Plant Ecol (2007) 193:31–38
DOI 10.1007/s11258-006-9246-9

ORIGINAL PAPER

How plants may benefit from their consumers: leaf-cutting ants indirectly improve anti-herbivore defenses in *Carduus nutans* L

Alejandro G. Farji-Brener

Received: 9 August 2006 / Accepted: 20 November 2006 / Published online: 27 December 2006

Abstract Although herbivores often have a negative impact on plant fitness, sometimes plants may benefit from their consumers. However, these positive interactions usually occur as a result of plant damage (e.g., overcompensation, defense induction). I present evidence of a novel way by which plants may benefit from their consumers without being eaten. Plants of *Carduus nutans* increased their physical defenses when grown in external refuse dumps of the leaf-cutting ant *Acromyrmex lobicornis*. Seedlings planted in refuse exhibited longer spines and tougher leaves than those planted in control soils. Pick-up assays with entire leaves and leaf discs demonstrated that these enhanced physical defenses prevented leaf-cutting ant harvest. Additionally, plants established in refuse dumps showed fewer insect herbivory than those in non-nest soils. The nutrient-rich refuse dump appeared to reduce the stage at which leaves are tender and thus more vulnerable to herbivory. This is the first case where plants may benefit from insect herbivores via waste products without the cost of being eaten. This illustrates how plants may plastically respond to reliable cues of the risk of herbivory.

A. G. Farji-Brener (✉)
Lab. Ecotono, Depto. de Ecología, CRUB,
Universidad Nacional del Comahue, 8400 Bariloche,
Argentina
e-mail: alefarji@crub.uncoma.edu.ar

Keywords *Acromyrmex lobicornis* · Herbivory risk · Induced defenses · Patagonia · Phenotypic plasticity · Refuse dumps

Introduction

Although herbivores often have a negative impact on plant growth and fitness (Marquis 1992), plants may benefit from their consumers (Agrawal 2000). Plants can respond to herbivory with an increase in their productivity (i.e., overcompensating). Consequently, some plant species produce more biomass when they are cropped by consumers (McNaughton 1983). Herbivory may stimulate plant branching generating an increase in the number of leaves, flower and fruits per plant (Paige and Whitham 1987), and result in better support in plants with aerial roots (Simberloff et al. 1978). Leaf damage may also stimulate anti-herbivore defenses. A growing body of evidence indicates that herbivore attacks may induce chemical, mechanical and biotic defenses in plants; and that these induced defenses can decrease herbivore damage (Agrawal 1998a, b, 2000; Abdala-Roberts and Parra-Tabla 2005). Plants may also benefit if the nutrient-rich waste products of consumers are deposited at the base of the attacked plant (Stadler et al. 1998). This ‘‘positive’’ relationship between consumers and plants, opposite to the traditional antagonistic view, was first formally postulated twenty five years ago (Owen 1980) but remains controversial (Belsky et al. 1993; Mathews 1994; Vail 1994; Järemo et al. 1999; Rautio et al. 2005). Much of this controversy results from the fact that the above described relationships always imply some level of plant damage. Therefore, whether plants have a net positive outcome (i.e., enhanced reproduction) or not is sometimes difficult to establish (Järemo et al. 1999; Callaway et al. 2003). However, there is a way in which plants may benefit from their consumers without being eaten. Here I present evidence of how the leaf-cutting ant *Acromyrmex lobicornis* increases the anti-herbivore defenses in plants of *Carduus nutans* (Asteraceae) without harvesting them; and how, as a result, this plant species is better defended against leafcutters and insect herbivory in general.

