

# Insect herbivory in climber–host shrubs associations: Benefit or detriment?

YAMILA SASAL\* AND MARÍA LAURA SUAREZ

*Laboratorio Ecotono, Instituto de Investigación en Biodiversidad y Medioambiente (INIBIOMA),  
Universidad Nacional del Comahue-CONICET, Pasaje Gutiérrez 1125, (8400), S. C. de Bariloche,  
Río Negro, Argentina (Email: yamila.sasal@conicet.gov.ar; shamilacony@gmail.com)*

**Abstract** Spatial proximity between different plant species could modify the sign (positive or negative) of plant–herbivore interaction. The chance of a plant being detected and colonized by herbivorous insects depends not only on the plant’s own traits but also on the identity of the neighbouring plants that grow with it. The closest proximity between plants occurs in climbers and their host. We conducted a field experiment to assess the effect of spatial association between a climber plant, *Vicia nigricans* (Fabaceae), and two host shrubs, *Berberis buxifolia* (Berberidaceae) and *Schinus patagonica* (Anacardiaceae), on insect herbivory levels, reproductive output and growth. The presence and identity of the host shrubs affected the herbivory levels of the climber *V. nigricans*, but not the reproductive output. For the climber, the probability of being attacked by insects could depend on the characteristics of the host shrub. Taking the opposite perspective, climber association affected different traits of the host shrubs. The association with the climber decreased leaf damage (positive), tended to decrease leaf production (negative) and did not affect reproductive output (neutral). Our findings suggest that spatial association between plant species could change the sign of the interactions between plants and insects affecting different traits. By taking into account the perspective of both plants involved in the association, this study shows and emphasizes that plant–animal interactions strongly depend on the community context.

**Key words:** *Berberis buxifolia*, Patagonia, plant–plant interaction, *Schinus patagonica*, *Vicia nigricans*.

## INTRODUCTION

Herbivory is a major factor determining plant survival and fitness (Strauss 1991a; Hulme 1996; Strauss & Agrawal 1999). Traditionally, herbivory has been viewed as a two-part interaction (Zamora *et al.* 1999). However, most plant species interact with more than one plant or animal species at the same time. An increasing number of studies show that plant–herbivore interactions strongly depend, in a predictable way, on the community context (Björkman & Hambäck 2003; Stiling *et al.* 2003; Strauss & Irwin 2004; Baraza *et al.* 2006). The strength and even the sign (positive or negative) of the interaction between two species may change in the presence of other species through indirect effects (Strauss 1991b). For example, spatial association between plant species could affect the chances of a focal plant being detected and colonized by herbivorous insects (Karban 1997; Hambäck *et al.* 2000; Stiling *et al.* 2003; Barbosa *et al.* 2009).

The intensity of herbivory experienced by the focal plant species is often affected by the identity and proximity of its neighbouring vegetation (Atsatt &

O’Dowd 1976; Huntly 1991; Callaway 1995; Hambäck *et al.* 2000). Neighbours may be beneficial or detrimental to a focal plant. For example, a palatable plant surrounded by unpalatable plants could be ignored by herbivores. This positive interaction has been described as ‘associational resistance’ (Tahvanainen & Root 1972). Alternatively, some plant species may experience much greater herbivory (negative interaction) when associated with certain other species than when they are alone; this is called ‘associational susceptibility’ (Brown & Ewel 1987; Karban 1997; White & Whitham 2000). Thus, the outcome of the interaction will be positive (+) for the focal plant in cases of associational resistance, and negative (–) in cases of associational susceptibility, while the impact on neighbouring plants can be neutral, positive or negative.

Foliar herbivory levels and neighbour association could affect plant fitness. From the point of view of an individual plant, herbivory could affect its fitness either positively or negatively. Some focal plants that suffer herbivory were negatively affected by reducing growth or reproduction, and increasing mortality (Bergvall *et al.* 2006). However, some plants benefit from being consumed by herbivores. For example, some plants overcompensate the damage produced by

\*Corresponding author.

Accepted for publication November 2010.

herbivores (Agrawal 2000); these damaged plants have higher fitness level than related plants that are undamaged. In addition, plant neighbours may simultaneously modulate herbivore impacts in two contrasting ways. Plant neighbours may increase plant tolerance to herbivory by reducing environmental stresses that might otherwise limit compensation (Callaway 1995). Alternatively, plant neighbours may compete for limiting resources, thereby magnifying the negative effects of herbivory on fitness (Rand 2004). Therefore, plant fitness could be affected positively or negatively by herbivory levels, or by neighbour's effect.

