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Abstract Studies of herbivory and its consequences on the growth of native and exotic plants could help elucidate some processes involved in plant invasions. Introduced species are likely to experience reduced herbivory in their new range due to the absence of specialist enemies and, thus, may have higher benefits if they reduce the investment in resistance and increase their compensatory capacity. In order to evaluate the role of herbivory in disturbed areas within the Patagonian steppe, we quantified and compared the leaf levels of herbivory of four native and five exotic species and recorded the associated insect fauna. We also performed greenhouse experiments in which we simulated herbivory in order to evaluate the compensatory capacity of native and exotic species under different herbivory levels that resembled naturally occurring damage. Natural herbivory levels in the field were similar between the studied exotic and native plants. Field observations confirmed that they both shared some herbivore insects, most of which are generalists. In the greenhouse experiments, both exotic and native plants fully compensated for herbivory. Our results suggest that the studied exotic plants are not released from herbivory in the Patagonian steppe but are able to fully compensate for it. The capacity to recover from herbivory coupled with other potential adaptations, such as a better performance under disturbance and greater competitive ability than that of the native species, may represent some of the mechanisms responsible for the success of plant invasion in the Patagonian steppe.

Keywords Herbivorous insect · Leaf herbivory · Plant compensation · Plant invasion · Tolerance

Introduction

Herbivory is a key interaction in most terrestrial communities. Since native and exotic plants may suffer from different amounts of leaf damage and respond differently to the loss of foliar tissue, studies of herbivory and its consequences on the growth of native and exotic plants are crucial to understanding processes involved in plant invasions.

Introduced species are likely to experience reduced herbivory in their new range due to the absence of specialist enemies (one of the premises of the enemy release hypothesis; Elton 1958; Keane and Crawley 2002). This decrease in regulation by herbivores and other natural enemies in the invaded region may result in a rapid increase in the distribution and abundance of the invader. Evidence gathered so far supporting this hypothesis is still poor and contradictory (Colautti et al. 2004; Liu and Stiling 2006). There are even some studies showing that herbivory can have strong negative effects on invader establishment and individual performance (Levine et al. 2004). This is because many exotic plants may escape their co-evolved herbivores when they invade a new region, but suffer considerable pressure from the native generalist herbivores in their new ranges.

Herbivores can often severely damage plant tissues and negatively affect plant reproduction (Strauss and Agrawal 1999). Thus, they exert an important selective force that favors anti-herbivore defenses, i.e., traits that allow plants to resist or tolerate consumption (Stowe et al. 2000). Tolerance is the ability to re-grow and/or reproduce after damage (Rosenthal and Kotanen 1994; Strauss and Agrawal 1999). Several mechanisms are involved in the plants' recovery from herbivory; for instance, increased net photosynthetic rate, high relative growth rates, increased branching or tillering after release of apical dominance, and the ability to shunt

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carbon stores from roots to shoots (Strauss and Agrawal 1999). The plants' origin (i.e., exotic or native) could affect their responses to herbivory. A higher investment in tolerance is expected in invasive plants in their new range if released from their enemies. This is a consequence of the existing trade-off between resistance and tolerance (the evolution of increased competitive ability hypothesis, or EICA hypothesis: Blossey and Nötzold 1995; Strauss and Agrawal 1999). Several studies support this idea (Blossey and Nötzold 1995; Rogers and Siemann 2004; Stastny et al. 2005; Zou et al. 2008). In invaded areas of arid Patagonia (Argentina), it is unknown whether exotic plants are released from herbivory or whether they have higher compensatory capacity than native plants, although these factors could help to clarify the mechanisms that favor their invasion.

Exotic plant species occur frequently in the Argentinean Patagonia (Rapoport 1993; Speziale and Ezcurra 2011), where they are considered one of the most significant threats to the native biota (Aizen et al. 2002). Disturbed areas such as roadsides usually present a high abundance of invasive species such as *Carduus thomeri*, *Verbascum thapsus* and *Marrubium vulgare*, a reduced abundance of the native plant species such as *Pappostipa speciosa* and *Mulinum spinosum* (Margutti et al. 1996), and are considered key areas for the dispersion of exotic plants (Rapoport 1991; Farji-Brener and Ghermandi 2008). Some studies have focused on herbivory in the Patagonian steppe, most of which examine the effects of livestock grazing on community functioning (e.g., Aguiar and Sala 1998; Golluscio et al. 2011). Roadside areas have a low presence of mammalian herbivores since livestock is fenced out of roads and kept inside nearby ranches ("estancias"). In these areas, insects seem to be responsible for most of the damage observed on plants. For example, the leaf-cutter ant *Acromyrmex lobicornis* harvests great quantities of plant material from at least 30 species, half of them exotics (Franzel and Farji-Brener 2000). There are also aphids, which occur in both exotic and native plants (Lescano and Farji-Brener 2010). Aside from these studies, there is no information on the interaction between insect herbivores and plants in this region.

The aim of this study was to quantify and compare leaf herbivory levels of native and exotic species and to study the associated insect fauna in a disturbed area of the Patagonian steppe. We further performed two greenhouse experiments in which we simulated herbivory in order to evaluate the compensatory capacity of native and exotic species under different herbivory levels. If enemy release is a plausible hypothesis for explaining the high abundance of exotic plant species in this area, we expect lower herbivory to occur on exotic plant species than on native plant species, and we predict a negative effect of foliar damage on plant growth. According to the evolution of the increased competitive ability hypothesis, we also expect the native plants' growth to be more affected than the exotic plants' growth. Through this study, we intend to expand the

understanding of some mechanisms, such as enemy release and increased competitive ability, which may be involved in biological invasions.

Methods

Study area

The study was carried out at the eastern border of the Nahuel Huapi National Park, located in northern Patagonia, Argentina (41°S, 72°W). Sampling was performed in a continuous area in roadside steppes along 20 km of both sides of the National Road 40 (~80 ha). Disturbance, caused mainly by the presence of the road, was homogeneous within this area, as was the altitude, with a mean of 728 m a.s.l. The dominant vegetation is a mix of native species typical of the Patagonian steppes (e.g., *Pappostipa speciosa*, *Mulinum spinosum*, *Imperata condensata* and *Plagiobotris tinctorius*), and exotic herbs (e.g., *Bromus tectorum*, *Onopordon acanthium*, *Carduus thomeri* and *Verbascum thapsus*) (Correa 1969–1998).

Most exotic species in the area were introduced after the settlement of Europeans, around 300 years ago. However, the distribution of exotic species has increased greatly over the last 30 years. In particular, Nahuel Huapi National Park has shown a noticeable increase of exotic species (e.g., Ezcurra and Brion 2005; Margutti et al. 1996). A recent study in northwestern Patagonia, Speziale and Ezcurra (2011), found a negative relationship between the richness of the alien species and the distance from urbanized areas in the steppe, suggesting that these plants are spreading outward from the cities.

