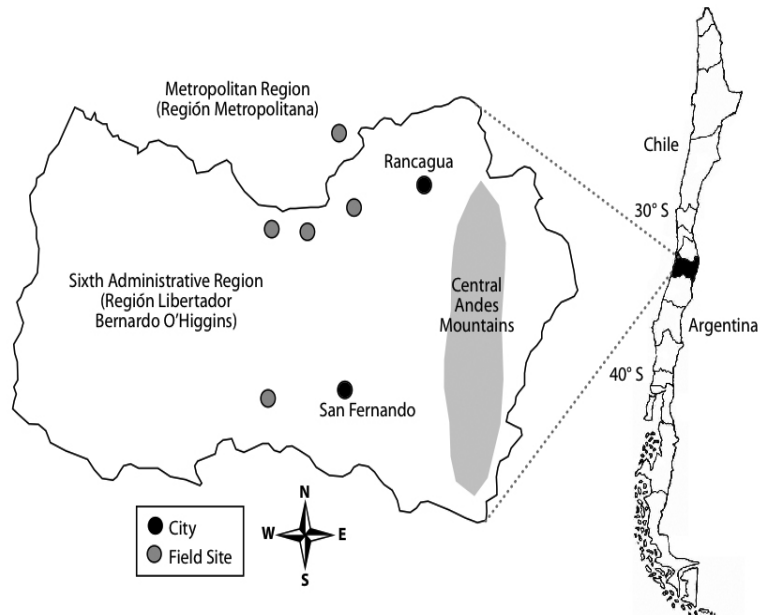


Figure 1. Field site locations for sampling *Nothofagus* trees of the coastal mountains of central Chile.

Figura 1. Ubicación de los sitios del campo para el muestreo de árboles de *Nothofagus* de las montañas costeras de Chile central.

ranges between 600-2100 m.a.s.l. Climate is mediterranean with cool, wet winters and hot dry summers. Annual average rainfall at a centrally located, low elevation point in the area is 527 millimeters and annual average temperature 13.3 °C (Instituto de Investigaciones Agropecuarias 1989). All sites are characterized by rugged mountain terrain and comprised mixed-aged, secondary growth southern beech stands with an important presence of evergreen, sclerophyll species (e.g., *Lithraea caustica* Hook and Arn; *Peumus boldus* Mol) in the canopy. The high elevation site of Altos de Cantillana included some species (e.g., *Berberis* L.) and vegetative forms (dwarfed shrubs) not found at the lower altitude sites. The Rinconada de Yaquil site had mixed stands of *N. macrocarpa* and *N. glauca* while the other stands were pure for one of the southern beech species. Foliage of these species in the study area begins to flush in September-October.

Study design

Data in the field were collected between mid-March and early April of 2008 corresponding to the end of central Chile's growing

season and the start of leaf senescence in deciduous species. Southern beech trees were haphazardly selected depending on terrain and crown access. A minimum of 10 m was maintained between sampled individuals. Collection of insect folivore damage data involved the extraction of eight terminal branches (10-15 cm in length) from each tree selected from variable canopy strata using a pole pruner. Four branches corresponded to "sun foliage" and four to "shade foliage". Sun and shade branch selection was based on canopy position (e.g., perimeter vs. interior), shading from associated vegetation, and aspect. Individual branches corresponded to natural light gradients across the canopy relative to each light availability category. For each branch leaves were extracted and digitally photographed with a Canon Powershot A560 (7.1 megapixels). For collection of plant community attribute data a 2.5x2.5 m quadrat was centered around each host tree and the following data were retrieved: host (southern beech) aerial cover at 0-3 m and >3 m; non-host aerial cover 0-3 m and >3 m; number of vascular plant species present; and host tree diameter at breast height (DBH). Aerial cover was used as an indicator of foliage production and measured by visual estimation in 5%

increments; diameter at breast height (DBH) was used as an indicator of host chronological age.

For *N. macrocarpa*, differences in community attributes were detected between the high elevation site (Altos de Cantillana) and lower elevation sites (Table 1). It was further assumed that climatic variables were different between the high and lower elevation sites. To discern the degree of similarity between *N. macrocarpa* sites, measured community attribute variables of non-host cover classes (e.g., >3 m aerial cover), number of vascular species, host DBH and leaf LWR (see below) were submitted to a discriminant function analysis (DFA). The DFA uses discriminant functions (eigenvector matrices) to classify individuals into groups based on their characteristics. The variable non-host cover 0-3 m could not be transformed to meet normality requirements and therefore was not included in the analysis. One datum outlier and one datum corresponding to missing data were not included in the analysis. However, because of concerns about meeting statistical requirements (e.g., equality of covariances) for this analysis the statistical results (e.g., Wilks' Lambda test) are not presented. Nevertheless, the DFA graphic of the discriminant function scores is presented to give a general idea of site heterogeneity (Figure 2). Based on the distribution of data points it is clear from the graphic that the high elevation site is distinct from the two lower elevation sites. This result, in conjunction with the data summarized in Table 1, prompted the creation of two data sets based on elevation for use in the statistical analyses: lower elevation site pooled data (low) (n=26) and high elevation site data (high) (n=8).