Among plants, the closest proximity occurs in climbers and their host plants. Climbers (weak-stemmed) and lianas (woody-stemmed) consist of plants that are rooted in the ground but need support for their stems, and generally can not be avoided by host plants (Gentry 1991). The interaction between lianas and trees has been of great interest because of the detrimental effect that lianas have on their tree hosts (Schnitzer & Bongers 2002). However, interactions between herbaceous climbers and shrubs have been poorly studied. This closeness could affect the herbivory levels, reproductive output and growth of both the climbers and their host plants. To our knowledge, studies focused on how these associations affect both climbers and hosts have not been reported yet.

In the temperate forest of Patagonia, annual and perennial climbers are important components of the vegetation community, with 22 species belonging to 12 families (Arroyo *et al.* 1996). Their host plants include shrubs and trees in different habitat types, ranging from wet ecosystems like Valdivian rain forest to semi-arid shrublands. Disturbance regime within these ecosystems is dominated by fires (Veblen *et al.* 1992), which may benefit climber abundance (Schnitzer & Bongers 2002). The dominance of resprouting shrubs facilitates the colonization by climbers after fire. A post-fire environment was selected as a key habitat for studying the present interaction because of the abundance of climber and shrubs. Additionally, after fire resprouting shrubs and climbers may facilitate or prevent tree species establishment of the main canopy tree species *Nothofagus sp.* (Nothofagaceae) (Suarez & Kitzberger 2008).

The present study analyses the reciprocal interaction between an abundant climber and two dominant shrubs in a post-fire forest environment. We assessed insect herbivory levels and reproductive output of both the climber and host shrub species, and growth only in host shrubs. We addressed the following bidirectional questions: (i) Are herbivory levels and reproductive output of the climber plant affected by the identity of the host shrubs? and (ii) Are herbivory levels, reproductive output and growth of host shrubs affected by the climber association?

## METHODS

### Study site and species

The present study took place at Nahuel Huapi National Park (41°14'S, 71°24'W; 850 m a.s.l.), Río Negro, Argentina. Mean annual precipitation in the area is approximately 1600 mm, mean temperature in January (Austral summer) is 23°C, and mean temperature in July (Austral winter) is -2°C (Barros *et al.* 1983). The native forest in the area can be described as South American Temperate Forest of the Subantarctic biogeographical region, and the predominant tree genus is the evergreen southern beech *Nothofagus* (Nothofagaceae) (Cabrera 1994).

The period of highest insect activity occurs during the Austral spring and summer. For this reason, field work was conducted in two consecutive springs and summers (2004 and 2005), 5 years after a widespread wildfire at the study area (1999). At the time of this study, vegetation community was in an early successional stage of recovery. In this post-fire community, resprouting plant species are common and include shrubs and climbers. The plant system under study was composed of a predominant climber and two dominant shrub species as host plants. The climber *Vicia nigricans* Hook. & Arn. (Fabaceae) is an annual herb, with slender and delicate stems that climb over different shrubs and can reach 2 m long, especially in forest gaps. Leaves are compound with many elliptical-ovate leaflets and branched tendrils. The inflorescence is a raceme made up of 15–19 dark pink flowers and the fruit is a legume (Brion *et al.* 1988; Correa 1988). Flowering extends from December to January and the fruiting period lasts from December to February (Paritsis *et al.* 2006). One of the host shrubs is *Berberis buxifolia* Lam. (Berberidaceae), an evergreen spiny shrub that reaches 2 m tall. Branch pattern is horizontal and not overlapped. Leaves are simple in fascicles of up to 10, each one having a spine at the end (Correa 1988). The stems have three spines at the base of the fascicles. The flowers are yellow, solitary and pendulum. The fruit is a bluish black berry, 0.8 cm across, containing 7–11 seeds (Brion *et al.* 1988). *Berberis buxifolia* flowers from October to November and fruits mature between November and January (Paritsis *et al.* 2006). The other host shrub is *Schinus patagonica* (Phil.) I.M. Johnst. (Anacardiaceae), an evergreen shrub that reaches 5 m tall. Branch pattern is overlapped with dense foliage. Leaves are simple and alternate. Flowers are unisexual. Fruits are black drupes, 5–7 mm across, with one seed. *Schinus patagonica* flowers from December to January and fruits mature between November and January (Paritsis *et al.* 2006). All the studied species are entomophilous. These three species together account for approximately 40% of total plant cover within the burned forest (E. Raffaele *et al.* 2004, unpubl. data), and are characteristic of the vegetation type in the region (Raffaele & Veblen 1998). Botanical nomenclature follows Ezcurra and Brion (2005).

