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**EFFECTO DE LA HERBIVORIA SOBRE LA SOBREVIVENCIA  
FOLIAR DE *NOTHOFAGUS ALPINA* Y *NOTHOFAGUS OBLIQUA***

Tesis

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por

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Director de Tesis: Dr. Italo Serey Estay



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A Marcos, Marquitos  
y mis padres



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## RESUMEN

Una estrategia clave en la obtención de recursos para las plantas es la longevidad de sus hojas individualmente, o la sobrevivencia de la población de hojas de la planta. El patrón de sobrevivencia foliar puede ser explicado por una serie de factores, tales como las condiciones ambientales, morfología de sus yemas, o herbivoría. Por otra parte, como las plantas son organismos modulares, la sobrevivencia foliar puede ser estudiada en distintos niveles jerárquicos: una planta o individuo, población de árboles o para la especie.

*Nothofagus alpina* y *N. obliqua* presentan una arquitectura morfológica similar y bajo las mismas condiciones ambientales presentan diferentes patrones de sobrevivencia foliar con diferentes grados de herbivoría. El objetivo de esta tesis fue determinar si una interacción biológica como la herbivoría puede explicar las diferencias en sobrevivencia foliar de estas especies analizando tres niveles jerárquicos: árbol, población de árboles y especie.

Los resultados mostraron que a nivel de los árboles, sólo algunos son afectados por la herbivoría en su sobrevivencia foliar y este efecto puede ser de aumentar o disminuir la sobrevivencia foliar en ambas especies. A nivel de la población de árboles, la herbivoría no afecta la sobrevivencia foliar de *N. alpina* pero si de *N. obliqua*, disminuyendo la sobrevivencia. En este nivel, la herbivoría daría cuenta en parte de las diferencias en sobrevivencia foliar entre *N. alpina* y *N. obliqua*, específicamente a edades intermedias de las hojas. A

nivel de la especie, nuevamente en *N. alpina* no hay efecto por la herbivoría, pero si un efecto indirecto, ya que esta especie estaría compensando con un aumento de sobrevivencia según la cantidad de daño. En tanto, *N. obliqua* tendría una compensación débil y su resultado es un efecto negativo de la herbivoría en la sobrevivencia de sus hojas. En el análisis interespecífico los resultados indicaron que la herbivoría no es la causa de las diferencias interespecíficas y que factores intrínsecos de las plantas podrían estar explicando dichas diferencias. Sin embargo, con el análisis de estos tres niveles se concluye que la herbivoría modula en parte estas diferencias, pero no es la única causa. Análisis de este tipo, en que un problema es mirado desde diferentes niveles de jerarquías, proporciona una mirada más completa y biológica de la herbivoría.

## ABSTRACT

A key strategy in plants obtaining resource, is the longevity of their individual leaves, or the survival of the leaf population of the plant. The foliar survival pattern could be explained by a series of factors, such as environmental conditions, shoot morphology or herbivory. On the other hand, as plants are modular organisms, foliar survival can be studied in different hierarchical levels: a plant or individual, population of trees or by species.

*Nothofagus alpina* and *N. obliqua* present a similar morphological architecture and under the same environmental conditions, they exhibit different foliar survival patterns with different degrees of herbivory. The objective of this thesis was to determine if a biological interaction, such as herbivory, could to explain the differences in foliar survival of these species, check three hierarchical levels: tree, population of trees and species.

The results showed that at the tree levels, only some are affected by herbivory in their foliar survival and this effect could result in increasing or decreasing the foliar survival in both species. At the population level of the trees, herbivory does not affect the foliar survival of *N. alpina* but that of *N. obliqua* is affected, decreasing the survival. At this level, herbivory partially explains differences in foliar survival between *N. alpina* and *N. obliqua*, specifically in the leaves of middle ages. At the species level, again in *N. alpina* there was no overall effect of herbivory, but an indirect effect, given that this

species would compensate with an increase in survival following the amount of damage. As such, *N. obliqua* had a weak compensation and the result is a negative effect of herbivory for foliar survival. In the interspecific analysis, the results indicated that herbivory is not the cause of the differences between species, and that intrinsic factors of the plants could explain said differences. However, with this analysis of three levels, it is concluded that herbivory modulates in part these differences, but is not the only cause. Analysis of this type, in which a problem is viewed from different hierarchical levels, allows a more complete and biological understanding of herbivory.

## INTRODUCCION

Las plantas son organismos modulares constituidos por unidades que pueden ser estudiadas con un enfoque demográfico, dado que cada una de sus unidades forma una población en sentido estricto (Harper, 1977; White, 1979; Porter, 1983 a y b; Jones, 1985). Las hojas constituyen una unidad interesante de estudio, ya que éstas contribuyen directamente a la adecuación biológica de las plantas (Harper, 1989). En una especie, la sobrevivencia de sus hojas es un parámetro poblacional que refleja su estrategia para utilizar la luz y maximizar la ganancia de carbono (Chabot & Hicks, 1982). La sobrevivencia foliar de una especie puede ser afectada por la radiación solar, la posición de sus ramas en la planta, el habitat o la herbivoría (Harper, 1977; Tallak, 1986; Dirzo, 1984; Pritchard & James, 1984). Entre especies, las diferencias en sobrevivencia foliar pueden estar dadas por la morfología de sus yemas o la intensidad de la herbivoría (Kikuzawa, 1982, 1983, 1984; Dirzo, 1984; Nuñez-Farfán & Dirzo, 1989). El efecto de la herbivoría promueve una respuesta fisiológica individual de las hojas, quienes podrían acelerar o retardar la senescencia, afectando así la sobrevivencia foliar (Thomas, 1980; Harnett & Bazzaz, 1984).

En los últimos años se ha enfatizado la importancia de estudiar la herbivoría en distintas escalas espaciales: hoja, rama, zonas de la copa, árbol, sitio, tipo de bosque y continente, así como también entre especies, comunidades y ecosistemas (Coley, 1983a y b; Dyer & Shugart, 1992; Lowman, 1997). Estos enfoques proporcionan una visión más completa de la

herbivoría, pero hasta el momento, pocos son los estudios que analizan más de un nivel y las relaciones entre distintos niveles es aún más escasa. Dentro de este contexto, el efecto de la herbivoría en la sobrevivencia foliar puede ser estudiado a distintas escalas según se defina la población de hojas. A nivel específico, la población de hojas está constituida por un conjunto de hojas, independiente del árbol que provengan. En una población de árboles, cada árbol constituye una réplica de la población de hojas. En un individuo, la población de hojas esta dada por el conjunto de hojas del árbol. Por otra parte el efecto de la herbivoría en la sobrevivencia foliar podría ser también analizado entre especies, en cada uno de los niveles mencionados.

*Nothofagus alpina* (Poepp. & Endl.) y *Nothofagus obliqua* (Mirb.) son dos especies arbóreas deciduas, típicas del bosque nativo de Chile. Se les puede encontrar formando bosques puros o mixtos (Gajardo, 1994). Poseen yemas preformadas de la estación de crecimiento anterior y comparten el mismo modelo arquitectural (Soumoy et al., 1995). Por otra parte, la sobrevivencia foliar es diferente entre éstas especies. *Nothofagus obliqua* tiene una sobrevivencia foliar menor respecto de *N. alpina*, en una misma localidad. Dado que *N. obliqua* presenta un mayor número de hojas dañadas por acción de insectos, y además presenta una mayor diversidad de insectos asociados (Grandon, 1996), las diferencias en sobrevivencia foliar entre éstas especies podrían ser explicadas por la herbivoría (Serey et. al , no publicado). Bajo estas circunstancias *N. alpina* y *N. obliqua* constituyen un buen sistema de

estudio para determinar si la herbivoría produce diferencias en la sobrevivencia foliar de estas especies.

En este contexto, los objetivos de esta tesis son a) conocer el efecto de la herbivoría sobre la sobrevivencia foliar de *N. alpina* y *N. obliqua* , considerando la población de hojas en tres niveles; especie, población de árboles e individual (árbol); b) determinar si la herbivoría es la responsable de las diferencias en sobrevivencia foliar de estas especies cuando se examina la población de hojas a nivel de especie y población de árboles.

## CAPITULO 1

### EFFECTS OF HERBIVORY IN THE LEAF SURVIVAL OF TWO SOUTHERN BEECH: *NOTHOFAGUS ALPINA* AND *N. OBLIQUA*

#### INTRODUCTION

Leaves could be considered modules in higher plants and foliage as populations with properties such as age structure, survival, life expectancy and mortality (Harper, 1977; Porter, 1983 a and b; Jones, 1985). Leaf population is affected by several factors that determine populations parameters, such as physical local conditions or biological interactions, i. e. herbivory (Harper, 1977; Dirzo, 1984).

The leaves show several responses to herbivory ranging from chemical changes to abscission. Chemical changes that are triggered by herbivory include rearrangement in the carbon balance, secondary metabolites induction, increase in photosynthetic capacity, hormonal changes and resource reallocation (Haukioja & Niemela, 1979; Montenegro et al., 1980; Chabot & Hicks, 1982; Coley, 1983; Toumi et al., 1984; Coley et al., 1985; Coley & Barone, 1996; Haukioja & Honkanen, 1997). Other types of responses are shown at the phenological level. Plants with higher levels of herbivory show a fast and simultaneous foliar expansion, reducing the damage time (Coley, 1983 a and b; Aide & Londoño, 1989; Aide, 1992; 1993; Aizen & Patterson, 1995; Coley & Barone, 1996), and saturating the food supply for herbivory. Nevertheless, there are species that produce new leaves to replace the lost surface area (Chabot & Hicks, 1982). Pritchard & James (1984) showed that



leaves damaged by miner insects in *Fagus sylvatica* and *Quercus ilex*, present a early abscission. Also, the palatability and the damage rate by herbivory are inversely correlated with the leaf life-expectancy (Southwood et al., 1986).

In leaves of seedlings of tropical species, Dirzo (1984) experimentally showed that there is an increase in the mortality rate and reduced life-expectancy with the increase of intensity of defoliation. Comparisons in field experiments show significant differences between damaged and non-damaged leaf survival in three of five species. Nuñez-Farfán & Dirzo (1989) found that herbivory was negatively correlated with leaf survival in seedlings of invader species. One of them, *Heliocarpus appendiculatus* has episodic mortality of leaves when the herbivory achieved 70 % of the foliar area, but in *Cecropia obtusifolia* the mortality was not affected.

The genus *Nothofagus* is one of most important tree taxa in Chile, because its species have economic value for timber and its current conservation status. The herbivory studies have been focused in the identification of the species of the insect assemblages, detecting the tree *Nothofagus* species showing the greater species richness and abundance of insects, the detection of secondary compounds, volatile substances and the bioactivity patterns (Welch, 1988; Grandon, 1996; Quiroz et al., 1999; Russell et al., 2000).

Preliminary studies of leaf survival suggest that herbivory could determine the differences of survival patterns of leaves in two deciduous species *N. alpina* and *N. obliqua* growing in a mixed forest (Serey et.,

unpublished data). *Nothofagus obliqua* has a higher number of leaves damaged by herbivory and lower survival values than *N. alpina* leaves, it associated with that *N. obliqua* has the higher species richness of defoliator insects (Welch, 1988; Grandon, 1996).

In this context, the objective of this work was a) to evaluate the effect of herbivory in foliar survival of *N. alpina* and *N. obliqua*; and b) to determine if herbivory is the factor determining the differences in foliar survival between *Nothofagus* species. The hypothesis is that "if the herbivory is the cause of the differences of survival between *N. obliqua* and *N. alpina*, then the survival patterns between species should be similar when herbivory is excluded". To achieve this objective, we performed a set of field experiments with leaves from different trees and branches, an approach used in several studies (Kikuzawa, 1982; 1983 a y b; Dirzo, 1984; Nuñez-Farfán & Dirzo, 1989; Kanda, 1996).