In the laboratory, three leaves from each digital photo were randomly selected for digital image analysis. Foliar damage from insects (folivory from other animal groups is not a factor here except in seedlings) was measured based on lamina removal and lamina necrosis. Lamina removal consisted of a complete absence of the lamina and included a range of damage (e.g., border and interior hole chewing) attributed primarily to external chewing insects. Lamina necrosis was assessed as brown, non-photosynthesizing tissue and

also included a range of damage (e.g., leaf rolling, piercing-and-sucking). Lamina necrosis from leaf drying or burning could be recognized and was not considered. Outward signs of foliar pathogens were infrequently observed and therefore it was assumed that necrosis attributed to them was minimal. It is important to indicate that insect folivore damage assessed here is known as primary consumption, or direct consumption, whereas secondary consumption includes damage as a result of leaf abscission (Lowman 1995a). Leaf abscission can be attributed to a range of factors (e.g., insect damage, nutrition, hydric stress) and their interactions, the importance of which are difficult to determine. There also exists the possibility that an important quantity of leaves were completely consumed and not included in the assessment. This seems unlikely though since lamina removal rarely reached >50%.

For each leaf the area corresponding to lamina removal, lamina necrosis and the entire leaf was estimated using Adobe Photoshop CS3 Extended software. For leaves so damaged (e.g., >30% lamina removal) that their original dimensions could not be visually determined, linear regression formulas applicable to each species and based on the modeling of leaf length and leaf width measurements across sites were calculated for use in estimation of leaf area. Estimation of leaf area based on this method was only applied in more extreme cases since leaf area reconstruction based on observation of adjacent leaves was assumed to be more precise. For the leaf thinness analysis leaf length (inferior lobe to apex) and leaf width (greatest lateral breadth) were measured using the digital images and the ruler tool in Adobe Photoshop; the leaf length-width ratios (LWR) were then generated.

Insect damage estimations for the three leaves from each digital photo (one branch) were averaged and subsequently branch values averaged to estimate the percent lamina removal and percent necrosis damage per tree. Thereafter, data were analyzed statistically based on the two categories of lamina removal (complete absence of the lamina) and folivore damage (lamina removal and necrosis). Lamina removal data were analyzed separately since the importance of this damage type has been

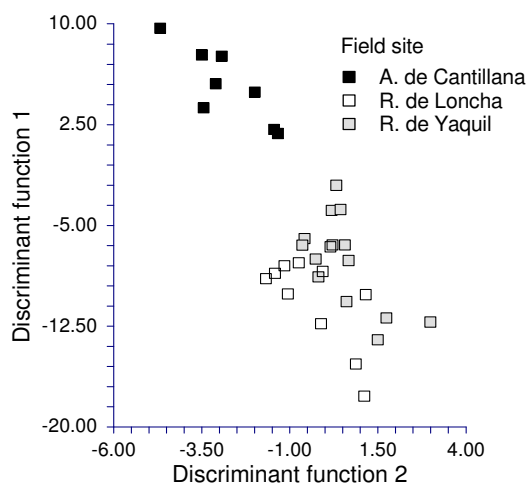


Figure 2. Discriminant function analysis (DFA) of community attribute data associated with *N. macrocarpa* trees by field site. The segregation of the high elevation discriminant function scores (black squares) from the lower elevation scores (white and grey squares) indicates a difference in site conditions between elevational gradients.

Figura 2. Análisis de función discriminante (AFD) de los datos de atributos de la comunidad asociados con árboles de *N. macrocarpa* por sitio de campo. La segregación de los valores de la función discriminadora para la alta elevación (cuadros negros) de los valores de la baja elevación (cuadros blancos y grises) indica una diferencia en condiciones ambientales a lo largo de un gradiente elevacional.

evidenced in many studies including one on *Nothofagus* trees of central Chile (Lanfranco et al. 2001).

The strength of association between independent variables and damage data and tests of differences in damage within and between species were conducted at the tree level: $n=26$, *N. macrocarpa* (low); $n=8$, *N. macrocarpa* (high); $n=18$, *N. glauca*, with the exception of testing the variable leaf LWR which was also considered at the branch level (see below). To test the association of aerial cover classes (e.g., host aerial cover) with damage data, aerial cover strata estimates (e.g., >3 m) were aggregated based on the assumption that the aggregate values were reasonable indicators of overall foliage production. Aerial cover values for host

and non-host vegetation were aggregated to test the prediction that *N. macrocarpa* foliage within less densely vegetated areas was more susceptible to insect folivory than *N. macrocarpa* foliage within more densely vegetated areas. To test for differences in damage in relation to light availability, sun

