RESEARCH ARTICLE

Temperature and foliage quality affect performance of the outbreak defoliator *Ormiscodes amphimone* (F.) (Lepidoptera: Saturniidae) in northwestern Patagonia, Argentina

La temperatura y la calidad del follaje afectan el desempeño del defoliador epidémico *Ormiscodes amphimone* (F.) (Lepidoptera: Saturniidae) en el noroeste de la Patagonia argentina

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ABSTRACT

In the temperate forests of Chile and Argentina the phytophagous moth *Ormiscodes amphimone* (F.) causes severe defoliation on the southern beech tree *Nothofagus pumilio* (Poepp. & Endl.) Krasser. The recent increase in defoliation frequency in some areas appears to be influenced by a warmer climate. To evaluate the effects of temperature and the spatial heterogeneity of foliage quality on the performance and relative consumption rate of *O. amphimone* in northwestern Patagonia, Argentina we conducted a factorial experiment. Larval performance was measured as relative growth rate, developmental time, larval survival, and pupal weight. Larvae of *O. amphimone* were reared under two constant temperature regimes (15 °C and 20 °C) and fed with two *N. pumilio* foliage types (from a mesic and from a xeric site). Larvae at the higher temperature and fed with leaves from the mesic site showed higher performance and consumption rate than larvae in the other treatments. Higher temperature and mesic foliage had positive effects on *O. amphimone*'s relative growth rate, development time and relative consumption rate. However, pupal weight was positively influenced by mesic foliage but not by temperature, and larval survival did not show significant differences among treatments. Our results preliminarily suggest that *O. amphimone* performance and consumption rate may increase under higher temperature conditions, especially in the mesic portions of the precipitation gradient. However, these findings should be carefully interpreted as further research is necessary to assess the influence of higher temperatures on the foliar quality of *N. pumilio*.

Key words: herbivory, *Nothofagus pumilio*, outbreaks.

RESUMEN

En los bosques templados de Chile y Argentina la polilla fitófaga *Ormiscodes amphimone* (F.) genera severas defoliaciones sobre la lenga (*Nothofagus pumilio* [Poepp. & Endl.] Krasser). El reciente aumento en la frecuencia de defoliación en algunas áreas de la Patagonia parecería estar influenciada por un clima más cálido. Para evaluar los efectos de la temperatura y la heterogeneidad espacial en la calidad del follaje sobre el desempeño y la tasa de consumo relativo del defoliador *O. amphimone* en el noroeste de la Patagonia argentina llevamos a cabo un experimento factorial. El desempeño larval fue medido como tasa de crecimiento relativo, tiempo de desarrollo, supervivencia larval y peso de las pupas. Las larvas de *O. amphimone* fueron criadas bajo dos temperaturas constantes (15 °C y 20 °C) y alimentadas con dos tipos de follaje de *N. pumilio* (de un sitio mésico y de uno xérico). Las larvas criadas a la temperatura más alta y alimentadas con hojas del sitio mésico exhibieron desempeños y tasas de consumo más elevadas que las larvas en los otros tratamientos. La temperatura más alta y el follaje del sitio mésico tuvieron efectos positivos en la tasa de crecimiento relativo, el tiempo de desarrollo y la tasa de consumo relativo. Sin embargo, el peso de las pupas fue influenciado positivamente por el follaje mésico pero no por la temperatura, y la supervivencia larval no mostró diferencias significativas entre tratamientos. Nuestros resultados sugieren preliminarmente que el desempeño y la tasa de consumo de *O. amphimone* podrían aumentar bajo condiciones de temperatura más elevadas, especialmente en los sitios mésicos del gradiente de precipitación. Sin embargo, estos resultados deben ser interpretados en forma prudente ya que más estudios son necesarios para evaluar los efectos de temperaturas elevadas sobre la calidad foliar de *N. pumilio*.

Palabras clave: defoliaciones, herbivoría, *Nothofagus pumilio*.

INTRODUCTION

In the temperate forests of Chile and Argentina in South America, *Ormiscodes amphimone* (F.) (Saturniidae, Hemileucinae), a phytophagous moth species, causes severe defoliation on the widely distributed southern beech tree, *Nothofagus pumilio* (Poepp. & Endl.) Krasser (Bauerle et al. 1997, Baldini & Alvarado 2008, Paritsis et al. 2010). *Ormiscodes amphimone* is one of the most widespread *Ormiscodes* species in Chile and Argentina ranging from ca. 34° S in central Chile to 55° S in Tierra del Fuego (Lemaire 2002, Angulo et al. 2004) and matching closely the distribution of *N. pumilio*. Although *O. amphimone* has been reported to feed on over 20 species of native and exotic plants (see Paritsis et al. 2010 for a species list), it feeds preferentially on the broad-leaved canopy tree *N. pumilio* (Baldini & Alvarado 2008), which is one of the most important native timber species in Patagonia (Martínez-Pastur et al. 2010).