## MATERIALS AND METHODS

### Study Site

The study was performed at Pitrilón, in the neighbourhood of the Pangué Hydroelectric Power Plant (37°30'S; 71°10'W) in central Chile at 1000 masl in the piedmont of Andes Mountains. The climate is Mediterranean-type with a dry season from December to March, a mean maximum temperature of 20.1 °C and a mean minimum temperature of 8.1 °C. Precipitation in the year of study was 3817 mm measured in the Pangué Meteorological Climate Station. The vegetation included a mixed forest with Mediterranean sclerophyllous, temperate *Nothofagus* and broad leaved species (Gajardo, 1994).

### Methods

Twenty trees of both *N. alpina* and *N. obliqua* were randomly selected and tagged. To evaluate the effect of herbivory, two conditions were defined for each tree: a) treatment with insecticide (TWI) to exclude herbivores, aspersing a solution of a contact organophosphoride insecticide (Gusathion M 35% WP; Bayer<sub>MR</sub>), and b) treatment with water (TWW), aspersing with water since the insecticide was dissolved in water. Aspersing was performed every 15 days during nine months. The study period considered the complete growing season of this species.

At each tree and for both treatments, two terminal shoots were tagged at a low level of the crown. Shoots were formed from the last growing season, but leaves of the actual season were identified according to shoot position with

numeration started at the base of shoot. The length of each leaf was measured with a calliper and the foliar area damage by herbivores was assessed visually in discrete categories (see below) every 15 days from the emergence time to abscission time of leaves. For each observation, the presence of insects was evaluated at the tagged shoot for both treatments.

### **Damaged foliar area**

Six percentage classes of damage were defined : Category 0: leaves with 0% of lost foliar area; Category 1: 1-6 %; Category 2 : 7-12%; Category 3 : 13-25%; Category 4 : 26-50 % and Category 5 : > 50% (Domínguez et al., 1989). The frequency distribution of damage categories were compared with a Kolmogorov- Smirnov test to evaluate the effects between species for both damage types, miners and chewers (Zar, 1984). A proportion test was used to evaluate the differences between a) treatments within each species, and b) the same treatment between species (Zar, 1984).

### **Survival Curves**

The classic approach to assess leaf survival is to tag a cohort of leaves, but the dynamic shows that leaf emergence is a more continuous process, and several leaves could be excluded from the records started at time zero. To avoid this difficulty we used the Kaplan-Meier method (Kaplan-Meier, 1958) that estimated the individual probability of one leaf to survive to a specific-age. Additionally, this method includes censored data, i.e. individual

leaves that are not recorded as dead at the end of study or lost in the study. The survival of a population of leaves for each treatment and damage category was evaluated. To compare two survival curves we performed Log-rank, a non-parametric test (Shoukri & Pause, 1999). When three or more curves were compared, the non-parametric generalized test of Wilcoxon was performed (Prentice & Marek, 1979). All tests were performed using Statistica Software.

## RESULTS

### 1.- Morphological characteristics of leaves of *Nothofagus alpina* and *N. obliqua*

The growing season lasted from October 1997 to July 1998, with a period of 270 days. The leaves of *N. alpina* have a mean size of  $9.8 \pm 7.8$  cm<sup>2</sup> (s.d.) with a half-life of  $193.9 \pm 32$  days ( $n = 489$ ). The leaves of *N. obliqua* have mean size of  $2.5 \pm 2.3$  cm<sup>2</sup> days, with a half-life of  $161.5 \pm 48$  days ( $n = 519$ ). The measurements were performed from leaves sampled from the with water treatment. The leaves of *N. alpina* show a higher density and longer trichomes than *N. obliqua* (Fig.1 and 2).

### 2.- Herbivory

During the growing season, two episodes of herbivory were present. The first when the growing season is beginning, and leaves are expanding. The first burst was due to insect larvae of Geometridae, and the second one was produced by the miner larvae of Heliozelidae.

The percentage of damaged leaves is shown in Table 1. *Nothofagus alpina* showed a higher percentage of damaged leaves than *N. obliqua* in the TWW (Proportion test,  $Z = 2.9$ ;  $P = 0.001$ ). In the TWI the proportion of damaged leaves between species was similar ( $Z = 0.6$ ;  $P = 0.25$ ).

The frequency distribution of damage between species for chewer and miner larvae was similar (Kolmogorov-Smirnov test,  $D = 0.10$ ,  $P = 0.33$  and  $D = 0.008$ ,  $P = 0.99$ , respectively, Fig.3 and 4).

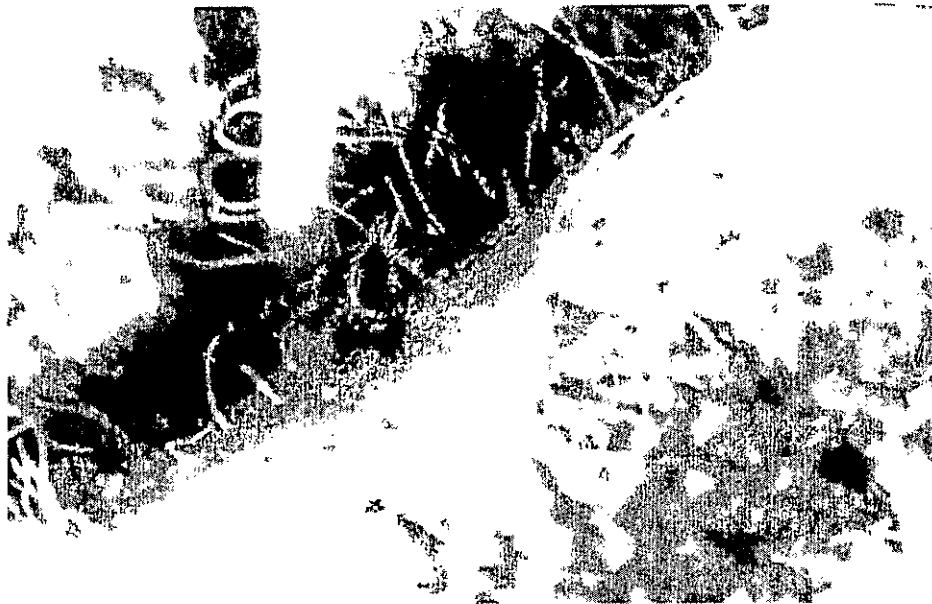


Figure 1. Trichomes in *N. alpina*



Figure 2. Trichomes in *N. obliqua*

Table 1.- Percentage of damaged leaves for treatment with insecticide and with water for each species.

Species	<i>N. alpina</i>		<i>N. obliqua</i>	
	With insecticide	With water	With insecticide	With water
% damage leaves	54,4	68,9	51,9	59,9
N	500	489	302	519

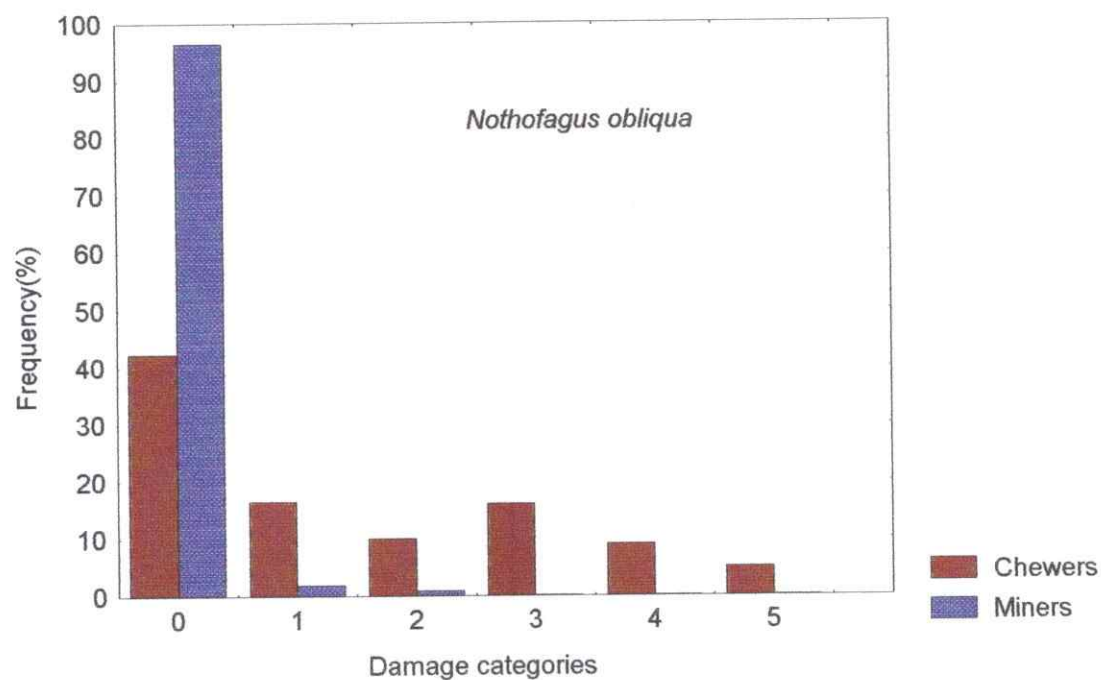


Figure 4.- Frequency distributions of damage categories for *N. obliqua* leaves for two types of herbivore larvae, chewers and miners,  $n = 533$ .

### 3.- Insect abundance between treatments

The insect abundance for each shoot was diminished by insecticide application in both species *N. alpina* and *N. obliqua*, (Wilcoxon, for repeated measures,  $n = 8$ ,  $Z = 2.2$ ,  $P = 0.02$  and  $n = 8$ ,  $Z = 1.89$ ,  $P = 0.05$  respectively, Figure 5)



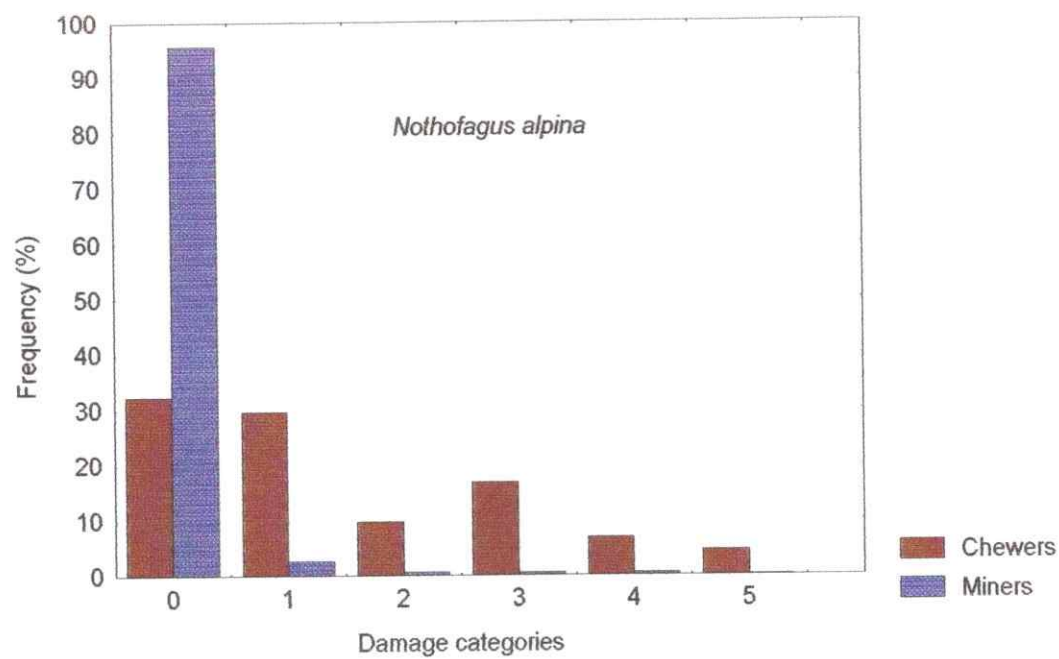


Figure 3.- Frequency distributions of damage categories for *N. alpina* leaves for two types of herbivore larvae, chewers and miners, n = 495.