Field measurements

Foliar herbivory

We measured herbivory in five exotic and four native species (Table 1). These species were chosen because they are abundant in the area where we conducted our

Table 1 Family, life form, life cycle and origin of plant species used in this study

Plant species	Family	Life form, life cycle	Origin
<i>Carduus thomeri</i>	Asteraceae	Forb, biennial	E
<i>Lactuca serriola</i>	Asteraceae	Forb, annual	E
<i>Marrubium vulgare</i>	Lamiaceae	Forb, perennial	E
<i>Onopordon acanthium</i>	Asteraceae	Forb, biennial	E
<i>Verbascum thapsus</i>	Scrophulariaceae	Forb, biennial	E
<i>Baccharis salicifolia</i>	Asteraceae	Shrub, perennial	N
<i>Conyza lechleri</i>	Asteraceae	Forb, annual	N
<i>Oenothera odorata</i>	Onagraceae	Forb, biennial	N
<i>Solidago chilensis</i>	Asteraceae	Forb, annual	N

E Exotic, N native

study, the driest part of Nahuel Huapi National Park, Argentina, and are representative of the local flora (Farji-Brener and Ghermandi 2000, 2004; Farji-Brener et al. 2010; see also Correa 1969–1998). The exotic species are highly invasive; they occur in the area of our study, as well as in a big sector of Argentina (they are present in 10–19 out of 23 provinces of Argentina) and in adjacent countries (Brazil, Chile, Paraguay and Uruguay) (Zuloaga et al. 2008). In particular, Speziale and Ezcurra (2011) found that *Carduus thomeri*, *Lactuca serriola* and *Verbascum thapsus* are among the 24 most invasive species in northwestern Patagonia. Unfortunately, there were no congeneric pairs of native and exotic species in the area, which would have allowed us to make phylogenetically controlled comparisons (Agrawal and Kotanen 2003). We are aware that this is a limitation of our approach, and we will discuss its implications for our results.

We used two different techniques to measure foliar herbivory in the field: punctual measurements and an estimation of herbivory rates (Coley 1980). The former consists of measuring the consumed area in several random leaves at one point in time in order to account for the extent of the herbivory a leaf had suffered before our measurement. The latter consists of measuring herbivory in previously marked leaves, obtaining information on the consumed area per unit time, i.e., herbivory rates. Although punctual measurements are used frequently because they are a faster method for estimating herbivory, we assessed herbivory rates as well, because punctual measures do not include totally consumed leaves, and therefore may underestimate the actual herbivory rates (García-Robledo 2005).

Foliar herbivory was measured in 20 randomly chosen adult individuals of each species (Table 1) during the summer (January–March 2008). We selected individuals that were separated from each other by at least 10 m, and we made sure that the floristic composition in their neighborhood was similar. For punctual herbivory, the percentage of damaged tissue in each leaf of an individual (first year rosettes in *Carduus thomeri*, *Onopordon acanthium* and *Verbascum thapsus*) or a randomly chosen branch (*Baccharis salicifolia*, *Marrubium vulgare*, *Oenothera odorata*) was measured. As for herbivory rates, an expanding leaf of each individual was marked with a thin aluminum strip placed around the petiole. After 4 weeks, each marked leaf was examined and the damaged area was estimated.

In order to estimate leaf damage by herbivores, we visually assessed the missing or altered area of the leaf and assigned each leaf to the following categories: 0, 0.1–5, 5.1–25, 25.1–50 and 50.1–100 % area consumed. To test the accuracy of our field observations, we photographed ten leaves of different individuals per species and compared visual estimations of herbivory in the field using the program Sigma Scan Pro. In 91 % of the cases ($N = 90$) categories were well assigned.

For the punctual herbivory technique, we estimated the percentage of individuals and of leaves with signs of

herbivory. The percentage of foliar damage per individual was calculated by multiplying the number of leaves of each damage category by the mid-point of each category (i.e., 0, 2.5, 15, 37.5 and 75 %, respectively) and dividing that result by the total number of leaves of the individual. For the herbivory rate technique, we estimated the percentage of marked leaves with signs of herbivory, and the mean percentage of the damaged area among all marked leaves. Since each sampling technique had a different experimental unit (i.e., the individual for punctual herbivory and the leaf for rates of herbivory), we chose random leaves from the punctual herbivory technique sample for statistical comparisons of the results of both techniques. The percentage of leaf damage was compared using a Wilcoxon matched paired test per species, where leaves from the same individual but measured with the different techniques constituted a pair. In this case, N was often lower than 20 since several marked leaves died during the 4 weeks encompassing the rates of herbivory technique.

We recorded the type of foliar herbivory damage in the same sampled individuals, which provides indirect information about the identity of the consumers. We assigned leaf damage to three categories: (1) complete tissue loss, either on the leaf edge or as holes in the leaf lamina, which evidences the presence of leaf chewing insects (mainly Lepidoptera larvae and Coleoptera); (2) consumed inner tissue with the dry epidermis remaining, which indicates the action of leaf miners or borers (most likely Diptera, Coleoptera, Lepidoptera and Hymenoptera); and (3) leaf deformations, such as curling or wilting, which indicate the presence of sucking insects (such as Hemiptera and Homoptera). A single leaf could have more than one type of damage.

The percentage of (1) individuals with foliar herbivory, (2) leaves with herbivory per individual, (3) leaf damaged tissue per individual, (4) complete tissue loss, and (5) consumed inner tissue was compared between exotic and native species. The Chi-square independence test was used for (1), while a nested ANOVA was used for (2–5). Species was considered as a random factor, nested within origin (exotic or native). Tukey contrasts were used to compare the variables between species. All response variables were examined to meet ANOVA assumptions and transformed when necessary.

Herbivore assemblage

In order to characterize the insect fauna associated with the studied plant species, we recorded observations of insects on individuals of all studied species, and collected specimens when possible. Observations and collections took place on the same individuals in which herbivory levels were measured, and on random individuals in the study area throughout the sampling season. A total of 79 observations and collections were made in 60–70 plant individuals per species. Specimens were stored in 90 % ethanol and identified to Order

and species (when possible) or morphospecies in the laboratory.

We were not able to assess the degree of specialization of most insects found on the plants due to the lack of information available. However, we categorized insects into exclusive (i.e., those found only in a single plant species), and shared, (i.e., those found on at least two species), which likely act as surrogates of specialists and generalists, respectively. We compared the frequency of both categories between exotic and native species with a Chi-square independence test.

