

# Site, Tree and Silvicultural Factors Influencing the Infestation of Xylophagous Insects on *Nothofagus* Forests

Rosa M. Alzamora<sup>1\*</sup>, Luis A. Apiolaza<sup>2</sup>, Cecilia Ruiz<sup>3</sup>, Dolly Lanfranco<sup>3</sup>

<sup>1</sup>Departamento de Manejo de Bosques y Medio Ambiente, Universidad de Concepción, Victoria 631, Concepción, Chile; <sup>2</sup>School of Forestry, University of Canterbury, Private Bag 4800, Christchurch, New Zealand; <sup>3</sup>Instituto de Conservación, Biodiversidad y Territorio, Universidad Austral de Chile, Independencia 641, Valdivia, Chile

## ABSTRACT

This study assessed infestation of *Proholopterus chilensis* in *Nothofagus obliqua* trees in the Valdivia Province, Chile. *P. chilensis* is a native xylophagous insect that produces internal galleries in the stem during larval stage, decreasing value recovery in the most profitable log of the tree. The objectives of the study were to evaluate the current infestation of *P. chilensis* in Valdivia Province, to investigate the relationships among infestation, trees, site and flora attributes, to increase information about *P. chilensis* infestation patterns, and to make suggestions about silvicultural practices that could reduce damage. Results indicated that the level of infestation was low, compared with previous data. Hierarchical logistic regression models showed that estimated tree height and stand density were significant to explain probability of a tree being attacked by *P. chilensis*. Site altitude, flora diversity and Importance Value Index of *Chusquea quila* and Shannon-Weaver index were not significant predictors of infestation.

**Keywords:** Xylophagous; *Nothofagus* forests; *Proholopterus chilensis*; Infestation patterns

## INTRODUCTION

Most of the insects living in the Chilean natural forests are native, and some of them cause economic damage, but in very specific areas; however, they cannot be considered as a pest since they are part of the growth, development, and dynamics of these forests. Moreover, they have contributed to design the forests ecosystems that we have today [1]. Preliminary studies of infestation patterns of *Proholopterus chilensis* (Col: Cerambycidae) in *Nothofagus obliqua* (Mirb.) Oerst have shown that tree diameter and environmental humidity have significant effects on infestation [2,3]. However, this knowledge is insufficient to develop silvicultural approaches that reduce the damage, particularly in the Valdivia Province of Chile, where infestation has been historically high.

*P. chilensis* is a native xylophagous insect with a long life-cycle (2-4 years); however, the economic damage occurs during the larval stage, when larvae remain protected inside the tree and dedicated to feed and grow [4,5]. This insect is associated with living trees, and the galleries are mainly located in the first 4 m from the base of the stem, which concentrates up to 60% of the tree volume [6-9]. Butt logs of infested trees are downgraded from appearance lumber or veneer end-use and, instead, they are used as fuel wood or chips

for the wood-composite industry [10-12]. Thus, most of the studies that report the damage of xylophagous insects, such as *P. chilensis*, are mostly referred to as wood value loss, because infestation rates that have been registered have not affected the biodiversity of the ecosystems where the Chilean *Nothofagus* forests grow. Thus, Díaz [13] reported that there is no intersection between galleries of different larvae; thus, there would be no competition for the resource with other native xylophagous insects.

*N. obliqua* is a native tree with a broad distribution in the South-Central part of Chile between 33° and 41° 30' latitude South in the Andes Mountains, Central Valley, and Coastal Mountains [14]. This species is highly valued due to its wood quality and durability for appearance and structural end-uses. In the Valdivia Province, there are 130,430 ha of *Nothofagus* forests with *N. obliqua*, and according to CONAF [15], these forests could produce around 321.4 million m<sup>3</sup> of timber; nevertheless, only 63% of this volume would be commercial due to forest health problems [16].

Valdivia is the most frequently infested province by *P. chilensis*, with Díaz [17] reporting 22.4%, 43.5% and 9.5% of infestation, respectively. Kruuse [6] explained that the high environmental humidity and the quality of wood tissue of *Nothofagus* trees growing in Valdivia would be optimal for insect proliferation. In contrast,

**Correspondence to:** Rosa M. Alzamora, Departamento de Manejo de Bosques y Medio Ambiente, Universidad de Concepción, Victoria 631, Concepción, Chile, Tel: +56 41 220 4000; E-mail: ralzamora@udec.cl