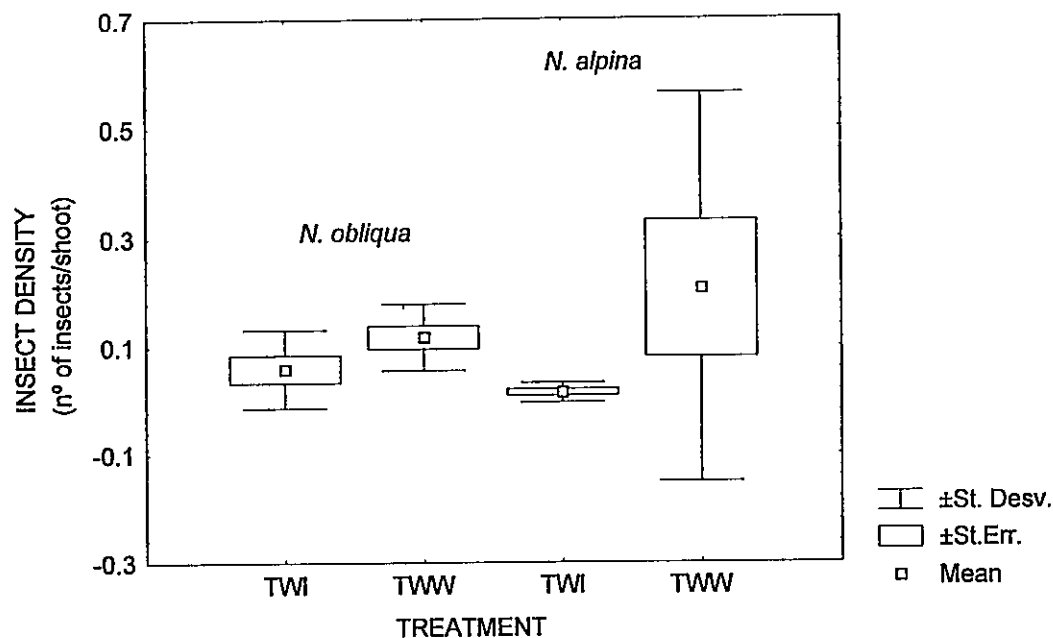


Figure 5.- Insect density by shoots for treatment with insecticide (TWI) and treatment with water (TWW) in *N.alpina* and *N.obliqua*.

#### 4.- Foliar survival

##### 4.1.- Foliar survival: intraspecific analysis

The foliar survival in *N. alpina* was similar between TWI and TWW (Log rank = 0.57;  $P = 0,28$  ; Fig. 6). The half-life of leaves for both TWI and TWW was  $189 \pm 45$  (s.d.) days ( $n = 506$ ) and  $193 \pm 37$  (s.d.) days respectively (Mann-Whitney,  $U = -0,97$ ,  $P = 0.10$  ). However, *N. obliqua* showed significant differences between the treatments ( Log Rank = -2.98 ;  $P = 0.001$ ), where the survival in TWW was lowest. The half-life was significantly lower in TWI than the survival in TWW ( $163 \pm 40$  (s.d.),  $n=313$  and  $148 \pm 53$  (s.d.) days ,  $n = 528$ , respectively; Mann-Whitney ,  $U = 70647$ ,  $P < 0.05$  , Fig. 6) .

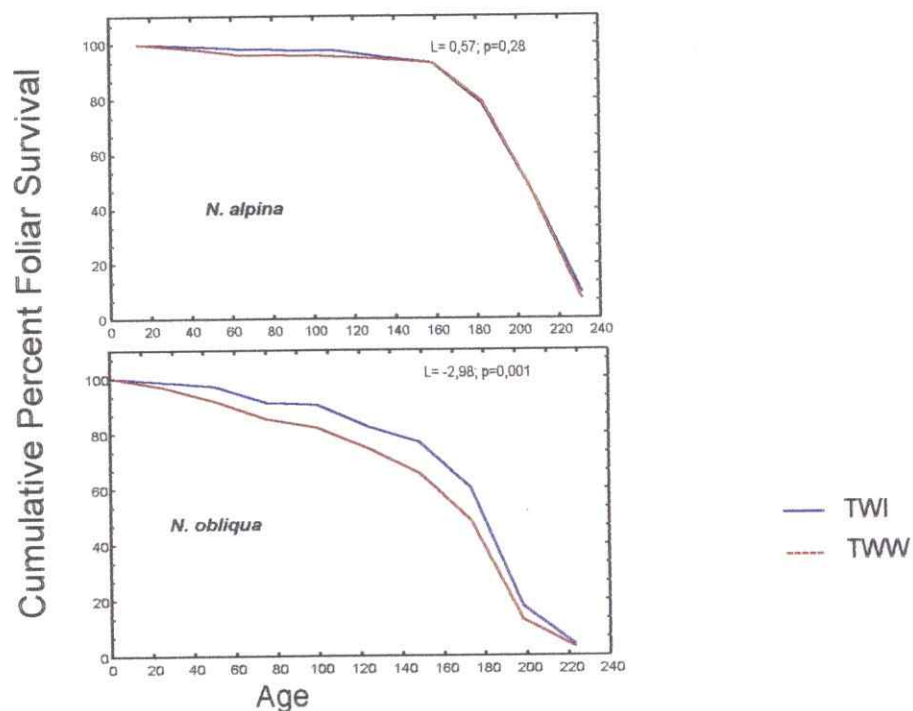


Figure 6. Foliar survival between treatments with insecticide (TWI) and treatment with water (TWW) in *Nothofagus alpina*,  $n_{TWI} = 506$ ,  $n_{TWW} = 499$  and *Nothofagus obliqua*,  $n_{TWI} = 313$ ,  $n_{TWW} = 528$ .

#### 4.2. Foliar survival in function of damage categories : intraspecific analysis

The foliar survival in the six damage categories of *N. alpina* in the TWW were different ( $\chi^2 = 33.6$  ; d.f. = 5;  $P < 0.05$ ; Fig. 7) . Category 0 presented the lowest survival similar to survival in Category 5, which includes leaves with

more than 50% of damage (Table 2). Nevertheless, *N. obliqua* presented significant differences when we compared the values of damage categories ( $X^2 = 18.2$ ; d.f. = 5;  $P < 0.05$ ; Fig. 8). However, the difference was produced only in Category 1 which was higher than Category 0. Category 1 shows a higher survival than all other categories which are all similar in survival (Table 2).

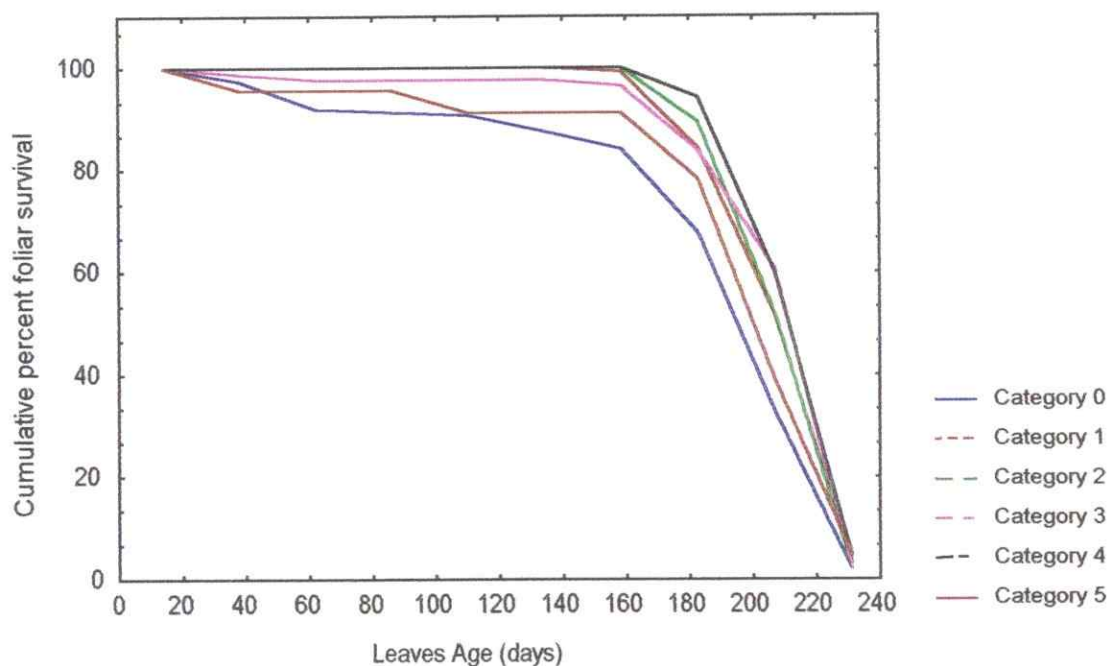


Figure 7. Foliar survival in treatment with water (TWW) of *N. alpina* for the six damage categories. Category 0 = intact; Category 1 = 1-6%; Category 2 = 6-12%; Category 3 = 13-25%; Category 4 = 26-50%; Category 5 = 50-100% of lost leaf area.

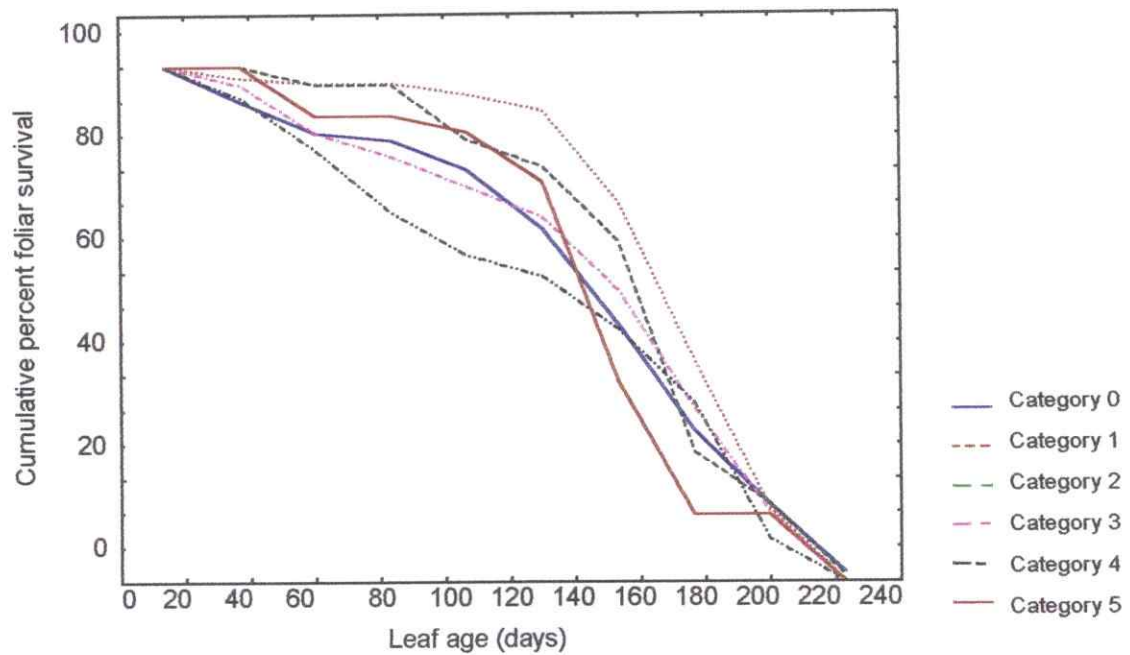


Figure 8. Foliar survival in treatment with water (TWW) of *N. obliqua* for the six damage categories. Category 0 = intact; Category 1 = 1-6%; Category 2 = 6-12%; Category 3 = 13-25%; Category 4 = 26-50%; Category 5 = 50-100% of lost leaf area.

Table 2. Values of paired comparisons between the damage categories in treatment with water of *N. alpina* and *N. obliqua*. (L = Log-Rank test, \* = P < 0, 05).