Leaf-cutting ants are known as the most voracious herbivores in the Americas, harvesting up to 17% of the production of leaves in forests (Cherrett 1989). However, leafcutters can benefit plants indirectly. This benefit generally implies the exploitation of ant debris by the plants. Leaf-cutting ants selectively collect large quantities of fresh vegetation from a large area and carry it to their nest chambers where the plant material is degraded by a mutualistic fungus (Cherrett 1989). The waste material from the fungal decomposition (hereafter refuse dumps) is carried to specific external or internal disposal areas (Farji-Brener and Medina 2000). This refuses is several times richer in organic carbon and nutrients than non-nest soils, enhancing the growth and performance of plants around the nest area (Haines 1978; Farji-Brener and Ghermandi 2000, 2004; Farji-Brener and Illes 2000; Moutinho et al. 2003; Wirth et al. 2003). For example, adult trees may benefit from the internal refuse chambers through their deep roots (Farji-Brener and Medina 2000; Moutinho et al. 2003), while seedlings and small plants near the nest may benefit from the external refuse dump (Farji-Brener and Medina 2000; Wirth et al. 2003; Farji-Brener and Ghermandi 2004). However, to grow on a refuse dump may be a problem for the plant.

Although refuse dumps are known to delay leaf-cutting harvest because they harbor microorganisms harmful to the ant colony (Hart and Ratnieks 2001), plants that grow on external refuse dumps are attacked by the ants because they are in close proximity to the nest (Farji-Brener and Sasal 2003). Consequently, plants that establish and grow on external refuse dumps have a benefit but also a risk: they can exploit a nutrient-rich source but are easily found by leaf-cutting ants. However, to grow on ant debris may confer a benefit for the plants that has been little studied: the increase of antiherbivore defenses.

It is known that the soil nutrient condition influences the physical and chemical traits of leaves (Chapin et al. 1987), and the susceptibility of a plant to herbivores (Nichols-Orians 1991). Under high nutrient conditions (e.g., in refuse dumps) plants may shunt more resources into production of antiherbivore defenses (Nichols-Orians 1991) or growth, decreasing the period when leaves are more vulnerable to herbivory. I investigated this indirect positive effect of ant debris on plants using *Acromyrmex lobicornis* leaf-cutting ants and the plant *Carduus nutans*. I experimentally tested whether *C. nutans* plants growing in refuse dumps contained higher anti-herbivore defenses than those growing in non-nest soil, and whether these enhanced defenses prevented leaf-cutting ant attack and reduced general insect herbivory.

Material and methods

Study area, plant and leaf-cutting ant species

The study area is located on the eastern border of the Nahuel Huapi National Park, Northwest Patagonia, Argentina (41°S, 71°W), and is covered by herbaceous and shrub steppe vegetation. The mean annual temperature is 8°C and the mean annual precipitation is 600 mm. We conducted surveys in steppe areas near road verges where both *Carduus nutans* and the leaf-cutting ant *Acromyrmex lobicornis* are common (Farji-Brener and Ghermandi 2004). *Carduus nutans* (musk thistle) is a naturalized, biennial, monocarpic plant species with the ability to colonize widely and spread quickly (Rapoport et al. 1997).

Seeds in the laboratory or the field may germinate in 14–21 days of shedding. Soon after germination a rosette is formed. Rosettes are protected from grazing animals by numerous sharp spines located on the leaf border (Lee and Hamrick 1983). *C. nutans* is very abundant near *A. lobicornis* nests, and forms an important part of their diet (Farji-Brener and Ghermandi 2000, 2004; Franzel and Farji-Brener 2000). *Acromyrmex lobicornis* Emery is the only leaf-cutting ant species inhabiting NW Patagonia (Farji-Brener and Ruggiero 1994). *Acromyrmex lobicornis* construct a mound of twigs, soil and dry plant material, which may reach a height and width of 1 m. Inside this mound, ants grow fungus to feed their larvae. Organic debris from the fungus culture are removed from the internal fungus garden and dumped on the soil surface in external dumps. The ant debris is deposited in a few large, flat piles on the soil surface near the mound, which makes them accessible to nearby plants. Refuse dumps of *A. lobicornis* show 5–10 times more organic matter, nitrogen and phosphorous than non-nest soils (Farji-Brener and Ghermandi 2000).

