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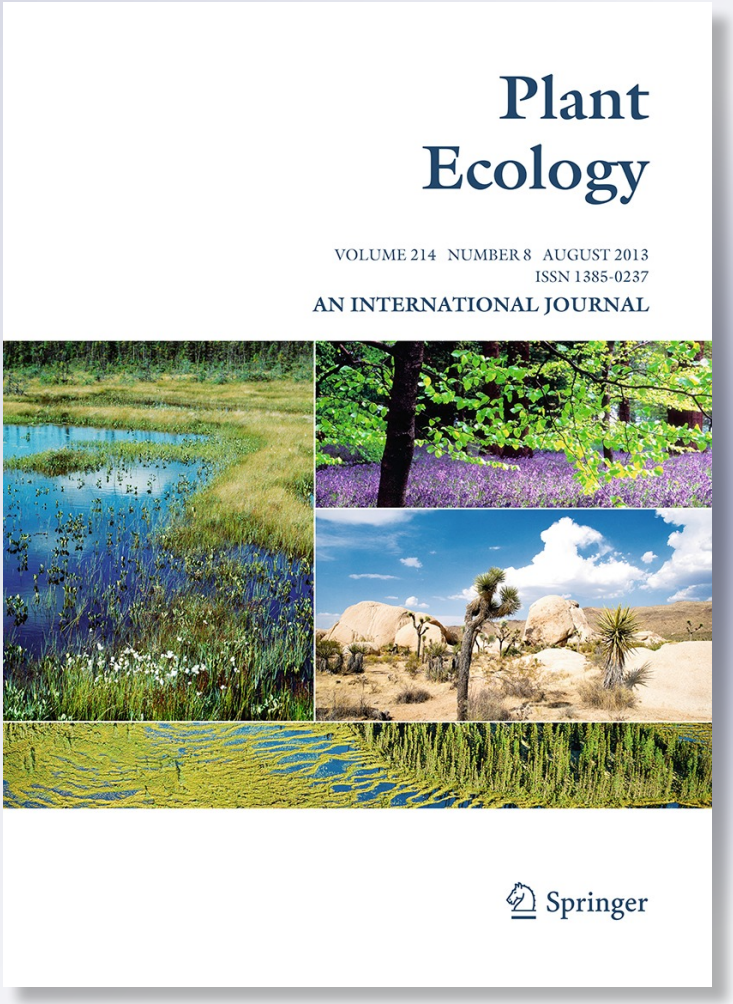
Plant Ecology
An International Journal

ISSN 1385-0237
Volume 214
Number 8

Plant Ecol (2013) 214:1059-1070
DOI 10.1007/s11258-013-0231-9



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Received: 27 March 2013 / Accepted: 21 June 2013 / Published online: 28 June 2013
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Abstract Compensation, the degree of plant recovery after herbivory, is influenced by nutrient availability. The compensatory continuum hypothesis (CCH) predicts that the more abundant the resources in an environment, the greater the potential for compensation. Nutrient-rich patches generated by leaf-cutting ants near their nests could modify plants' responses to damage. We performed a greenhouse and a field experiment to evaluate the effects of refuse dumps (RDs) created by *Acromyrmex lobicornis* on plant compensation for foliar herbivory in roadside areas of the Patagonian steppe. We expected higher tolerance in plants growing in RDs than in adjacent non-nest soils (NNSs). We also assessed whether compensation differed between native and exotic species common in the area. We expected higher compensation in exotic than native plants since they perform better in RDs. Native and exotic plants fully compensated for simulated herbivory resembling natural levels. In the greenhouse, clipped plants achieved similar biomass as control plants and in the field reproductive output was similar between treatments. However, compensation was not higher in RDs than NNSs or in exotic than native plants as expected. Both native and exotic plants in roadside areas may have traits associated with disturbance which allow them to tolerate natural occurring herbivory without compromising their performance. Our study, the first one to test the CCH on RDs, shows that enhanced levels of resources do not always determine higher tolerance to herbivory.

Keywords *Acromyrmex lobicornis* · Disturbance · Herbivory · Patagonian steppe · Tolerance

Electronic supplementary material The online version of this article (doi:10.1007/s11258-013-0231-9) contains supplementary material, which is available to authorized users.

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Introduction

Herbivores can severely damage plant tissues and consequently affect plant growth and reproduction. Thus, there is an important selective force which favors anti-herbivore defenses (Stowe et al. 2000). Among defensive strategies, resistance includes physical, morphological and chemical mechanisms which reduce the probability of a plant being consumed. On the other hand, tolerance includes traits that confer upon plants the ability to re-grow and/or reproduce after herbivory. Most studies on plant adaptations to consumers have focused on the evolution of resistance traits, but plant tolerance to herbivory in natural populations did not receive much attention until about three decades ago (Rosenthal and Kotanen 1994; Strauss and Agrawal 1999; Stowe et al. 2000).

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Compensation is the degree of recovery that plants exhibit after being damaged by herbivores. The mechanisms involved include an increased net photosynthetic rate (Mabry and Wayne 1997), high relative growth rates (Houle and Simard 1996), an increased branching or tillering after release of apical dominance (Rosenthal and Welter 1995; González-Teuber and Gianoli 2007), and the ability to translocate carbon stores from roots to shoots (Mabry and Wayne 1997). As a result, plants' fitness may suffer no changes (full compensation), may increase (overcompensation), or decrease (undercompensation) (Belsky 1986). The reaction norm of fitness across a damage gradient is plastic and not only depends on the species, but also on the environmental conditions plants face. Among them, inter- and intra-specific competition (Hjältén et al. 1993), timing and intensity of herbivory (Maschinski and Whitham 1989), water (Cox and McEvoy 1983; Levine and Paige 2004) and nutrient availability (Maschinski and Whitham 1989; Rosenthal and Kotanen 1994; Hawkes and Sullivan 2001; Wise and Abrahamson 2005) may influence the impact of herbivores on plant compensation.

