

## Leaf traits and herbivore selection in the field and in cafeteria experiments

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**Abstract** Despite the vast diversity and complexity of herbivores, plants and their interactions, most authors agree that a small number of components of leaf quality affect preference by generalist herbivores in a predictable way. However, herbivore preference is determined not only by intrinsic plant attributes and herbivore biology but also by the environmental context. Within this framework, we aimed to analyse general interspecific trends in the association between herbivory and leaf traits over a wide range of angiosperms from central Argentina. We (i) tested for consistent associations between leaf traits, consumption in the field, and preference of generalist invertebrate herbivores in cafeteria experiments; (ii) assessed how well herbivore preferences in cafeterias matched leaf consumption in the field; and (iii) developed a simple conceptual model linking leaf traits, herbivore preference in cafeterias and consumption in the field. In general, we found that tender leaves with higher nutritional quality were preferred by herbivores, both in the field and in cafeteria experiments. According to our model, this relationship between field and cafeteria consumption and leaf quality is observed when generalist herbivores and plants of high accessibility are considered. However, differences between leaf consumption in the field and in cafeteria experiments can also be found. At least two reasons can account for this: (i) specialized plant–herbivore relationships often occur in the field, whereas cafeteria experiments tend to consider only one or a few generalist herbivores; (ii) different plant species growing in the field often differ in their degree of accessibility to herbivores, whereas in cafeteria experiments all species are equally accessible. Our results add new evidence to a growing consensus that, although herbivory in the field is determined by many factors, consistent patterns of differential susceptibility to foliar feeders can be found in leaves differing in nutritional quality and thus in resource-use strategy.

**Key words:** carbon, comparative ecology, leaf toughness, nitrogen, plant functional traits.

### INTRODUCTION

Herbivores are taxonomically and ecologically diverse, and they affect plant communities in many ways. There is evidence that plant species that differ in taxonomic status and ecological strategy also differ in terms of palatability and susceptibility to foliar feeders (Scriber & Feeny 1979; Coley *et al.* 1985; Grime *et al.* 1996). Despite the vast diversity and complexity of herbivores, plants, and their interactions, most authors agree that a small number of components of leaf quality affect preference by generalist herbivores in a predictable way (Feeny 1990; Herms & Mattson 1992; Singer 2000).

Foliar nutrient content, especially nitrogen content, is considered a key factor in plant–herbivore interactions. The leaves of fast-growing species are often rich in nitrogen (Lambers & Poorter 1992; Cornelissen *et al.* 1997; Garnier *et al.* 1997), and they thus tend to

be preferred by herbivores over the leaves of slow-growing species, which are richer in complex carbon compounds not involved in photoassimilation (Feeny 1970; Crawley 1983; Herms & Mattson 1992). High investment in these carbon compounds strongly reduces leaf palatability (Coley 1988).

Foliar water content, which tends to be higher in the fast-growing plants of Northern Hemisphere floras (Cornelissen *et al.* 1996; Wilson *et al.* 1999), has been reported to be a limiting factor for chewing insects (Scriber 1977; Tabashnik 1982). Physical characteristics are also important in reducing herbivory.

Most of the information on plant–herbivore interactions comes from studies that have either (i) analysed a small number of species; (ii) included very functionally similar plants; or (iii) analysed specific plant defences against specific herbivores (Tsingalia 1989; Scheidel & Bruelheide 1999; Lawler *et al.* 2000; Hanley & Lamont 2002). ‘Cafeteria’ experiments (*sensu* Krebs 1989), analyse consumption of plant parts belonging to several species or populations when offered simul-

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taneously to herbivores under standardized conditions. These experiments can provide useful information about herbivore preference for a broad range of plants (Grime *et al.* 1996; Cornelissen *et al.* 1999).