Methodology

To evaluate the effect of refuse dumps on the antiherbivore defenses of *C. nutans*, I (a) measured the presence of insect herbivory in plants of *C. nutans* growing in refuse dumps and non-nest soils; (b) planted seeds from randomly selected *C. nutans* plants in refuse dumps and non-nest soil plots in a greenhouse. Ten weeks later I measured leaf toughness, spine number and spine length of all planted seedlings; and (c) offered entire leaves and leaf discs from the above described experimental plants to leaf-cutting ants in field pick-up assays.

To monitor whether the presence of insect herbivory on *C. nutans* was related to the substrate in which the plants grow, I recorded the presence of leaf damage in a total of 120 *C. nutans* plants growing on refuse dumps on different ant nests and 120 growing in non-nest soils in the field in 1999, 2001, and 2004. Plants in each treatment were randomly selected. A Chi-square test with Yates correction was used to analyze the independence between the presence of insect herbivory and the substrate on which plants grew.

To experimentally assess the effect of refuse dumps on the level of physical antiherbivore defenses of *C. nutans* I conducted the following experiment. First, in an area of 10 ha, I collected 20 seeds each from 20 *C. nutans* plants established in non-nest soils. Second, I collected refuse samples from 20 randomly selected active *A. lobicornis* nests, and soil samples from nearby non-nest sites. Non-nest sites were chosen by selecting a random distance between 3 and 6 m from each nest-mound at a random angle from 0 to 360°. Each refuse dump and non-nest soil sample was pooled from three cores of 10-cm diameter and 15-cm depth (300 cm^3 each). All samples were sterilized in the laboratory in a drying chamber (60°C) for one week. A random sub sample was placed in a greenhouse and watered every 2 days for 5 weeks. No plants germinated in the sample period, verifying that this treatment had killed all seeds in the seed bank of the soil and refuse. Third, in the greenhouse, each sterilized refuse dump and non-nest soil sample from the same site ($n = 20$) was placed in a plot of 10 × 20 × 10 cm. Ten of the 20 collected seeds per plant were sown in a refuse dump plot and the other 10 in a non-nest soil plot. I planted a total of 400 seeds from 20 plants (20 seeds per plant), 200 seeds in refuse dump plots ($n = 20$ plots) and 200 on non-nest soil plots ($n = 20$ plots). Refuse dump and non-nest soil plots were watered every two days. After 10 weeks I randomly selected three plants per plot to measure leaf toughness and the number and length of spines. I determined the toughness of the two largest leaves per seedling using a penetrometer (Nichols-Orians 1991). The response variable was the grams required to break the leaf blade. Five readings were taken per leaf and the ten measures averaged. In the same leaves, spine number and length were measured in two sectors of 4-cm of leaf border. All measures per seedling were averaged per site ($n = 20$) and analyzed using paired t-tests to control plant and site effects; leaf-toughness, spine density and spine length were the response variables.

Acceptability bioassays

To analyze whether the physical features measured in the seedlings from the greenhouse experiment (or other unmeasured chemical leaf traits) affect leaf-cutting ant preferences, I carried out two different pickup assays in the summer (beginning of March) of 2002. This type of experiment is designed to determine preferences between leaf types based on plant defenses or nutritional quality, and is widely used in leaf-cutting ant studies (Howard 1987, 1988; Nichols-Orians 1991; Farji-Brener 2001). In the first pickup assay, two whole leaves (~7 cm length and 3 cm maximum width) from different seedlings, one for each treatment (refuse dump and non-nest soil), were presented to the ants simultaneously in the field. Both seedlings came from seeds of the same plant. The leaves were placed in a single line besides an active ant trail (~5 cm) at 2–5 m from the nest entrance. Each assay lasted for 30 min, beginning when the ants first started to cut any leaf. To eliminate possible position effects, the order of the leaf from different treatments with respect to the nest entrance was changed in each trial. Tracings of leaves were made before and after cutting and the resulting difference in leaf area was measured with a leaf area meter. The area harvested was expressed as a percentage. All palatability measurements were initiated within 1 h and completed within 3 h from time to collection, prior to the appearance of observable induced changes in plant chemistry (Howard 1987). This field test was conducted at a total of 20 times in 20 different colonies (one per colony); each trial was replicated twice per colony during the peak of foraging activity, and the replicates were averaged.