Category	<i>N. alpina</i>	<i>N. obliqua</i>
0 y 1	L= 3,0; p=0,001 *	L= 2,2; p=0,01 *
0 y 2	L= 2,5; p=0,005 *	L= 0,5; p=0,29
0 y 3	L= 3,5; p=0,0002 *	L=-0,08; p=0,46
0 y 4	L= 4,1; p=0,0001 *	L=-0,9; p=0,17
0 y 5	L= 0,7; p=0,24	L=-0,8; p=0,19
1 y 2	L= 0,3; p=0,36	L=-1,4; p=0,06
1 y 3	L= 1,1; p=0,13	L=-2,1; p=0,01 *
1 y 4	L= 2,4; p=0,006 *	L=-2,4; p=0,008 *
1 y 5	L=-1,0; p=0,15	L=-2,5; p=0,006 *
2 y 3	L= 0,6; p=0,26	L=-0,4; p=0,31
2 y 4	L= 1,6; p=0,04 *	L=-1,0; p=0,15
2 y 5	L=-1,0; p=0,14	L=-1,4; p=0,08
3 y 4	L= 1,6; p=0,05	L=-0,6; p=0,26
3 y 5	L=-1,6; p=0,05	L=-0,7; p=0,21
4 y 5	L=-2,1; p=0,01 *	L=-0,2; p=0,41

#### 4.2.- Foliar survival: interspecific analysis

The foliar survival for the TWW between the species was different (L = -16.4; P << 0.001; Fig.9). Similarly for TWI the foliar survival was different (L = -12.6; P << 0.001; Fig.9).

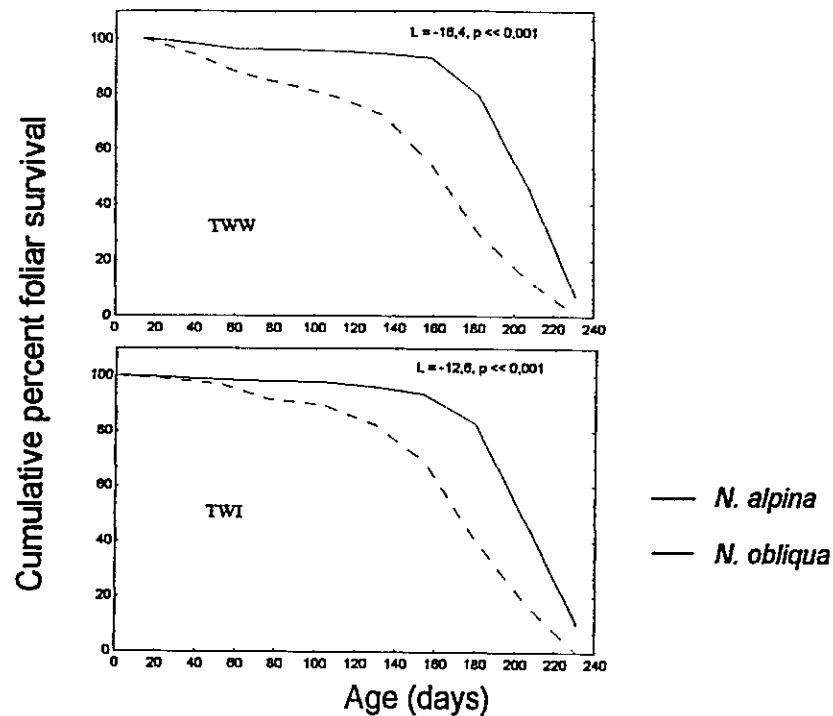


Figure 9. Foliar survival between *N. alpina* and *N. obliqua* in the treatment with insecticide (TWI) and treatment with water (TWW).

## DISCUSSION

The results showed that the percentage of damaged leaves was higher in *N. alpina* associated to a higher abundance of herbivory than in *N. obliqua*. However, during 1995-1996 *N. obliqua* was more affected (Serey et al., unpublished) supporting the idea that the important difference related to species depends on the growing season. However, during 1997-1998 the damage distribution was similar between both species. This fact is interesting because

the mean surface area of *N. alpina* leaves is three times the mean surface area of *N. obliqua* leaves. Herbivory produced by miners was lower compared to that of chewers. The damage due to miners in these two southern beeches is low and similar to that found in *Fagus sylvatica* and *Quercus ilex* (Pritchard & James, 1984) *Quercus hemisphaerica*, *Q. nigra* and *Q. falcata* (Faeth et al. 1981).

The longevity and senescence of leaves is controlled by several genetic and physiological factors. The senescence process could be delayed or advanced depending of several environmental factors, such as light, temperature, nutrient resources or biological interactions such as herbivory. Specifically, herbivory reduces leaf ability for carbon gain, increasing the time to compensate the building cost and increasing the photosynthetic capability of the remaining surface area (Chabot & Hicks, 1982). The senescence of leaves could also be advanced because the rest of the leaf is exposed to the action of pathogens (Thomas & Stoddart, 1980). The triggering of senescence is more dependent on environmental factors and is therefore related to the fast change of survival of individual leaves in the growing season. Some species could repair the damaged tissue with a new growth the leaves. The longevity of leaves determines the strategies of leaf survival of one species (Chabot & Hicks, 1982).

Intraspecific analysis shows that leaf survival in *N. alpina* was not changed by the effects of herbivory, but in *N. obliqua* leaf survival was reduced. This fact supports the idea that the response to herbivory is species-



specific, when the analysis is performed on an assembly of leaves as a population for each species. However, in *N. alpina* the fraction of the leaf population with damage shows an increased survival and suggests the existence of a compensatory mechanism. In *N. obliqua* the increase in survival only occurs when the leaves have a percentage damage of 1-6 %, and then the compensation is weak, but for the leaf population the net effect is a reduction of survival. Others species of the Fagaceae family also show a reduction in the leaf survival due to the effects of herbivory as in *Fagus sylvatica*, *Quercus ilex*, *Q. nigra*, *Q. Hemisphaerica* (Faeth et al., 1979, Pritchard & James, 1984).

The differences between species are usually explained by physical environmental variables (Chabot & Hicks, 1982; Kikuzawa, 1984; Kanda, 1996), but this study was performed at the same time and locality. Other explanations are based in morphological bud characteristics, where different bud types show different leaf survival curves (Kikuzawa, 1982, 1983) but both *Nothofagus* species are similar in architectural and morphological characteristics of shoots (Soumoy et al, 1996). Another explanation is an ecological interaction such as herbivory. We studied the effect of herbivory considering leaves as populations and we can analyse the differences between species by looking at the effect of herbivory on leaf survival and use the results to compare two species of trees. In this interspecific analysis, the leaf survival was different in the treatment without herbivores, so that the herbivory was not the explicative mechanism and the proposed hypothesis is rejected. The differences could be

explained by other mechanisms related to the characteristic of the leaf growth and foliage dynamics, particularly those determining leaf survival and shoot growth. An alternative mechanism to explain the differences between species is that in *N. obliqua*, the leaf population included leaves developed in the middle of the growing season, coming from a fraction of shoots with polycycle growth, a low frequency phenomena in the shoots of *N. alpina*. The polycyclism is a frequent phenomena in the Chilean *Nothofagus* species. This study showed that herbivory as an ecological pressure, does not account for differences in leaf survival and therefore we suggest that observed leaf survival was modelled by past environmental pressure. Leaf survival is apparently a conservative attribute and differences between species are only modulated by herbivory.

#### Acknowledgements

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## CAPITULO 2

### **EFFECT OF THE HERBIVORY IN THE SURVIVAL OF LEAVES OF *NOTHOFAGUS ALPINA* AND *N. OBLIQUA*: INDIVIDUAL AND POPULATION LEVEL**

#### INTRODUCTION

The modular approach to plant studies regards the leaves as an elemental unit capturing energy and nutrients to the plant, and considers that the leaf has a value for the individual plant (Harper, 1989). Herbivory could affect demography of modules or others units in a important way, producing changes in the biological fitness. The direct effect is changing the demographic parameters of the leaves (Harnett & Bazzaz, 1984; Marquis, 1984; Ruohomäki et al., 1997).

Recent studies have enhanced the interest to understand the herbivory at different hierarchical levels: leaf, shoot, tree or individual, tree population, community and ecosystems (Dyer & Shugart, 1992; Lowman & Heatwole, 1992; 1997). The modular structure of plants facilitates the hierarchical studies of demographic processes (White, 1979; Jones, 1985). Foliar demography, studies leaves commonly as a populations of metameric parts, disregarding the relationship as pertains to one particular leaf of a specific individual tree (Harper, 1977; Kikuzawa, 1982; 1983; 1984; Dirzo, 1984; Kanda, 1996). In this approach the leaf survival generally is known for the species, but unknown for the individuals of the same species and its population consequences. On the



other hand, damage to leaves by insects is not uniform and varies widely among different individuals resulting in large variability at population level (Coley, 1983; Lowman & Heatwole, 1992; Marquis, 1992). The herbivory can affect the leaf survival in a direct or indirect form: diminishing survival by induced chemical changes in the leaf, accelerating the abscission, increasing the photosynthetic rate of the remnant foliar area and diminishing the life of the leaf, retarding the senescence of the leaf due to construction cost, or, increasing the mortality of the leaves to facilitate the entrance of pathogens (Chabot & Hicks, 1982; Thomas & Stoddart, 1980)

In this context, the objectives of this work was to evaluate the effect of the herbivory on the foliar survival for two species at two levels: i) considering the individual tree as units and then comparing within each individual, an intraspecific analysis. The hypothesis to be evaluated was "if the herbivory affects the leaf survival, then excluding the presence of herbivores the leaf survival will be increased"; and ii) considering the trees as a population and performing an intraspecific and interspecific comparisons. At this level the hypothesis to be evaluated were a) "if the herbivory affects the leaf survival of the population tree, then without herbivory the leaf survival will be increased" and b) "if the herbivory affects the leaf survival between tree populations of *N. alpina* and *N. obliqua*, then, excluding herbivory the leaf survival will be similar".

## MATERIALS AND METHODS

### Study Site

The study was performed at Pitrilón, in the neighbourhood of the Pangué Hydroelectric Power Plant (37°30'S; 71°10'W) in central Chile at 1000 masl in the piedmont of Andean Mountains. The climate is Mediterranean-type which has a dry season from December to March, with a mean maximum temperature of 20.1 °C and a mean minimum temperature of 8.1 °C. Precipitation in the year of study was 3817 mm measured at the Pangué Meteorological Climate Station. The vegetation included a mixed forest with Mediterranean sclerophyllous and temperate *Nothofagus* and broad leaved species (Gajardo, 1994).

### Methods

Twenty trees of both *N. alpina* and *N. obliqua*, were randomly selected and tagged. At each tree and for both treatments, two terminal shoots were tagged at the underside of the crown. Shoots were formed from the last growing season, with leaves of the actual season identified according to shoot position and numeration started at the base of shoot. To evaluate the effect of herbivory two conditions were defined for each tree: a) treatment with insecticide (TWI), for excluding the herbivores, aspersing a solution of contact organophosphoride insecticide (Gusathion M 35% WP; Bayer MR), and b) treatment with water (TWW), aspersing with water because the insecticide was dissolved in water.

Each treatment included two terminal shoots from the underside of the crown. Aspersing was performed every 15 days respectively. The study period considered the complete growing season of nine months.

Herbivory was quantified by determining visually the total leaf area and damaged portions every 15 days from the emergence time to abscission time of leaves. For each observation, the presence of insects was evaluated for the tagged shoot of both treatments.

### **1) Individual level:**

#### **Damage foliar area**

In each species, the mean percentage of leaf area lost was evaluated by tree and compared between treatments by using the non-parametric test of Mann-Whitney (Zar, 1984).

#### **Survival curves**

For all trees the survival curves in each treatment were determined using the Kaplan-Meier method (Kaplan-Meier, 1958). The method estimates the individual probability of one leaf to survive to a specific-age. Additionally, this method could include censored data, i.e. individual leaves that are not recorded as dead or those lost by the end of study. To compare the two survival curves, we performed a non-parametric test, Log-rank (Shoukri & Pause, 1999)

## 2) Population of tree level

### Herbivory

Estimates of levels of herbivory were determined by the percentage of leaf area eaten, using the following categories: Category 0: leaves with 0%; Category 1: 1-6 % of lost foliar area; Category 2 : 7-12%; Category 3 : 13-25%; Category 4 : 26-50 % and Category 5 : > 50%. The score for each leaf was used to define an index of damage (ID) per tree as:

$$ID = \sum n_i(C_i)/N$$

where,  $i$  is the category of damage,  $n_i$  is the number of leaves in the  $i$ th category of damage,  $C_i$  is each category and  $N$  is the total number of leaves on the tree (Domínguez et al., 1989).