Defoliation caused during epidemic population levels of this moth apparently does not generate widespread mortality of mature *N. pumilio* trees, probably due to the short duration of these outbreaks (i.e. one season; Veblen et al. 1996, Paritsis 2009). Nevertheless, defoliation significantly reduces *N. pumilio*'s radial growth (Paritsis et al. 2009) and has been suggested as a predisposing factor for the partial crown dieback observed in multiple *N. pumilio* stands (Veblen et al. 1996). Furthermore, defoliation by this insect is known to cause economic losses by killing saplings and reducing timber production and also by diminishing forest aesthetic value for tourism (Bauerle et al. 1997, Baldini & Alvarado 2008). Since the late 20th century there has been an increase in *Ormiscodes* outbreak frequency in southern Patagonia (Paritsis & Veblen 2011) coinciding with the well-documented climate warming in the region that started in the mid-1970s (Villalba et al. 2003). Although there is evidence implying that warming favors the occurrence of *O. amphimone* outbreaks (Paritsis & Veblen 2011), the mechanisms involved in the apparent increase in the frequency of outbreaks over the past several decades remain largely unknown.

Spatially, *O. amphimone* defoliation events appear to occur more extensively towards the mesic portion of the distribution gradient of *N. pumilio*. In a study conducted in study areas in northern and southern Patagonia (Nahuel Huapi and Los Glaciares National Parks, respectively) defoliation occurred more extensively than expected towards the mid- to high precipitation portions of the gradient (Paritsis 2009). This spatial pattern is also supported by studies conducted in our study area that show higher incidence of chewing insects on *N. pumilio* leaves at wetter sites compared to drier sites (Mazía et al. 2004, 2009). In one of these studies, the guild of leaf chewing insects (including defoliators such as *O. amphimone*) was responsible for almost two thirds of foliar damage towards the mesic end of the precipitation gradient, while it only caused one third of foliar damage towards the xeric portion of the gradient (Mazía et al. 2004). These observations suggest that mesic *N. pumilio* forests could be more favorable for *O. amphimone* herbivory than xeric forests, but the mechanisms responsible for the observed spatial pattern of herbivory were not studied. Thus, the first necessary step to explore the causes of this spatial pattern is to evaluate the physiological response of *O. amphimone* to foliage from these two contrasting locations along the precipitation gradient.

Temperature and host plant quality are key factors that have strong influences on insect performance, acting either individually or in combination (Lindroth et al. 1997, Levesque et al. 2002, Kingsolver et al. 2006). For instance, the effects of temperature on consumption and growth rates of herbivorous insects may be significant when insects feed on diets of certain quality but not on others (Kingsolver et al. 2006). Consequently, insect responses to the synergistic effects of temperature and plant quality may generate complex population processes, such as colonization, extirpation, and outbreaks, which are difficult to predict without understanding potential interactions between temperature and plant quality. Furthermore, responses of phytophagous insects to temperature, host plant quality, and to the interactions between these factors are highly variable in space and time, which has important implications for insect population dynamics (Karban & Agrawal 2002, Auslander et al.

2003), particularly under current and future climate warming scenarios. Recent large-scale outbreaks of forest insects in the northern hemisphere have been attributed to temperature increases and have been modulated by the spatial heterogeneity of the quality of the resource (i.e. host plants) over the landscape (Powers et al. 1999, Logan et al. 2003). However, the precise mechanisms through which temperature and the spatial heterogeneity of plant host quality may influence population dynamics of phytophagous insects are extremely diverse and thus, must be assessed on a case specific basis.