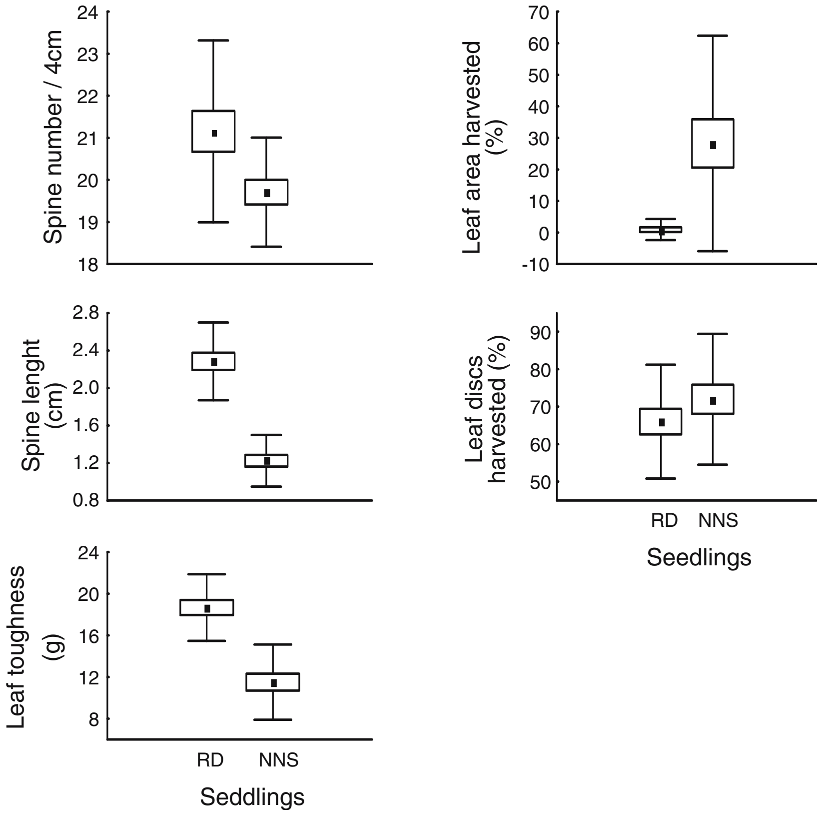
To determine the relative importance of physical versus chemical defenses, I repeated the experiment described above in the same 20 nests using leaf discs instead of entire leaves. While both mechanical and chemical leaf traits affect the acceptability of entire leaves, only chemical leaf traits affect the preference of leaf discs because every barrier against leaf cutting is removed (see Howard 1988; Nichols-Orians and Schultz 1990). Two leaf discs of a given leaf type (refuse dump and non-nest soil) were produced with a standard paper punch and placed with a disc of a highly preferred control, *Salix humboltiana*, beside active trails. The use of preferred items in leaf-cutting pick-up assays is widely used to control for fluctuations in ant activity (Nichols-Orians 1991; Farji-Brener 2001). When one disc was removed it was replaced by a disc of the same type. The acceptability of each leaf type was expressed as the number of test leaf discs removed when 20 control discs had been removed, averaged over three replicate trials. Data of both pick-up assays were analyzed with paired *t*-tests, and nests ($n = 20$) were considered as the replicates.