**Received:** April 19, 2020, **Accepted:** May 15, 2020, **Published:** May 22, 2020

**Citation:** Alzamora RM, Apiolaza LA, Ruiz C, Lanfranco D (2020) Site, Tree and Silvicultural Factors Influencing the Infestation of Xylophagous Insects on *Nothofagus* Forests. 9:226. doi: 10.35248/2168-9776.20.9.226

**Copyright:** © Alzamora RM, et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

trees growing in areas farther North are not affected by *P. chilensis*, as those sites present lower humidity and higher temperature that preclude mating, oviposition and larvae survival [17]. In the same way, a study carried out in Valdivia concluded that *N. obliqua* trees facing South (lower radiation and lower temperatures) had more damage than trees facing North [3]. Besides environmental humidity, infestation depends on tree attributes, flora biodiversity, site, and silviculture.

Suárez and Cabrera [2,3] showed a positive relationship between tree diameter at breast height (dbh) and infestation. Suárez [2] analyzed the influence of flora biodiversity on xylophagous infestation when studying herbivory patterns of *P. chilensis* and *Cheloderus childreni* (Col: Oxypeltidae) on *N. obliqua* and *Nothofagus dombeyi*, respectively. They concluded that the number of understory species had a negative influence on *C. childreni* infestation but no influence on *P. chilensis*. These results could be extended to study the relationships between xylophagous infestation and individual understory species, such as *Chusquea quila* (Poaceae: Bambuseae), which has been shown to obstruct the establishment and growth of trees, especially *Nothofagus* sp. [18].

Altitude is another variable that could influence *P. chilensis*, since altitudinal gradients are correlated to temperature changes that vary the structure and the ecosystem processes in the forest. Temperature decreases by around 0.5°C per 100 m of elevation [14]. Altitude affects habitat quality for wood-boring insects, because their reproductive behavior is stimulated by sun exposure [19]. Baldini and Oltremari [20] reported that stands located under 250 masl displayed more insect attacks in the Araucanía Region (North of our study sites). These authors also pointed out that as the stocking increases the infestation decreases, although there would be an attack preference for stockings lower than 500 stem per ha.

There is no much information about the effect of silviculture on *P. chilensis* infestation; however, stocking appears to influence insect attack in other species. Amman [21] found a negative correlation between *Pinus contorta* stand density and mountain pine beetle-caused mortality (*Dendroctonus ponderosae*). However, in the case of Douglas-fir beetle (*Dendroctonus pseudotsugae*), high stand density is positively correlated with infestation [22]. These examples show that density management treatments, such as thinning, are expected to play a role in the management of infestation problems.

This study was conducted to explore relationships among *P. chilensis* infestation, trees, site and flora attributes in the Valdivia Province, aiming at increasing information about *P. chilensis* infestation patterns, as well as suggesting silvicultural approaches that could reduce *P. chilensis* damage.

## MATERIALS AND METHODS

### Location and selections of study plots

The study established 36 non-permanent 400 m<sup>2</sup> square plots between December 2012 and January 2013, covering the eight communes of the Valdivia Province in Los Ríos Region, Chile. The number of plots per commune was as follows: Corral (3 plots), Lanco (3 plots), Los Lagos (7 plots), Máfil (3 plots), Mariquina (4 plots), Paillaco (3 plots), Panguipulli (9 plots) and Valdivia (4 plots) (Figure 1 and Table 1).

### Climate and soils

The Valdivia Province presents temperate rainy climate with Mediterranean influence, with an average annual relative humidity of 76%, and an average annual precipitation of 1780 mm [23]. There are three major soil groups: organic-rich andisols, aquatic andisols and red clay. Organic-rich andisols occupy about 86% of the study area and correspond to andesitic-basaltic volcanic soils. In general, these soils are deep to very deep with good drainage [24,25].

### Variables collected in the field

Each plot was georeferenced and assessed for slope, elevation, tree stocking and for a visual density factor to define open-stands and closed-stands. Information on flora composition and biodiversity was generated by two vegetation censuses based on plots of 64 m<sup>2</sup>. Censuses were carried out by following the phytosociological principles of the South-European School [26]. Field records included the species list and the abundance-dominance score per species (degree of cover), which was estimated visually by using [27]. Sampling points were selected according to physiognomic and floristic homogeneity. Lists of plant species were analyzed to estimate two indicators: the Shannon-Weaver index of understory species and the Importance Value Index (IVI) of *C. quila*. The Shannon-Weaver index is a diversity measure that accounts for both evenness and abundance of species present in the community. IVI is an efficient indicator to compare species in terms of their importance within the community [28].