Plants growing in resource-poor environments require a greater fraction of their net production to replace the tissue lost or damaged by herbivores than plants growing in resource-rich environments (Coley et al. 1985). The compensatory continuum hypothesis (CCH) predicts that the more abundant the resources in an environment, the greater the potential for compensation (Maschinski and Whitham 1989). Although the CCH has been taken as a truism, over the years some studies have shown lower tolerance in resource rich-environments (e.g., Mutikainen and Walls 1995; Irwin and Aarssen 1996). Even though plants do grow and reproduce better in situations with either high resources or no herbivory, the interaction of these factors is far more complex than previously thought and the outcome may depend on the plants' functional groups. For example, monocots and dicot herbs and woody plants show qualitatively different responses to herbivory (Hawkes and Sullivan 2001). Plants' origin could also influence the response to herbivory under different resource conditions. Exotic plants may use nutrients more efficiently than native plants by virtue of particular morphological and/or physiological traits (Davis and Pelsor 2001; Farji-Brener et al. 2010). Plus, in the absence of natural enemies, they have higher benefits if they reduce the investment in resistance and increase their compensatory capacity (the evolution of increased competitive ability hypothesis, or EICA hypothesis; Blossey and Nötzold 1995). Therefore, more studies analyzing the effect of nutrient availability on plant tolerance to herbivory in exotic and native plants are needed.

Availability and spatial distribution of resources in ecological communities can be greatly affected by the activity of resident organisms. In particular, ants redistribute soil and organic matter through nest excavation and the accumulation of organic waste resulting from colony activity (Hölldobler and Wilson 1990; MacMahon et al. 2000). Consequently, nest-soils often differ from adjacent soils in chemical and physical traits, causing edaphic enrichment (Carlson and Whitford 1991; Farji-Brener and Silva 1995; Farji-Brener and Illes 2000). This soil enrichment may accelerate nutrient cycling and benefit plant growth (Beattie and Culver 1977; Loucks, Plumb-Mentjes and Rogers 1985; Woodell and King 1991) and generally persists after the colony dies or is abandoned (Buckley 1982; Farji-Brener and Ghermandi 2000). Hence, nutrient-rich patches associated with ant colonies could modify plants' responses to damage. Most studies on the influence of resources on plants' tolerance manipulate soil nutrient content by adding commercial fertilizers (e.g., Meyer and Root 1993; Rogers and Siemann 2002). However, experiments using naturally occurring nutrient patches, generally associated with decomposing organic matter, could demonstrate how the CCH operates in nature. To date no studies have explored how ants' nutrient-rich patches may affect tolerance to herbivory of associated plants.

Leaf-cutting ants (Formicidae, Attini) produce dramatic edaphic changes. They move an extraordinary quantity of soil to construct and maintain their nests, cut and concentrate a large amount of vegetation, and deposit large piles of organic waste in external or internal disposal areas (Farji-Brener and Illes 2000). In NW Patagonia, Argentina, *Acromyrmex lobicornis* deposits the waste material externally, forming refuse dumps (RDs) on the soil surface near the nest. These RDs have a higher water retention capacity and 5–10 times more N, K, P and organic carbon than adjacent soils (Farji-Brener and Ghermandi 2008). This increase in resource concentration enhances local diversity of native and exotic plants, but especially favors the performance of exotic

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vegetation (Farji-Brener and Ghermandi 2000, 2004, 2008; Farji-Brener et al. 2010).

We performed a greenhouse and a field experiment to evaluate the effects of *A. lobicornis* RDs on plant compensation for foliar herbivory in the Patagonian steppe. We expect that plants growing in RDs tolerate better foliar damage than those growing in NNSs, as the CCH predicts. We also evaluated whether the compensation for foliar damage differs between native and exotic species. Taking into account the better performance of exotic than native plants in RDs (Farji-Brener et al. 2010) we expect a higher compensation in exotic than native plants growing in RDs.

Materials and methods

Study area and species

Field experiments and seed, soil, and refuse dump collection took place at the eastern border of the Nahuel Huapi National Park, located in northern Patagonia, Argentina (41°S, 72°W). The study site was located in roadside steppes along 20 km of both sides of the National Road 40 (~80 ha). Mean annual temperature in this area is 8 °C and mean annual rainfall is about 600 mm.

The dominant vegetation is a mix of native species typical of Patagonian steppes (e.g., *Stipa speciosa*, *Mulinum spinosum*, *Imperata condensata*, *Oenothera odorata* and *Plagiobotris tinctorius*), and exotic herbs (e.g., *Bromus tectorum*, *Onopordon acanthium*, *Carduus thoermeri* and *Verbascum thapsus*) (Correa 1969–1998). The six plant species studied here (Table 1) are abundant in the study area and representative of the local flora (Farji-Brener and Ghermandi 2000, 2004; Farji-Brener et al. 2010; see also Correa 1969–1998). All of them were observed growing in RDs and performed well in the greenhouse. They are either annual or biennial forbs belonging to three families. Half of them are native and half exotic. Most exotic species in the area were introduced after the settlement of Europeans, around 300 years ago and their distribution has increased greatly over the last 30 years (Margutti et al. 1996; Ezcurra and Brion 2005). Unfortunately, in the area there were not congeneric pairs of native and exotic species, which would have allowed us to make phylogenetically controlled comparisons (Agrawal and Kotanen 2003). Two exotic and two native species belong to the family Asteraceae and all species, to different genera (Table 1). Natural foliar herbivory levels (% damaged leaf tissue) of the studied exotic species were on average ~11 % for *Carduus thoermeri* and ~1 % for *Onopordon acanthium* and *Verbascum thapsus*. For the native species, they were ~3 % for *Solidago chilensis* and *Oenothera odorata*, and 0.2 % for *Conyza lechleri* (see Pirk and Farji-Brener 2012 for more details).

Acromyrmex lobicornis Emery is the only leaf-cutting ant which inhabits Patagonia. In the study area it is more abundant near road borders (Farji-Brener and Ghermandi 2000, 2008). Its nests are about 1 m deep, with a dome-shaped mound of twigs, soil and dry plant material. RDs are located on the soil surface near the mound in one or a few large piles.