Herbivore preference is determined not only by intrinsic plant attributes and the biology of herbivores but also by the environmental context (Grime *et al.* 1970; Mattson 1980). If cafeteria experiments are to be useful for understanding nature, a good match between their results and consumption patterns in the field is essential. Despite this, studies comparing herbivore preference in laboratory tests with herbivory or preference in the field are rare (Grime *et al.* 1970; Scheidel & Bruelheide 1999).

Within this context, we aimed to analyse general trends of association between herbivory and leaf traits over a wide range of angiosperms from central Argentina. Specifically, we (i) tested for consistent associations between leaf quality (nitrogen content, C:N ratio, water content, specific leaf area, tensile strength, pubescence and cuticle thickness), consumption in the field and preference of invertebrate generalist herbivores in cafeteria experiments; (ii) assessed how well herbivore preferences in cafeteria experiments matched leaf consumption in the field; and (iii) developed a simple conceptual model linking leaf quality, herbivore preference in cafeteria experiments and consumption in the field.

## MATERIALS AND METHODS

### Study area and species collection

Plant material and data on field consumption were collected along a regional climatic gradient in central Argentina (31°25'–32°S, 64°10'–68°37'W), with a range in annual precipitation of >800 mm, a range in annual temperature of 11°C, and a range in altitude of >1500 m. The gradient stretches from the subhumid high plateaus of the Córdoba Mountains to the western semiarid and arid plains (Diaz *et al.* 1998). The consideration of this steep climatic gradient allowed us to select a wide range of plant families and functional types, ranging from maximum allocation to assimilation and growth, to maximum allocation to storage and defence (Diaz & Cabido 1997; Pérez-Harguindeguy *et al.* 2000; Vendramini *et al.* 2000). A total of 52 Angiosperm species common in natural areas of central Argentina were selected (Appendix I).

### Field herbivory

In order to minimize differences due to factors other than leaf quality, field herbivory was measured on at

least 10 leaves (subreplicates) from a minimum of 10 individuals (replicates) per species. At sites along the regional gradient where each species was most abundant, individuals were chosen randomly among healthy-looking sexually mature plants. Leaves of each individual were chosen randomly among fully expanded, non-senescent sun leaves. Consumption was measured in late spring and in late summer by direct observation of percentage of area consumed in each leaf or leaf analogue (categories were 0, 5, 25, 50, 75, and 90% of leaf area consumed). Because in all cases consumption in late summer was higher than in late spring, and many of the species were still not available in spring, all results presented here are based on late summer measurements.

### Herbivore preference

The method for quantifying herbivore preference was a cafeteria (*sensu* Krebs 1989) in which generalist herbivores were allowed to feed selectively on 10 1-cm<sup>2</sup> samples cut out from fresh leaves of a whole range of species distributed in random positions on a feeding arena (Grime *et al.* 1996). For narrow leaves, from which it was not possible to cut a 1-cm<sup>2</sup> sample, an equivalent area was produced by cutting an appropriate number of 10-mm lengths from the mid-leaf section. In the case of highly succulent and aphyllous species, a 1-cm<sup>2</sup> fragment of epidermis and mesophyll (relatively young photosynthetic tissue) was used as a leaf analogue. Each sample of fully expanded, non-senescent leaves was collected from typical habitats of the species on the day before the experiment was started. All leaves were kept in sealed bags at 4–5°C until processed. Herbivore preference was assessed in two independent feeding trials. In the first cafeteria experiment, a garden snail was used (*Helix aspersa*), which is known to have generalist feeding habits (Grime *et al.* 1996). Considering that snails consume few graminoids (Grime *et al.* 1996), and that a second generalist herbivore could contribute to a better discrimination within this group of plants (Godan 1983; Fraser 1996), we carried out another experiment, using the native generalist grasshopper *Schistocerca cancellata* (Gastón 1969). Herbivores were starved for 48 h before the experiments (Grime *et al.* 1996). We ensured that the model herbivores had no previous experience with the plants included in the trials. Both model herbivores were bred, or collected when young and raised in captivity in the case of snails, in laboratory conditions, and they did not feed on any of the plants included in the cafeteria experiments. This, and the pretrial starvation are considered important in cafeteria experiments, because they avoid biased results due to preconditioning.