### Sampling methods

In the spring and summer of 2004 and 2005, we conducted observational and experimental studies on (i) *V. nigricans*

growing alone – support was provided with a dead branch, which mimicked the structure of shrubs, because plants can experience more herbivory when growing prostrate (Gianoli & Molina-Montenegro 2005); (ii) *B. buxifolia* alone – with manual extraction of the climber; (iii) *S. patagonica* alone – with manual extraction of the climber; (iv) *V. nigricans*–*B. buxifolia* – naturally found; and (v) *V. nigricans*–*S. patagonica* – naturally found. We selected 10 plants, alone or in pairs, per treatment per year, and in treatments 4 and 5 we measured both plant species. In an area of 2 ha we selected plants of the three species, similar in size, either alone or associated, and 2–50 m apart. In the second year (2005) new climbers, alone and associated, were marked in similar places as those in 2004. Manual extraction of climbers in treatments 2 and 3 were made at the beginning of the spring when *V. nigricans* was growing and was approximately 10 cm tall. In treatments 4 and 5 (climber-associated shrubs) the climber covered between 40 and 60% of the shrubs foliage. We measured herbivory levels in two consecutive years (2004 and 2005) and reproductive output and growth only in 2005. To avoid measuring herbivory on leaves of different ages, at the beginning of the growing season we marked two or three new branches on each plant (depending on plant size). Herbivory was measured in 10–15 leaves randomly collected from the marked branches from each plant at the end of the summer. For each leaf, herbivory was quantified as leaf area removed or damaged by insects; measures were performed with the software Sigma ScanPro 5.1. The actual leaf area (ALA) was measured directly, and the potential leaf area (PLA), that is the area before herbivory, was measured by reconstructing the missing area (filling the holes, redrawing leaf margins). We calculated the proportion of leaf area removed by herbivores as  $1 - (ALA / PLA)$  for each leaf (Rodríguez-Auad & Simonetti 2001). Then we averaged the proportion of leaf area removed of the 10–15 leaves per plant per year. The sampling unit was each plant. Damage levels represent cumulative herbivory within each growing season, which is direct evidence of insect abundance and consumption.

During the second year (2005) we measured reproductive output and growth of the studied plants. We estimated fruit production as an indicator of plant fitness. On the three species we recorded the number of fruits on five randomly selected branches per plant, and then we calculated the average of fruit production per plant. We sampled the total number of leaves produced in the marked branches from the two host shrubs, as a non-destructive indicator of plant growth. We were unable to count the climber's leaves due to their fragility and their complex ramifications; any manipulation of the stems would have killed the entire plant.

## Data analysis

We assessed the effects of the host shrubs' presence and identity on the climber by analysing the following treatments: 1 (climber alone), 4 (association *V. nigricans*–*B. buxifolia*) and 5 (association *V. nigricans*–*S. patagonica*). The effect of the climber on host shrubs was addressed considering as factors climber association (shrubs alone and associated), shrubs species (*B. buxifolia* and *S. patagonica*) and years (2004 and 2005). We combined treatments 2 (*B. buxifolia* alone), 3 (*S. patagonica* alone), 4 (association *V. nigricans*–*B. buxifolia*) and 5 (association *V. nigricans*–*S. patagonica*) to order data in factors. Herbivory levels, reproductive output and growth in all treatments were tested fitting generalized linear models (GLMs) to the data. Our response variables were counts, ratios and proportions, with non-normally distributed errors, even after applying different transformation. Thus, the application of GLMs allowed us to preserve the nature of the response variables under study in all analyses (McCullagh & Nelder 1989). Although most error distributions and link functions are commonly related to a particular response variable, we first fitted each model by using all applicable link functions, and then selected the one that minimized the deviance of the model (Table 1). Climatic conditions are known to affect insect activity, particularly because 2005 was a dry year for northern Patagonia (–1SD in annual aridity index; 'Servicio Meteorológico Nacional'). Consequently, we included study year as a factor in accounting for interannual variability in herbivory levels. Comparisons between two treatment levels were performed by using a post hoc contrast linear hypothesis test for GLMs by using the 'lht' function in the car package (Wald  $\chi^2$ ). Analyses were conducted by using the 'glm' function in the stats package of R statistical software (version 2.10.1, R Development Core Team 2009, <http://www.r-project.org>).