Despite the current importance of *O. amphimone* as a defoliator in the *N. pumilio* forests of southern South America and its potential to increase its impact on ecosystem processes under a warmer future, there are no published studies specific to the ecology of this key species (Baldini & Alvarado 2008). Consequently, we address the question of how *O. amphimone* responds physiologically to the combined effects of increased temperature and the spatial variation of foliage quality in northwestern Patagonia. To evaluate the response of *O. amphimone* to temperature and *N. pumilio* foliage quality we conducted a laboratory experiment to examine the simultaneous effects of these two key variables on the performance and consumption rate of *O. amphimone*. Foliage quality was measured as foliar water content, leaf toughness, nutrients, and total phenolics, all of which are key variables known to influence insect performance (Mattson 1980, Scriber & Slansky 1981, Ohmart & Edwards 1991, Lawrence et al. 1997, Sanson et al. 2001). Our specific objective was to evaluate the independent and interacting effects of two temperature regimes and two types of foliage of *N. pumilio* on the performance (measured as relative growth rate, development time, larval survival, and pupal weight) and relative consumption rate of the outbreak defoliator *O. amphimone*.

METHODS

Study sites

We selected two contrasting study sites from where *N. pumilio* foliage was collected. Both sites are located on the eastern slopes of the Andes in Northwestern

Patagonia, Argentina, where there is a steep west-to-east gradient of decreasing precipitation associated with the rain shadow effect of the Andean divide (Veblen et al. 1996). The climate in this region is characterized by cold and wet winters, and mild but dry summers with the growing season occurring mainly from November to February. The mesic site is located at Paso Puyehue (40°43' S; 71°55' W; 1150 m) on a relatively flat area with a mean annual precipitation of ca. 3000 mm (Barros et al. 1983). This is a relatively dense *N. pumilio* stand with an open understory of forbs and small shrubs (e.g., *Adenocaulon chilensis* Less., *Ribes maguellanica* Poer., *Berberis serratodentata* Lechl.). The xeric site is located 67 km to the southeast at Cerro Otto (41°08' S; 71°20' W; elev. 1120 m) on a northeast-facing slope with a mean annual precipitation of ca. 1000 mm (Barros et al. 1983). This *N. pumilio* stand has a more open canopy than the mesic site and the understory species are mainly shrubs such as *Schinus patagonicus* (Phil.) I. M. Johnst. and *Berberis buxifolia* Lam.

Experimental design

The study was conducted during the 2006-2007 austral summer in the northern Patagonian Andes at Nahuel Huapi National Park, Argentina. In mid-December 2006 we collected 12 family-groups of *O. amphimone* larvae, each from a different female, at the mesic site Paso Puyehue. Family-groups had 40 to 120 larvae, which were in their second instar. Because females lay eggs in discrete masses and larvae are gregarious until their reach the 5th and last instar, we were certain that each group of larvae collected was the offspring of a single female. We divided each family-group into four subgroups that were assigned to one of four combinations of temperature and foliage treatments; hence, family-group was not a factor in the experiment. The 2 x 2 factorial design consisted of two temperature treatments of 15 °C (low) and 20 °C (high), and two *N. pumilio* foliage types (i.e. diets) collected from a mesic site and a xeric site. Foliage collection was conducted every four days or less in both sites and was preserved at 5 °C to provide constant fresh leaves to larvae. For all treatments, we reared larvae in growth chambers with a 14:10 L:D photoperiod. The low temperature treatment was chosen to match the average summer (December to February) temperature recorded at the Bariloche meteorological station (41°09' S, 71°16' W; elev. 825 m; 1976-2006). The high temperature was selected to approximately match the highest expected warming of ca. 4 °C over the 21st century predicted by the A1Fl climate scenario of fossil fuel emissions used by the Inter-governmental Panel on Climate Change (IPCC 2007).

Each replicate consisted of a group of 10 to 30 larvae to emulate the gregarious behavior of *O. amphimone* in natural conditions. We started the experiment with 12 replicates for each of the four treatments representing 934 larvae. Groups of larvae (i.e. replicates) were kept in 1000 cm³ plastic containers each and fed at least every other day with fresh *N. pumilio* leaves, assuring constant foliage availability. At the fifth instar, when larvae become solitary in natural populations, each replicate was reduced to four larvae per container to simulate natural conditions. Because of parasitoid-related deaths, sample size diminished to nine replicates per treatment by the end of the experiment. Nevertheless, parasitoid-caused deaths were minimal in the remaining nine

replicates (i.e. ca. 10 %) and did not differ among treatments (F = 0.23; df = 3, 32; P = 0.87). Voucher specimens were deposited at the Museo Nacional de Historia Natural in Santiago, Chile.