Results

In the field, the presence of insect herbivory in *C. nutans* plants was associated with the substrate where the plants grew. While only 15 of 120 seedlings growing on refuse dumps showed insect herbivory signs, 96 of 120 growing in non-nest soils showed some level of leaf damage (X^2: 41.2, $P < 0.0001$). Leaf damage occurred mainly in the younger leaves and included signs of herbivory not caused by leafcutters (e.g., caterpillars and beetles). In the greenhouse, seedlings grown in refuse dump plots showed higher levels of physical defenses than those grown in non-nest-soil plots (Fig. 1). Although each pair of compared seedlings came from seeds of the same adult plant, the means of spine length, number of spines/4 cm, and leaf toughness were higher in seedlings in refuse-dump plots than in seedlings in non-nest soil plots (paired *t*-test = 12.03, 2.4, and 8.5, respectively, all $P < 0.03$, $N = 20$ each, Fig. 1).

These physical traits affected the susceptibility of leaves to leaf-cutting ants. When entire leaves were exposed to ant attack, leaves from non-nest soil seedlings were by far harvested more often than leaves from refuse-dump seedlings (paired $t = 3.7$, $P < 0.001$, $N = 20$, Fig. 1). Moreover, 17 of 20 leaves from refuse-dump seedlings were not cut, while 10 of the 20 leaves from the non-nest soil seedlings greater than 20% of the leaf was removed. The less tough leaves from non-nest soil seedlings were easily cut by ants, while

Fig. 1 Physical antiherbivore defenses in seedlings established in refuse dump plots (RD) and non-nest soil plots (NNS) (left side); and results of the pick-up assays in where whole leaves (above) and leaf discs (below) of both types of seedlings were offered to leaf-cutting ants (right side). All results are statistically significant (paired t-test, $P < 0.003$), except the pick-up assay with leaf-discs ($P = 0.34$, see text). Points represent the mean, box standard errors, and whisker values standard deviations



leaf-cutters found the thornier and tougher leaves from refuse-dump seedlings very difficult to manipulate and cut. However, when leaf discs were offered to the ants instead of entire leaves, leaf discs from non-nest soil and refuse-dump seedlings were equally harvested (paired $t = 1.1$, $P = 0.34$, $N = 20$, Fig. 1).

Discussion

Growing on refuse dumps of *A. lobicornis* increased the level of physical antiherbivore defenses in *C. nutans.* These enhanced defenses deterred leaf-cutting ant attacks and reduced the herbivory level caused by other insects. Seedlings that grew in refuse dump plots showed an increase of 100% in spine length, 10% in spine number, and 50% in leaf toughness compared to seedlings growing in non-nest soil plots. Entire leaves from non-nest soil seedlings were harvested 25 times more than entire leaves from refuse dump seedlings, while leaf discs of both types of seedlings were equally preferred by the ants (Fig. 1). These results strongly suggest that physical differences between leaves, and not other chemical leaf traits that were not measured, influenced the acceptability of leaves to leafcutters. Plant selection by leaf-cutting ants is affected by secondary chemistry and nutrients (Howard 1987; Nichols-Orians 1991), but physical defenses often deter leaf-cutting ant attack (Howard 1988; Nichols-Orians and Schultz 1990). First, larger and denser spines on the leaf edge prevent the adoption of the preferred cutting posture of leafcutters (Barrer and Cherrett 1972; Wetterer 1991). Second, ants often avoid cutting tough leaves because it is energetically and time demanding (Nichols-Orians and Schultz 1990).

Leaves of *C. nutans* are tender with small spines in the first weeks, but become tougher and thornier as the seedling grows. However, leaves from seedlings of the same age but established in different substrates showed great differences in their physical leaf traits (Fig. 1). These results do not permit discrimination whether the enhanced physical traits in refuse seedlings may be a consequence of the shunt of more resources into the production of physical defenses, and/or the result of faster growth. Whatever the mechanism is, the final effect is the reduction of the stage in which leaves are tender and thus more vulnerable to herbivory. Reducing this “window of vulnerability” may have key repercussions for plants because defense of young leaves is a major determinant of plant fitness (Coley and Barone 1996; Kursar and Coley 2003).