## RESULTS

Overall, we measured a total of 693 leaves in 2004 and 804 leaves in 2005 ( $n = 70$  plants for both years). The proportion leaf area removed by insects per plant varied between 0 and 0.3 in 2004 and between 0 and 0.2 in 2005. All plants were attacked by herbivores of many feeding guilds, like beetles and lepidopteran larvae chewers; there were sap-sucking bugs and aphids and there were some lepidopteran larvae that

**Table 1.** Summary of variables, measurement units and generalized linear model parameters used in this study to test for differences between plants growing alone or associated

Variable	Measurement units	Generalized linear model parameters		
		Error distribution	Link function	Fixed effect
Herbivory	Proportion leaf area removed by insects	Gamma	Log	Treatment, species, year
Reproduction	Fruits per plant	Quasipoisson	Log	Treatment, species
Growth	Number of leaves per branch	Quasipoisson	Log	Treatment, species

skeletonized leaves (Y. Sasal 2004, pers. obs.). The reproductive output, assessed as the average number of fruits per plant, was different for each species. The climber *V. nigricans* produced between 5 and 13 legumes per branch; the shrub *B. buxifolia* produced 0–18 berries per branch; and the shrub *S. patagonica* produced 1–38 drupes per branch. The leaves production, measured only in shrub species, was different for each species. The shrub *B. buxifolia* produced 3–114 leaves per branch, and the shrub *S. patagonica* produced 8–137 leaves per branch.

#### Climber–shrub association: climber’s point of view

On the climber *V. nigricans*, herbivory levels varied with the presence and identity of the host shrubs (Table 2, Fig. 1a). In the *V. nigricans*–*B. buxifolia* association, the climber suffered the highest level of herbivory (Fig. 1a). However, in the *V. nigricans*–*S. patagonica* association, the climber suffered the lowest level of foliar damages (Fig. 1a); whereas *V. nigricans* alone, which are growing over dead branch mimicking the structure of shrubs, showed intermediate herbivory levels (Fig. 1a). Between the two analysed years, herbivory levels were higher in 2004 ( $0.13 \pm 0.009$ , mean  $\pm$  SE) than in 2005 ( $0.05 \pm 0.008$ ; Table 2). On the other hand, the reproductive output of the climber, assessed as the average fruit production per plant, was not affected by the host’s presence or identity (Table 2; Fig. 1b).

#### Climber–shrub association: shrub’s point of view

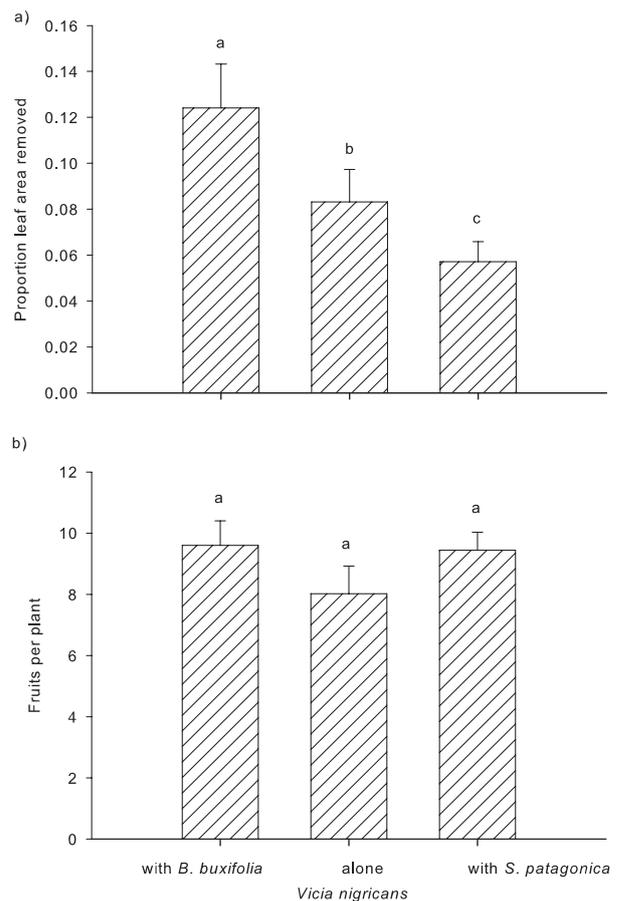
The climber association affected different traits of host shrub species. Host shrubs alone suffered higher

**Table 2.** Comparison of the proportion of leaf area removed by insects and fruits production between the climber *Vicia nigricans* alone, associated with host shrub *Berberis buxifolia* and associated with host shrub *Schinus patagonica*