Foliar quality assessment

Several measures of foliage quality were made: leaf water content (% fresh mass), leaf toughness (measured as strength to fracture; g mm^{-2}), nitrogen (% dry mass), phosphorous (% dry mass), organic matter (% dry mass), and total phenolics content (% Gallic Acid Equivalents, dry mass). To characterize foliage quality we collected samples from 11 *N. pumilio* individuals at each site in early January (i.e. early summer). We collected foliage from a mixture of saplings (ca. 70 %) and mature trees (ca. 30 %) matching the proportion of these types of foliage to larval diet. At the time of foliage collection, leaves at both sites were fully expanded but not senescent; thus, differences in leaf phenology between sites, which may be a confounding factor in comparative studies (Mopper & Simberloff 1995), were not likely to bias foliar quality measures between sites. Three small branches from different orientations and heights were collected per replicate (i.e. tree). Foliage was preserved at ca. 5 °C for 48 hours until analyses were performed. Water content was quantified gravimetrically by measuring the percentage of water in fresh leaves. The amount of force needed to fracture foliage (defined here as toughness) was assessed by randomly selecting 30 mature leaves per individual and measuring the weight needed to punch each leave with a 2 mm^2 steel rod (Sanson et al. 2001). Organic matter was estimated by calcinating the samples and weighing the ashes (Schlesinger & Hasey 1981). Phosphorous was assessed by sample mineralization (Richards 1993) and nitrogen was quantified using the semi-micro Kjeldahl method (Bremner 1996). Total phenolics were measured as gallic acid equivalents using the Folin-Ciocalteu technique (Waterman & Mole 1994).

Bioassays

We evaluated *O. amphimone* performance as larval growth rate, development time, percentage of larval survival, and pupal weight. To examine the independent as well as synergistic influence of the treatments on larval growth rate we weighed larvae (in groups) every five days until pupation, and we estimated the individual larval weight per replicate as the ratio between total weight and number of larvae in the sampling unit. Hence, although larvae were not weighed individually, all the nutritional indices in this study are calculated on a per larva basis using the average weight per sample. We calculated larval relative growth rate (RGR) per sampling unit at each five-day feeding period (Bowers et al. 1991, Rath et al. 2003). A mean value of RGR was subsequently obtained per treatment averaging the RGRs obtained at each five-day feeding period, which ranged from eight to 15 depending on the treatment. Wet larval weight was used instead of dry weight to avoid killing larvae and the consequent reduction in sample size. We quantified development time as the mean number of days it took for each group of larvae to pupate from the beginning of the experiment (i.e. when larvae were at their second instar). To calculate percentage of larval survival we excluded parasitoid-caused mortality (easily identified by the conspicuous cocoon that the hymenopteran parasitoids form within

the body of larvae) because these were not directly affected by the treatments. One week after pupation, all the pupae were weighed and sexed. We used female pupal weight as a measure of herbivore performance since it is known to be a good indicator of fitness in non-feeding adult Lepidoptera species (as is the case with *O. amphimone*) and is often linearly associated with egg number (Awmack & Leather 2002). The sex of the pupae was determined examining the ventral portion of the last abdominal segments (Tuskes et al. 1996) and was verified at adult emergence for at least 30 % of the pupae.

To calculate foliage consumption rate we conducted foliar consumption trials with recently molted fifth-instar larvae. Small branches with fresh leaves were weighed and placed in containers with the larvae. After 48 hours, the branches with the remaining leaves were weighed again to calculate foliar mass consumed. To account for leaf wilting we weighed and placed foliage in control containers (i.e. without larvae) that were re-weighed after 48 hours. The percentage of water lost by transpiration (weight/weight) was incorporated into the calculation of the relative consumption rate (RCR), which is the wet weight of the consumed foliage divided by the product of multiplying the duration of feeding (days) by the larval mean wet weight (calculated as: [initial weight + final weight] / 2) (Bowers et al. 1991, Rath et al. 2003). We used wet-weight because it has been suggested that it reflects short term feeding responses of caterpillars more realistically than dry weight (Kingsolver 2000).

Statistical analyses

Foliar quality variables from the mesic and the xeric sites were compared using t-tests for independent samples. Two-way analysis of covariance (ANCOVA) was performed to determine if there were significant differences in performance and foliar RCR among larvae reared under the different treatments and to evaluate potential interactions between treatments. Initial larval weight was used as a covariate to control for potential differences among groups of larvae at the beginning of the experiment. Where significant effects existed, post-hoc pair-wise comparisons were conducted to examine differences among individual treatment combinations using Tukey post-hoc tests. All percentage data were transformed with an arcsine square root to reduce variance heterogeneity (Zar 1999).