Plants are highly plastic. For example, individuals within a species that grow on different substrates may vary by orders of magnitude in size, growth rates, reproduction, and chemical and physical leaf traits (Sultan 2000; Callaway et al. 2003). I demonstrated that seeds from the same plant can produce seedlings with different levels of physical leaf traits depending on the substrate in which they grow. Thus, the presence of external ant debris is acting as a developmental environment (*sensu* Weis 1992) because it influences the phenotypic expression throughout the ontogenetic development of a character. Moreover, this plastic response of *C. nutans* in contact with ant debris may be an example of an induced defense.

Given that herbivory reduces plant fitness (Marquis 1992), inducible responses to herbivory should be more adaptive if adjusted to the risk of herbivory rather than after herbivore attack (Karban et al. 1999). Why is defense induction by herbivory more widespread than responses to herbivore cues before attack? Perhaps it is because past or current herbivory is the most reliable predictor of future risk of herbivory (Karban et al. 1999). However, if consumers generate reliable cues detected by plants before attack, plants may evolve adaptive responses against herbivores before being eaten reducing the cost of losing leaf area. Several cues associated with herbivores, including disturbance, may influence plant response before the attack. For example, in the ant defended *Cecropia* and *Acacia* trees, noise or branch movement caused by mammalian herbivores (e.g., monkeys) induces a significant increase in the number of patrolling ants (Agrawal 1998b; AG Farji-Brener, personal observations). The external refuse dumps of leaf-cutting ants should be considered as a reliable cue of herbivore risk for plants because it implies close proximity of the ant nest. However, there is no selective evidence for this aspect yet. The association between herbivore risk and defense responses can be imposed by herbivores and/or shaped by physiological constraints. For example, plants growing in nutrient-rich environments other than ant debris might shorten the stage when leaves are tender independently of herbivore risk. Whatever the selection force is that induced the enhanced physical defenses found here, the ecological consequence for the plant is better protection against herbivory when growing on ant debris.

Here I showed that plants of *C. nutans* increased their physical defenses when they grow in external refuse dumps of *A. lobicornis*, and that these increased level of defenses reduced herbivore damage. However, the ultimate question is whether it benefits the plants in terms of fitness, a topic not measured in this work. Nonetheless, a parallel study demonstrated that plants that grow in refuse dumps have more seeds than plants that grow in non-nest soils (A.G. Farji-Brener, unpublished data). Therefore, it is likely that the increased level of anti-herbivore defenses in refuse-plants also imply a net beneficial effect in terms of reproduction.

The effect of *A. lobicornis* debris stimulating a plastic anti-herbivore response in *C. nutans* might also occur in other plant species and deter other insect herbivores. First, it has been shown that the nutrient-rich refuse dumps of leaf-cutting ants often promote rapid growth in a broad number of plant species (Lugo et al. 1973, Farji-Brener and Ghermandi 2000, 2004; Moutinho et al. 2003). As discussed earlier, the time reduction of the stage of young leaves is an effective antiherbivore defense in a range of plant species (Coley and Kursar 2003). Second, physical leaf traits effectively deter a broad number of herbivores (Coley and Barone 1996). Hence, tougher and thornier leaves may prevent attack of other generalist herbivores aside from leaf-cutting ants. The lower level of general insect herbivory in field plants grown in refuse dumps compared with those grown in non-nest soils supports this hypothesis. This effect may be particularly important in temperate regions as studied here, where the peak of herbivore activity often coincides with the first stage of plant development.