At tree-level, each *N. obliqua* individual was evaluated for social status, diameter at breast height (dbh), height and form. Infestation was recorded as attacked or non-attacked tree, by detecting external signs such as sawdust drain orifices and emergence orifices in the stem.

### Data analysis

At tree-level, infestation was managed as a dichotomous variable 1/0, where 1 represented presence of damage signs (infestation) and 0 their absence (no infestation). Trees were grouped according to infestation and compared on dbh using a t-test. We fitted a hierarchical linear mixed model with a logistic link function. The fixed-effects included a factor for stand density (Open Stand versus Closed Stand) and estimated tree height as a covariate. The random effects considered a separate intercept (in the logit scale) for each plot. Residuals were assumed to be independent of each other and to follow a binomial distribution.

All models were fitted using the lme4 package [29] in the R Statistical System (R Core Team). R code and data are available as supplementary materials.

$$\Pr(\text{infestation}_{ij} = 1) = \text{logit}^{-1}(\alpha_j + \beta_1 \text{height}_{ij})$$

$$\alpha_j = \gamma_0 + \gamma_1 \text{stand}_j + \gamma_2 \log(\text{altitude})_j + \eta_j$$

$$\text{, with } \eta_j \sim N(0, \sigma_{\eta_j}^2)$$

Stand density and altitude were fitted at the plot level, while total height entered the model at the tree level.

**Table 1:** Summary of *P. chilensis* damage indicators and stand variables per commune, where codes are CO (Corral), LA (Lanco), LL (Los Lagos), MF (Máfil), MQ (Mariquina), PC (Paillaco), PG (Panguipulli), and VD (Valdivia).

Plots Communes	Trees/ ha	Trees/ plot	Attacked Trees	N° damage signs	Basal Area/ plot	Mean dbh (cm)	Elevation (masl)	Slope Range (%)	Density factor
CO01	1575	63	1	1	18.47	10.13	124	20	Closed Stand
CO02	775	31	0	0	20.54	16.52	51	35	-
CO03	375	15	6	6	24.06	26.50	87	25	Open Stand
LA01	675	27	4	5	53.67	30.63	183	30	Closed Stand
LA02	800	32	0	0	33.77	21.53	183	30	Closed Stand
LA03	800	32	5	6	62.89	29.89	230	10	Closed Stand
LL01	1425	57	1	1	34.18	13.32	404	20	Closed Stand
LL02	775	31	3	4	39.11	23.13	101	10	Open Stand
LL03	775	31	1	1	37.63	23.40	148	33	Closed Stand
LL04	900	36	2	2	53.37	24.94	158	0	Closed Stand
LL05	2075	83	11	12	68.65	19.04	220	-	Closed Stand
LL06	800	32	1	1	34.49	21.09	295	5	Closed Stand
LL07	1350	54	0	0	30.47	15.15	277	30	Closed Stand
MF01	925	37	4	5	42.78	21.80	202	50	Closed Stand
MF02	1275	51	1	1	49.27	18.15	239	37	Closed Stand
MF03	1350	54	7	9	61.11	21.09	113	35	Closed Stand
MQ01	725	29	3	7	32.45	20.72	139	20	Open Stand
MQ02	875	35	5	6	32.12	19.77	125	20	Open Stand
MQ03	1100	44	6	6	32.53	17.77	160	33	Closed Stand
MQ04	550	22	3	3	27.04	23.95	209	20	Closed Stand
PC01	1375	55	5	6	16.23	10.93	132	18	Closed Stand
PC02	1425	57	9	13	46.62	18.35	79	15	Closed Stand
PC03	2050	82	16	17	22.74	11.27	89	20	Open Stand
PG01	550	22	13	19	36.10	28.30	253	2	Open Stand
PG02	925	37	7	7	58.84	25.68	281	15	Closed Stand
PG03	775	31	1	1	43.86	24.18	471	30	Closed Stand
PG04	600	24	2	2	48.23	30.46	348	28	Open Stand
PG05	525	21	6	7	60.72	37.05	270	30	Closed Stand
PG06	925	37	0	0	45.43	23.53	539	15	Closed Stand
PG07	1225	49	2	2	56.66	21.19	524	40	Closed Stand
PG08	525	21	0	0	37.29	28.12	464	15	Open Stand
PG09	1175	47	0	0	55.04	22.98	600	15	Closed Stand
VD01	2175	87	0	0	37.10	13.06	266	5	Closed Stand
VD02	1650	66	13	16	35.76	14.65	34	10	Open Stand
VD03	1975	79	20	27	51.09	16.91	39	2	Closed Stand
VD04	2275	91	6	8	39.24	12.58	28	30	Closed Stand