Greenhouse experiment

To evaluate the effects of RDs on tolerance to herbivory in exotic and native species, we performed a greenhouse experiment simulating herbivory with three exotic and three native species (Table 1).

In September 2008 we planted seeds of these species (harvested during the previous summer from ~10 randomly chosen individuals per species) in single celled seedbeds with fertile commercial soil and placed them in a greenhouse. In January 2009, we extracted 40 seedlings of each species from the

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

Plant species	Family	Life form, life cycle	Origin
Carduus thoermeri	Asteraceae	Forb, biennial	Exotic
Onopordon acanthium	Asteraceae	Forb, biennial	Exotic
Verbascum thapsus	Scrophularuiaceae	Forb, biennial	Exotic
Conyza lechleri	Asteraceae	Forb, annual	Native
Oenothera odorata	Onagraceae	Forb, biennial	Native
Solidago chilensis	Asteraceae	Forb, annual	Native

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commercial soil and transplanted them individually into $13 \times 10 \times 4$ cm^3 trays. Each seedling was randomly assigned a substrate type, i.e., half of them were planted in RDs and half in NNSs. RDs came from 10 randomly selected active *A. lobicornis* nests, and soil samples from nearby non-nest sites (blocks). These sites were placed at a random direction and distance (between 3 and 6 m) from each nest-mound. According to previous measurements in the same study site, RDs show much higher contents of OM, C, N, P, Ca, K, Mg and Na than NNSs, but pH and relative content of silt, sand and clay is similar (Table 2; see Farji-Brener and Ghermandi 2008). A systemic insecticide was sprayed on the plants and soil to prevent natural herbivory inside the greenhouse. Trays were regularly watered and kept at field capacity. They also were regularly weeded to remove non-target plants. We randomly assigned a treatment (simulated herbivory or control) to each plant to achieve a full factorial design, with ten replicates (blocks) of each combination of factors: treatment (two levels), species (six levels) and substrate (two levels). Few *Conyza lechleri* seeds germinated in the seedbeds so there were only five replicates of each treatment (Total initial $N = 220$). We counted the initial number of leaves (Li), and measured the initial height (Hi) and surface cover (Ci) of all individuals, right after inflicting damage to the simulated herbivory treatment group. We estimated surface cover as the product of maximum width (w1) and width of the axis perpendicular to it (w2), and π (i.e., an oval shape was assumed). We simulated leaf damage by clipping two-thirds of 50 % of the leaves (i.e., 33 % leaf loss) in assigned individuals. We applied this type of damage because complete tissue loss is the most common type of foliar damage in these species and in general, fewer than 50 % of the leaves suffered herbivory (see Pirk and Farji-Brener 2012). As for the amount of tissue loss, we wanted to represent high levels of herbivory, yet realistic ones ($\sim$33 % is the maximum value observed in the field; Pirk and Farji-Brener 2012). We randomly selected a control young leaf (i.e., not clipped), marked it and estimated its initial area (CL1i) and its final area at week 4 (CL1f) by taking photos and analyzing them with the program Sigma Scan Pro. We did not measure them further because leaves were already becoming senescent. At week 8 we marked another set of control leaves, measured their surface (CL2i) and re-measured them at week 12 (CL2f). The experiment ended at week 12, and after measuring final height (Hf), surface cover (Cf) and number of leaves (Lf), we removed plants from the substrate, washed and dried them at 60 °C for one week. Total, root and shoot dry biomass was then weighed for each individual. *Oenothera odorata*, *Solidago chilensis* and *Conyza lechleri* produced basal sprouts and *Conyza lechleri* also branches. We counted the number of branches and sprouts to analyze their potential role in compensation.

We calculated change in plant height Hf/Hi, surface cover Cf/Ci and number of leaves Lf/Li for the 12-week period. We also estimated change in area of the first (weeks 0–4) and second (weeks 8–12) set of control leaves CLf/CLi. Finally, we calculated total dry biomass (Bf) and root:shoot ratio. Growth variables (change in plant height, surface cover, number of leaves and leaf area) provide information on the potential mechanisms involved in plant compensation. For example, change in plant height and cover describe variations in plant architecture after damage, and change in number of leaves and in leaf area could be involved in increasing photosynthetic activity. Also, root:shoot ratio was estimated to evaluate if damaged plants reallocate carbon stores from roots to shoots after damage. Each of the seven variables was

Table 2 Chemical and physical parameters (mean ± SE) of RDs and NNSs in the study area (modified from Farji-Brener and Ghermandi 2008)

	RD	NNS
OM	13.8 ± 2.5	2.5 ± 1.0
C	8.1 ± 1.4	1.4 ± 0.2
N	0.76 ± 0.09	0.13 ± 0.01
P	597.4 ± 61.4	56.5 ± 4.5
Ca	20.6 ± 1.4	13.1 ± 0.8
K	6.9 ± 1	0.8 ± 0.1
Mg	6.7 ± 0.7	2.6 ± 0.2
Na	0.14 ± 0.01	0.09 ± 0.02
pH	6.9 ± 0.2	6.8 ± 0.11
Clay	9.7 ± 1.6	7.7 ± 0.5
Silt	22.5 ± 2.8	26.9 ± 1
Sand	67.7 ± 3.7	65.3 ± 1.8

Contents of clay, silt, sand, OM (organic matter), C (carbon) and N (nitrogen) are expressed in percentages; P (phosphorous) in ppm; Ca (calcium), Mg (magnesium), K (potassium) and Na (sodium) in meq/100 g. All parameters differ between RDs and NNSs except for pH, clay, silt and sand (MANOVA)

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separately analyzed in a nested ANOVA. Factors were origin (exotic or native), species (nested within origin), treatment (simulated herbivory or control), substrate (RD or NNS) and block (ten random RDs and adjacent NNSs). According to the CCH, we expected a significant substrate × treatment interaction, where response variables in clipped plants are higher in RD than in NNS. Moreover, if plant origin affects their capacity to tolerate foliar damage, we also expected a significant substrate × treatment × origin interaction, where response variables in clipped plants have the highest values for exotic plants growing in RDs. We analyzed number of branches in *C. lechleri* and sprouts in *O. odorata* and *S. chilensis* in two-way ANOVAs, with treatment and substrate as factors. We also analyzed number of sprouts in *C. lechleri* in a one-way ANOVA with treatment as the only factor since sprouts were only present in RDs.