The Herbivory Index was compared among treatments for each species using non-parametric Wilcoxon matched pairs test (Zar, 1984). The frequency distributions of damage categories among species and treatments were compared using Goodness fit test.

### Survival curves

The survival curves of the population tree by species were compared among treatments in function of age, showing the variability of the survival of leaves between the individuals that represent the population. The age-specific survival was compared among treatments for each species and between species for the treatment with insecticide and treatment with water, using the non-parametric

test Mann-Whitney (Zar, 1984). All tests were performed using Statistica Software.

## RESULTS

### 1. Leaf Survival and damage area for individual trees of *N. alpina* and *N. obliqua*

#### 1.1.- Damaged foliar area

The record of damage area of leaves, on each individual, showed that *N. alpina*, has a tendency to lose higher surface percentage in TWW conditions, but was significant for eight trees (trees N° 1, 2, 3, 5, 7, 10, 19 and 20; Fig.1). For *N. obliqua*, we observed the same tendency for individuals, but only one tree has significant differences (tree, N° 9; Fig.2).

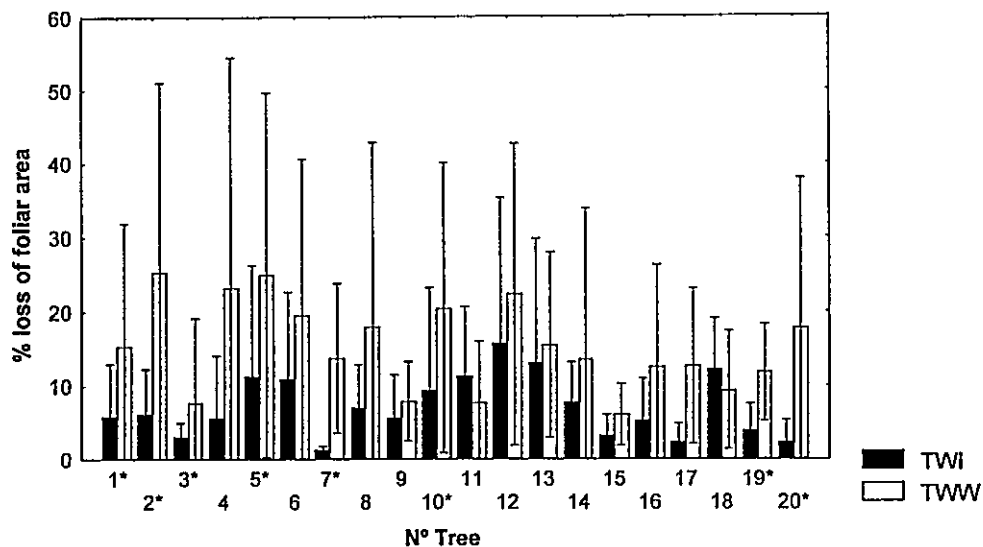


Figure 1. - Percentage of leaf area lost in *N. alpina*, by tree and treatment with insecticide (TWI) and treatment with water (TWW). \* Significant differences between treatments (Mann - Whitney,  $P < 0,05$ ).

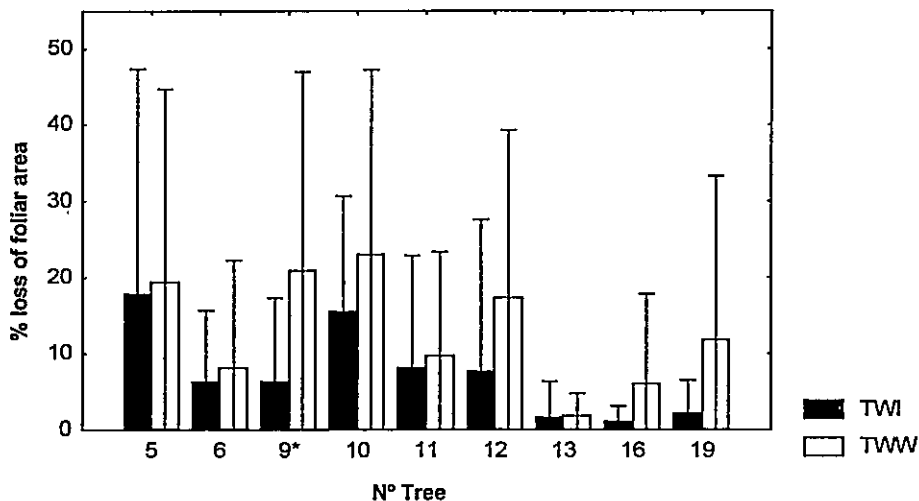


Figure 2.- Percentage of leaf area lost in *N. obliqua*, by tree and treatment with insecticide (TWI) and treatment with water (TWW). \* Significant differences between treatments (Mann - Whitney,  $P < 0,05$ ).

## 1.2.- Leaf Survival

We compared the pattern of leaf survival between experiments TWI and TWW for each individual. The results show that ten individuals of *N. alpina* have not significant difference, six individual show a significant reduction in leaf survival (negative effect, tree N° 2, 8, 11, 16, 17 and 19; Fig.3) and four remaining trees show an increase in leaf survival (positive effect, tree N° 1, 4, 6 and 14; Fig.3) in TWW.

The same experiment was performed with *N. obliqua* but with a reduced sample size because the parrot *Enicognathus leptorhynchus* broke some tagged shoots. There were nine remaining trees. Two trees did not have significant differences, six showed a reduction of leaf survival (negative effect, trees N ° 5, 6, 9, 11, 12 and 16; Fig.4) and only one tree had increased leaf survival (tree N° 19; Fig.4) in TWW.

## 2. Herbivory and leaf survival at the tree population level

### 2.1. Damaged foliar area

The percentage of foliar damage area of the population of *N. alpina* was significantly higher in TWW with a mean damage area of  $11.64\% \pm 6.0$  (s.d.) than in TWI with a mean damage area of  $4.01\% \pm 2.6$  (Wilcoxon paired samples,  $n=20$ ;  $T=7$ ;  $P=0.0001$ ). For *N. obliqua*, the percentage of foliar damage was significantly higher in TWW with a mean percentage of  $13.04\% \pm 7.8$ , than in TWI with a mean of  $7.44\% \pm 5.8$  (Mann-Whitney,  $n_{TCl}=11$  y

$n_{TSI}=16$ ;  $U=50$ ,  $P= 0.03$ ; Wilcoxon paired samples,  $n=9$ ;  $T=0$ ;  $P=0.003$ ).

In the interspecific comparison, the percentage of foliar damage area was similar between species in the TWI (Mann-Whitney,  $n_{alpina} = 20$  y  $n_{obliqua} = 11$ ;  $U= 63$ ,  $P = 0.052$ ). The percentage of foliar damage area was also similar between species in TWW (Mann-Whitney,  $n_{alpina} = 20$  y  $n_{obliqua} = 16$ ;  $U= 135$ ,  $P = 0.42$ ).



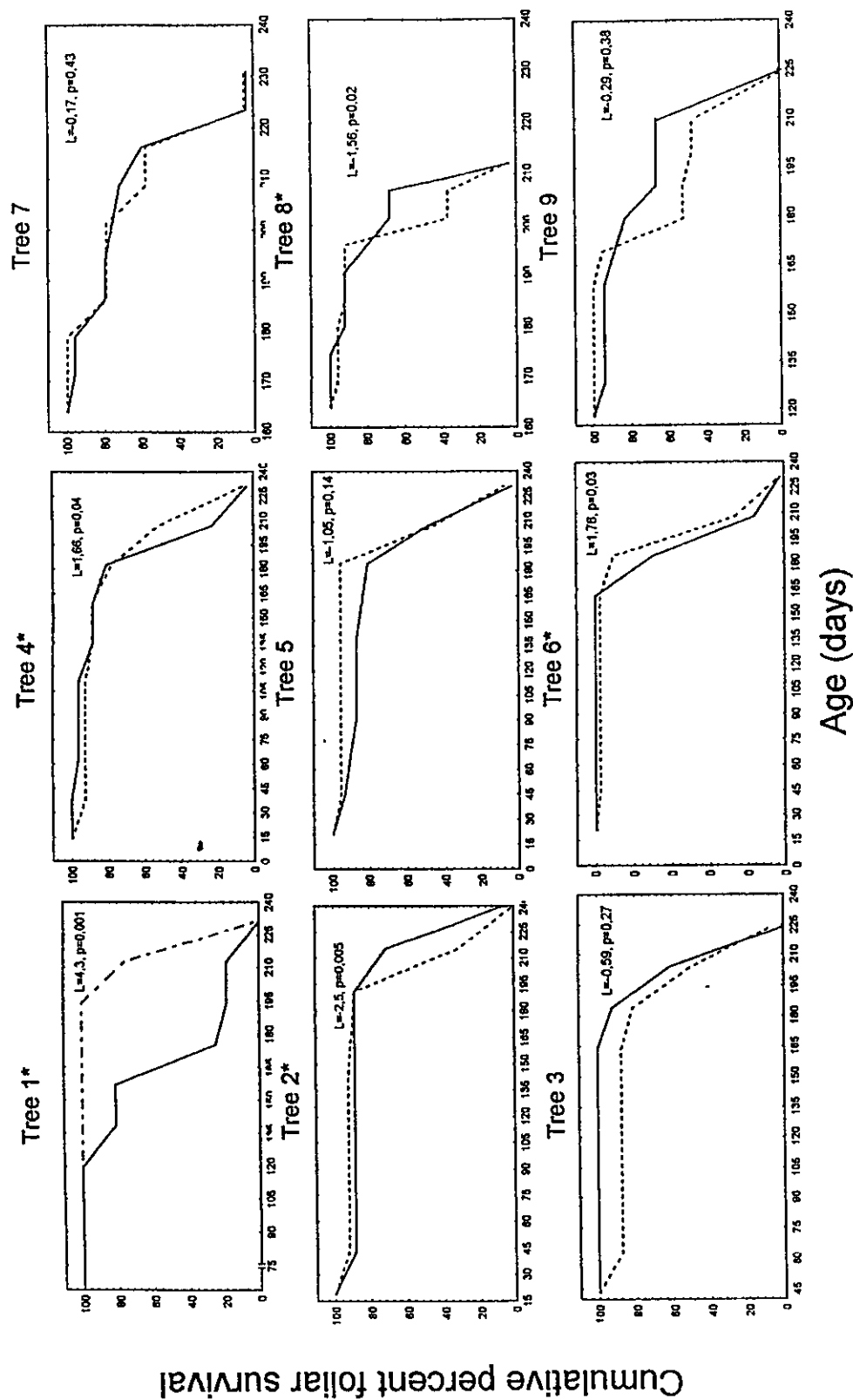


Figure 3. Foliar survival of the individuals of *Nothofagus alpina* in treatments with insecticide (—) and treatment with water (---).