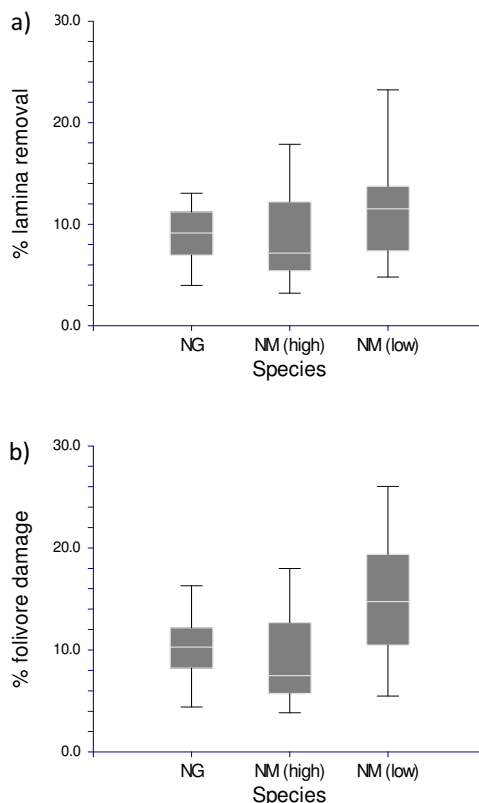


Figure 3. a) Box-plots of insect lamina removal (complete absence of lamina); b) insect folivore damage (lamina removal and necrosis), corresponding with the end of the 2007-2008 productive season in *Nothofagus* trees. Each box-plot displays the median (horizontal line inside box) and 25th and 75th percentiles (ends of the box). NG=*N. glauca*; NM=*N. macrocarpa*; low=low elevation sites; high=high elevation site.

Figura 3. a) Diagramas de caja de remoción de lámina (ausencia completa de lámina) por insectos; b) daño de folivoría (remoción y necrosis de lámina) por insectos, correspondientes al final de la estación productiva 2007-2008 en árboles de *Nothofagus*. Cada caja muestra la mediana (línea horizontal dentro de la caja) y los percentiles 25 y 75 (terminaciones de la caja). NG=*N. glauca*; NM=*N. macrocarpa*; low=sitios de baja elevación; high=sitio de alta elevación.

branch and shade branch data were averaged separately at branch and then tree level. The strength of association of leaf thinness (i.e., leaf LWR) with damage categories (Stone & Bacon 1995) was also tested at the branch level. Independence of samples at this level was promoted by using data from one randomly chosen sun and one shade branch per tree. Branches which included leaves whose area and dimensions were determined using the linear regression models were excluded from the analysis (n=46, *N. macrocarpa* (low); n=15 *N. macrocarpa* (high); n=31, *N. glauca*).

Statistical analyses

Data were analyzed and summarized statistically using NCSS 2007 software. For the strength of association analyses extreme outliers were removed. Requirements of data normality and constant variance were determined through NCSS tests (e.g., Shapiro-Wilk) and through examination of variable and residual distributions. Insect damage, host DBH and non-host aerial cover data were transformed (Log 10) where possible and when necessary to satisfy requirements. For strength of association between variables the simple linear regression (r_{LR}) and the Spearman-rank correlation coefficient (r_s) were used. For testing statistical differences between sample groups, t-tests [paired; two sample equal and non-equal variance) (t)], and a non-parametric test (Mann-Whitney U (z)) was used. A multiple regression model of the independent variables against damage

category data was considered but was not carried out given the minimum number of data recommended for this type of analysis (Neter et al. 1996; Tabachnick & Fidell 1996).

RESULTS

Three *N. macrocarpa* and four *N. glauca* leaves could not be analyzed due to problems with the digital photos. Lamina removal and folivore damage were found in more than 94% of leaves of the three plant groups. Lamina removal of *N. macrocarpa* (low) was significantly greater than that of *N. glauca* (t=-2.1, P=0.04) whereas lamina removal of *N. macrocarpa* (high) did not statistically differ from the other groups (Figure 3a). Folivore damage in *N. macrocarpa* (low) was greater than folivore damage in *N. glauca* (t=-3.19, P=0.003) and than in *N. macrocarpa* (high) (t=3.26, P=0.003; Figure 3b).

Lamina removal for *N. macrocarpa* (low) negatively correlated with aerial cover of host and non-host species (P=0.01; Figure 4) whereas I did not find a significant correlation for *N. macrocarpa* (high) (P=0.49) and *N. glauca* (P=0.96). Lamina removal in *N. glauca* was significantly greater in sun foliage than in shade foliage (t=5.62, P<0.0001) and there were statistically marginal differences for *N. macrocarpa* (low) (t=-1.96, P=0.06) but not for *N. macrocarpa* (high) (t=-0.54, P=0.60; Figure 5a). Folivore damage of sun foliage was also greater than that of shade foliage for *N. glauca* (t=4.2, P<0.0001; Figure 5b). At the branch level

Table 1. Means of southern beech plant community attributes by field site (ac=aerial cover, RY=Rinconada de Yaquil, RL=Robleria de Loncha, AC=Altos de Cantillana, HM=Hijuela del Medio, AP=A Pino property).