	<i>t</i> -value	<i>P</i> -value
Proportion leaf area removed		
Climber alone–associated with <i>B. buxifolia</i>	2.1	0.04
Climber alone–associated with <i>S. patagonica</i>	3.1	0.003
Years (2004–2005)	9.9	<0.001
Fruits per plant		
Climber alone–associated with <i>B. buxifolia</i>	1.3	0.21
Climber alone–associated with <i>S. patagonica</i>	1.4	0.16

Generalized linear models results. See Table 1 for model details applied to each response variable.

herbivory than those associated with the climber (Table 3, Fig. 2a). Furthermore, the climber association affected herbivory differently in each of the analysed years (Table 3). In 2004, herbivory levels were higher alone than associated (alone  $0.053 \pm 0.013$  and associated  $0.031 \pm 0.006$ ). However, in 2005, herbivory levels were higher associated than alone (alone  $0.045 \pm 0.009$  and associated  $0.049 \pm 0.012$ ). The reproductive output, assessed as the number of fruits per plant, was similar in association with the climber or alone for host shrubs (Table 3; Fig. 2b). Finally, the growth rate, assessed as leaf production, was lower in the host shrubs associated with the climber than shrubs alone; however, this result was marginally significant (Table 3; Fig. 2c). We did not



**Fig. 1.** (a) Herbivory level measured as proportion leaf area removed by insects (Walt  $\chi^2 = 27.7$ ,  $P < 0.001$ ) and (b) reproductive output measures as fruits per plant (Walt  $\chi^2 = 0.02$ ,  $P = 0.89$ ) on the climber *Vicia nigricans* associated with host shrub *Berberis buxifolia*, alone and associated with host shrub *Schinus patagonica* (Means  $\pm$  SE). Different letters above error bars denote significant differences. Comparisons between two treatment levels were performed by using contrast linear hypothesis test for generalized linear models (Walt  $\chi^2$ ).

**Table 3.** Effect of association with climber (alone–associated), host shrubs species (*Schinus patagonica*–*Berberis buxifolia*) and year (2004–2005) on the proportion of leaf area removed by insect, fruits per plant and number of leaves per branch

	<i>t</i> -value	<i>P</i> -value
Proportion leaf area removed		
Treatment (alone–associated with climber)	–2.7	0.01
Species ( <i>B. buxifolia</i> – <i>S. patagonica</i> )	1.3	0.19
Year (2004–2005)	0.7	0.46
Treatment × species	1.3	0.18
Treatment × year	2.0	0.05
Species × year	–1.8	0.07
Treatment × species × year	–0.7	0.48
Fruits per plant		
Treatment (alone–associated with climber)	–0.29	0.77
Species ( <i>B. buxifolia</i> – <i>S. patagonica</i> )	2.19	0.04
Treatment × species	–1.64	0.11
Number of leaves per branch		
Treatment (alone–associated with climber)	–1.91	0.06
Species ( <i>B. buxifolia</i> – <i>S. patagonica</i> )	–2.89	0.006
Treatment × species	0.56	0.58

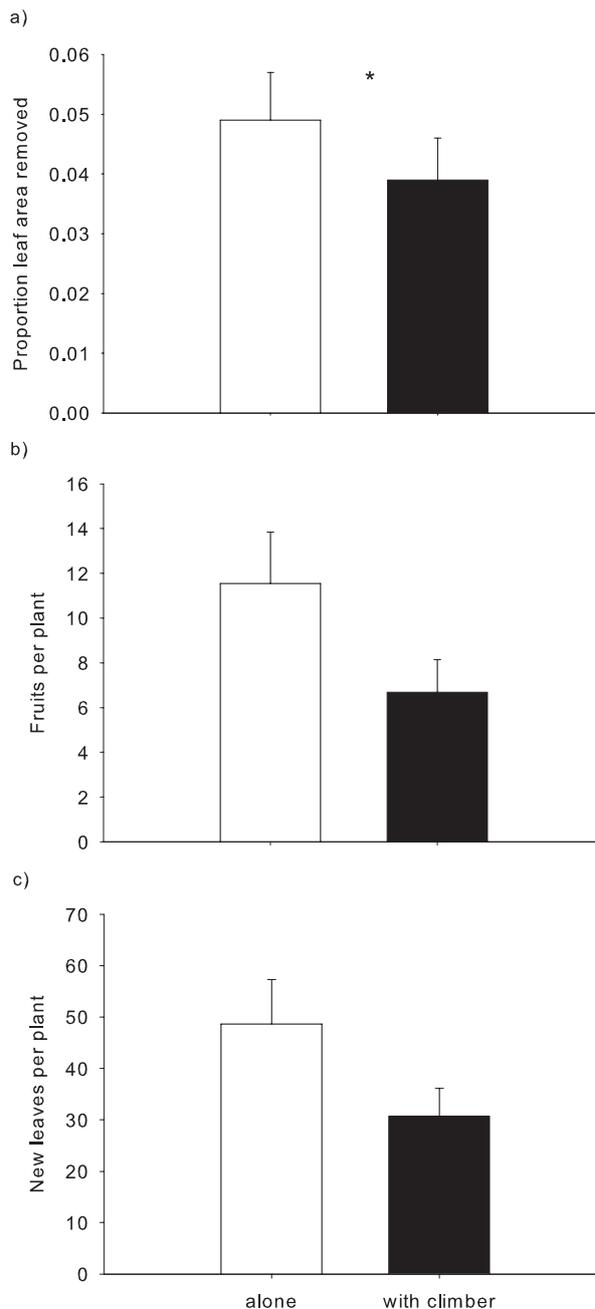
Generalized linear models results. See Table 1 for model details applied to each response variable.