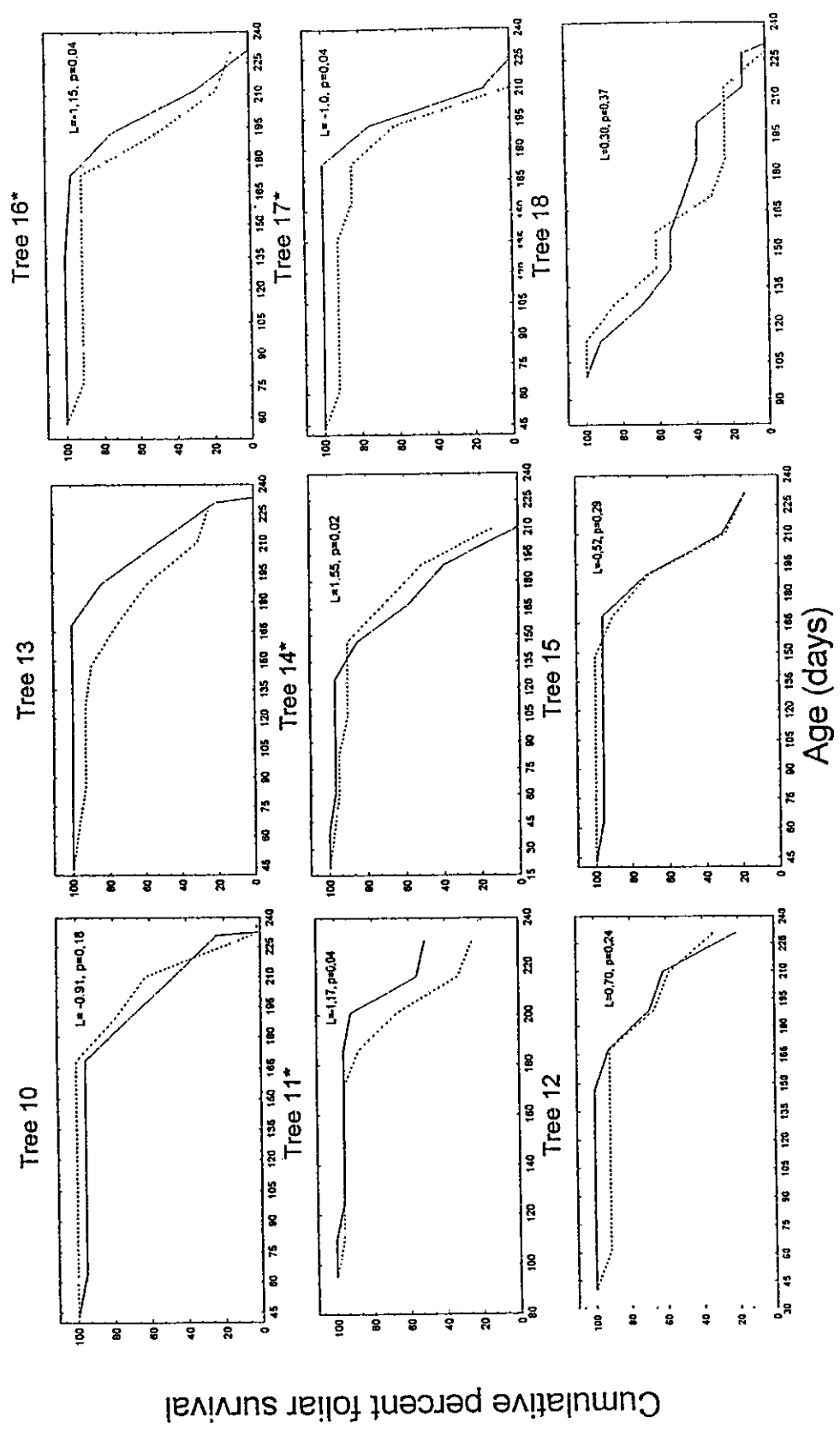
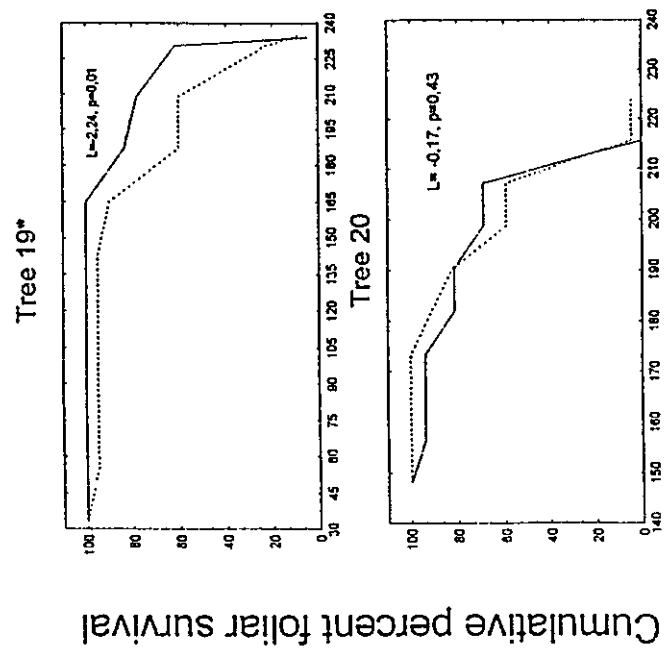


Figure 3. Foliar survival of the individuals of *Nothofagus alpina* in treatments with insecticide (—) and treatment with water (---).



Age (days)

Figure 3. Foliar survival of the individuals of *Nothofagus alpina* in treatments with insecticide (—) and treatment with water (---).

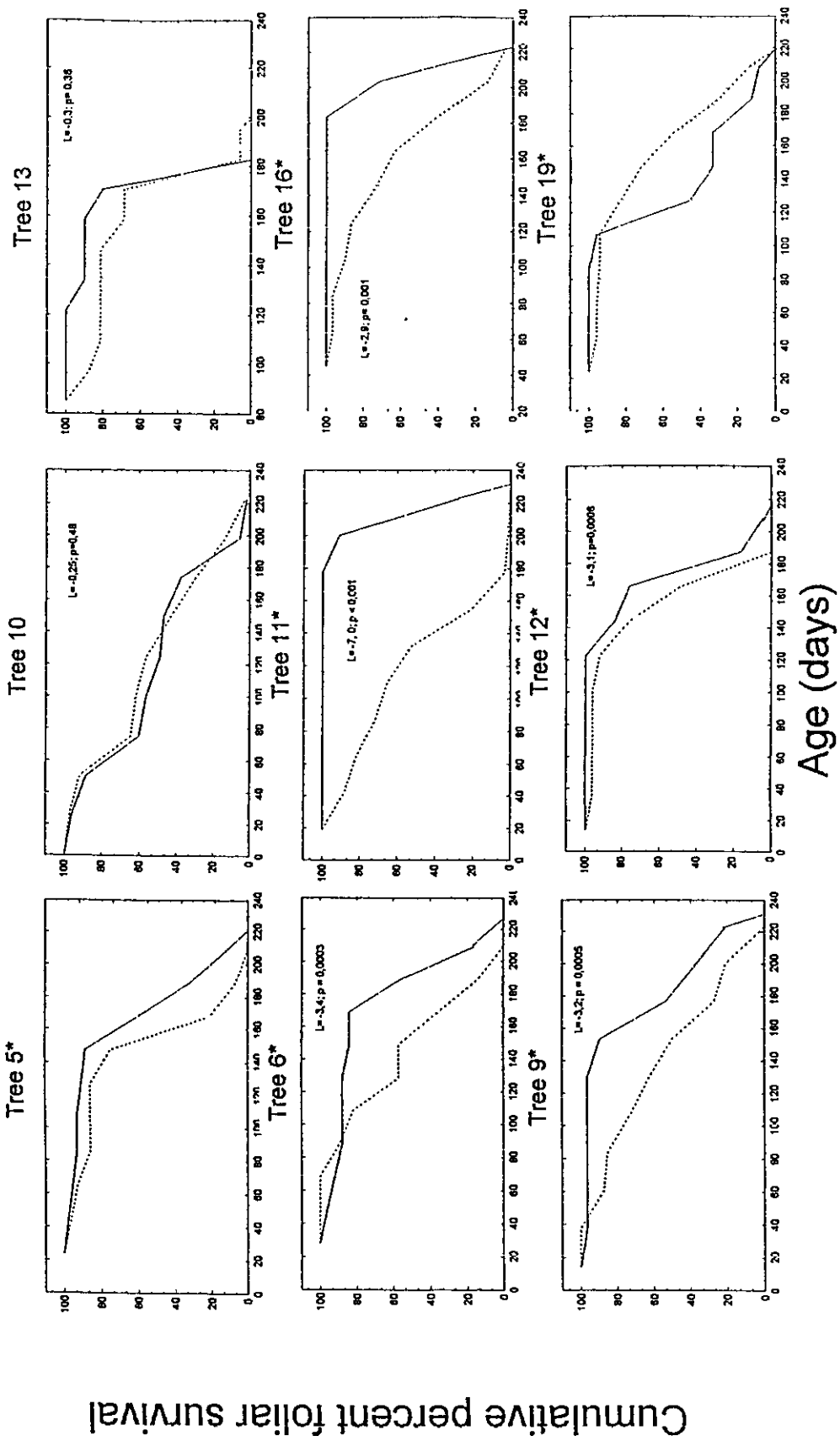


Figure 4. Foliar survival of the individuals of *Nothofagus obliqua* in treatments with insecticide (—) and treatment with water (---).

## 2.2 Herbivory Index

The Herbivory Index showed that for both *N. alpina* and *N. obliqua*, the TWW was higher than the TWI experiment (Wilcoxon matched pairs test,  $N_{N. alpina} = 20$ ,  $T = 10$ ,  $P < 0.05$ ;  $N_{N. obliqua} = 9$ ,  $T = 1$ ,  $P = 0.01$ ; Table 1). An unexpected result was that the Herbivory Index and damage distributions were similar between *N. alpina* and *N. obliqua* in TWW experiments (Mann-Whitney,  $N_{N. alpina} = 20$ ,  $N_{N. obliqua} = 16$ ,  $U = 159$ ,  $P = 0.98$ ;  $\chi^2 = 4.9$ , d.f.=5,  $P=0.42$ ). Similarly, in the TWI the Herbivory Index was similar between species (Mann-Whitney,  $N_{N. alpina} = 20$ ,  $N_{N. obliqua} = 11$ ,  $U = 79$ ,  $P = 0.2$ ), but the damage distributions were statistically different ( $\chi^2 = 18.2$ , d.f.=5,  $P=0.01$ ).

Table 1. Herbivory Index the *N. alpina* and *N. obliqua* in treatments with insecticide (TWI) and with water (TWW).

N° Tree	<i>N. alpina</i>		<i>N. obliqua</i>	
	TWI	TWW	TWI	TWW
1	0.7		-	1.9
2	0.7	2.3	-	0.3
3	0.2	1.1	-	-
4	0.63	1.31	-	2.3
5	1.24	2.7	1.6	2.15
6	1.32	1.51	1.1	1.14
7	0.42	1.67	-	2.5
8	0.75	1.26	-	1.7
9	1.0	1.2	1.0	2.17
10	1.14	2.27	2.1	2.4
11	1.8	1.3	1.36	1.41
12	0.77	1.75	0.8	1.9
13	0.68	1.43	0.4	0.38
14	0.9	1.3	1.19	-
15	0.4	0.4	-	0.87
16	0.8	1.1	0.6	0.9
17	0.5	1.0	-	-
18	1.1	0.8	0.93	-
19	0.7	1.8	0.5	1.2
20	0.6	2.0	-	0.4
I.H ± sd	0.82 ± 0.37	1.50 ± 0.56	1.05 ± 0.51	1.5 ± 0.8

## 2.3 Leaf Survival

### 2.3.1 Intraspecific analysis

Leaf survival in *N. alpina* trees was similar between treatments (Wilcoxon for paired samples  $n=15$ ,  $T=27,5$ ,  $P=0,116$ ) at the tree population level. Leaf survival was similar at each age between treatments (Table 2). The

results suggest that an increase in age is associated with an increased variability in survival (Fig. 5).

Leaf survival in *N. obliqua* showed significant differences between treatments (Wilcoxon for paired samples,  $n=15$ ,  $T= 1$ ,  $P=0,001$ ). The survival was similar in almost all age classes. Only one age (181, days) showed a significant difference with a lower value in TWW (Mann-Whitney;  $U= 46$ ,  $P= 0,038$ ; Table 3). Starting with the leaves of a younger age, the variability of leaf survival increased towards the middle-age leaves and diminished toward higher ages (Fig.6).

Table 2. Leaf survival in tree populations in *N. alpina*, between treatments TWI, n=20 and TWW, n=20.

Age Class (Days)	<i>Cumulative foliar survival</i>		Mann-Whitney P
	TWW	TWI	
0	1.000	1.000	-
16	0.975 ± 0.009	0.976 ± 0.008	0.578
33	0.948 ± 0.016	0.949 ± 0.028	0.447
49	0.913 ± 0.037	0.923 ± 0.034	0.456
66	0.889 ± 0.044	0.901 ± 0.039	0.489
82	0.867 ± 0.050	0.878 ± 0.045	0.625
99	0.845 ± 0.055	0.857 ± 0.051	0.645
115	0.824 ± 0.061	0.835 ± 0.058	0.714
132	0.800 ± 0.074	0.798 ± 0.082	0.704
148	0.770 ± 0.10	0.767 ± 0.09	0.473
165	0.739 ± 0.10	0.722 ± 0.14	0.786
181	0.675 ± 0.14	0.663 ± 0.16	0.655
198	0.507 ± 0.14	0.549 ± 0.13	0.180
214	0.288 ± 0.16	0.363 ± 0.19	0.250
231	0.055 ± 0.08	0.162 ± 0.17	0.055



Table 3. Leaf survival in tree populations in *N. obliqua*, between treatments TWI, n=11 and TWW, n=16, \* P<0.05.