Field experiment

Although plant size is considered a good estimator of fecundity (Horvitz and Schemske 2002), the final impact of herbivory on fitness could not be assessed in the greenhouse due to the absence of pollinators and the extent of the experiment. Thus, we performed a similar experiment under field conditions to have a more realistic estimation of the impact of herbivory on fitness. In this case, we could achieve a reasonable number of replicates only for the two most abundant species growing in RDs, i.e., *Carduus thoermeri* and *Onopordon acanthium*. Both are biennial and have a vegetative phase as a rosette during the first year and elongate and flower in mid-summer of next year. In January and February 2009 we marked 160 first year rosettes of each species, 80 in RDs and 80 in adjacent soils. Plants in the field were not watered, and thus, they were exposed to natural moisture conditions of the system. We removed plants growing in the neighborhood to minimize competition. Even if this removal makes conditions less natural, the presence of competing plants would have made our results more difficult to interpret due to the difficulty of quantifying their actual effect on resources available to focal plants. Removal was performed in both RDs and NNSs, so it implied no bias towards any substrate type. Before inflicting leaf damage we counted the number of leaves (Li) and measured height (Hi) and surface cover of each individual (Ci). We also estimated naturally occurring leaf damage by visually assessing the missing or altered area of the leaf. Each leaf was assigned to the following categories: 0, 0.1–5, 5.1–25, 25.1–50 and 50.1–100 % area consumed (see Pirk and Farji-Brener 2012). We calculated the percentage of foliar damage per individual by multiplying the number of leaves of each damage category by the mid-point of that category (i.e., 0, 2.5, 15, 37.5 and 75 %, respectively) and dividing it by the total number of leaves of the individual. Then we randomly selected half of the individuals growing on each substrate to receive 33 % leaf removal (see Greenhouse experiment). In January 2010 we performed the same measurements, but this time we estimated herbivory in 20 random leaves. We also counted total number of inflorescences per individual (a good surrogate of seed production in both species; Farji-Brener and Ghermandi 2008).

We analyzed data with an ANCOVA for each variable: change in plant height, surface cover, number of leaves, and total number of inflorescences. Species, substrate and treatment were the main factors and mean herbivory levels in the first and second year was the co-variable. As CCH proposes, we expected a significant treatment × substrate interaction, where compensation is highest in plants growing on RDs.

Results

Greenhouse experiment

Substrate and origin did not affect compensatory capacity. Damaged plants showed similar change in height, surface cover, leaf number, dry biomass, root:shoot ratio and leaf area in both substrates (RDs and NNSs) and in exotic and native species (i.e., substrate × treatment × origin interaction was not significant for all variables; Figs. 1, 2, 3; Tables 3, 4, 5).

Simulated herbivory treatment affected change in surface cover and leaf area in the first set of control leaves (CL1). Both variables increased 12 % more in damaged than control plants (Supplementary Table 1). However, this trend was independent of type of substrate or plant origin (Figs. 1, 3; Tables 3, 5).

Type of substrate and plant origin affected plant growth. Height, leaf number and leaf area (CL2) increased about 15 % more in plants growing in RDs

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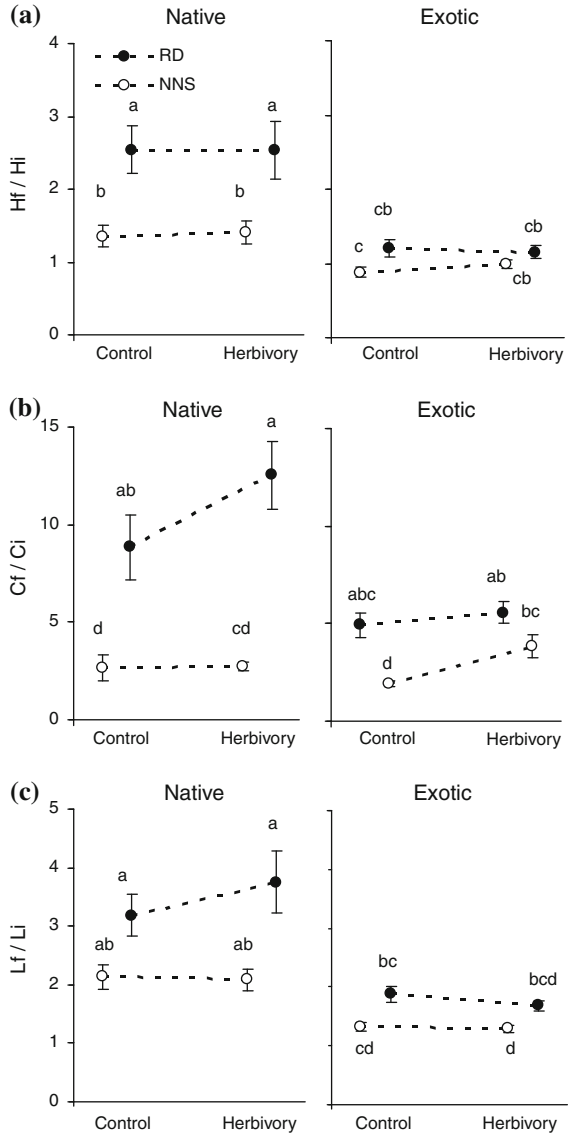