Greenhouse experiments

To evaluate the effects of foliar herbivory on plant growth in exotic and native species and the potential mechanisms involved in compensation, we performed two greenhouse experiments simulating herbivory. The first experiment (Exp. 1) involved three exotic (*Carduus thoermeri*, *Onopordon acanthium* and *Verbascum thapsus*) and one native species (*Oenothera odorata*). This subgroup of plant species was selected based on their performance under greenhouse conditions and on seed availability. In January–February 2008, we planted seeds of these species (harvested during December 2007 and January 2008 from around ten randomly chosen individuals per species) in single celled seedbeds with fertile commercial soil and placed them in a greenhouse. In March 2008, 20 seedlings of each species were transplanted individually into 13 × 10 × 4 cm trays with soil from the study area, which was collected in ten randomly chosen sites (blocks). It took several weeks for the plants to overcome the transplanting effect, so we started the experiment the following spring (November 2008) when the weather was warm again. We assigned each plant randomly to a treatment (simulated herbivory or control), with ten replicates of each combination per species, each one corresponding to a different soil sample. A systemic insecticide was sprayed on the plants and soil to prevent natural herbivory inside the greenhouse. Trays were regularly watered and always kept at field capacity. Before inflicting leaf damage, we measured the height (H_i) and the surface cover of each individual (C_i). The surface cover was estimated as the product of maximum width (w_1) and width of the axis perpendicular to it (w_2), and π , (i.e., an oval shape was assumed). We simulated leaf damage on assigned individuals by clipping one quarter of 50 % of the leaves, i.e., constituting a total of 12.5 % leaf area loss. We chose to apply this type of damage because, the most common type of damage was complete tissue loss, and, in general, fewer than 50 % of the leaves suffered herbivory (see “Results”). As for the amount of tissue loss, we wanted to represent the mean maximum levels of natural herbivory observed across species (~10 % leaf tissue loss). At week 12, after measuring the height (H_i) and the surface cover (C_i), we removed plants from the substrate and washed and dried them at 60 °C for 1 week. Total, root and shoot dry

biomass was then weighed for each individual. *Oenothera odorata* was the only species to produce flowers during the experiment. We recorded the total number of flowers produced per individual during the experiment.

The second experiment (Exp. 2) differed from Exp. 1 in the number of species included, the timing, and the level of damage applied. In this case, two other native species (*Conyza lechleri* and *Solidago chilensis*) survived in the greenhouse and were therefore included in the experiment, resulting in a total number of six species, three exotic and three native. The seeds of the six species were planted in seedbeds in September 2008 and transplanted into experimental trays in January 2009. We kept the same proportion of damaged leaves as in Exp. 1 (i.e., 50 %), but this time, we clipped two-thirds of each leaf, i.e., we simulated 33 % area loss, the maximum value observed in the field (*Carduus thoermeri*). Applying higher levels of herbivory would have been unrealistic. We measured the same variables as in Exp. 1 before inflicting the damage and after 12 weeks. Few *Conyza lechleri* seeds germinated in the seedbeds, so there were only five replicates for each treatment initially performed. In this experiment, *Conyza lechleri* produced branches and *Oenothera odorata* and *Solidago chilensis* had basal sprouts. We counted the number of branches and sprouts in order to analyze their potential role in compensation.

The percentage increase in plant height $H_f/H_i \times 100$ and the surface cover $C_f/C_i \times 100$ was calculated for the 12-week period for each experiment. These variables, as well as the total final dry biomass and the root:shoot ratio were analyzed in a nested ANOVA per variable. The factors included were origin (exotic or native), species (random and nested within origin), treatment (simulated herbivory or control), and soil samples (random blocks). Also, the number of *Oenothera odorata* flowers in Exp. 1, and the number of branches in *C. lechleri* and sprouts in *Oenothera odorata* and *Solidago chilensis* in Exp. 2 were analyzed in one-way ANOVAs, with treatment as the factor.

Results

Field measurements

The percentage of leaf damage did not differ between punctual herbivory and herbivory rate techniques. Comparisons were not significant for any species (Wilcoxon matched paired test, Table 2), which means that both techniques are equivalent in the studied system. Therefore, we only report data with the punctual herbivory technique since sampling was more exhaustive (we measured all the leaves within individuals).

The percentage of individuals with foliar herbivory did not differ between exotic and native species (70 and 79 % for exotic and native respectively; $X_1^2 = 1.76$, $P = 0.18$; inset in Fig. 1a). In all species, except for *Conyza lechleri*, half or more of the inspected individuals

Table 2 Comparison of percentage of leaf damage (mean \pm SE) estimated with punctual herbivory and herbivory rates techniques. Significance of Wilcoxon matched paired test (P) is shown for each species

Species	Leaf damage (%)		N	P
	Punctual herbivory	Herbivory rates		
<i>Carduus thoermeri</i> (E)	17.5 \pm 3.3	23.5 \pm 6.2	17	0.31
<i>Lactuca serriola</i> (E)	0.3 \pm 0.2	4.7 \pm 4.7	16	1
<i>Marrubium vulgare</i> (E)	0	0	17	1
<i>Onopordon acanthium</i> (E)	1.0 \pm 0.3	1.3 \pm 0.8	19	0.71
<i>Verbascum thapsus</i> (E)	0.1 \pm 0.1	0.1 \pm 0.1	20	1
<i>Baccharis salicifolia</i> (N)	0.3 \pm 0.2	0.8 \pm 0.3	16	0.31
<i>Conyza lechleri</i> (N)	0	0	11	1
<i>Oenothera odorata</i> (N)	3.2 \pm 2.3	5.9 \pm 4.3	17	0.55
<i>Solidago chilensis</i> (N)	0.3 \pm 0.2	7.7 \pm 5.4	15	0.20

E Exotic, N native

showed signs of foliar herbivory. This percentage was especially high for *Carduus thoermeri* (100 %), *Baccharis salicifolia*, *Solidago chilensis*, *Oenothera odorata* (90 %) and *Verbascum thapsus* (80 %) (Fig. 1a).

Plant origin did not affect the percentage of leaves with herbivory per individual ($F_{1,171} = 0.03$, $P = 0.95$), but plant species had a significant effect ($F_{7,171} = 19.9$, $P < 0.001$; ANOVA). *Carduus thoermeri* had the highest percentage of leaves with herbivory (> 50 %), while *Marrubium vulgare* and *Conyza lechleri* had the lowest (< 3 %). The other species showed intermediate levels of leaves with herbivory ($P < 0.05$, Tukey test; Fig. 1b).

The percentage of damaged leaf tissue was similar between exotic and native species ($F_{1,171} = 0.19$, $P = 0.67$). Again, significant differences were detected among species ($F_{7,171} = 20.04$, $P < 0.001$; ANOVA). The percentage of damaged leaf tissue was highest in *Carduus thoermeri* (11 %), intermediate in *Baccharis salicifolia*, *Solidago chilensis* and *Oenothera odorata* (2–3 %) and below 1 % in the other species ($P < 0.05$, Tukey test; Fig. 1c).