## RESULTS

### Infestation and damage signs

A total of 1602 trees were evaluated, and 164 of them showed damage signs produced by *P. chilensis*. The damage was concentrated in the commune of Valdivia (51 signs in 39 trees). The infestation per plot ranged from 1.5 to 59.1% among the 36 plots. Average infestation, at the commune level, did not exceed 14%. The lowest infestation was observed in Los Lagos (5.18%), Máfil (8.56%) and Lanco (10.13%) communes, whereas the highest occurred in Valdivia (12.87%), Mariquina (12.90%), Panguipulli (13.56%) and Corral (13.83%) (Table 1).

According to Table 1, plots had similar slope; however, variables such as average dbh, and elevation were highly variable among plots. Average infestation was 12%, and only 4 plots presented infestation levels higher than 25%, two in Panguipulli (59.1% and 28.5%), one in Corral (40%) and one in Valdivia (27.3%).

### Tree-level damage models

A *t*-test assessed statistical differences between mean dbh of infested trees and non-infested trees. That difference was statistically significant ( $p < 0.05$ ). A mixed-effects logistic regression model was fitted to explain *P. chilensis* infestation at tree level (Table 2). Elevation, dbh, *C. quila* IVI, Shannon-Weaver index, estimated tree height and stand density factor were also tested as explanatory variables but did not help explaining infestation.

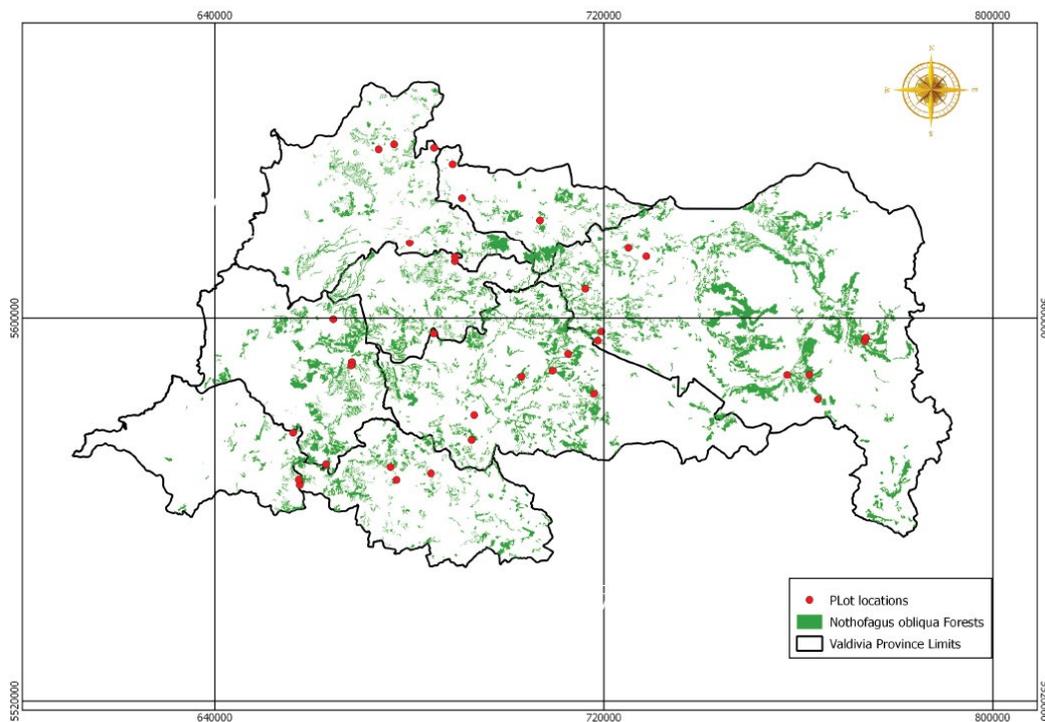


Figure 1: Distribution of plots in Valdivia province.