Fig. 1 Growth variables in the greenhouse experiment. (**a**) Change in height (Hf/Hi), (**b**) surface cover (Cf/Ci) and (**c**) leaf number (Lf/Li) of exotic and native species with (Herbivory) and without (Control) simulated herbivory treatment growing in *NNS* non-nest soils and *RD* refuse dumps. *Different letters* indicate significant differences with Tukey contrasts ($p < 0.05$). See Table 3 for more statistical results

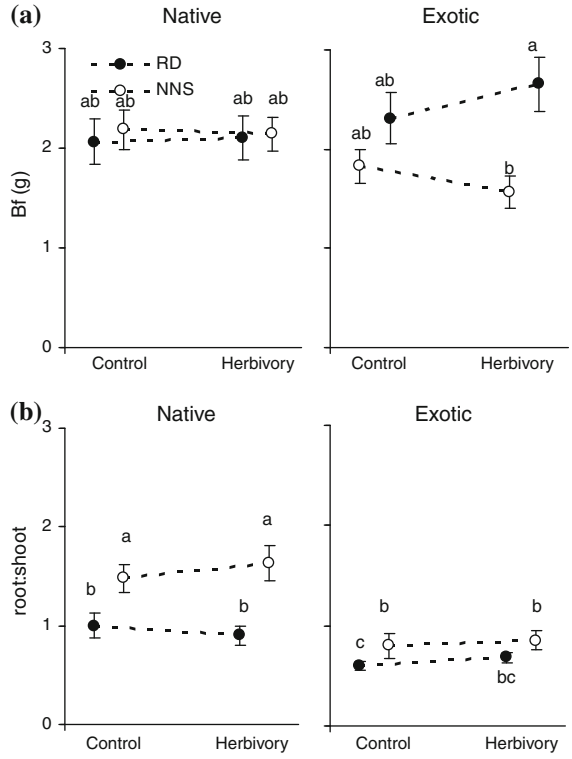

Fig. 2 Final biomass of plants in the greenhouse experiment. (**a**) Total final dry biomass (Bf) and (**b**) root:shoot ratio of exotic and native species with (Herbivory) and without (Control) simulated herbivory treatment growing in *NNS* non-nest soils and *RD* refuse dumps. *Different letters* indicate significant differences with Tukey contrasts ($p < 0.05$). See Table 4 for more statistical results

than in those growing in NNSs. Change in height and leaf number were 13 and 18 % greater in native than exotic plants (Figs. 1, 3; Tables 3, 5; Supplementary Table 1). In addition, change in surface cover was especially greater in native plants growing in RDs (i.e., interaction origin × substrate was significant; Table 3). Increase in surface cover of native plants in RDs doubled that of exotics and was four times greater than plants of any origin growing in NNS (Supplementary Table 1). However, total dry biomass showed a different trend. While exotic plants achieved greater total biomass in RDs than in NNSs (2.5 ± 0.1 vs. 1.7 ± 0.1 g), native plants showed similar values between substrates (2.1 ± 0.2 and 2.2 ± 0.2 g in RDs and NNS, respectively; Supplementary Table 1). On the other hand, root:shoot ratio of native plants in NNSs doubled that of exotic plants (Fig. 2; Table 4; Supplementary Table 1).

Number of basal sprouts per individual did not differ between control and clipped plants neither in *Oenothera odorata* ($F_{1,22} = 0.09$, $P = 0.76$; two-way ANOVA), *Solidago chilensis* ($F_{1,22} = 0.001$, $P = 0.97$; two-way ANOVA) nor in *Conyza lechelri* ($F_{1,5} = 1.75$, $P = 0.24$; one-way ANOVA) (Fig. 4). These variables were not affected by type of substrate

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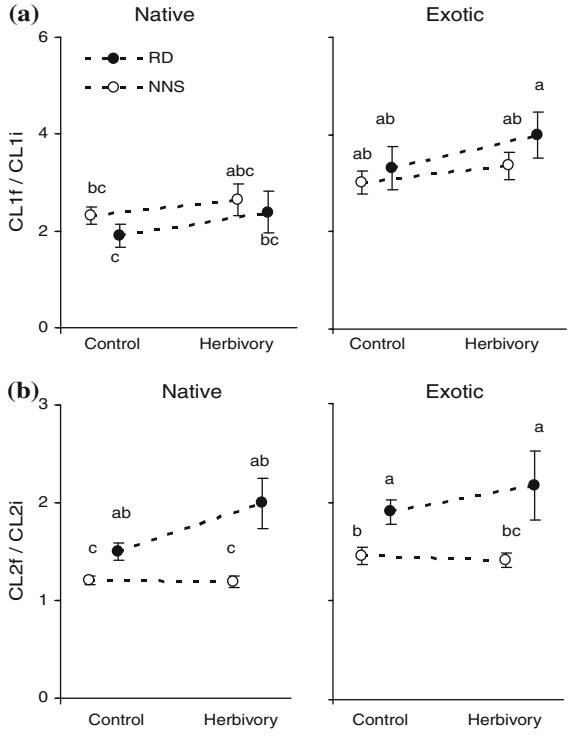

Fig. 3 Change in area of (**a**) CL1 control leaf 1, and (**b**) CL2 control leaf 2 of exotic and native species with (Herbivory) and without (Control) simulated herbivory treatment growing in *NSS* non-nest soils and *RD* refuse dumps. *Different letters* indicate significant differences with Tukey contrasts ($p < 0.05$). See Table 5 for more statistical results

in *O. odorata* ($F_{1,22} = 3.55$, $P = 0.07$; two-way ANOVA) and in *S. chilensis* ($F_{1,22} = 0.49$, $P = 0.49$; two-way ANOVA), but *C. lechleri* only presented sprouts in plants growing on RDs. Number of branches in *C. lechleri* was similar between substrates and herbivory treatments ($F_{1,13} = 0.94$, $P = 0.35$ for treatment and $F_{1,13} = 0.05$, $P = 0.81$ for substrate; two-way ANOVA) (Fig. 4).