The most common type of damage in all species (except for *Lactuca serriola*), was complete tissue loss (i.e., performed by chewing insects). No differences were detected in this variable between native and exotic species ($F_{1,125} = 1.17$, $P = 0.31$). However, species differed significantly in the percentage of leaves that showed complete tissue loss ($F_{7,125} = 5.26$, $P < 0.001$; ANOVA), with *Lactuca serriola* presenting the lowest values and *Carduus thoermeri* and *Verbascum thapsus*, the highest ones (Fig. 2a). The proportion of inner tissue consumed, which indicates the action of leaf miners or borers, did not differ between exotic and native ($F_{1,125} = 0.27$, $P = 0.61$), but differed among species ($F_{7,125} = 7.16$, $P < 0.001$; ANOVA). *Lactuca serriola* and *Oenothera odorata* presented the highest proportions of this type of damage while *Verbascum thapsus*, *Carduus thoermeri* and *Solidago chilensis*, had the lowest ones (Fig. 2b). Leaf deformations, which indicate the presence of sucking insects, were observed only in *Bac-*

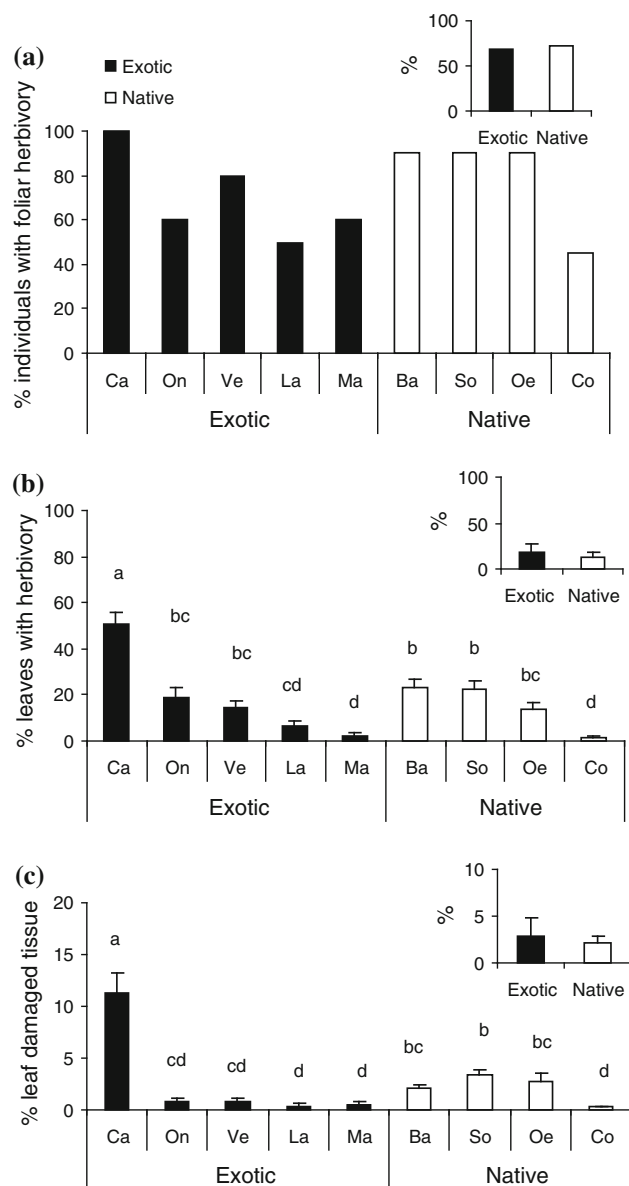


Fig. 1 Percentage of **a** individuals and mean percentage (+SE) of **b** leaves with herbivory, and **c** leaf area damaged, of *Carduus thoermeri* (Ca), *Onopordon acanthium* (On), *Verbascum thapsus* (Ve), *Lactuca serriola* (La), *Marrubium vulgare* (Ma), *Baccharis salicifolia* (Ba), *Solidago chilensis* (So), *Oenothera odorata* (Oe) and *Conyza lechleri* (Co). Insets Frequencies (a) and mean percentage (+SE) (b, c) of all exotic and native species. In b and c different letters indicate significant differences ($P < 0.05$) with Tukey comparisons

charis salicifolia, *Solidago chilensis* and *Conyza lechleri*, and in a very low percentage of leaves (5.6 ± 2.5 , 0.3 ± 0.3 and 5.6 ± 5.6 % of leaves, respectively).

A total of 42 insect morphospecies belonging to six Orders (Coleoptera, Hemiptera, Homoptera, Hymenoptera, Orthoptera and Lepidoptera) were identified among the 79 collections and observations made on the studied plants (Fig. 3). Insects of the Order Coleoptera predominated on *Carduus thoermeri*, *Verbascum thapsus*, *Lactuca serriola* and *Oenothera odorata*. Hymenoptera

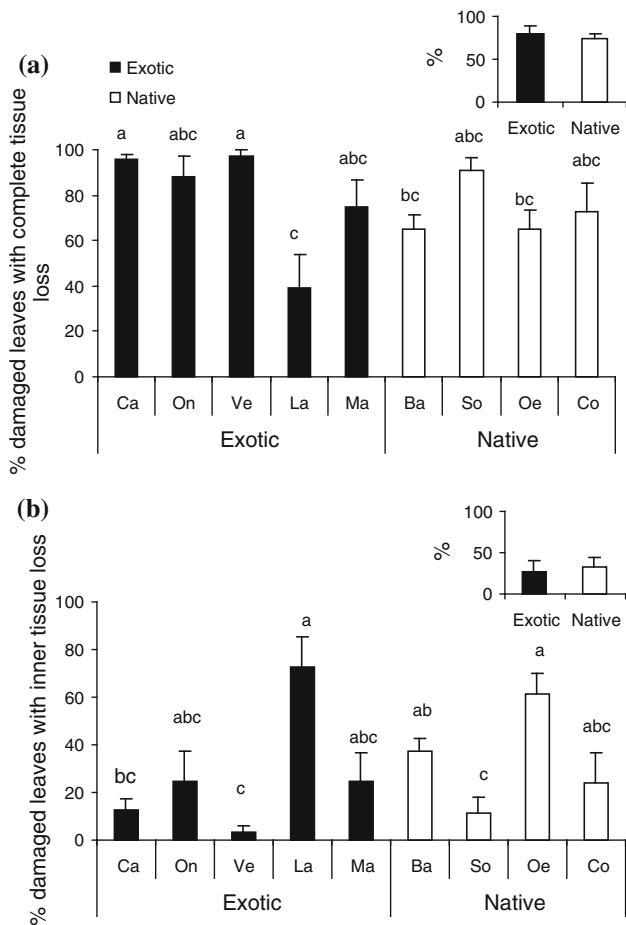


Fig. 2 Mean percentage (+SE) of damaged leaves with **a** complete tissue loss and **b** with inner tissue loss of *Carduus thoermeri* (Ca), *Onopordon acanthium* (On), *Verbascum thapsus* (Ve), *Lactuca serriola* (La), *Marrubium vulgare* (Ma), *Baccharis salicifolia* (Ba), *Solidago chilensis* (So), *Oenothera odorata* (Oe) and *Conyza lechleri* (Co). Insets Mean percentage (+SE) of all exotic and native species. Different letters indicate significant differences ($P < 0.05$) with Tukey comparisons