RESULTS

Foliar quality

Foliar water content and organic matter were significantly higher in the mesic than in the xeric site (Table 1). Total phenolics were significantly higher in foliage from the mesic site than in foliage from the xeric site (Table 1). Although marginally significant, leaf toughness was slightly higher in the xeric than in the mesic site (Table 1). Leaf N and P showed no significant difference between foliage from the two sites (Table 1).

Bioassays

Temperature and foliar quality affected most of the *O. amphimone* performance variables and consumption rate (Figs. 1A, 1B and 1C, Table 2). However, contrary to our expectations, no significant interactions of temperature and foliar quality were observed on any of the measured performance variables and consumption rate (Table 2). Larvae reared at the warmer temperature and fed with leaves from the mesic site had significantly higher RGR than larvae in the other treatments (Fig. 1A, Table 2). In addition, larvae growing under the high temperature treatment pupated significantly earlier compared to those growing under the low temperature treatment (48 ± 5 versus 67 ± 5 days, respectively; mean ± SE) (Fig. 1B, Table 2). Larvae feeding on mesic foliage pupated significantly earlier than those feeding on xeric foliage, indicating that foliage quality also had a significant effect on development time (Fig. 1B, Table 2). Larval survival rates were not significantly different among treatments (Table 2). Finally, groups of larvae feeding on mesic foliage had significantly higher female pupal weight (1.07 ± 0.05 g; mean ± SE) than larvae feeding on xeric foliage (0.83 ± 0.02 g; mean ± SE) (Fig. 1C) but there was no significant effect of temperature on pupal weight (Table 2).

Temperature and foliar quality had a significant effect on the consumption rate of *O. amphimone* fifth-instar larvae (Fig. 2, Table 2).

Larvae in the mesic-high temperature treatment showed the highest RCR among the four treatments, which was nearly twice that of larvae in the xeric-high temperature treatment and more than three times that of larvae in the xeric-low temperature treatment (Fig. 2). There were no significant differences in RCR among the xeric-high, mesic-low, and xeric-low temperature treatments (Fig. 2).

DISCUSSION

Foliar quality

Water content and total phenolics were higher and leaf toughness was lower in leaves from the mesic compared to the xeric site. Generally, high water content and lower leaf toughness are considered to be characteristic of higher quality food for insect herbivores (Schoonhoven et al. 2005), and thus may be responsible for the positive effect of mesic foliage on the performance variables reported here. Interestingly, the slightly higher concentration of total phenolics in the mesic foliage reported in the current study had no negative effects on *O. amphimone* performance. Potentially, the lack of negative effects are related to the high chemical diversity of defensive compounds of *N. pumilio* leaves (Thoison et al. 2004), which is not apparent when measuring total phenolics alone.

TABLE 1

Mean (± SE) *Nothofagus pumilio* foliar quality traits in the mesic and xeric sites (n = 11 trees per site). Percentages are based on foliar dry weight (except for water content).

Media (± EE) de las características de calidad foliar de *Nothofagus pumilio* en el sitio mésico y en el xérico (n = 11 árboles por sitio). Los porcentajes están basados en peso seco (excepto para el contenido de agua).

	Mesic	Xeric	t	df	P
Water content (%)	64.5 ± 0.4	61.1 ± 0.8	3.2	20	< 0.001
Toughness (g mm ≥)	41.3 ± 1.1	44.5 ± 1.3	-1.9	20	0.07
Nitrogen (%)	2.38 ± 0.05	2.24 ± 0.09	2.1	20	0.1
Phosphorus (%)	0.19 ± 0.01	0.2 ± 0.01	-0.7	20	0.1
Organic matter (%)	95.7 ± 0.13	93.5 ± 0.23	8.9	20	< 0.001
Total phenolics (% GAE[a])	9.3 ± 0.4	7.9 ± 0.3	2.7	20	0.015