Tabla 1. Los promedios de atributos de la comunidad del roble del hemisferio del sur por sitio de campo. (ac=cobertura aérea, RY=Rinconada de Yaquil, RL=Robleria de Loncha, AC=Altos de Cantillana, HM=Hijuela del Medio, AP=propiedad de A. Pino).

Attribute	N. macrocarpa			N. glauca		
	RY	RL	AC	RY	HM	AP
Host ac 0-3m	25%	23%	57%	40%	40%	44%
Host ac >3m	68%	52%	66%	61%	69%	59%
Associated ac 0-3	38%	26%	23%	22%	13%	34%
Associated ac >3	6%	2%	0%	2%	1%	0%
Host DBH	15	17	23	16	21	18
#vascular spp.	15	12	2	9	7	10
Altitude (m.a.s.l.)	650-750	850-950	2000-2100	650-750	600-700	800-900

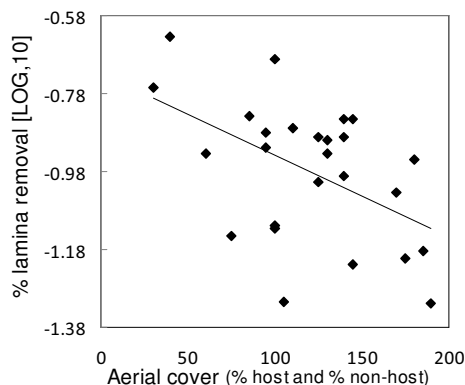


Figure 4. Inverse correlation of aerial cover (host and non-host) with insect lamina removal (complete absence of lamina) for *N. macrocarpa* trees (low) of central Chile.

Figura 4. Correlación inversa de cobertura aérea (huésped y no-huésped) con remoción de lámina por insectos (ausencia completa de lámina) para árboles de *N. macrocarpa* (low) de Chile central.

lamina removal of *N. macrocarpa* (low) was positively associated with leaf length-width ratio ($P=0.03$, Figure 6a), whereas a weak, but not significant correlation was noted for folivore damage ($P=0.10$). Weak to moderate positive trends at this level were also noted for *N. macrocarpa* (high): lamina removal ($P=0.16$); folivore damage ($P=0.14$). Correlations of leaf

LWR with *N. glauca* damage were very weak and not significant. Lamina removal in *N. macrocarpa* (low) negatively correlated with host diameter at breast height ($P=0.01$; Figure 6b) and a similar trend was noted for folivore damage ($P=0.07$). No significant correlations were found for this variable with damage classes for *N. macrocarpa* (high) and *N. glauca*. Finally, no significant correlations were found between vascular plant richness with damage classes for either species.

DISCUSSION

This study is important since it provides baseline data on damage levels from insect folivores in South American southern beech, and evidences the importance of bottom-up community attributes to that damage, most notably in relation to *N. macrocarpa*. The baseline data presented here can be contrasted with insect folivore damage data for these and other *Nothofagus* spp. of South America and damage data on a larger geographic scale, to get an initial “snapshot” of damage intensity in these species. Furthermore, damage patterns detected here can be related to potential mechanisms. However, sustained research is necessary to verify and extend these results and to experimentally test potential mechanisms.

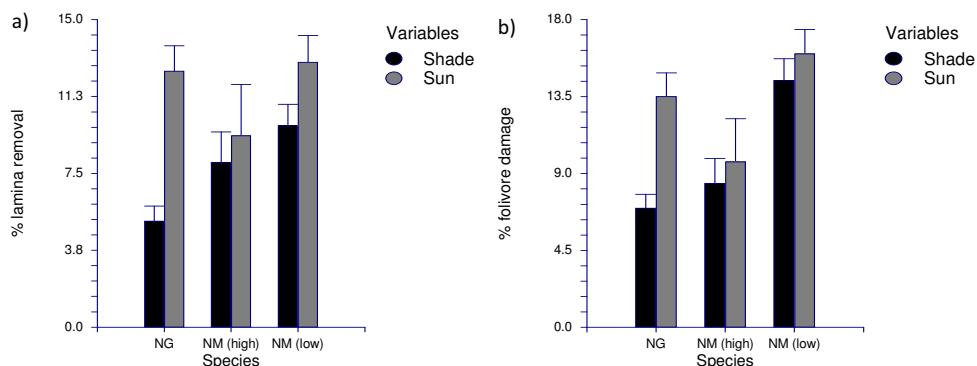


Figure 5. a) Insect lamina removal (complete absence of lamina); b) insect folivore damage (lamina removal and necrosis), based on light availability (sun vs. shade) in foliage of *Nothofagus* trees of central Chile. NG=*N. glauca*; NM=*N. macrocarpa*; low=low elevation sites; high=high elevation site. Vertical bars= \pm SE.

Figura 5. a) Remoción de lámina (ausencia completa de lámina) por insectos; b) daño de folivoría (remoción y necrosis de lámina) por insectos, sobre la base de la disponibilidad de luz (sol vs. sombra) en follaje de árboles de *Nothofagus* de Chile central. NG=*N. glauca*; NM=*N. macrocarpa*; low=sitios de baja elevación; high=sitio de alta elevación. Barras verticales= \pm ES.