Field experiment

In the field, type of substrate affected the compensatory capacity but this effect depended on the species and the response variable (i.e., there was a significant species × substrate × treatment interaction only in change in height; Fig. 5; Table 6). Clipped *Onopordon acanthium* plants showed a two-fold increase in height in RDs compared to control plants, whereas in *Carduus thoermeri* no differences were detected between treatments in RDs (Fig. 5).

Simulated herbivory treatment also affected change in surface cover. Growth was about two times greater in clipped than control plants (Supplementary Table 2), but independent of substrate type (Table 6). Substrate type also affected plant growth. Change in surface cover, in leaf number and number of inflorescences were 7, 9 and 11 times greater, respectively, in RDs than in NNSs (Table 6; Supplementary Table 2).

Discussion

RDs resulting from the activity of leaf-cutter ants benefit plant growth and reproduction in the Patagonian steppe but do not provide any special advantage to compensate for damage. The studied native and exotic plants fully compensated for simulated

Table 3 ANOVA results of change in height, surface cover and number of leaves of plants grown in the greenhouse

Source	Effect	df	Change in height			Change in surface cover			Change in number of leaves		
			SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Origin	Fixed	1	103068	8.23	**0.04**	41	0.01	0.95	1.19	10.99	**0.03**
Species (origin)	Random	4	55193	6.22	**<0.01**	43691	5.42	**<0.01**	0.47	5.37	**<0.01**
Treatment	Fixed	1	1361	0.61	0.43	45622	22.65	**<0.01**	0.01	0.11	0.74
Substrate	Fixed	1	61471	27.7	**<0.01**	171770	85.28	**<0.01**	0.64	29.12	**<0.01**
Block	Random	9	14304	0.72	0.7	37205	2.05	**0.04**	0.28	1.39	0.19
Origin × substrate	Fixed	1	7724	3.48	0.06	9105	4.52	**0.03**	0.01	0.06	0.81
Origin × treatment	Fixed	1	1086	0.49	0.48	510	0.25	0.62	0.01	0.05	0.82
Treatment × substrate	Fixed	1	2702	1.22	0.27	2112	1.05	0.31	0.01	0.09	0.77
Origin × substrate × treatment	Fixed	1	568	0.26	0.61	3673	1.82	0.18	0.01	0.03	0.86
Error		178	395042			358533			3.94		

Significant effects ($p < 0.05$) are indicated in bold

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Table 4 ANOVA results of final dry biomass and root:shoot ratio of plants grown in the greenhouse

Source	Effect	df	Final dry biomass			Root:shoot		
			SS	*F*	*P*	SS	*F*	*P*
Origin	Fixed	1	960	0.03	0.88	65195	0.89	0.40
Species (origin)	Random	4	164237	20.38	**<0.01**	327499	89.73	**<0.01**
Treatment	Fixed	1	491	0.243	0.62	9	0.01	0.92
Substrate	Fixed	1	6783	3.37	0.07	52562	57.60	**<0.01**
Block	Random	9	93921	5.18	**<0.01**	37625	4.58	**<0.01**
Origin × substrate	Fixed	1	23169	11.50	**<0.01**	4091	4.48	**<0.01**
Origin × treatment	Fixed	1	365	0.18	0.67	2564	2.81	0.09
Treatment × substrate	Fixed	1	831	0.41	0.52	121	0.131	0.72
Origin × substrate × treatment	Fixed	1	4853	2.41	0.12	1477	1.62	0.20
Error		178	2014			162423		

Significant effects ($p < 0.05$) are indicated in bold

Table 5 ANOVA results of change in leaf area of control leaves from weeks 0–4 (CL1) and 8–12 (CL2) of the greenhouse experiment

Source	Effect	df	Change in area of CL1			Change in area of CL2		
			SS	*F*	*P*	SS	*F*	*P*
Origin	Fixed	1	7.07	3.58	0.13	93964	3.67	0.13
Species (origin)	Random	4	8.79	12.12	**<0.01**	113958	14.87	**<0.01**
Treatment	Fixed	1	0.76	4.21	**0.04**	47	0.02	0.87
Substrate	Fixed	1	0.06	0.35	0.56	90950	47.47	**<0.01**
Block	Random	9	1.99	1.22	0.28	47	0.02	0.87
Origin × substrate	Fixed	1	0.62	3.42	0.07	147	0.08	0.78
Origin × treatment	Fixed	1	0.01	0.05	0.82	1093	0.57	0.45
Treatment × substrate	Fixed	1	0.11	0.62	0.43	1238	0.60	0.42
Origin × substrate × treatment	Fixed	1	0.01	0.01	0.92	567	0.30	0.59
Error		178	32.26			341001		

Significant effects ($p < 0.05$) are indicated in bold

herbivory resembling natural levels of foliar damage, but the general trend did not show higher compensatory growth in RDs than in NNSs, as we expected under the CCH.

Both native and exotic plants growing in RDs performed better than plants in NNSs (i.e., they grew higher, had more leaves, surface cover and dry biomass) as observed in previous greenhouse and field studies (Farji-Brener and Ghermandi 2008; Farji-Brener et al. 2010). Nevertheless, the benefits provided by the RDs did not translate into a better compensatory capacity, as the CCH proposes (Maschinski and Whitham 1989). Our results could be explained in the framework of the limiting resource model (LRM, Wise and Abrahamson 2005, 2007), which takes into account the factors limiting plant fitness, the resources that are affected and the way that damage affects resource acquisition. In our study the focal resource (i.e. the one being manipulated) is actually a group of nutrients enhanced in RDs (Farji-Brener and Ghermandi 2008) and simulated foliar herbivory primarily affects carbon levels (Wise and Abrahamson 2005), an alternate resource. Given these premises, the LRM provides several scenarios resulting in equal tolerance in high versus low levels of the focal resource (i.e., between RDs and NNSs). Firstly, that the focal resource is not limiting plant fitness in the low focal resource environment. This is unlikely