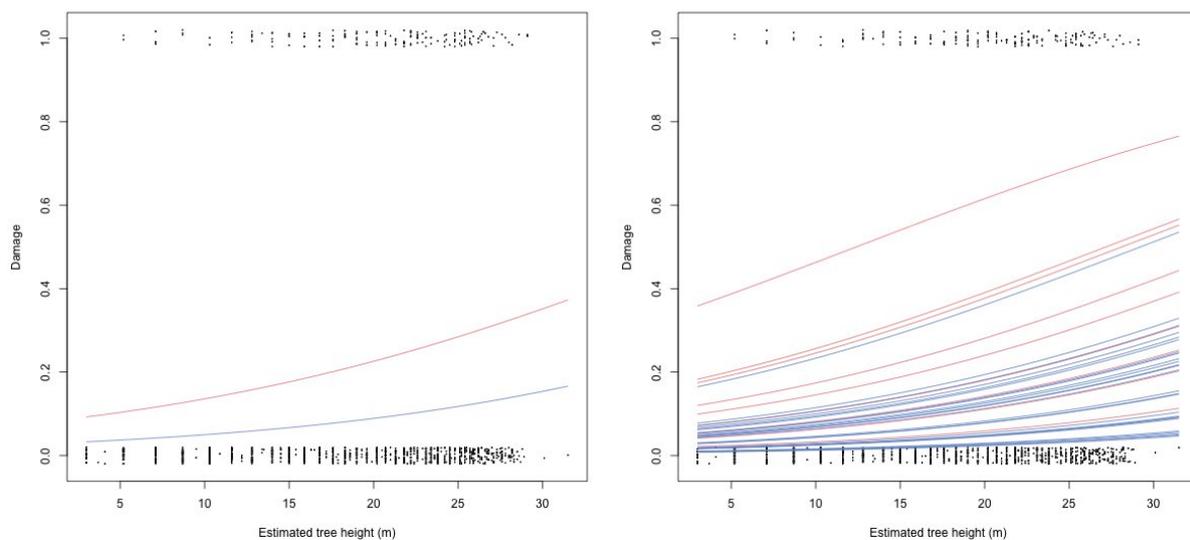


Figure 2: Mixed-effects coefficients model with probability of damage increasing with tree height for both open (red) and closed (blue) stands. Left panel shows only fixed effects of the model, while right panel also displays plot-level random effects.

Table 2: Fixed-effects coefficients in the logit scale. The random effect plot variance is 1.08.

Variables	Estimate	Std. Error	z-value	Pr (>  z )
Intercept	-2.46951	0.56227	-4.392	1.12e-05
Estimated tree height	0.06192	0.01885	3.284	0.00102
Stand density factor	-124.325	0.46479	-2.675	0.00748

Figure 2 summarizes the model with the probability of damage increasing with tree size. The left panel displays only the fixed effects of the model, using red for open stands and blue for the closed stands. The right panel introduces the plot random effects, showing the large between-plot variability for open (red) and closed stands (blue).

Elevation was not statistically significant to explain the probability of a tree being attacked by *P. chilensis*. Concerning tree attributes, estimated height was better predictor than tree dbh; although most of studies so far indicate that tree dbh have significant effect on xylophagous damage. Thus, probability of attack increases as tree dbh increases [2]. Results indicated the probability of a tree being attacked increased significantly with tree height (0.06%). Density

factor, which describes how closed is a stand, was also significant to explain *P. chilensis* attack. Our results indicated that the probability of infesting a tree decreased significantly with stand density, matching the trend observed by Baldini and Oltremari [20] when looking for factors influencing xylophagous infestation.

## DISCUSSION

Infestation levels were occasionally over 12% in the 36 plots, and just 4 plots in communes of Panguipulli, Corral and Valdivia presented infestation higher than this percentage, which represent 11% of the total plots. Thus, our study does not support the idea of a generalized xylophagous infestation problem in Valdivia Province. On the other hand, these results differ significantly from those obtained in previous studies, in Los Ríos Region, by Díaz [17] who reported levels of infestation of 22.4%, 43.5% and 9.5% respectively. These results could be explained because the selected places had high infestation levels, or due to variations on insect population cycles.

We consider that most of the forests analyzed in this study are growing with a natural health, according to the expected host-guest relationship between two native species [1]. However, it became interesting to assess site, flora and tree variables that explain the variability of infestation and damage signs, as a way to contribute to the knowledge of this insect, and to make suggestions about silvicultural practices that could reduce *P. chilensis* damage.

Using a mixed-effects logistic model helped identify variables that contribute to increase the probability of a tree being attacked. As a result, estimated tree height was highly associated with this probability (Table 2). This study confirms that the most severe attack of *P. chilensis* occurs in dominant and codominant trees, which are the largest trees of a stand [2,17]. Most of studies concerning to *P. chilensis* report that dbh would be the tree variable that mostly explains *P. chilensis* attack; thus, both dbh and tree height would be plausible variables to represent damage trends.