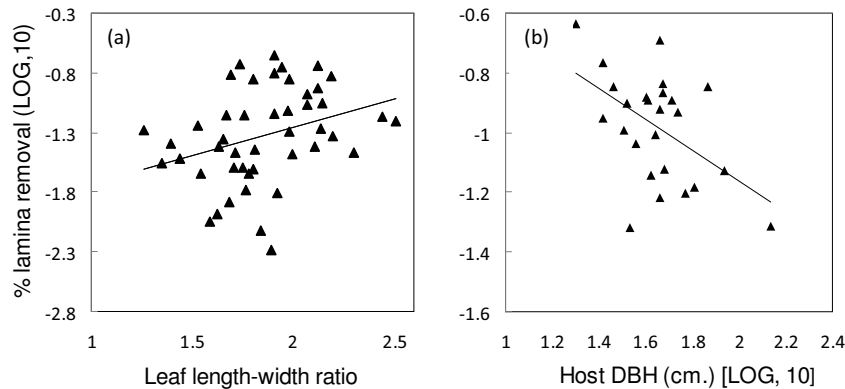


Figure 6. Correlation of lamina removal of *N. macrocarpa* (low) trees of central Chile with (a) leaf length-width ratio (LWR) at the branch level, and (b) host diameter at breast height (DBH).

Figura 6. Correlación de la remoción de lámina en árboles de *N. macrocarpa* (low) de Chile central con (a) la proporción del largo-ancho (PLA) nivel de rama, y (b) el diámetro a la altura de pecho (DAP) del huésped.

Insect damage levels assessed can be compared to results of other *Nothofagus* studies and to damage levels in other geographic areas. Estimates of insect folivore damage in *Nothofagus* spp. of Chile ranged from a maximum mean of >20% for *N. antarctica* (G. Forst) Oerst. to a minimum mean of <3% for *N. alessandrii* Espinoza (both species native to Chile) (Russell et al. 2000). In another study estimates of mean seasonal (1998-2007) lamina area damaged in *N. pumilio* from chewing insects were in the range of 0.2-7% (Mazía et al. 2009). The high percentage of leaves with lamina removal damage evidenced in the current study (e.g., 94.5% for *N. macrocarpa*) is consistent with findings for *N. obliqua* (Mirb.) Oerst. trees of southern Chile (Lanfranco et al. 2001). Damage levels reported here are considerably greater than the mean 7.1% annual damage calculated for temperate species across 13 studies (Coley & Barone 1996). Conversely, in Australia insect folivores were attributed to a mean 13% annual leaf area removal in trees of a “healthy dry sclerophyll woodland” (Lowman 1995b).

A difference in damage levels between the two species was evidenced for lower elevation trees. This agrees with the study of Russell et al. 2000 where a mean <5% leaf feeding damage was reported for *N. glauca*, which was less than that of *N. macrocarpa*. The differences in damage levels between studies may be a result of the timing of data collection, annual

variability, and/or sampling methodologies. The lower damage observed in *N. glauca* may be attributed in part to an enhanced structural defense in its leaves. Based on tactile manipulation *N. glauca* leaves were perceived to be more sclerophyll (i.e., having qualities of hardness, toughness and/or stiffness) than *N. macrocarpa* leaves, a quality which has been associated with deterring insect folivory (Lowman & Box 1983; Choong et al. 1992; Read et al. 2006). Surprisingly, damage levels in sun foliage were similar in both species (Figure 5) while shade foliage damage levels were comparatively much lower in *N. glauca*. This suggests that for *N. glauca* insect folivores have a strong preference for sun foliage and that sun foliage in this species is as palatable as sun foliage in *N. macrocarpa*. The relationship between light availability and degree of sclerophyll with insect folivore levels has been little studied although it is likely important to insect folivory in these species. Marques et al. (1991) evidenced a positive correlation of light availability with leaf sclerophyll in *Sebastiania myrtilloides* (Mart.) Pax of southeastern Brazil. Alternatively, it was suggested that a greater sclerophyll found across Australian understory vs. overstory species was related to decreasing light availability from the upper to lower canopy (Specht & Rundel 1990).

A number of explanations, or combinations thereof, may be elicited to explain the inverse correlation found between aerial cover (host