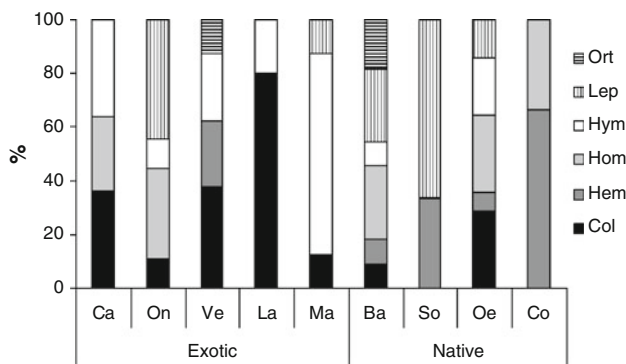


Fig. 3 Composition of insect herbivore assemblage observed on *Carduus thoermeri* (Ca), *Onopordon acanthium* (On), *Verbascum thapsus* (Ve), *Lactuca serriola* (La), *Marrubium vulgare* (Ma), *Baccharis salicifolia* (Ba), *Solidago chilensis* (So), *Oenothera odorata* (Oe) and *Conyza lechleri* (Co). Ort Orthoptera, Lep Lepidoptera, Hym Hymenoptera, Hom Homoptera, Hem Hemiptera, Col Coleoptera

(specially the leaf cutting ant *Acromyrmex lobicornis*) were found frequently on *Carduus thoermeri* and *Marrubium vulgare*, while Lepidoptera predominated on *Onopordon acanthium*, *Baccharis salicifolia* and *Solidago chilensis*. Finally, Homoptera (mainly aphids) were common on *Carduus thoermeri*, *Onopordon acanthium*, *Baccharis salicifolia*, *Oenothera odorata* and *Conyza lechleri*, and Hemiptera were found in a high percentage on *Conyza lechleri* (Fig. 3).

The type of damage recorded on leaves matched insect observations and collections, implying that insects found on the studied plants were most likely eating them. The most common type of damage was that inflicted by chewing insects and most plant species were characterized by Coleoptera, Lepidoptera and Hymenoptera (mainly leaf-cutting ants *Acromyrmex lobicornis*), which include a great number of chewing species. Moreover, leaf deformations were observed in *Conyza lechleri*, *Baccharis salicifolia* and *Solidago chilensis*, all of them characterized by Hemiptera and Homoptera (Fig. 3).

The frequency of exclusive insects was low and similar between native and exotic species: 37 and 32 % of insects found on native and exotic, respectively, were exclusive ($X^2_1 = 0.14$, $P = 0.29$), indicating that exotic species probably do not have a lower frequency of specialist insects and that there is a predominance of generalist insects consuming most species.

Greenhouse experiments

The increase in height, surface cover, final dry biomass, and root:shoot ratio of plants grown in the greenhouse were not affected by any simulated herbivory treatment or origin (Tables 3, 4). However, there were differences among species for the four variables in Exp. 1 and in increase in height, final dry biomass, and root:shoot ratio in Exp. 2 (Table 3). The number of flowers produced by *Oenothera odorata* individuals during Exp. 1 did not differ between treatments. Control plants produced 1.7 ± 0.3 flowers and treated plants 2.1 ± 0.5 flowers ($F_{1,9} = 2.25$, $P = 0.17$, one-way ANOVA). In Exp. 2, the number of branches per individual of *Conyza lechleri* was similar between treatments (5.4 ± 1.1 and 4.4 ± 0.7 , for control and treated plants, respectively; $F_{1,9} = 0.36$, $P = 0.58$, one-way ANOVA). Also, the number of basal sprouts in *Oenothera odorata* and *Solidago chilensis* was similar between treatments. *O. odorata* control plants had 1.1 ± 0.4 sprouts and treated plants had 1.2 ± 0.3 ($F_{1,9} = 0.06$, $P = 0.81$, one-way ANOVA). Control individuals of *Solidago chilensis* presented 2.3 ± 0.5 sprouts and treated individuals 1.7 ± 0.4 ($F_{1,9} = 1.32$, $P = 0.28$, one-way ANOVA).

Discussion

The level of natural foliar herbivory experienced by the measured plant species in roadsides within the

Patagonian steppe did not depend on their origin. The three response variables analyzed (percentage of individuals with foliar herbivory, leaves with herbivory per individual, and leaf damaged tissue per individual) showed consistently similar levels of foliar damage between exotic and native plants. These results differ from those of other studies that support the enemy release hypothesis, where exotic species experienced significantly lower leaf herbivory than native species in the same community (Carpenter and Cappuccino 2005; Cincotta et al. 2009). However, other studies also found similar estimates of herbivore damage between exotic and native species (Radho-Toly et al. 2001). Our results may be affected by phylogenetic constraints since we could not perform a rigorous phylogenetically controlled comparison between exotic and native species due to the absence of congeneric exotic and native pairs in the study area. We chose plants based on their abundance to better resemble natural conditions, with most exotic and native species belonging to the family Asteraceae and all of them, to different genera. Thus, phylogenetic variation was distributed similarly among exotic and native species.

The most important variations in herbivory levels occurred at the species level. Thus, the degree of foliar damage by native herbivores seems to be more dependent on species-specific traits than on plant origin. The studied plant species vary in their physical and chemical defenses and in their nutritional quality (Woodman and Fernandes 1991; de la Fuente et al. 1994; Zunino et al. 1997; Jordon-Thaden and Louda 2003; Schmeda-Hirshmann et al. 2005; Bushman et al. 2006; Farji-Brener et al. 2010), and local herbivorous insects may forage on different plant species depending on their feeding preferences, the chemical leaf quality, and the possibilities of avoiding plant defenses. For example,

Lactuca serriola contains latex, which has been reported to be toxic to most herbivores (Ramos et al. 2010). *Carduus thoermeri* and *Onopordon accanthium* have relatively high levels of foliar nutrients (Farji-Brener and Ghermandi 2008; Farji-Brener et al. 2010), and this could explain their high damage levels reported in this study. Thus, plants in this study have a great variety of defenses, even when six of them belong to the same family.

When we studied the herbivore assemblage associated with the studied plants, we found that the exotic species had a similarly low frequency of exclusive insects, likely specialists, as did the native species, and that there were many shared insects among the exotic and native plants. The most common herbivore was the leaf-cutting ant, *Acromyrmex lobicornis*, which was observed harvesting six out of the nine studied plant species. This is not surprising since a previous study in the same area shows that these ants have a wide diet, including around 30 species, half of them exotics (Franzel and Farji-Brener 2000). This native ant species is conspicuous in the area and has a high colony density (43 nests ha⁻¹; Farji-Brener 2000). It has increased its natural range in the last decades through roads and rivers (Farji-Brener 1996). Consequently many of the exotic species that are expanding along disturbed areas, as well as many of the native species, may be subjected to herbivory by this ant. Also, several exotic and native species share the same aphid species, which are very common in the study site (Farji-Brener et al. 2009; Lescano and Farji-Brener 2010). Other studies have also reported the attack of introduced plants by generalist aphids (Memmott et al. 2000). Therefore, some exotic plants are hit upon by a diversity of generalist insects able to consume them when introduced in the Patagonian steppe, as has been observed in other systems (Parker and Hay 2005).