This is the first case, to my knowledge, which demonstrates that plants can benefit from insect herbivores via their waste products without the cost of being eaten. The closest examples may be the deposition of sugar honeydew by aphids beneath their host plant, which provide an energy source for free-living nitrogen-fixing bacteria (Owen 1980; Stadler et al. 1998) and the importance of caterpillar frass under the consumed tree for the plant's induced defenses (Haukioja and Neuvonen 1985). However, in these cases the plant has the cost of being eaten. If the effect found here occurs in a range of plant species, leaf-cutting ant refuse dumps may be viewed as an herbivore-safe site for plants, illustrating a novel way of how plants may benefit from their consumers.

Acknowledgments I thank W Eberhard, MC Castellanos, E Gianoli and two anonymous referees for their comments on the manuscript; and B O'Neill and N Wiggins for their English help. I also thank L Ghermandi for field and laboratory assistant. CONICET (PIP 5101), Fundación Antorchas and FONCYT (PICT 25314) partially funded this research.

References

Abdala-Roberts L, Parra-Tabla V (2005) Artificial defoliation induces trichome production in the neotropical shrub *Cndoscolus aonitifolius*. Biotropica 37:251–257

Agrawal A (2000) Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. Trend Plant Sci 5:309–313

Agrawal A (1998a) Induced responses to herbivory and increased plant performance. Science 279:1201–1202

Agrawal A (1998b) Leaf damage an associated cues induces aggressive ant recruitment in a neotropical ant-plant. Ecology 79:2100–2112

Barrer P, Cherrett JM (1972) Some factors affecting the site and pattern of leaf-cutting ant activity in the ant *Atta cephalotes*. J Entomol 47:15–27

Belsky AJ, Carson W, Jensen C, Fox G (1993) Overcompensation by plants: herbivore optimization or red herring. Evol Ecol 7:109–121

Callaway R, Pennings S, Richards C (2003) Phenotypic plasticity and interactions among plants. Ecology 84:1115–1128

Chapin III F, Bloom A, Field C, Waring R (1987) Plant responses to multiple environmental factors. BioScience 37:49–57

Cherrett JM (1989) Leaf-cutting ants, biogeographical and ecological studies. In: Lieth H, Werger M (eds) Ecosystem of the world 14b, tropical rain forests ecosystem. Elsevier, New York, pp 473–488

Coley P, Barone J (1996) Herbivory and plant defenses in tropical forests. Ann Rev Ecol Syst 27:305–335

Farji-Brener AG (2001) Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? an evaluation of the palatable forage hypothesis. Oikos 92:169–177

Farji-Brener AG, Ruggiero A (1994) Leaf-cutting ants (*Atta* and *Acromyrmex*) inhabiting Argentina: patterns in species richness and geographical ranges sizes. J Biogeogr 21:535–543

Farji-Brener AG, Illes A (2000) Do leaf-cutting ant nests make 'bottom up' gaps in neotropical rain forests? A critical review of the evidence. Ecol Lett 3:219–227

Farji-Brener AG, Medina C (2000) The importance of where to dump the refuse: seed banks and fine roots in nests of the leaf-cutting ants *Atta cephalotes* and *Atta colombica*. Biotropica 32:120–126

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, Sasal Y (2003) Is dump material an effective small-scale deterrent to herbivory by leaf-cutting ants? Ecoscience 10:151–154

Farji-Brener AG, Ghermandi L (2004) Seedling recruitment in the semi-arid Patagonian steppe: facilitative effects of refuse dumps of leaf-cutting ants. J Veg Sci 15:823–830

Franzel C, Farji-Brener AG (2000) Oportunistas o selectivas? Plasticidad en la dieta de la hormiga cortadora de hojas *Acromyrmex lobicornis* en el N-O de la Patagonia. Ecol Austral 10:159–168

Haines B (1978) Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. Biotropica 10: 270–277

Hart A, Ratnieks F (2001) Task partitioning, division of labor and nest compartmentalization collectively isolate hazardous waste in the leaf-cutting ant *Atta cephalotes*. Behav Ecol Sociob 49: 387–392