and non-host) and lamina removal in *N. macrocarpa* (low). One possibility implicates the plant vigor hypothesis. As previously discussed environments with reduced foliage indicate less competition for resources which may result in higher quality host foliage for insect folivores (Price 1991). This may be based on a greater availability of soil moisture, soil nutrients and/or light. Light may be especially important here since a trend was detected whereby foliage with greater light exposure was more damaged than foliage with less light exposure. With less foliage present more light would be able to penetrate the canopy. While the effect of light availability on insect folivore abundances and damage levels is still an open question, many studies examining the issue have evidenced the effect that light has on foliage quality for consumption, especially in terms of nitrogen and secondary defenses (e.g. phenolics). Components of foliar nutrition, including secondary defenses, have been evidenced to vary between species based on sunlight availability (Schoonhoven et al. 2005; Osier & Jennings 2007; Muth et al. 2008). Nonetheless, a word of caution is important here since damage in shade vs. sun foliage may have been influenced by other factors besides sunlight (e.g., canopy position). Yet another possibility is that the sparsely vegetated areas actually reflect low productive potential due to a limiting resource (e.g., soil moisture) and insect folivores are responding to the resultant leaf quality associated with the stress (White 1969). Of course, an understanding of the mechanisms behind insect folivore damage must also consider grazing in terms of whether consumption increases with poorer quality leaves (fitness consumption) or increases with better quality leaves (luxury consumption), or if both patterns are present. Perhaps the simplest explanation of the pattern is the idea of "resource dilution" whereby areas with fewer plant resources (e.g., foliage) are hypothesized to manifest more insect damage than areas with greater resources, assuming relatively equal insect abundances (Rhainds & English-Loeb 2003).

A concept which has received relatively little attention in terms of insect folivore interaction with its host plant, leaf thinness was found to be important to lamina removal in *N. macrocarpa* (low). The positive correlation of

leaf LWR with lamina removal at the branch level is contrary to an investigation where at the branch level for *Eucalyptus largiflorens* F. Muell an inverse correlation was found between missing leaf area and an estimation of leaf LWR (Stone & Bacon 1995). In another investigation a positive correlation was found between leaf length and leaf miner presence across Australian species (Sinclair & Hughes 2008). In many plants the relationship of leaf length with leaf area is strong. In an investigation of 51 plant species, the importance of plant phenology to insect folivore damage was demonstrated when it was found that larger leaves (positively correlated with longer leaves) expanded at a slower rate and showed more insect damage than smaller leaves (Moles & Westoby 2000). The importance of larger leaves to insect folivore fitness has been attributed to greater leaf nutrition among other factors (Whitham 1978; Bultman & Faeth 1986). Additionally, thinner leaves may interact with environmental conditions (e.g., temperature) in a distinct manner relative to other leaf sizes and/or shapes, which will ultimately determine the conditions of the leaf tissue (e.g., CO₂ stomata exchange) and its importance to insect folivores (Fonseca & Fleck 2006).

An unexpected result was the inverse association of host diameter at breast height with lamina removal for *N. macrocarpa* (low). This pattern also invokes the plant vigor hypothesis since more juvenile plants and plant parts often have greater vigor (Price 1991). Developmental stages in plants include physical and chemical changes (Poethig 1990) which are central to herbivorous insect use of a plant as a resource. For example, the quality of leaves as food (Boege 2005) and shoots for oviposition sites (Price et al. 1987) have been experimentally related to developmental and ontogenetic stages (i.e., maturation) in host plants. Plant development is also important to higher trophic levels and local abiotic conditions both of which can effect interaction of herbivorous insects with the host plant. And developmental shifts in host defensive traits may be associated with dramatic changes in insect herbivore damage levels (Fonseca & Fleck 2006). Of potential importance to results here, a recent meta-analysis on insect herbivory and its relationship with

plant ontogenesis indicated a general trend in juvenile woody plants to exhibit greater physical defenses (e.g., more sclerophyll foliage) with age (Barton & Koricheva 2010). It is important to note that for *N. macrocarpa* (low) no significant correlation was detected between host diameter at breast height and aerial cover ($r_{LR}=0.11$, $P=0.60$) as might be suspected, which strengthens the idea that these variables can act independently and are important.

This study is important in so far as it provides insect folivore damage data for *Nothofagus* spp. of South America and evidences novel patterns of this damage relative to southern beech community attributes. This data and information can be applied to future investigations on *Nothofagus* spp. Annual collection of folivore damage data across environmental gradients and throughout the productive season should proceed in order to develop databases on insect damage which could be applied to predict insect outbreaks and patterns in relation to anthropogenic factors. Among the many possibilities to extend the investigation of insect folivore interaction with *Nothofagus* spp. consideration should be given to the relationship of insect folivore abundances and damage levels with: 1) nutritional and defensive attributes of host foliage in relation to a range of plant production and light availability regimes, and host age classes, 2) host physiognomic (e.g., branch length, tree height) and leaf morphological traits (e.g., leaf sclerophylly), and 3) insect predator and parasite richness and abundances also in consideration of their interaction with aforementioned variables. Of these studies the first is arguably the most important since current literature reinforces the idea that foliage quality in terms of nutrition and plant defenses is an overriding driver of insect folivory.

ACKNOWLEDGEMENTS

The author would like to express his gratitude to M. van Sint Jan, L. Cornejo, A. Pino, J. Solo de Zaldivar, the Tello family, and three anonymous manuscript reviewers for their assistance with this investigation.