Table 3 ANOVA results from the greenhouse simulated herbivory experiments

Source	Effect	df	Increase in height (%)			Increase in surface cover (%)			Final dry biomass			Root:shoot		
			SS	F	P	SS	F	P	SS	F	P	SS	F	P
Exp. 1														
Origin	Fixed	1	14.82	8.11	0.10	32.96	1.64	0.33	0.79	0.10	0.79	2.19	1.11	0.40
Species (origin)	Random	2	3.61	4.44	0.02	39.71	8.88	<0.01	16.31	16.87	<0.01	3.87	52.65	<0.01
Treatment	Fixed	1	0.51	1.27	0.27	0.16	0.07	0.79	0.01	0.02	0.88	0.01	0.42	0.51
Block	Random	9	3.15	0.86	0.56	77.77	3.87	<0.01	34.92	8.03	<0.01	0.75	2.26	0.03
Origin × treatment	Fixed	1	0.04	0.11	0.74	0.17	0.08	0.78	0.13	0.27	0.60	0.02	0.53	0.46
Error	Fixed	64	26.00			143.06			30.92			2.35		
Exp. 2														
Origin	Fixed	1	7.01	3.93	0.12	0.14	0.025	0.88	7.28	1.24	0.33	16.29	2.25	0.20
Species (origin)	Random	4	7.51	4.78	<0.01	23.53	1.39	0.24	24.89	12.64	<0.01	30.86	66.76	<0.01
Treatment	Fixed	1	0.12	0.74	0.58	2.59	0.61	0.44	0.64	1.29	0.26	0.25	2.22	0.14
Block	Random	9	2.62	4.78	<0.01	36.43	0.96	0.48	24.79	5.59	<0.01	2.51	2.42	0.02
Origin × treatment	Fixed	1	0.07	0.30	0.67	6.66	1.58	0.21	0.30	0.61	0.43	0.07	0.60	0.44
Error	Fixed	93	36.51			392.70			45.79			10.75		

Exotic species were *Carduus thoermeri*, *Onopordon acanthium* and *Verbascum thapsus* and native species were *Oenothera odorata* in Exp. 1 and also *Conyza lechleri* and *Solidago chilensis* in Exp. 2 (see "Methods"). Treatment included control individuals with no clipping and treated individuals with 12.5 % (Exp. 1) and 33 % foliar area removed (Exp. 2)

Table 4 Mean \pm SE of increase in height (%), increase in surface cover (%), final dry biomass and root:shoot ratio of the exotic species (E) *Carduus thomeri* (Ca), *Onopodon acanthium* (On), *Verbascum thapsus* (Ve), and the native species (N) *Solidago chilensis* (So), *Oenothera odorata* (Oe) and *Conyza lechleri* (Co) subjected to no simulated herbivory (C) or 12.5 % (Exp. 1) and 33 % (Exp. 2) leaf tissue loss (H)

Origin	Species	Increase in height (%)		Increase in surface cover (%)		Final dry biomass		Root:shoot		
		C	H	C	H	C	H	C	H	
Exp. 1										
E	Ca	81.1 \pm 12.0	102.4 \pm 15.7	210.8 \pm 46.9	206.0 \pm 22.8	1.2 \pm 0.2	1.1.0 \pm 0.2	0.85 \pm 0.09	0.94 \pm 0.13	
	On	155.4 \pm 19.0	143.7 \pm 19.9	405.0 \pm 74.5	424.2 \pm 76.9	1.7 \pm 0.2	1.1.5 \pm 0.3	1.01 \pm 0.04	0.91 \pm 0.04	
	Ve	121.5 \pm 10.8	150.7 \pm 22.6	354.6 \pm 62.2	286.7 \pm 62.7	2.2 \pm 0.5	2.2.5 \pm 0.5	0.39 \pm 0.04	0.39 \pm 0.04	
N	Oe	213.5 \pm 16.7	237.5 \pm 34.9	164.1 \pm 45.8	164.6 \pm 34.1	1.4 \pm 0.2	1.1.5 \pm 0.2	0.4 \pm 0.02	0.34 \pm 0.04	
Exp. 2										
E	Ca	85.2 \pm 11.3	103.3 \pm 9.3	216.9 \pm 31.1	255.4 \pm 79.0	1.3 \pm 0.2	1.1.2 \pm 0.2	1.06 \pm 0.11	1.20 \pm 0.12	
	On	77.1 \pm 12.1	69.14 \pm 4.08	215.2 \pm 36.3	182.8 \pm 40.8	2.5 \pm 0.2	2.2.1 \pm 0.2	0.79 \pm 0.05	0.75 \pm 0.06	
	Ve	101.2 \pm 10.5	126.5 \pm 18.6	145.0 \pm 16.8	194.7 \pm 33.2	1.7 \pm 0.3	1.1.4 \pm 0.3	0.55 \pm 0.07	0.58 \pm 0.05	
N	Oe	142.3 \pm 20.9	119.8 \pm 10.2	384.6 \pm 179.1	208.8 \pm 33.5	1.4 \pm 0.2	1.1.6 \pm 0.2	0.67 \pm 0.09	0.62 \pm 0.09	
	Co	243.2 \pm 64.1	214.8 \pm 89.1	115.0 \pm 13.9	184.5 \pm 27.3	3.1 \pm 0.2	1.1.6 \pm 0.2	1.94 \pm 0.32	2.05 \pm 0.26	
	So	97.9 \pm 11.1	114.7 \pm 9.4	219.5 \pm 31.0	159.9 \pm 19.0	2.5 \pm 0.3	2.2.4 \pm 0.4	2.06 \pm 0.08	2.05 \pm 0.26	

Simulated herbivory treatment was not significant for any variable or species (nested ANOVA, Table 3)

The fact that several exotic plants in the Patagonian steppe are consumed by generalist herbivores may suggest the existence of biotic resistance to plant invasion. However, in the greenhouse experiments, exotic and native plants which had lost 12.5 and 33 % foliar biomass at an early stage had a similar increase in height and surface cover, and attained a similar final dry biomass as the control plants, implying a full compensation of herbivory. Consequently, herbivory at natural levels is not detrimental to the individual performance of either exotic or native species under greenhouse conditions. The main mechanism involved is probably higher growth rates, because when we considered plant dimensions after clipping as initial size, we found a higher increase in surface cover in plants with simulated herbivory. This mechanism was demonstrated in other species such as the invasive ecotypes of *Sapium sebiferum* (Rogers and Siemann 2004) and *Salix planifolia* in North America (Houle and Simard 1996). In our study, life histories of the chosen species may influence this type of response. All plants employed in the experiments were annual or biennial (Table 1), and thus, they need to maximize their growth and reproductive output in their short life span. Consequently, they are probably adapted to quickly overcoming factors that may damage them through an increased growth rate. Resource allocation from roots to shoots (observed in studies by Briske et al. 1996; and Mabry and Wayne 1997) is not likely an acting mechanism because the root:shoot ratio was similar in treated and untreated plants. Another potential mechanism of tolerance is branching or tillering (Rosenthal and Welter 1995). Here, we observed some branching and sprouting, but only in native species and it did not differ between treatments. Yet, other mechanisms not explored here such as increased photosynthetic or decreased leaf longevity could be co-acting to enable plants to compensate for the damage (Strauss and Agrawal 1999).