Haukioja E, Neuvonen S (1985) Induced long-term resistance of birch foliage against defoliators: defensive or incidental? Ecology 66:1303–1308

Howard JJ (1987) Leaf-cutting ant selection: the role of nutrients, water, and secondary chemistry. Ecology 68:503–515

Howard JJ (1988) Leaf-cutting ant diet selection: relative influence of leaf chemistry and physical features. Ecology 69: 250–260

Järemo J, Tuomi T, Nilsson P, Lennartsson T (1999) Plant adaptations to herbivory: mutualistic versus antagonistic coevolution. Oikos 84: 313–320

Karban R, Agrawal A, Thaler J, Adler L (1999) Induced plant responses and information content about risk of herbivory. Trend Ecol Evol 14: 443–447

Kursar T, Coley P (2003) Convergence in defense syndromes of young leaves in tropical rain forests. Biochem Syst Ecol 21: 929–949

Lee JM, Hamrick J (1983) Demography of two natural populations of musk thistle (*Carduus nutans*). J Ecol 71: 923–936

Lugo A, Farnworth E, Pool D, Jerez P, Kaufman G (1973) The impact of the leaf cutter ant *Atta colombica* on the energy flow of a tropical forest. Ecology 54:1292–1301

Marquis RJ (1992) The selective impact of herbivores. In: Fritz R, Simms E (eds) Plant resistance to herbivores and pathogens: ecology, evolution and genetics. Chicago University Press, Chicago USA, pp 301–332

Mathews J (1994) The benefits of overcompensation and herbivory: the difference between coping with herbivores and liking them. Am Nat 144: 528–533

McNaughton S (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329–336

Moutinho P, Nepstad D, Davidson E (2003) Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. Ecology 84:1265–1276

Nichols-Orians C (1991) Environmentally induced differences in plant traits: consequences for susceptibility to a leaf-cutter ant. Ecology 72: 1609–1623

Nichols-Orians C, Schultz J (1990) Interactions among leaf toughness, chemistry, and harvesting by Attine ants. Ecol Entomol 15:311–320

Owen D (1980) How plants may benefit from the animals that eat them. Oikos 35:230–235

Paige K, Whitham T (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. Am Nat 129:407–416

Rapoport E, Margutti L, Sanz E (1997) Plantas silvestres de la Patagonia Andina. Parte I: exóticas. UNICEF and Universidad Nacional del Comahue, Bariloche, Argentina

Rautio P, Huhta A, Piippo S, Tuomi J, Juenger T, Saari M, Aspi J (2005) Overcompensation and adaptive plasticity of apical dominance in *Erysimun strictum* in response to stimulated browsing and resource availability. Oikos 111:179–191

Simberloff D, Brown D, Lowrie S (1978) Isopod and insect root borers may benefit Florida mangroves. Science 201:630–632

Stadler B, Michalzik B, Muller T (1998) Linking aphid ecology with nutrient fluxes in a coniferous forest. Ecology 79:1514–1525

Sultan S (2000) Phenotypic plasticity for plant development, function and life history. Trend Plant Sci 5: 537–542

Vail S (1994) Overcompensation, plant-herbivory mutualism, and mutualistic coevolution: a reply to Mathews. Am Nat 144: 534–536

Weterrer J (1991) Allometry and the geometry of leaf-cutting in *Atta cephalotes*. Behav Ecol Sociobiol 29:347–351

Weis A (1992) Plant variation and the evolution of phenotypic plasticity in herbivore performance. In: Fritz R, Simms E (eds) Plant resistance to herbivores and pathogens: ecology, evolution and genetics. Chicago University Press, Chicago USA, pp 140–171

Wirth R, Herz H, Ryel R, Beyschlag W, Hölldobler B (2003) Herbivory of leaf-cutting ants. A case study on Atta colombica in the tropical rainforest of Panama. Ecol Stud 164, Springer