Stand density had a significant importance decreasing the probability of a tree being attacked. Suárez et al. [2] Tried the same predictor when analyzing infestation patterns of *P. chilensis* in Valdivia, Osorno and Llanquihue Provinces; however, their results indicated that this predictor was not significant ( $p > 0.05$ ). Stand density is associated with temperature and light decreasing effects, which affect habitat quality of organisms like wood-boring insects, since their reproductive behavior is stimulated by sunny exposure [30]. Stand manipulation by silviculture has been reported as a sustainable method to control insect damage [31-33]. However, it is necessary to first understand infestation patterns, because insects have different infestation strategies. A study developed in Canada by Gebeyehu and Wingfield [34] showed that the weevil *Pissodes nemorensis* Germar (Col: Curculionidae) moves around very little in shaded pine stands, since shade has a negative influence on the insect's visual response to attractive pine leads. In the same way, our results suggest a negative relationship between infestation and stand density factor (Table 2). Thus, we hypothesize that dense stands and shaded habitats would preclude *P. chilensis* development, because temperature and radiation levels that prevail in these conditions, limit feeding, oviposition and larvae development. Accordingly, we suggest creating low temperature and more cover shade conditions by keeping stand density over 500 stem per hectare. In this way,

thinning practices must be approached with a tree health criterion based on protocols designed to identify *P. chilensis* damage [35].

Elevation, flora biodiversity index and *C. quila* IVI were not significant at explaining the probability of a tree being attacked by *P. chilensis*. We hypothesized that increasing elevation would be associated with decreasing damage since the temperature decreasing effect is shown to affect *P. chilensis* infestation. Interactions between plants and herbivores vary with altitude; thus, herbivory at lower elevations can even limit the distribution range for some plant species [36,37]. Previous studies on *P. chilensis* showed an inverse relationship between damage and elevation. Thus, Díaz [17] climatic conditions; particularly temperature, limited *P. chilensis* infestations in higher altitude. In addition, at lower altitude anthropic alteration increases, which means best trees were felled and attacked trees in the stand are provoking infestation increase.

Concerning flora biodiversity, which was represented by Shannon-Weaver index, we hypothesized that trees growing in more biodiverse environments would present less damage since insects' herbivory, with very specific hosts, has shown to decrease in the presence of high vegetation biodiversity. In fact, Altieri and Landis et al. [38,39] explain that high biodiversity in plants sustains more parasitoids, predators and natural enemies. We also hypothesized that *C. quila* IVI would have negative effects on *P. chilensis* due to the microclimatic conditions that this Bambuseae creates by reducing temperature and light, which is comparable to maintain high stocking. This understory species has shown to obstruct the establishment and growth of trees, especially *Nothofagus*, but there are not studies that relate to their effect on xylophagous infestation [18].

Results also indicated that the most frequent attack of *P. chilensis* is in dominant and codominant trees, which imposes a complex scenario to put forward silviculture suggestions, because infestation increases with decreasing stand density. Therefore, in keeping denser stands, log production will be concentrated in smaller diameters, which have lower prices.

As height and diameter growth, and *P. chilensis* infestation are inversely related to stand density, stocking decisions will generate volume-damage tradeoffs that will affect the value recovery of the forest. An alternative silvicultural approach for balancing production and forest health is the application of uneven-aged management strategy, which has shown it can contribute to good ecosystem health, diversity and sustainability [40]. The advantages of uneven-age management are providing income at more frequent intervals, minimizing regeneration costs and offers wildlife habitat and recreational services. The main disadvantage of this approach is the complexity of achieving a balanced and sustained yield of forest products.

Although *P. chilensis* is native, its attack to *Nothofagus* forests beyond the natural balance between host and insect, could affect value recovery and sustainability; however, this study indicates that infestation in Valdivia Province is under 12%, which is lower than previous values reported in the literature.

This study confirm that stand density (stocking) is a statistically significant factor to explain the probability of a tree being attacked by *P. chilensis*, which suggests the possibility of managing stocking to

reduce damage in natural forests and applying such learning when establishing plantations based on *Nothofagus* species.

In testing climatic factors, altitude was not significant to explain the probability of a tree being attacked by *P. chilensis*; nevertheless, previous studies showed an inverse relationship between damage and elevation. For example, Díaz [17] indicated that, at higher altitude, temperature limits *P. chilensis* infestations. On the other hand, at lower altitude anthropic alteration is higher and forests are characterized by presenting a high proportion of attacked trees inducing increased infestation.