The final impact of herbivory on fitness could not be assessed in the greenhouse due to the absence of pollinators and the duration of the experiment (e.g., seed production was impossible to measure). Nevertheless, plant size is widely considered to be a good estimator of fecundity because, within a species, larger plants often produce more seeds (Horvitz and Schemske 2002 and references therein). The only species that produced flowers during the experiments was *O. odorata*. When we explored flower production between treated and untreated plants, we found no differences in the number of flowers per individual, which is consistent with results based on plant size. Thus, plant size could be a good indicator of plant fitness in natural conditions.

The fact that compensation did not differ between exotic and native plants is not surprising when taking into account that herbivory levels are also similar. It has been proposed that in the absence of natural enemies in their introduced ranges, invasive plants will have higher benefits if they reduce the investment in resistance and increase their compensatory capacity (Blossey and Nötzold 1995). However, exotic plants in the Patagonian steppe still need to prevent herbivory by generalists. A recent work in the same study site shows how physical defenses of *Carduus thomeri* are efficient in decreasing the harvest by the generalist leaf-cutting ant *Acromyrmex lobicornis* (Farji-Brener 2007). The comparison of resistance and tolerance in the native ecotypes of the studied exotic species would be necessary to prove if tolerance has actually changed with respect to their native ranges.

This study shows that herbivory is unlikely to regulate the growth of the studied species. It is unknown whether higher levels of herbivory could have different consequences on plants, but we wanted to recreate herbivory levels in the greenhouse that were as close as possible to the naturally occurring conditions. Herbivory regulation on population dynamics may differ under

field conditions where there are other processes, such as competition and pollination, and other variables, such as weather conditions and disturbance and resource heterogeneity, that could influence the performance of plants when they face herbivory. However, field data for two of the species show consistent results between the field and the greenhouse. It should also be taken into account that in this study we focused on foliar herbivory, but other guilds of enemies (e.g., soil microbes, foliar fungi, seed predators) could be attacking native and introduced species as well (Agrawal and Kotanen 2003; Agrawal et al. 2005). In our system, seed predation by granivorous birds and insects was observed in exotic species, especially in *Carduus thoermeri*. Seed losses in this species may have an important impact on population growth as observed in its native range (Jongejans et al. 2006). Hence, exotic species are not escaping from seed predation, suggesting potential demographic consequences.

Finally, the studied exotic plants are not released from herbivory in the Patagonian steppe, contrary to the prediction of the enemy release hypothesis. Moreover, both native and exotic plants are able to fully compensate for foliar damages, and exotic plants do not display higher compensation than native ones, contrary to the evolution of the increased competitive ability hypothesis. Thus, these mechanisms are not likely involved in plant invasions in the area. Much of the difficulty in explaining the causes of plant invasions may stem from seeking a single explanation when invasions are more likely to result from multiple traits interacting with multiple features of a new range (Schierenbeck et al. 1994). The ability to compensate for herbivory at natural levels could be coupled with other differential adaptations in exotic plants. For example, human perturbations (e.g., nutrient enrichment, overgrazing by domestic livestock, decreased water flow and climate change) can reduce the adaptation of native species to their environment, decreasing their competitive ability in relation to exotic species (Mack et al. 2000). Here, the study area is located close to an important national road, where maintenance is obviously a source of disturbance. On the other hand, exotic species might have a greater competitive ability than native species as a result of different evolutionary histories (e.g., faster uptake of limiting resources, ability to maintain dense monocultures and high levels of allelopathy) (D'Antonio and Mahall 1991; Hamilton et al. 1999; Ridenour and Callaway 2001). Both hypotheses are worth exploring in future studies.

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References

- Agrawal AA, Kotanen PM (2003) Herbivores and success of exotic plants: a phylogenetically controlled experiment. *Ecol Lett* 6:712–715
- Agrawal AA, Kotanen PM, Mitchell CE, Power AG, Godsoe W, Klironomos J (2005) Enemy release? An experiment with congeneric plant pairs and diverse above and belowground enemies. *Ecology* 86:2979–2989
- Aguiar MR, Sala OE (1998) Interactions among grasses, shrubs and herbivores in Patagonian grass-shrub steppe. *Ecol Austral* 8:201–210
- Aizen M, Vazquez D, Smith-Ramirez C (2002) Historia natural y conservación de mutualismos planta-animal del bosque templado de Sudamérica austral. *Rev Chil Hist Nat* 75:79–97
- Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. *J Ecol* 83:887–889
- Briske DD, Boutton TW, Wang Z (1996) Contribution of flexible allocation priorities to herbivory tolerance in C-4 perennial grasses: an evaluation with ^{13}C labeling. *Oecologia* 105:151–159
- Bushman BS, Scholte AA, Cornish K, Scott DJ, Brichta JL, Vederas JC, Ochoa O, Michelmore RW, Shintani DK, Knapp SJ (2006) Identification and comparison of natural rubber from two *Lactuca* species. *Phytochemistry* 67:2590–2596
- Carpenter D, Cappuccino N (2005) Herbivory, time since introduction and the invasiveness of exotic plants. *J Ecol* 93:315–321
- Cincotta C, Adams JM, Holzapfel C (2009) Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). *Biol Invasions* 11:379–388
- Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecol Lett* 7:721–733
- Coley PD (1980) Effects of leaf age and plant life history patterns on herbivory. *Nature* 284:545–546
- Correa MN (1969–1998) Flora Patagónica, vol 7. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires
- D'Antonio CM, Mahall BE (1991) Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *Am J Bot* 78:885–894
- de la Fuente M-A, Dyer LA, Bowers MD (1994) The iridoid glycoside, catalpol, as a deterrent to the predator *Camponotus floridanus* (Formicidae). *Chemoecology* 5:13–18
- Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London
- Ezcurra C, Brion C (2005) Plantas del Nahuel Huapi, catálogo de la Flora Vascular del Parque Nacional Nahuel Huapi. Universidad Nacional del Comahue, Bariloche
- Farji-Brener AG (1996) Posibles vías de expansión de la hormiga cortadora de hojas *Acromyrmex lobicornis* hacia la Patagonia. *Ecol Austral* 6:144–150
- Farji-Brener AG (2000) Leaf-cutting ant nests in temperate environments: mounds, mound damages and nest mortality rate in *Acromyrmex lobicornis*. *Stud Neotrop Fauna Environ* 35:131–138
- Farji-Brener AG (2007) How plants may benefit from their consumers: leaf cutting ants indirectly improve anti-herbivore defenses in *Carduus nutans* L. *Plant Ecol* 193:31–38
- Farji-Brener AG, Ghermandi L (2000) The influence of nests of leaf-cutting ants on plant species diversity in road verges of northern Patagonia. *J Veg Sci* 11:453–460
- Farji-Brener AG, Ghermandi L (2004) Seedling recruitment in a semi-arid Patagonian steppe: facilitative effects of refuse dumps of leaf-cutting ants. *J Veg Sci* 15:823–830
- Farji-Brener AG, Ghermandi L (2008) Leaf-cutting ant nests near roads increase fitness of exotic plant species in natural protected areas. *Proc R Soc Lond Ser B Biol Sci* 275:1431–1440