find evidence of a differential response of herbivory, fitness and growth between the two shrubs in the presence of the climber.

## DISCUSSION

The presence and identity of host shrubs affected herbivory levels but not the reproductive output of the climber *V. nigricans*. Taking the opposite perspective, the climber affected herbivory levels, tended to affect leaves production and did not affect reproductive output of host shrubs.

From the climber's point of view, the presence and identity of the two host shrubs had different effects. The climber associated with the host shrub *B. buxifolia* suffered higher herbivory than when growing alone, suggesting a case of associational susceptibility (Brown & Ewel 1987; Barbosa *et al.* 2009). This susceptibility could be explained by the leaf characteristics of both plants. Insect herbivores on *B. buxifolia* could prefer climber leaves, with high water content and probably high nitrogen content (Fabaceae), instead of coriaceous and spiny shrub leaves. Given that herbivores could rank their potential food hosts within a site (White & Whitham 2000), it is probable that they prefer the climber's leaves. On the other hand, the climber associated with the host shrub *S. patagonica* suffered less herbivory than when



**Fig. 2.** (a) Herbivory level measured as proportion leaf area removed by insects, (b) reproductive output measures as fruits per plant and (c) leaves production measured as new leaves per branch on both host shrubs (*Berberis buxifolia* and *Schinus patagonica*) alone and associated with the climber *Vicia nigricans* (Means  $\pm$  SE). Asterisk denotes significant differences.

growing alone, in agreement with the associational resistance effect (Tahvanainen & Root 1972; Barbosa *et al.* 2009). There are three mechanisms by which plants may gain associational resistance from neighbours: (i) neighbours may be host for predators that attack the herbivores of the focal plant individual;

(ii) neighbours may attract herbivores away from the focal individual; and (iii) neighbours may allow focal individuals to avoid detection or attack by herbivores (Atsatt & O'Dowd 1976; Barbosa *et al.* 2009). The third mechanism could occur in the climber associated with *S. patagonica*; this host shrub has abundant foliage and volatile compounds that can reduce the ability of herbivores to find the climber, and thus interfere with the host-finding process (Atsatt & O'Dowd 1976; Barbosa *et al.* 2009). However, we could not discard the other two mechanisms. Herbivory levels varied markedly in years, which could be a result of changes in abiotic conditions that can affect insect relationships with both food plants and natural enemies, and plant nutritional quality (Koricheva *et al.* 1998). Although association affects herbivory levels, the final effect on reproductive output was not affected by any of the shrubs; the reproductive output was similar for plants alone and for plants associated with shrubs. This could be resulting from the ability of climber plants damaged by insects to overcompensate through the production of more flowers and fruits (Agrawal 2000).

From the shrub's point of view, association with the climber affected different traits. Hosts shrubs associated with the climber suffered less leaf damage than alone; this was beneficial for host shrubs. Climbers often place their leaves above the shrubs or trees because they use them as mechanical support. Therefore, climbers could attract herbivore insects or hide their leaves from herbivores. This could explain the lower damage of shrubs when they grow in association with climbers, suggesting a case of associational resistance for the shrubs. This associational resistance was general for both shrubs species; we have no evidence of a differential response of herbivory between the two shrubs. This result is not consistent with the shrubs' identity effect on herbivory found in the climber's point of view. The outcome of the herbivory interaction in the association shrub–climber was positive for the shrubs and the sign depends on the identity of the shrub.