There is no single strategy able to confront phytosanitary challenges on *Nothofagus* forests. From a silviculture point of view, sustaining uneven aged structure, favoring flora diversity and maintaining high tree stocking have been argued to reduce damage of xylophagous insects. Donoso [41] points out that diverse systems are the best guarantee to maintain the balance between prey and predators, thus avoiding the proliferation of pests and positively impacting forest health.

## CONCLUSION

Our study did not find significant relationships between attack and flora diversity; in addition, sampled stands corresponded to second-growth forests with even-aged structure; so, it was not possible to study differences between uneven and even-aged structure. In the same way, our results do not evidence that *P. chilensis* is representing problems to crops or ecosystem services such as water quality neither is a threat to other native insects.

## ACKNOWLEDGEMENTS

This study was funded by the Natural Forest Grant of Chilean Forest Service (FIBN 006/2012, CONAF). We thank Ronnie Reyes and Jessica Pérez for their assistance in field work.

## REFERENCES

1. Estay S. Forest Pest and Disease Management in Latin America: Modern Perspectives in Natural Forests and Exotic Plantations. Springer Nature. 2020.
2. Suárez L, Aguilar A, Gonzáles W. Patrones de infestación por insectos xilófagos en renovales de *Nothofagus obliqua* Mirb. y *Nothofagus dombeyi* (Mirb.) Oerst. (Fagales: Nothofagaceae) Rev Chil Hist Nat. 2005; 78(1):23-32.
3. Cabrera P. Impacto de *Holopterus chilensis* Blanchard en renovales de *Nothofagus obliqua* (Mirb.) Oerst. en la provincia de Valdivia, Chile: Avances hacia la evaluación del daño. Bosque. 1997; 18(1): 9-19.
4. Thompson J. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insect. Entomol Exp Appl. 1988; 47:3-14.
5. Mayhew P. Adaptive patterns of host-plant selection by phytophagous insect. Oikos. 1997; 79(3):417-428.
6. Kruuse L. Algunos factores bióticos y abióticos que inciden en el nivel de ataque de *Holopterus chilensis* Blanch. (Col.: Cerambycidae) en *Nothofagus obliqua* (Mirb.) Oerst. Tesis Ing. Forestal. Facultad de Ciencias Forestales, Universidad Austral de Chile. Valdivia, Chile. 1981.
7. Baldini A, Pancel L. Agentes de daño en el bosque nativo. Editorial Universitaria, Santiago, Chile. 2000; p: 480.
8. Baldini A, Alvarado A. Manual de plagas y enfermedades del bosque nativo en Chile. Asistencia para la recuperación y revitalización de los bosques templados de Chile, con énfasis en los *Nothofagus* caducifolios. FAO/CONAF, Santiago, Chile. 2008; p:240.
9. Rojas E, Lanfranco D, Ruiz C. Barrenadores del xilema. In: Lanfranco D, Ruiz C (eds) Entomología Forestal en Chile. Ediciones Universidad Austral de Chile, Valdivia. 2010; pp.141-162.
10. Donoso P, Promis A. Silvicultura en Bosques Nativos. Avances en la investigación en Chile, Argentina y Nueva Zelandia. Estudios en Silvicultura de Bosques Nativos Marisa Cuneo Ediciones, Valdivia, Chile. 2013; 1:226.
11. Csóka G, Kovács T. Xilofág rovarok - Xylophagous insects. Hungarian Forest Research Institute. Erdészeti Tuományos Intézet, Agroinform Kiadó, Budapest. 1999; p:189.
12. Lotfalizadeh H, Khalghani J. Hymenopterous parasitoids (Hym: Chalcidoidea) of xylophagous beetles in Iran. Entomofauna. 2008; 29:249-264.
13. Díaz A. Evaluación del dano interno y estimación de pérdidas producidas por *Holopterus chilensis* (Blanch) en *Nothofagus obliqua* (Mirb.) Oerst., en la provincia de Valdivia, Decima Region. Dissertation, Universidad Austral de Chile, Valdivia. 1999.
14. Donoso C. Tipos forestales de los Bosques Nativos de Chile. Investigación y Desarrollo Forestal. CONAF/FAO Santiago, Documento de Trabajo. 1981:38.
15. CONAF. Catastro de los recursos vegetacionales nativos de Chile. Monitoreo de cambios y actualizaciones, período 1997-2011. Santiago, Chile: CONAF (Corporación Nacional Forestal). Santiago, Chile. 2011; p: 28.
16. INFOR. Boletín informativo N° 12, Instituto Forestal, Chile. 2008.
17. Díaz A. Gusanera del roble: *Holopterus chilensis*. In: Lanfranco D, Ruiz C (eds) Entomología Forestal en Chile. Ediciones Universidad Austral de Chile, Valdivia. 2011; p:337-348.
18. González ME, Veblen TT, Donoso C, Valeria L. Tree regeneration responses in a lowland *Nothofagus* dominated forest after bamboo dieback in South-Central Chile. Plant Ecol. 2002; 161(1):59-73.
19. Sundqvist MK, Sanders NJ, Wardle DA. Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. Annu Rev Ecol Evol Syst. 2013; 44:261-280.
20. Baldini A, Oltremari J. Bosques de *Nothofagus* en Chile: la amenaza de su degradación. Rev Agronom For. 2009; 37:15-17.
21. Amman GD. Why Partial Cutting in Lodgepole Pine Stands Reduce Losses to Mountain Pine Beetle. GTR-INT-262. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT. 1989; p:12.
22. Weatherby JC, Thier RW. A preliminary validation of a Douglas-fir beetle hazard rating system, Mountain Home