[a] Gallic Acid Equivalents
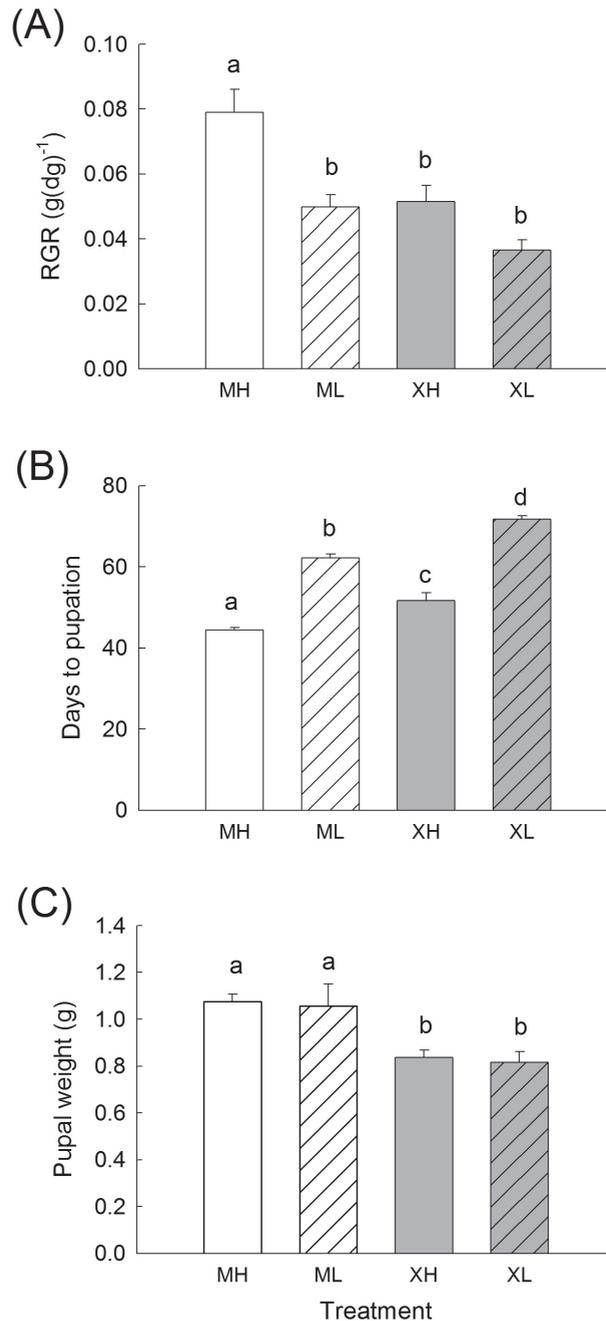
Fig. 1: (A) Mean (± SE) relative growth rate (RGR; see Methods for definition; *g*: grams; *d*: days) in the four treatments measured at five-day intervals. (B) Mean (± SE) development time (days to pupation) in the four treatments from the beginning of the experiment. (C) Mean (± SE) wet pupal weight (grams) of females for the four treatments. Treatments are: M, mesic foliage; X, xeric foliage; H, high temperature (20 °C); L, low temperature (15 °C). Bars designated with different letters indicate significant differences among treatments (Tukey test, P < 0.01).

(A) Media (± EE) de la tasa de crecimiento relativo (RGR; ver Métodos para la definición; *g*: gramos; *d*: días) en los cuatro tratamientos, medida a intervalos de cinco días. (B) Media (± EE) del tiempo de desarrollo (días hasta el pupado) en los cuatro tratamientos desde el comienzo del experimento. (C) Media (± EE) del peso húmedo (gramos) de las pupas hembra en los cuatro tratamientos. Los tratamientos son: M, follaje mésico; X, follaje xérico; H, temperatura alta (20 °C); L, temperatura baja (15 °C). Las barras con letras diferentes indican diferencias significativas entre tratamientos (prueba de Tukey, P < 0.01).

TABLE 2

Effects of temperature (high versus low) and foliage source (mesic versus xeric) on relative growth rate (RGR), development time, larval survival, female pupal weight, and relative consumption rate (RCR) tested by two-way ANCOVA (initial larval weight was used as a covariable).

Efectos de la temperatura (alta versus baja) y de la procedencia del follaje (mésico versus xérico) sobre la tasa de crecimiento relativa (RGR), el tiempo de desarrollo, la supervivencia larval, el peso de pupas hembra y la tasa de consumo relativo (RCR) evaluados mediante ANCOVA de dos vías (el peso inicial de las larvas fue usado como covariable).

	Source	df	F	P
RGR	Temperature	1, 32	20.69	< 0.001
	Foliage	1, 32	23.93	< 0.001
	Temperature x Foliage	1, 32	1.27	0.27
	Initial weight	1, 32	10.80	0.003
Development time	Temperature	1, 32	303.09	< 0.001
	Foliage	1, 32	58.51	< 0.001
	Temperature x Foliage	1, 32	1.12	0.28
	Initial weight	1,32	4.65	0.039
Larval survival	Temperature	1, 32	0.16	0.89
	Foliage	1, 32	0.26	0.61
	Temperature x Foliage	1, 32	2.91	0.09
	Initial weight	1, 32	4.57	0.04
Female pupal weight	Temperature	1, 32	0.05	0.82
	Foliage	1, 32	13.82	0.001
	Temperature x Foliage	1, 32	0.02	0.88
	Initial weight	1, 32	0.82	0.37
RCR	Temperature	1, 37	10.09	0.003
	Foliage	1, 37	22.86	< 0.001
	Temperature x Foliage	1,37	2.57	0.118
	Initial weight	1,37	22.06	< 0.001