REFERENCES

- ANDOW, DA. 1991. Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.* **36**:561-586.
- ATSATT, PR & DJ O'DOWD. 1976. Plant defense guilds. *Science* **193**:24-29.
- BALDINI, A & L PANCEL. 2000. *Agentes de daño en el bosque nativo*. Editorial Universitaria. Santiago, Chile. Pp. 409.
- BARTON, KE & J KORICHEVA. 2010. The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. *Am. Nat.* **175**(4):481-493.
- BOEGE, K. 2005. Herbivore attack in *Casearia nitida* influenced by plant ontogenetic variation in foliage quality and plant architecture. *Oecologia* **143**:117-125.
- BULTMAN, TH & SH FAETH. 1986. Leaf selection by leaf-mining insects on *Quercus emoryi* (Fagaceae). *Oikos* **46**:311-316.
- CAMPITELLI, BE; AK SIMONSEN; A RICO WOLF; JS MANSON & JR STINCHCOMBE. 2008. Leaf shape variation and herbivore consumption and performance: a case study with *Ipomoea hederacea* and three generalists. *Arthropod-Plant Interact.* **2**(1):9-19.
- CHOONG, MF; PW LUCAS; JSY ONG; B PEREIRA; HTW TAN; ET AL. 1992. Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytol.* **121**:597-610.
- COLEY, PD. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* **53**:209-233.
- COLEY, PD & JA BARONE. 1996. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* **205**:305-335.
- COLLINGE, SK & SM LOUDA. 1988. Herbivory by leaf miners in response to experimental shading of a native crucifer. *Oecologia* **75**:559-566.
- DONOSO, C. 1993. *Bosques templados de Chile y Argentina: variación, estructura y dinámica*. Editorial Universitaria. Santiago, Chile. Pp. 484.
- FONSECA, CR & T FLECK. 2006. Processes driving ontogenetic succession of galls in a canopy tree. *Biotropica* **38**(4):514-521.
- GAJARDO, R. 1994. *La vegetación natural de Chile, clasificación y distribución geográfica*. Editorial Universitaria. Santiago, Chile. Pp. 165.
- HECHENLEITNER VEGA, P; MF GARDNER; PI THOMAS; C ECHEVERRÍA; B ESCOBAR; ET AL. 2005. *Plantas amenazadas del centro-sur de Chile: distribución, conservación y propagación*. Universidad Austral de Chile and Royal Botanical Garden of Edinburgh. Chile. Pp. 188.