- Ranger District, Boise National Forest, 1992. USDA Forest Service, Intermountain Region, State and Private Forestry, Forest Pest Management, Report No. 1993; R4-93-05: p:7.
23. Fuenzalida H. Climatología de Chile: publicación interna de la sección meteorología. Depto. de Geofísica y Geodesia. Santiago, Chile. 1971; p:90.
  24. Schlatter J, Grez R, Gerding V. Manual para el reconocimiento de suelos. Universidad Austral de Chile. Valdivia, Chile. 2003.
  25. Casanova M, Salazar O, Seguel O, Luzio W. The Soils of Chile, World Soils Book Series. Springer Science+ Business Media, Dordrecht. 2013; p:185.
  26. Ellenberg H, Mueller-Dombois D. Aims and Methods of Vegetation Ecology. New York (NY). John Wiley and Sons. 1974; p:547.
  27. Dierschke H. Pflanzensoziologie: Grundlagen und Methoden. Verlag Eugen Ulmer, Stuttgart. 1994; p:683.
  28. Curtis JT, McIntosh RP. The interrelations of certain analytic and synthetic phytosociological characters. Ecology. 1950; 31(3):438-455.
  29. Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H. et al. Package 'lme4'. Convergence. 2015;12 (1).
  30. Rose AH. Some notes on the biology of *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae). Can Entomol. 1957; 89(12):547-553.
  31. Gottschalk KW. Silvicultural guidelines for forest stands threatened by the gypsy moth. General Technical Report-Northeastern Forest Experiment Station, USDA Forest Service. 1993; NE-171:49.
  32. McLean JA. Silvicultural control of the white pine weevil at the UBC Malcolm Knapp Research Forest. Proceedings of a symposium held on the white pine weevil: Biology, damage and management, January 19–21, Richmond, British Columbia. 1994.
  33. Taylor SP, Alfaro R, Delong C, Rankin LJ. The effects of overstorey shading on white pine weevil damage to interior white spruce. In Proceedings of a symposium held on the white pine weevil: Biology, damage and management, January 19–21, Richmond, British Columbia. 1994.
  34. Gebeyehu S, Wingfield MJ. Pine weevil *Pissodes nemorensis*: threat to South African pine plantations and options for control: review article. S African J Sci. 2003; 99(11-12): 531-536.
  35. Lanfranco D, Rojas E, Ríos R, Ruiz C. Insect defoliators of *Nothofagus obliqua* (Roble) in south Chile: Two years monitoring species and their damage. Proceedings: Integrated management and dynamics of forest defoliating insects. August 15-19; Victoria, BC. Gen. Tech. Rep. 1981; NE-277:117.
  36. Galen C. Limits to the distributions of alpine tundra plants: herbivores and the alpine skipper *Polemonium viscosum*. Oikos. 1990; 59(3):355-358.
  37. Miller T, Louda SM, Rose KA, Eckberg JO. Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. Ecol Monogr. 2009; 79(1):155-72.
  38. Altieri M. Biodiversidad, agroecología y manejo de plagas. Consorcio latinoamericano sobre agroecología y desarrollo. CETAL Ediciones, Valparaíso, Chile. 1992.
  39. Landis D, Wratten S, Gurr G. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu Rev Entomol. 2000; 45(1):175-201.
  40. Gamborg C, Larsen JB. "Back to nature": A sustainable future for forestry? For Ecol Manag. 2003; 179(1): 559–571.
  41. Donoso C. Bosques templados de Chile y Argentina. Variación Estructura y Dinámica. Editorial Universitaria. Santiago, Chile. 1993; p:483.