Although the reported variation in foliage quality between sites may have contributed to the observed differences in herbivore performance and consumption, it is probable that other foliar traits, such as specific phenolic compounds (e.g., flavonoids), were also important. Additionally, qualitative rather than quantitative variation in foliar nitrogen could be responsible for the observed differences in performance. Although generally not measured, variation in the protein quality in a diet can significantly affect the performance and survival of herbivorous insects (Felton 1996). Independently of which foliar traits are responsible for generating the observed differences in herbivore performance, it is clear that *O. amphimone* larvae fed with foliage from the mesic site showed higher performance and RCR than those fed with foliage from the xeric site.

In assessing food quality effects on insect performance it is important that the study subjects do not have prior preference for any of the food qualities offered (i.e. parental effects on feeding preference should be minimal). Insects growing on certain diets may produce offspring that perform better on similar diets, even if these are of lower nutritional quality (Rotem et al. 2003). Given that all the larvae in our experiment were collected at the mesic site, our experimental design may be limited in this aspect. In order to confirm that foliage from the mesic site favors *O. amphimone* performance independently from the origin of the larvae, we would have to include individuals from the xeric site in our experiment. In practice, this was not possible due to the extremely low density of *O. amphimone* populations in the xeric *N. pumilio* forests. Exhaustive searches

for *O. amphimone* egg clusters and larvae at several mesic and xeric sites during three consecutive seasons yielded a difference in egg cluster density of approximately 1:20 (xeric to mesic). This observation suggests that conditions in the xeric environments sustain markedly lower densities of *O. amphimone* than mesic sites. Therefore, although we cannot formally confirm that foliage from the mesic site favors *O. amphimone* performance independently of the origin of the larvae, our field observations and Mazía et al. (2004, 2009) findings on the incidence of herbivorous chewing insects imply that xeric foliage is less suitable for *O. amphimone* than mesic foliage.

Performance and consumption

Higher temperature and mesic foliage increased RGR and consequently shortened development time of *O. amphimone*. Our findings concur with multiple studies that have found positive relationships between development time of lepidopteran species, and

temperature and foliage quality (e.g., Stamp & Bowers 1990, Lindroth et al. 1997, Levesque et al. 2002). Nevertheless, there were no interactions between temperature and foliage quality on *O. amphimone* performance. Most of the previous studies that evaluated the combined effects of temperature and foliage quality found some interaction between these factors. The lack of interactions in the current study may be related to the small differences in foliage quality between treatments, as suggested by Levesque et al. (2002) in their study of forest tent caterpillar *Malacosoma disstria* Hübner.

Although higher temperature significantly shortened the feeding period of *O. amphimone*, pupal weight was not reduced in the high temperature treatments. One explanation for this observation is that although the feeding stage is commonly shortened at higher temperatures, larvae have higher consumption rates, attaining similar pupal weight as those with a longer larval stage (a process known as "compensatory feeding"; Slansky 1993). Compensatory feeding may explain why pupal
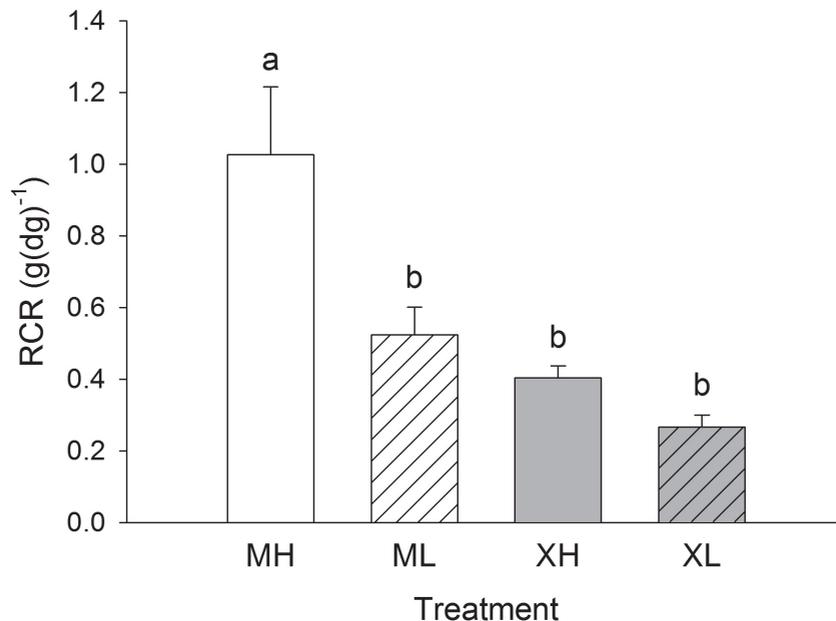
Fig. 2: Mean (± SE) relative consumption rate (RCR; see Methods for definition; g: grams; d: days) per fifth-instar larva per day for the four treatments: M, mesic foliage; X, xeric foliage; H, high temperature; L, low temperature. Different letters indicate significant differences among treatments (Tukey test, P < 0.05).