- Farji-Brener AG, Gianoli E, Molina-Montenegro M (2009) Small-scale disturbances spread along trophic chains: leaf-cutting ant nests, plants, aphids, and tending ants. *Ecol Res* 24:139–145
- Farji-Brener AG, Lescano N, Ghermandi L (2010) Ecological engineering by a native leaf-cutting ant increases the performance of exotic plant species. *Oecologia* 163:163–169
- Franzel C, Farji-Brener AG (2000) Oportunistas o selectivas? Plasticidad en la dieta de la hormiga cortadora de hojas *Acromyrmex lobicornis* en el noroeste de la Patagonia. *Ecol Austral* 10:159–168
- García-Robledo C (2005) Comparación de dos métodos para medir herbivoría ¿Es la herbivoría en el Neotrópico mayor de lo que creemos? *Rev Biol Trop* 53:111–114
- Golluscio RA, Cavagnaro FP, Valenta MD (2011) Arbustos de la estepa patagónica: ¿adaptados a tolerar la sequía o el pastoreo? *Ecol Austral* 21:61–70
- Hamilton JG, Holzapfel C, Mahall B (1999) Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* 121:518–526
- Horvitz C, Schemske D (2002) Effects of plant size, leaf herbivory, local competition and fruit production on survival, growth and future reproduction of a neotropical herb. *J Ecol* 90:279–290
- Houle G, Simard G (1996) Additive effects of genotype, nutrient availability and type of tissue damage on the compensatory response of *Salix planifolia* ssp. *planifolia* to stimulated herbivory. *Oecologia* 107:373–378
- Jongejans E, Sheppard AW, Shea K (2006) What controls the population dynamics of the invasive thistle *Carduus nutans* in its native range? *J Appl Ecol* 43:877–886
- Jordon-Thaden IM, Louda SM (2003) Chemistry of *Cirsium* and *Carduus*: a role in ecological risk assessment for biological control of weeds? *Biochem Syst Ecol* 31:1353–1396
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol Evol* 17:164–170
- Lescano MN, Farji-Brener A (2010) Exotic thistles increase native ant abundance through the maintenance of enhanced aphid populations. *Ecol Res* 26:827–834
- Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecol Lett* 7:975–989
- Liu H, Stiling P (2006) Testing the enemy release hypothesis: a review and meta-analysis. *Biol Invasions* 8:1535–1545
- Mabry CM, Wayne PW (1997) Defoliation of the annual herb *Abutilon theophrasti*: mechanisms underlying reproductive compensation. *Oecologia* 111:225–232
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Margutti L, Ghermandi L, Rapoport E (1996) Seed bank and vegetation in a Patagonian roadside. *Int J Ecol Environ Sci* 22:159–175
- Memmott J, Fowler SV, Paynter Q, Sheppard AW, Syrett P (2000) The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. *Acta Oecol* 21:213–222
- Parker JD, Hay ME (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecol Lett* 8:959–967
- Radho-Toly S, Majer JD, Yates C (2001) Impact of fire on leaf nutrients, arthropod fauna and herbivory of native and exotic eucalypts in Kings Park, Perth, Western Australia. *Austral Ecol* 26:500–506
- Ramos MV, Grangeiro TB, Freire ED, Sales MP, Souza DP, Araújo ES, Freitas CDT (2010) The defensive role of latex in plants: detrimental effects on insects. *Arthropod Plant Interact* 4:57–67
- Rapoport EH (1991) Tropical versus temperate weeds: a glance into the present and future. In: Ramakrishnan P (ed) *Ecology of biological invasion in the tropics*. ISF, New Delhi, pp 11–51
- Rapoport EH (1993) The process of plant colonization in small settlements and large cities. In: McDonnell M, Pickett S (eds) *Humans as components of ecosystems*. Springer, New York, pp 178–196
- Ridenour WM, Callaway RM (2001) The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. *Oecologia* 126:444–450
- Rogers WE, Siemann E (2004) Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree *Sapium sebiferum*. *J Appl Ecol* 41:561–570
- Rosenthal JP, Kotanen PM (1994) Terrestrial plant tolerance to herbivory. *Trends Ecol Evol* 9:145–148
- Rosenthal JP, Welter SC (1995) Tolerance to herbivory by a stem-boring caterpillar in architecturally distinct maize and wild relatives. *Oecologia* 102:146–155
- Schierenbeck KA, Mack RN, Sharitz RR (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology* 75:1661–1672
- Schmeda-Hirshmann G, Jordan M, Gerth A, Wilken D (2005) Secondary metabolite content in rhizomes, callus cultures and in vitro regenerated plantlets of *Solidago chilensis*. *Z Naturforsch C* 60:5–10
- Speziale KL, Ezcurra C (2011) Patterns of alien plant invasions in northwestern Patagonia, Argentina. *J Arid Environ* 75:890–897
- Stastny M, Schaffner U, Elle E (2005) Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? *J Ecol* 93:27–37
- Stowe KA, Marquis RJ, Hochwender CG, Simms EL (2000) The evolutionary ecology of tolerance to consumer damage. *Annu Rev Ecol Syst* 31:565–595
- Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. *Trends Ecol Evol* 14:179–185
- Woodman RL, Fernandes GW (1991) Differential mechanical defense: herbivory, evapotranspiration, and leaf-hairs. *Oikos* 60:11–19
- Zou J, Rogers WE, Siemann E (2008) Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum*. *Biol Invasions* 10:291–302
- Zuloaga FO, Morrone O, Belgrano MJ (2008) Catálogo de las plantas vasculares del Cono Sur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay). Missouri Botanical Garden Press
- Zunino MP, Novillo-Newton M, Maestri DM, Zygadlo JA (1997) Composition of the essential oil of *Baccharis crispa* Spreng. and *Baccharis salicifolia* Pers. grown in Cordoba (Argentina). *Flavour Fragr J* 12:405–407