- HUNTER, MD & PW PRICE. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**:724-732.
- INSTITUTO DE INVESTIGACIONES AGROPECUARIAS. 1989. *Mapa agroclimático de Chile*. Ministry of Agriculture of Chile. Santiago, Chile. Pp. 221.
- LAVFRANCO, D; E ROJAS; R RÍOS & C RUIZ. 2001. Pp. 91-103 in: Liebhold, AM; ML McManus; IS Otvos & SLC Fosbroke (eds.). Proceedings: integrated management and dynamics of forest defoliating insects. U.S. Department of Agriculture. Newton Square, USA.
- LAVANDERO, B; A LABRA; CC RAMÍREZ; NM NIEMEYER & E FUENTES-CONTRERAS. 2009. Species richness of herbivorous insects on *Nothofagus* trees in South America and New Zealand: the importance of chemical attributes of the host. *Basic Appl. Ecol.* **10**(1):10-18.
- LAWTON, JH. 1983. Plant architecture and the diversity of phytophagous insects. *Ann. Rev. Entomol.* **28**:23-29.
- LINCOLN, DE & HA MOONEY. 1984. Herbivory on *Diplacus aurantiacus* shrubs in sun and shade. *Oecologia* **64**(2):173-176.
- LOWMAN, MD. 1995a. Herbivory as a canopy process in rainforest trees. (18) Pp. 431-454 in: Lowman, MD & NM Nadkarni (eds.). *Forest canopies*. Academic Press. San Diego, USA. Pp. 624.
- LOWMAN, MD. 1995b. Herbivory in Australian forests - a comparison of dry sclerophyll and rain forest canopies. *P. Linn. Soc. N. S. W.* **115**:77-87.
- LOWMAN, MD & JD BOX. 1983. Variation in leaf toughness and phenolic content among five species of Australian rain forest trees. *Aust. J. Ecol.* **8**:17-25.
- MACKAY, DA & RE JONES. 1989. Leaf shape and the host-finding behaviour of two ovipositing monophagous butterfly species. *Ecol. Entomol.* **14**(4):423-431.
- MARQUES RODRIGUES, A; QS GARCÍA & G WILSON FERNANDES. 1991. Effects of sun and shade on leaf structure and sclerophylly of *Sebastiania myrtilloides* (Euphorbiaceae) from Serra do Cipó, Minas Gerais, Brazil. *Bol. Bot. Univ. Sao Paulo* **1999** **18**: 21-27.
- MAZÍA, CN; EJ CHANETON; T KITZBERGER & LA GARIBALDI. 2009. Variable strength of top-down effects in *Nothofagus* forests: bird predation and insect herbivory during an ENSO event. *Austral Ecol.* **34**:359-367.
- MOLES, AT & M WESTOBY. 2000. Do small leaves expand faster than large leaves, and do shorter expansion times reduce herbivore damage? *Oikos* **90**:517-524.
- MUTH, NZ; EC KLUGER; JH LEVY; MJ EDWARDS & RA NIESENBAUM. 2008. Increased per capita herbivory in the shade: necessity, feedback, or luxury consumption. *Ecoscience* **15**(2):182-188.
- NETER, J; MH KUTNER; CJ NACHTSHEIM & W WASSERMAN. 1996. *Applied linear statistical models*, 4th ed. Irwin. Chicago, USA. Pp. 1408.
- NORGHAUER, JM; JR MALCOLM & BL ZIMMERMAN. 2008. Canopy cover mediates interactions between a specialist caterpillar and seedlings of a neotropical tree. *J. Ecol.* **96**: 103-113.
- OSIER, TL & SM JENNINGS. 2007. Variability in host-plant quality for the larvae of a polyphagous insect folivore in midseason: the impact of light on three deciduous sapling species. *Entomol. Experimentalis et Applicata* **123**:159-166.
- PEARSON, T; DFRP BURSLEM; R GOERIZ & J DALLING. 2003. Interactions of gap size and herbivory on establishment, growth and survival of three species of neotropical pioneer tree. *J. Ecol.* **91**: 785-796.
- POETHIG, RS. 1990. Phase change and the regulation of shoot morphospecies in plants. *Science* **250**: 923-930.
- PRICE, PW. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* **62**:244-251.
- PRICE, PW; H ROININEN & J TAHVANAINEN. 1987. Plant age and attack by the bud galler, *Euura mucronata*. *Oecologia* **73**:334-337.
- READ, J; GD SANSON; M DE GARINE-WITCHATITSKY & T JAFFRÉ. 2006. Sclerophylly in two contrasting tropical environments: low nutrients vs. low rainfall. *Am. J. Bot.* **93**(11):1601-1614.
- RHAINDS, M & G ENGLISH-LOEB. 2003. Testing the resource concentration hypothesis with tarnished plant bug on strawberry: density of hosts and patch size influence the interaction between abundance of nymphs and incidence of damage. *Ecol. Entomol.* **28**(3):348-358.
- RIVERO-LYNCH, AP; VK BROWN & JH LAWTON. 1996. The impact of leaf shape on the feeding preferences of insect herbivores: experimental and field studies with *Capsella* and *Phyllotreta*. *Philos. T. Roy. Soc. B.* **351**(1348):1671-1677.
- RODRÍGUEZ R; M QUEZADA. 2003. Fagaceae *Dumort.* In: MARTICORENA C & RODRÍGUEZ R (eds.). Flora de Chile Vol. 2(2), Berberidaceae-Betulaceae, Universidad de Concepción, Concepción, Chile. Pp. 64-76.
- ROOT, RB. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* **43**(1):95-124.
- RUSSELL, GB; WS BOWERS; V KEESING; HM NIEMEYER; T SEVENET; ET AL. 2000. Patterns of bioactivity and herbivory on *Nothofagus* species from Chile and New Zealand. *J. Chem. Ecol.* **26**(1):41-56.

- RUSSELL, GB; EH FAUNDEZ & HM NIEMEYER. 2004. Selection of *Nothofagus* host trees by the aphids *Neuquenaphis staryi* and *Neuquenaphis edwardsi*. *J. Chem. Ecol.* **30**(11):2231-2241.
- SCHOONHOVEN, LM; JJA VAN LOON & M DICKE. 2005. *Insect-plant biology 2nd ed.* Oxford University Press. New York, USA. Pp. 421.
- SILVA, CA & JA SIMONETTI. 2009. Inquiring into the causes of depressed folivory in a fragmented temperate forest. *Acta Oecologica* **35**(3):458-461.
- SINCLAIR, RJ & L HUGHES. 2008. Incidence of leaf mining in different vegetation types across rainfall, canopy cover and latitudinal gradients. *Austral Ecol.* **33**:353-360.
- SOUTHWOOD, TRE; VK BROWN & PM READER. 1979. The relationships of plant and insect diversities in succession. *Biol. J. Linn. Soc.* **12**(4):327-348.
- SPECHT, RL & PW RUNDEL. 1990. Sclerophylly and nutrient status of Mediterranean-climate plant communities in southern Australia. *Aust. J. Bot.* **38**:459-474.
- STONE, C & PE BACON. 1995 Influence of insect herbivory on the decline of black box (*Eucalyptus largiflorens*). *Aust. J. Bot.* **43**(6):555-564.
- TABACHNICK, B & L FIDELL. 1996. *Using multivariate statistics, 3rd ed.* Harper Collins College Publishers. New York, USA. Pp. 880.
- TAHVANAINEN, JO & RB ROOT. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* **10**:321-346.
- TANAI, T. 1986. Phytogeographic and phylogenetic history of the genus *Nothofagus* Bl. (Fagaceae) in the southern hemisphere. *J. Fac. Sci., Hokkaido Univ.* **4**(21):505-582.
- WHITE, TCR. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* **50**:905-909.
- WHITHAM, TG. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. *Ecology* **59**(6):1164-1176.