Media (± EE) de la tasa de consumo relativo (RCR; ver Métodos para la definición; g: gramos; d: días) por larva por día en quinto instar en los cuatro tratamientos: M, follaje mésico; X, follaje xérico; H, temperatura alta; L, temperatura baja. Las letras diferentes indican diferencias significativas entre tratamientos (prueba de Tukey, P < 0.05).

weight was not reduced in the mesic-high temperature treatment compared to the mesic-low temperature treatment in which larvae experienced a longer feeding period. On the other hand, the similar pupal weight of *O. amphimone* between the xeric-high temperature and xeric-low temperature treatments cannot be entirely explained by compensatory feeding because larvae in the xeric-high temperature treatment did not show significantly greater RCR than larvae in the xeric-low temperature treatment. A potential explanation for the similar pupal weight between the two xeric foliage treatments may be related to larval assimilation efficiency. At lower temperatures, assimilation efficiency may have been reduced (Schroeder & Lawson 1992); thus, although larvae at the low temperature treatment had more time to feed, they gained less biomass due to low assimilation efficiencies.

Implications for O. amphimone *population dynamics*

Assuming that the general trends in the responses to temperature and food quality we documented for *O. amphimone* under laboratory conditions apply in natural ecosystems, our results suggest that under the current and predicted temperature increase in Patagonia (Carril et al. 1997, Villalba et al. 2003) the performance and consumption rate of *O. amphimone* may increase, primarily in areas located in the mesic portion of the gradient. Although warming is commonly expected to favor the occurrence of outbreak events for many insect species (Robinet & Roques 2010), insect populations have been shown to respond in multiple ways to climate warming trends. While some species of Lepidoptera, such as the pine processionary moth (*Thaumetopoea pityocampa* [Denis & Schiffermüller]) in north-central France, expanded their outbreak range to previously unaffected regions (Battisti et al. 2005); other species, such as larch bud moth (*Zeiraphera diniana* Gn.) in the Alps, have diminished the frequency of outbreak events with warming, apparently due to asynchrony between egg hatch and budburst (Büntgen et al. 2009). Furthermore, outbreaks of the same Lepidoptera species may respond differently to

the same climatic trend in different portions of the species' geographic range (Thomson et al. 1984, Swetnam & Lynch 1993). Consequently, despite the likelihood that warming may increase the performance and consumption of *O. amphimone* in *N. pumilio* forests, there are important sources of uncertainty in predicting future population dynamics of this defoliator and the frequency and severity of defoliation events.

Factors not examined in this study can also have significant effects on *O. amphimone* population dynamics and/or *N. pumilio* susceptibility to attack, which could override the direct effects of temperature and food quality. For instance, changes in temperature regimes can influence pathogen and parasitoid incidence (Ayres & Lombardero 2000, Stireman et al. 2005), which in turn can interact in complex ways with the direct effects of temperature. Furthermore, warmer temperatures may cause phenological asynchrony between larval emergence and budburst that may generate significant population fluctuations (van Asch & Visser 2007). Warming trends may also affect plant nutritional quality of foliage and defenses (Ayres & Lombardero 2000), which in turn may affect population dynamics of *O. amphimone*. Therefore, additional experimentation with temperature influences on predation rates, host plant quality (including defenses) and phenological synchrony are needed to better understand the *Ormiscodes-Nothofagus* system. Nevertheless, the findings of the current study combined with documented and reconstructed defoliation events (Paritsis & Veblen 2011) provide a preliminary expectation that warming temperatures will likely enhance the performance and consumption rate of *O. amphimone* in northwestern Patagonia, particularly in more mesic *N. pumilio* forests.

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