Furthermore, the shrubs associated with the climber tended to produce fewer leaves. Although this result was marginally significant, we will discuss this trend as we consider that biological effects could still be important. We base our decision on the considerable difference observed in the plants' responses to treatments and on the high variability observed among plants that increased the standard errors and could hide statistical significance. The climber association proved to be detrimental to hosts' leaves production, as climbers could be effective competitors for light. Trees that are heavily climber-laden grow more slowly and produce fewer fruits and seeds than climber-free trees (Stevens 1987); the same effects could be found in shrubs. The climber could be a hard competitor for

light, reducing 23% of the shrub's leaves production ( $P = 0.06$ ).

Finally, the reproductive output was not affected by the climber association. The fruits production was similar for shrubs alone and for shrubs associated with the climber. This could be a result of the compensation between herbivory and growth. Shrub plants alone suffer greater herbivory and produce more leaves; the opposite occurs in shrubs associated. These negative and positive interactions produce neutral effect on reproductive output. In summary, the climber–shrubs interaction could have different outcomes for the host shrubs depending on the studied variable response, positive effect being reducing herbivory, negative effect being reducing leaves production and with no effect on reproductive output.

In conclusion, the identity of the host shrubs affected the herbivory levels of the climber *V. nigricans*; however, the reproductive output was not affected. Taking the opposite perspective, the association affected particular traits of host shrubs. The association with the climber decreased leaf damage (positive), tended to decrease leaf production (negative) and did not affect reproductive output (neutral). Our findings suggest that spatial association between plant species could change the sign of the interactions between plants and insects, and could affect growth. We think that it is important to take the perspective of both plants involved in the association and include several plant species in this kind of studies. Additionally, cover and vigour of shrubs and climber plants presented in the understorey become key factors in either facilitating or preventing overstorey tree species' establishment after severe fire or in canopy openings (Kitzberger *et al.* 2000; Suarez & Kitzberger 2008). The climber could use tree saplings as mechanical support as they were shrubs, which could affect the trees' establishment and further have imprints on future forest composition. At least for this studied system, our results seem to be consistent with the theoretical framework of spatial associations and show clear effect of spatial associations on herbivory pressure. Our results suggest that future work should examine how association contributes to associational resistance or susceptibility in this system.

## ACKNOWLEDGEMENTS

We want to thank E. Perner, D. Sasal and E. Sasal for their help in the field. Also, thanks to A. Malizia, M. A. Nuñez, N. Tercero-Bucardo, A. G. Farji-Brener, E. Raffaele, M. A. Rodriguez-Cabal, G. Pirk and Elina Roldán for their comments on the manuscript. This project was funded by 'Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET)'.