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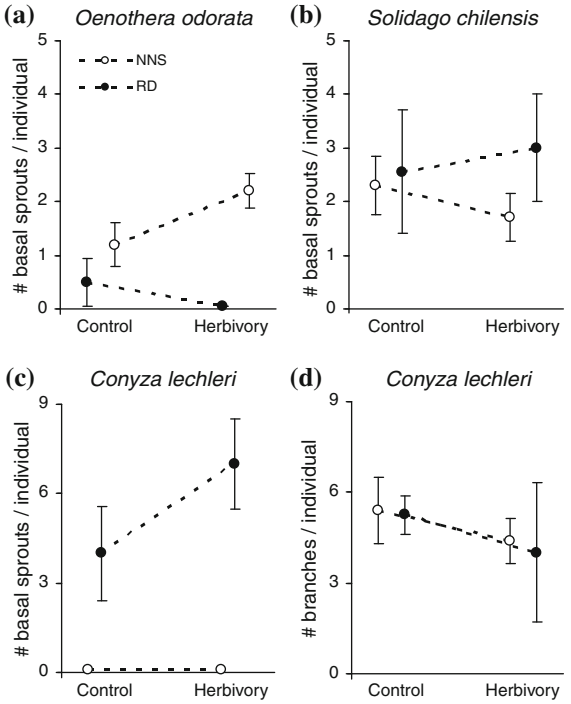

Fig. 4 Number of basal sprouts per individual in (**a**) *Oenothera odorata*, (**b**) *Solidago chilensis* and (**c**) *Conyza lechleri*, and (**d**) branches per individual in *Conyza lechleri* growing in *NSS* non-nest soils, and *RD* refuse dumps with (Herbivory) and without (Control) simulated herbivory treatment

since in our study and in previous ones (Farji-Brener and Ghermandi 2008; Farji-Brener et al. 2010) plants in RDs achieve more biomass than in NNSs, indicating that at least one of the resources enhanced in RDs is limiting plant growth. Next, given a limiting focal resource, the question is whether herbivory affects the acquisition/use of the focal or a different resource. Leaf herbivory primarily affects carbon, an alternate resource. According to the LRM, if the alternate resource affected by herbivory is not limiting plant fitness in the high focal resource environment, equal tolerance in both environments is expected. So, in our study, the equal tolerance in RDs and NNSs may be due to a lack of carbon limitation in RDs. Also, levels of herbivory inflicted were probably not sufficiently high to cause carbon to become limiting. The chosen amount of herbivory (i.e., 33 % leaf loss) represents the highest levels found in the field, and thus is realistic. Of course, although there is some evidence supporting the assumptions which lead to the expectation of equal tolerance between RDs and NNSs, each

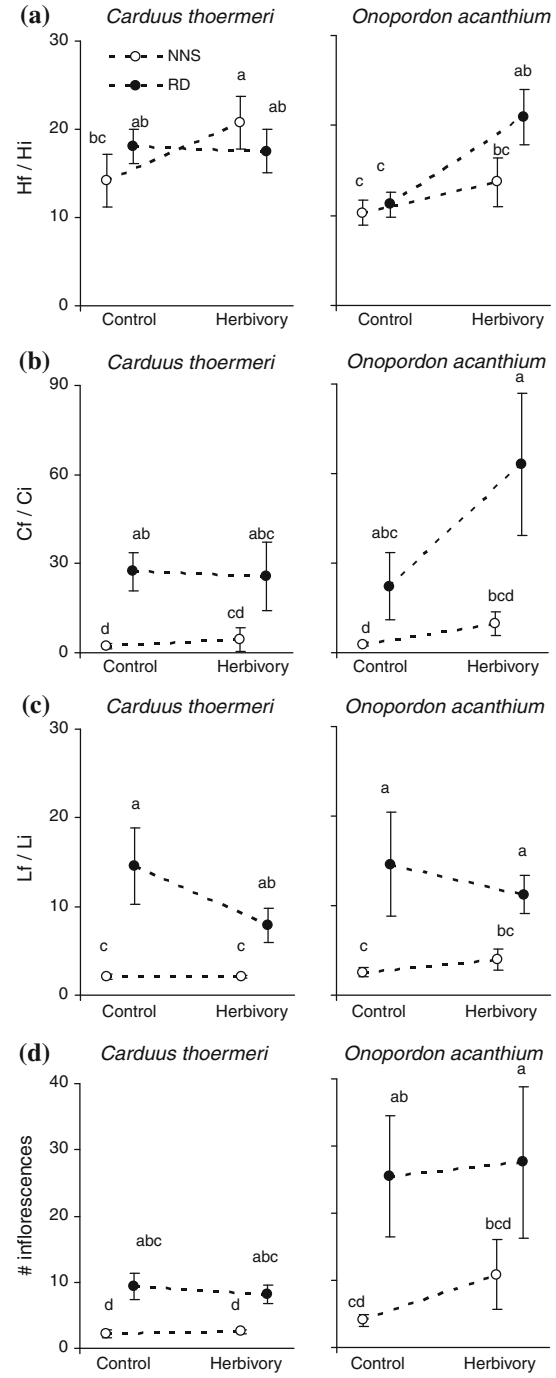

Fig. 5 Results of the field experiment. (**a**) Change in height (Hf/Hi), (**b**) surface cover (Cf/Ci) and (**c**) leaf number (Lf/Li), and (**d**) number of inflorescences per individual of *Carduus thoermeri* and *Onopordon acanthium* with (Herbivory) and without (Control) simulated herbivory treatment growing in *NSS* non-nest soils and *RD* refuse dumps in field experiments. *Different letters* indicate significant differences with Tukey contrasts ($p < 0.05$). See Table 6 for more statistical results

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Table 6 ANOVA results of change in height, surface cover, number of leaves and final number of inflorescences of *Onopordon acanthium* and *Carduus thoermeri* during field experiments