Age Class (Days)	<i>Cumulative foliar survival</i>		Mann-Whitney P
	TWW	TWI	
0	1.000	1.000	-
16	0.936 ± 0.15	0.971 ± 0.019	0.569
33	0.900 ± 0.16	0.942 ± 0.035	0.674
49	0.856 ± 0.16	0.912 ± 0.052	0.335
66	0.807 ± 0.17	0.862 ± 0.10	0.299
82	0.774 ± 0.18	0.838 ± 0.11	0.256
99	0.733 ± 0.18	0.812 ± 0.12	0.152
115	0.695 ± 0.18	0.784 ± 0.13	0.145
132	0.651 ± 0.18	0.709 ± 0.16	0.401
148	0.576 ± 0.17	0.656 ± 0.17	0.182
165	0.467 ± 0.19	0.584 ± 0.13	0.054
181	0.316 ± 0.19	0.467 ± 0.15	0.000*
198	0.224 ± 0.15	0.277 ± 0.18	0.401
214	0.113 ± 0.11	0.165 ± 0.16	0.385
231	0.047 ± 0.09	0.038 ± 0.06	0.825

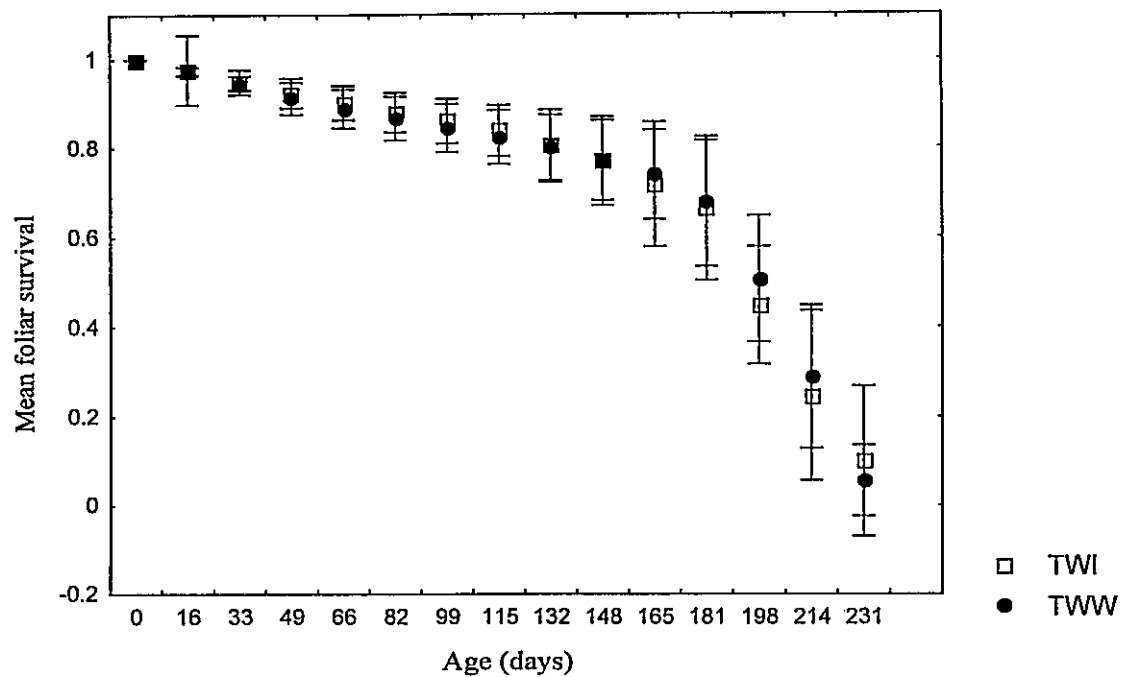


Figure 5. Mean leaf survival in the population of *N. alpina* trees, between treatments TWI and TWW.

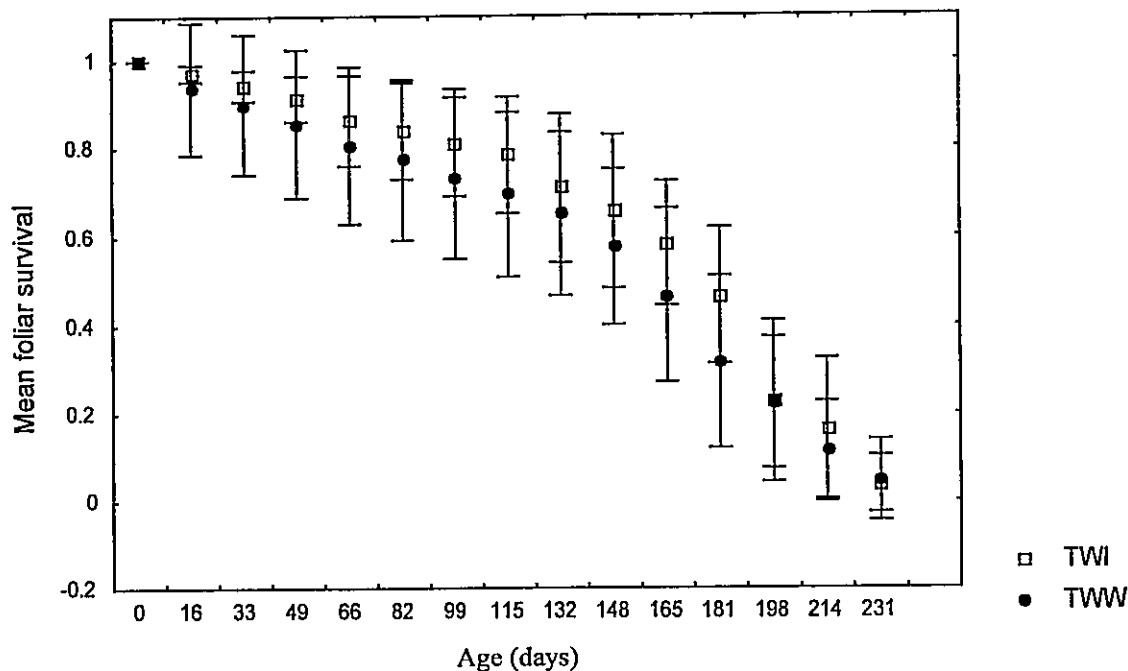


Figure 6. Mean leaf survival in the population of *N. obliqua* trees, between treatments TWI and TWW.

#### 2.3.1.1. Survival Curves

The survival curves of each tree showed that there are three responses to the herbivory : a group without effects ; a second group that presents a reduction of survival and a third group that showed an increased survival. This pattern is present in both species, *N. alpina* and *N. obliqua*. The effect on tree population level for the *N. alpina* showed that the probability to affect the survival curve positively or negatively is similar (Sign Test,  $n=10$ ;  $T=4$ ,  $P=0.37$ ) and the same response was found with *N. obliqua* (Sign Test  $n=7$ ,  $T=1$ ,  $P=0.062$ ).

### 2.3.2 Interspecific Analysis

The interspecific comparison in TWW showed that there is significant differences between species ( Sign test,  $n=14$ ,  $z = 3.47$ ,  $P<0.05$ ). *Nothofagus alpina* has a higher survival than *N. obliqua*. The leaf survival was similar for the first five age classes, but the age from classes six to fourteen showed significant differences and the last class showed similar survivals (Table 4).

The comparison between both species in TWI showed significant differences (Sign test,  $n=14$ ,  $z=3.47$ ,  $p<0.05$ ). *Nothofagus alpina* showed a higher survival than *N. obliqua*. Leaf survival was similar for the first ten classes and the last class, and only four classes showed significant differences (Table 5).

Tabla 4. Leaf survival of the population of trees in the treatment with water between *N. alpina* and *N. obliqua*.

Age Class (Days)	Cumulative foliar survival		Mann-Whitney P
	<i>N. alpina</i>	<i>N. obliqua</i>	
0	1.000	1.000	-
16	0.975 ± 0.009	0.936 ± 0.15	0,873
33	0.948 ± 0.016	0.900 ± 0.16	0,774
49	0.913 ± 0.037	0.856 ± 0.16	0,308
66	0.889 ± 0.044	0.807 ± 0.17	0,085
82	0.867 ± 0.050	0.774 ± 0.18	0,041*
99	0.845 ± 0.055	0.733 ± 0.18	0,014*
115	0.824 ± 0.061	0.695 ± 0.18	0,003*
132	0.800 ± 0.074	0.651 ± 0.18	0,001*
148	0.770 ± 0.10	0.576 ± 0.17	0,000*
165	0.739 ± 0.10	0.467 ± 0.19	0,000*
181	0.675 ± 0.14	0.316 ± 0.19	0,000*
198	0.507 ± 0.14	0.224 ± 0.15	0,000*
214	0.288 ± 0.16	0.113 ± 0.11	0,001*
231	0.055 ± 0.08	0.047 ± 0.09	0,588

Table 5. Leaf survival of the population of trees in the treatment with insecticide between *N. alpina* and *N. obliqua*.

Age (Days)	Cumulative foliar survival		Mann-Whitney P
	<i>N. alpina</i>	<i>N. obliqua</i>	
0	1.000	1.000	-
16	0.976	0.971	0.934
33	0.949	0.942	0.901
49	0.923	0.912	0.950
66	0.901	0.862	0.788
82	0.878	0.838	0.917
99	0.857	0.812	0.885
115	0.835	0.784	0.591
132	0.798	0.709	0.256
148	0.767	0.656	0.072
165	0.722	0.584	0.003*
181	0.663	0.467	0.002*
198	0.549	0.277	0.000*
214	0.363	0.165	0.012*
231	0.162	0.038	0.082

## DISCUSSION

There is a higher variability in the amount of herbivore caused damage on the leaves of *N. alpina* and *N. obliqua* southern beeches. The explanations are complex, because there are many factors, such as genotypes and environment that could be interacting to determinate the damage level. The genotype could determine the surface area affected by herbivores and the herbivore density by plant. Simultaneously, the morphological properties of plants could change according to the environmental gradient and change the damage levels (Hunter, 1997; Lowman & Shugart, 1992; Marquis, 1992). The leaf survival was also different among individuals, and the hypothesis "if herbivory affects leaf survival, then by excluding the presence of herbivores, leaf survival should be increased" was accepted in some tree individuals. For others tree individuals, the hypothesis was rejected because there is a compensation or no effect of herbivory upon leaf survival. However, the percentage of foliar damage does not explain the plant responses. Furthermore, the timing of damage and type of damage cannot explain differences because of the similarity among individuals. The architectural organization of plants could be explored to evaluate if the leaf number affected by shoots could be used to explain the leaf mortality.

When we consider the tree individuals from a population point of view, the individuals' differences are cleared and a population parameter, such as the mean survival damage, emerges (tree population level). The hypothesis at the

intraspecific level is: "if herbivory affects leaf survival of the tree population, then leaf survival without herbivories must be higher", was rejected for *N. alpina* but accepted for *N. obliqua*. Herbivory was significant different between treatments, but it does not affect the leaf survival in *N. alpina*, however in *N. obliqua* the higher values of herbivory indicates a reduction of leaf survival. This difference of response to herbivory suggests that there are species-specific responses, and we cannot formulate a general pattern. At the interspecific level the hypothesis is: "if herbivory affects leaf survival between tree populations of *N. alpina* and *N. obliqua*, then by excluding herbivory, the leaf survival should be similar", was rejected, because the experiments without herbivores showed a significant difference in leaf survival, particularly in the last age class. However, in this same experiment the analysis by age class showed that the herbivory has an influence, because in the middle age class, the leaf survival in *N. obliqua* is reduced, and therefore increasing the differences between species (Table 4 and 5). Herbivory affects leaf survival enhancing the differences between species because *N. obliqua* has a higher sensitivity to herbivory, probably by morphological and chemical characteristics that provide a better leaf palatability than the other species of *Nothofagus* (Barrera & Meza, 1993; Russell et al., 2000). An interesting factor is that *N. obliqua* attracts a higher diversity of foliage insects (Grandon, 1996), which suggests that *N. obliqua* is a more profitable resource for insects species, but it is necessary to experimentally evaluate this hypothesis. Specific chemical



analysis of defensive compounds and nutrients could be performed. Other leaf survival differences could be explained by genetic differences between individuals and species.