## REFERENCES

- Agrawal A. A. (2000) Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. *Trends Plant Sci.* **5**, 309–13.
- Arroyo M. T. K., Caviries L., Peñalosa A., Riveros M. & Faggi A. M. (1996) Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sudamérica. In: *Ecología de los bosques nativos de Chile* (eds J. J. Armesto, C. Villagrán & M. T. K. Arroyo) pp. 71–99. Editorial Universitaria, Santiago.
- Atsatt P. R. & O'Dowd D. J. (1976) Plant defense guilds. *Science* **193**, 29.
- Baraza E., Zamora R. & Hódar J. A. (2006) Conditional outcomes in plant-herbivore interactions: neighbors matter. *Oikos* **113**, 148–56.
- Barbosa P., Hines J., Kaplan I., Martinson H., Szczepaniak A. & Szendrei Z. (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. *Annu. Rev. Ecol. Evol. Syst.* **40**, 1–20.
- Barros V., Cerdón V., Moyano C., Mendez R., Forquera J. & Pizzio O. (1983) *Cartas de precipitación de la Zona Oeste de las Provincias de Río Negro y Neuquén. Primera Contribución*. Facultad de Ciencias Agrarias, Universidad Nacional del Comahue, Cinco Saltos.
- Bergvall U. A., Rautio P., Kesti K., Tuomi J. & Leimar O. (2006) Associational effects of plant defenses in relation to within- and between-patch food choice by mammalian herbivore: neighbor contrast susceptibility and defense. *Oecologia* **147**, 253–60.
- Björkman C. & Hambäck P. (2003) Context-dependence in plant-herbivore interactions. *Oikos* **100**, 3–5.
- Brión C., Puntieri J., Grigera D. & Calvelo S. (1988) *Flora de Puerto Blest y sus alrededores*. Universidad Nacional del Comahue, General Roca.
- Brown B. J. & Ewel J. J. (1987) Herbivory in complex and simple tropical successional ecosystems. *Ecology* **68**, 108–16.
- Cabrera A. L. (1994) *Regiones Fitogeográficas Argentinas*. Editorial Acme S.A.C.I.C., Buenos Aires.
- Callaway R. M. (1995) Positive interactions among plants. *Bot. Rev.* **61**, 306–49.
- Correa M. N. (1988) *Flora Patagónica (República Argentina)*. Colección Científica del I.N.T.A., Capital Federal.
- Ezcurra C. & Brión C. (2005) *Plantas del Nahuel Huapi. Catálogo de la flora vascular del Parque Nacional Nahuel Huapi, Argentina*. Universidad Nacional del Comahue & Red Latinoamericana de Botánica, S. C. de Bariloche.
- Gentry A. H. (1991) The distribution and evolution of climbing plants. In: *The Biology of Vines* (eds F. E. Putz & H. A. Mooney) pp. 3–50. Cambridge University Press, Cambridge.
- Gianoli E. & Molina-Montenegro M. A. (2005) Leaf damage induces twining in a climbing plant. *New Phytol.* **167**, 385–90.
- Hambäck P. A., Agren J. & Ericson L. (2000) Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. *Ecology* **81**, 1784–94.
- Hulme P. E. (1996) Herbivory, plant regeneration, and species coexistence. *J. Ecol.* **84**, 609–15.
- Huntly N. (1991) Herbivores and the dynamics of communities and ecosystems. *Annu. Rev. Ecol. Syst.* **22**, 477–503.
- Karban R. (1997) Neighborhood affects a plant's risk of herbivory and subsequent success. *Ecol. Entomol.* **22**, 433–9.
- Kitzberger T., Steinaker D. F. & Veblen T. T. (2000) Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology* **81**, 1914–24.
- Koricheva J., Larsson S. & Haukioja E. (1998) Insect performance on experimentally stressed woody plants: a meta-analysis. *Annu. Rev. Entomol.* **43**, 195–216.
- McCullagh P. & Nelder J. A. (1989) *Generalized Linear Models*. Chapman & Hall, London.
- Paritsis J., Raffaele E. & Veblen T. T. (2006) Vegetation disturbance by fire affects plant reproductive phenology in a shrubland community in northwestern Patagonia, Argentina. *NZ J. Ecol.* **30**, 387–95.
- R (2009) R-A language and environment for statistical computing. The R Foundation for Statistical Computing, Mendoza, Argentina.
- Raffaele E. & Veblen T. T. (1998) Facilitation by nurse shrubs of resprouting behavior in post-fire shrubland in northern Patagonia, Argentina. *J. Veg. Sci.* **9**, 693–8.
- Rand T. A. (2004) Competition, facilitation, and compensation for insect herbivory in an annual salt marsh forb. *Ecology* **85**, 2046–52.
- Rodríguez-Auad K. & Simonetti J. A. (2001) Evaluación de la folivoria: una comparación de dos métodos. *Ecol. Bol.* **36**, 65–9.
- Schnitzer S. A. & Bongers F. (2002) The ecology of lianas and their role in forest. *Trends Ecol. Evol.* **17**, 223–30.
- Stevens G. C. (1987) Lianas as structural parasites: the *Bursera simaruba* example. *Ecology* **68**, 77–88.
- Stiling P., Rossi A. M. & Catell M. (2003) Associational resistance mediated by natural enemies. *Ecol. Entomol.* **28**, 587–92.
- Strauss S. Y. (1991a) Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. *Ecology* **72**, 543–58.
- Strauss S. Y. (1991b) Indirect effects in community ecology: their definition, study and importance. *Trends Ecol. Evol.* **6**, 206–10.
- Strauss S. Y. & Agrawal A. A. (1999) The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.* **14**, 179–85.
- Strauss S. Y. & Irwin R. E. (2004) Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annu. Rev. Ecol. Evol. Syst.* **35**, 435–66.
- Suarez M. L. & Kitzberger T. (2008) Recruitment patterns following a severe drought: long-term compositional shifts in Patagonian forests. *Can. J. For. Res.* **38**, 3002–10.
- Tahvanainen J. O. & Root R. B. (1972) The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* **10**, 321–46.
- Veblen T. T., Mermoz M., Martín C. & Kitzberger T. (1992) Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. *Conserv. Biol.* **6**, 71–83.
- White J. A. & Whitham T. G. (2000) Associational susceptibility of cottonwood to a box elder herbivore. *Ecology* **81**, 1795–803.
- Zamora R., Hódar J. A. & Gómez J. M. (1999) Plant-herbivore interaction: beyond a binary vision. In: *Handbook of Functional Plant Ecology* (eds F. I. Pugnaire & F. Valladares) pp. 677–718. Marcel Dekker, Inc., New York.