Source	df	Change in height			Change in surface cover			Change in number of leaves			Number of inflorescences		
		SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Natural herbivory	1	172.26	2.24	0.14	4.11	2.71	0.10	0.04	6.14	**0.01**	2029.71	3.63	0.06
Species	1	70.30	0.92	0.34	2.00	1.32	0.25	0.04	5.42	**0.02**	4594.87	8.22	**<0.01**
Treatment	1	533.33	6.95	**<0.01**	12.95	8.53	**<0.01**	0.01	0.01	0.98	129.21	0.23	0.63
Substrate	1	35.92	0.47	0.50	63.30	41.72	**<0.01**	0.39	56.08	**<0.01**	18242.53	32.65	**<0.01**
Species × treatment	1	54.66	0.71	0.40	0.28	0.18	0.67	0.01	0.14	0.71	1056.87	1.89	0.17
Species × substrate	1	96.08	1.25	0.27	5.53	3.64	0.06	0.01	1.31	0.25	210.13	0.38	0.54
Substrate × treatment	1	2.56	0.03	0.85	0.15	0.10	0.75	0.01	0.08	0.77	101.23	0.18	0.67
Species × substrate × treatment	1	324.06	4.22	**0.04**	5.03	3.31	0.07	0.01	0.78	0.38	371.25	0.66	0.42
Error	91	6982.16			138.09			0.63			50839.25		

Significant effects ($p < 0.05$) are indicated in bold

of them of needs to be adequately tested to reach solid conclusions.

Exotic plants achieve more biomass in RDs than native plants. These results were similar to a previous study (Farji-Brener et al. 2010) despite using a smaller set of species, which shows that this trend is strong. In spite of this supposed advantage, exotic plants' compensatory capacity is not enhanced in RDs under levels of simulated herbivory damage administered here. Neither exotic nor native species are better at compensating for herbivory in either substrate. Moreover, in the study area exotic plants are not released from herbivory (Pirk and Farji-Brener 2012) and thus, are probably not particularly benefited if they reduce the investment in resistance and increase their compensatory capacity (the evolution of increased competitive ability hypothesis, or EICA; Blossey and Nötzold 1995). Small amounts of leaf herbivory can have major detrimental effects on plant growth and survival. Only 10 % loss of leaf area significantly reduced fitness in *Piper arieianum* plants in Costa Rica (Marquis 1984). The fact that plants included in this study were not affected by the levels of simulated herbivory inflicted, may be related to natural history. All species are common in roadsides of the Patagonian steppe and adapted to disturbance. Some are annual and others biennial, with high growth rates which allow them to reproduce within one or two growing seasons. Native plants in these disturbed areas probably share some typical traits of invasive species: fast growth rates, high seed production (van Kleunen et al. 2010), high competitive ability (D'Antonio and Mahall 1991), and high phenotypic plasticity (Funk 2008). It has recently been pointed out that invasive alien plants usually have the same general suite of traits exhibited by most successful plants in the world today, irrespective of their alien or native status (Thompson and Davis 2011). In particular, a study in Australia has shown that natives of disturbed, fertile habitats are indistinguishable from aliens of similar habitats (Leishman et al. 2010). Thus, the rapid and efficient response of the studied plants to damage could be a consequence of their particular life history traits which made them successful in this disturbed environment, regardless of their origin.

As for the mechanisms involved in plant compensation, in the greenhouse experiment growth variables suggest that similarity of the final biomass between clipped and control individuals is achieved through a

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compensatory increase in foliar area right after the damage. Surface cover and leaf area experienced higher increases in clipped plants. This means that when leaves are damaged, plants respond by producing more foliar area. This response occurs immediately after damage since treatment effect was only evident in the first set of control leaves (from the onset of the experiment until week 4). The increase in surface cover is a consequence of this increased foliar area rather than a higher leaf production, because change in leaf number did not differ between treatments. In the field, the similar reproductive output between clipped and control plants may also be related to an increase in surface cover, as well as an increase in height. The latter was only relevant in the field probably because the production of stalks and inflorescences occurs during the second year, significantly increasing plant height. Plant's energy investment in producing more foliar area is likely rapidly compensated for through a higher area available for photosynthesis, which aids plants to quickly achieve a full recovery, i.e., no effect on total plant biomass. This mechanism is hypothetical since we did not perform physiological measures. However, our results suggest alternative explanations are less likely. For example, it is unlikely that damaged plants shunt carbon stores from roots to shoots to achieve a higher foliar area since final root:shoot ratio was not affected by simulated herbivory treatment. However, as this variable was only measured at the end of the experiment (it involves total destruction of plants), it is unknown if this mechanism may temporarily occur after damage. Increased branching or tillering did not depend on treatment so it is unlikely that this mechanism is involved in compensation. In sum, the compensatory increase under simulated foliar damage appears to be more related with a rapid production of foliar area than with other alternatives, such as increasing leaf number or branching.

Finally, by using two different approaches (i.e., a greenhouse and a field experiment) with different virtues and drawbacks (e.g., in the greenhouse environmental variables are more controlled but the field experiment is more realistic) similar results were obtained. This confers robustness to our main conclusion that RDs do not provide any special advantage to compensate for damage. Our study, the first one to date performed to test the CCH on ants' RDs, corresponds with other studies that show that enhanced levels of resources do not always determine higher tolerance to herbivory (e.g., Hawkes and Sullivan 2001; Wise and Abrahamson 2005). The outcome may depend on the type of resources that are increased (either limiting or not), and the amount and type of herbivory experienced by plants. Moreover, the degree in which plants compensate for herbivory may be influenced by their life histories, rather than their origin. Plants associated with disturbances may have traits that allow them to tolerate natural occurring herbivory without compromising their performance.

Acknowledgments We thank R. Dirzo and E. Gianoli for their critical reading and comments on an earlier draft of this manuscript. We are also grateful for the contributions of two anonymous reviewers. N. Lescano, S. González, C. Ezcurra, J. Franzese, C. Ziperovich, and L. Ghermandi helped at several stages of this study. GP was supported by a postdoctoral fellowship from CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas) and financial support was partially supplied by Agencia Nacional de Promoción Científica y Tecnológica of Argentina (lately through PICT 2008-0352).

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