The hierarchical studies of herbivory were performed to evaluate the different levels or spatial scale in plants, and to obtain evidence of damage variability (Lowman, 1997). Few studies of herbivory have been developed based on this hierarchical point of view (Dyer & Shugart, 1992). This work showed the effect of herbivory on one parameter (leaf survival) as seen from the individual and population level, and providing the best insight to understanding the herbivory phenomena in plants. At the individual level there is ample variation in the response to herbivory, but at the population level herbivory diminished leaf survival, a phenomenon that is not explain by a uniform response of individual trees.

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## CONCLUSIONES GENERALES

### Especies

En este nivel se concluyó que la herbivoría no es el mecanismo por el cual las especies difieren en su sobrevivencia foliar, pero podría formar parte de los factores que diferencian a las especies, ya que intraespecíficamente las especies responden distintas a la herbivoría. *Nothofagus alpina* sobrecompensaría más según la intensidad de la herbivoría, probablemente porque los costos de construcción pueden ser mayores en esta especie. Posee hojas más grandes, con mayor cantidad de tricomas y la frecuencia de policiclismos es muy baja. Sin embargo, *N. obliqua*, el poseer hojas pequeñas, pocos tricomas y mayor frecuencia de policilismo, sugieren que es pobremente defendido y la compensación es muy débil. Esta idea se relaciona con el hecho de que efectivamente *N. obliqua* posee una mayor riqueza de especies herbívoras.

### Individuos

Se concluyó que la herbivoría afecta la sobrevivencia foliar de algunos individuos, pero el porcentaje de área foliar perdida promedio no se relaciona con las diferencias en la sobrevivencia foliar entre los tratamientos al interior de cada árbol, seguramente porque hay mucha variación de daño en las hojas y existen muchas hojas que no son dañadas. En este aspecto particular se requiere aumentar el número de hojas al interior de los individuos para

comparar la sobrevivencia de sus hojas con distintas categorías de daño. Lo interesante es que se pueden encontrar tres situaciones en ambas especies, individuos en los cuales la sobrevivencia aumenta, en otros disminuye, y otros en los cuales no tienen ningún efecto por la herbivoría.

#### Población de árboles

En este nivel, para *N. alpina* la herbivoría no tiene efecto en su sobrevivencia, pero sí en *N. obliqua*. Interespecíficamente, se concluyó que la herbivoría es al menos uno de los factores que afecta en la diferencia de la sobrevivencia foliar entre las especies. Este efecto estaría dado porque en *N. obliqua* las hojas de edades medias reducen su sobrevivencia foliar, pero en edades adultas de las hojas pueden existir otros factores que aumentan las diferencias y que pueden ser considerados como diferencias genéticas, propias de las especies.

#### Implicancias de realizar un análisis jerárquico de la herbivoría

Analizar la herbivoría en cada uno de estos niveles otorgó mayor riqueza biológica a la comprensión de este fenómeno. Aunque la pregunta podía responderse en cualquiera de los tres niveles, la información de los tres niveles fue esencial para comprender que la herbivoría puede ser parte del proceso, en que momento operaría y cómo lo haría al interior de cada especie. De haber analizado sólo el nivel específico, no sabríamos que la herbivoría a cierta edad de las hojas es importante para explicar las diferencias en sobrevivencia de las

hojas entre las especies o que existen individuos con respuestas diferentes al mismo proceso. De haber analizado sólo el nivel de la población de árboles no sabríamos que *N. alpina*, que aparentemente no presenta efecto por la herbivoría, podría estar compensando en sobrevivencia de sus hojas. Y finalmente el analizar sólo el nivel individual no permite distinguir diferencias entre las especies, ya que en ambas los individuos presentan el mismo patrón, individuos con respuestas positivas, negativas y neutras en cuanto a la sobrevivencia foliar por herbivoría. Lo interesante de una aproximación jerárquica en esta interacción biológica, es que cada nivel aporta información distinta al problema. Por ende, se hace necesario especificar el nivel jerárquico en el cual se está trabajando en herbivoría.



**TASA DE CONSUMO FOLIAR DE INSECTOS MASTICADORES  
(GEOMETRIDAE) Y MINADORES (HELIOZELIDAE) EN *NOTHOFAGUS*  
*ALPINA* Y *N. OBLIQUA***

Foliar consumption rate of chewer (Geometridae) and miner (Heliozelidae)  
insects in *Nothofagus alpina* and *N. obliqua*

**RESUMEN**

Se evaluó la tasa de consumo foliar de dos especies de insectos, una especie masticadora *Omaguacua longibursae* (Geometridae), y una especie minadora de la familia Heliozelidae, sobre el follaje de *Nothofagus alpina* y *N. obliqua* que tienen diferencias en su morfología foliar. La tasa de consumo foliar es similar sobre los dos *Nothofagus*, sugiriendo que las diferencias morfológicas y posiblemente químicas son irrelevantes en la alimentación de los estados larvarios de estos insectos.

Palabras claves: Tasa de consumo foliar, Geometridae, Heliozelidae, *Nothofagus*.

## ABSTRACT

The foliar consumption rate of two insect species, one chewer species *Omaguacua longibursae* (Geometridae) and one miner (Heliozelidae) species was evaluated when feeding on the foliage of *Nothofagus alpina* and *N. obliqua*, which present different leaf morphology. The foliar consumption rate was similar between the two *Nothofagus*, suggesting that morphological and possible chemicals differences are irrelevant for feeding of larval stage of these insects.

Keywords: Foliar consumption rate, Geometridae, Heliozelidae, *Nothofagus*.

Los estudios de herbivoría foliar en el género *Nothofagus* en Chile han estado centrados en la identificación del ensamble de insectos defoliadores y sus ciclos de vida, la tipificación de los daños, la evaluación de la defoliación y en el reconocimiento de metabolitos secundarios y sustancias volátiles (Gentili & Gentili, 1988; Grandon, 1996; Quiroz et al., 1999, Russel et al., 2000). Entre los insectos defoliadores es frecuente encontrar varias especies de insectos que consumen el follaje de dos o más especies de *Nothofagus*, como por ejemplo *Epistomentis pictus* (Buprestidae) que se alimenta de *N. alpina*, *N. dombeyi*, *N. obliqua* y *N. pumilio* (Grandon, 1996). Sin embargo, el que los insectos incluyan en su dieta a más de una especie no significa que se alimenten a la misma tasa en todas. La tasa de consumo foliar está

determinada por la calidad del alimento, es decir, por el contenido de nitrógeno, agua, metabolitos secundarios y morfología foliar (Mattson, 1980; Montenegro et al., 1980; Southwood et al., 1986; Coley & Barone, 1996). Como en algunos *Nothofagus* existen diferencias en estas características (Barrera et al., 1993; Hevia et al., 1999; Russell et. al., 2000), cabe preguntarse desde el punto de vista de los insectos, si tendrán el mismo comportamiento de consumo foliar frente a dos especies que son parte de su dieta.

*Nothofagus alpina* y *N. obliqua* se encuentran formando bosques mixtos en la Cordillera de los Andes, sector Altos del Bio-Bio (Gajardo, 1994). En 1997-1998 se identificaron dos taxas de insectos en ambos *Nothofagus*; una especie masticadora, *Omaguacua longibursae* (Geometridae) (Parra & Beeche, 1986) la cual estuvo presente en ambos árboles al comienzo de la estación de crecimiento, cuando las hojas están en plena expansión en Octubre de 1997. El otro taxón corresponde a un Heliozelidae minador, el cual emerge hacia la mitad de la estación de crecimiento (Enero, 1998) en *N. obliqua* y hacia fines de la estación (Abril, 1998) en *N. alpina*. El objetivo de este trabajo fue determinar la tasa de consumo foliar de *Omaguacua longibursae* (masticadora) y *Heliozelidae* (minadora) en *N. alpina* y *N. obliqua*.

Para determinar la tasa de consumo foliar de *O. longibursae*, se colectaron 28 larvas y se colocaron 14 individuos separadamente en capsulas Petri con 2 cm<sup>2</sup> de hoja de *N. alpina*, y otras 14 larvas, con la misma superficie foliar de *N. obliqua*. La edad de las hojas de ambas especies fue de 16 días. Al

cabo de una hora se retiraron las hojas y se midió el área foliar consumida. La tasa de consumo foliar fue determinada como:

$$(1) \quad \text{TCF} = (X_i - X_f)/t$$

donde  $X_i$  corresponde al área inicial de 2 cm<sup>2</sup>,  $X_f$  corresponde al área final después de consumida en el tiempo (t) de una hora.

Para Heliozelidae, se colectaron 126 hojas que contenían larvas minadoras en *N. alpina* y 62 en *N. obliqua*. En cada hoja se marcó la superficie foliar afectada por minadores sobre láminas transparentes al momento de la colecta, y al cabo de 24 horas se volvió a marcar la nueva superficie consumida la que representó la tasa de consumo foliar por día (TCF= Área consumida/ día).

La tasa de consumo foliar de *O. longibursae* sobre *N. alpina* fue de  $0,12 \pm 0,05$  cm<sup>2</sup>/hr (media  $\pm$  e.e.) mientras que para *N. obliqua* la tasa de consumo foliar fue de  $0,09 \pm 0,04$  cm<sup>2</sup>/hr. La tasa de consumo de *O. longibursae* en hojas de ambas especies *N. alpina* y *N. obliqua* no difiere significativamente (Mann-Whitney,  $n = 28$ ,  $U = 92$ ,  $P = 0,78$ ). En tanto, para insectos minadores (Heliozelidae), la tasa de consumo foliar sobre *N. alpina* fue de  $0,12 \pm 0,02$  cm<sup>2</sup>/día y  $0,15 \pm 0,02$  cm<sup>2</sup>/día sobre *N. obliqua*. La tasa de consumo foliar de insectos minadores tampoco difiere significativamente entre *N. alpina* y *N. obliqua* (Mann-Whitney,  $n = 188$ ,  $U = 3318$ ,  $P = 0,09$ ).

*Nothofagus alpina* y *N. obliqua* presentan diferencias en la morfología de sus hojas. *Nothofagus alpina* posee gran cantidad de tricomas y glándulas

(Barrera et al., 1993). En bioensayos *N. obliqua* presenta una mayor palatabilidad para insectos enrolladores de hojas y el extracto de sus hojas no afecta la producción de ninfas de áfidos, contrario a lo observado en *N. alpina*. Estos bioensayos sugieren diferencias químicas entre estos dos *Nothofagus* (Russell et al., 2000). Sin embargo, estas diferencias químicas y morfológicas serían irrelevantes para la alimentación en los estados larvarios de *O. longibursae* y de Heliozelidos. En términos proteicos, falta conocer el contenido de nitrógeno foliar de *N. alpina* para hacer una mejor interpretación, sólo se conoce algunos *Nothofagus* y en que *N. obliqua* tiene mayor contenido de nitrógeno foliar que *N. pumilio* (Hevia et al., 1999). En los insectos minadores, si bien la tasa de consumo foliar es igual sobre ambas especies de *Nothofagus*, el período de emergencia es distinto, en *N. obliqua* tendrían más tiempo para completar su desarrollo que aquellas larvas que emergen hacia el final de la estación vegetativa en *N. alpina*. En otras especies de la familia Fagaceae se ha encontrado que insectos minadores aceleran la abscisión de las hojas (Faeth et al., 1981; Pritchard & James, 1984), de ocurrir así, *N. obliqua* sería el más afectado en términos de sobrevivencia foliar.

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