### Leaf trait measurements

All leaf trait measurements were carried out on randomly chosen, fully expanded non-senescent sun leaves from healthy looking, sexually mature individuals. At least six leaves (subreplicates) were measured from at least six individuals (replicates) of each species for all trait measurements. Carbon content was estimated as 50% of ash-free biomass (Schlesinger 1977; McClaugherty *et al.* 1985; Gallardo & Merino 1993). Nitrogen content was measured by an Auto-analyser RFA 300-Alphen.

Leaf water content (LWC) was measured to indicate approximate leaf density and it was calculated on a fresh weight basis ( $1 - \text{dry mass/fresh mass}$ ) (Garnier & Laurent 1994; Shipley 1995; Cunningham *et al.* 1999). Full hydration was assured by collecting leaves in the morning immediately after rainfall. Samples were stored in sealed plastic bags (which were moistened in the case of mesophytic species, but not in the case of succulent and resinous species), and kept at 4–5°C in the dark during transport to the laboratory. In most cases, samples were measured on the day of collection. Samples were blotted dry using tissue paper to remove any surface water and immediately weighed. Samples were then oven-dried in paper bags at 70°C until a constant weight was achieved, then reweighed to produce a dry weight value.

Specific leaf area (SLA) was measured as  $\text{mm}^2 \text{ leaf area mg}^{-1} \text{ dry weight}$ . Samples were kept at 4–5°C in the dark in nylon bags until measurement. Leaves were then arranged between a sheet of white paper and a sheet of glass and scanned with a manual scanner. The average leaf area of each replicate was calculated by using Optimetrics Software (Bioscan, Edmonds, USA). Compound leaves were treated as a

whole, without separating leaflets. Leaves were then oven-dried at 70°C until a constant weight was achieved. To estimate the SLA of aphyllous species and some thick-stemmed succulents, fragments of photosynthetic tissue of known area were dried and weighed.

Leaf tensile strength (or leaf toughness) was measured with a dynamometer constructed following Hendry and Grime (1993), and expressed as force per unit of width needed to tear a fresh leaf sample ( $\text{N mm}^{-1}$ ). In the case of highly succulent or aphyllous species, a 1-cm<sup>2</sup> fragment of young photosynthetic tissue (epidermis and mesophyll) was used for the measurements of tensile strength.

Pubescence and cuticle thickness were measured by direct observation under a light microscope on at least six leaves from six different individuals per species. Cuticle thickness was expressed in mm. Pubescence was recorded as categorical data relating to three types of hairs (vertical, horizontal or water-absorbing), and within each hair type we recognised three levels of pubescence according to hair density (0, no hairs present; 1, less than 10% of leaf area covered by hairs; 2, more than 10% leaf area covered by hairs).

### Data analysis

Because the data distributions were not normal, Spearman's rank correlations were used to test the relationships between field consumption, preference in cafeteria experiments and leaf traits (Hollander & Wolfe 1972). Kruskal–Wallis and Wilcoxon rank tests (Norusis 1992) were used for comparisons between snail and grasshopper preferences for monocotyledons and eudicotyledons (*sensu* Soltis *et al.* 2000).

**Table 1.** Spearman rank correlations between leaf traits, field consumption, and preference in cafeteria experiments

	Field consumption	Preference in cafeteria experiments	
		Snails	Grasshoppers
Leaf N content	0.49** <i>n</i> = 48	0.49*** <i>n</i> = 52	0.45** <i>n</i> = 52
Leaf C : N ratio	-0.48** <i>n</i> = 46	-0.52*** <i>n</i> = 50	-0.44** <i>n</i> = 50
Leaf tensile strength	-0.48** <i>n</i> = 44	-0.57*** <i>n</i> = 48	-0.38* <i>n</i> = 48
SLA	0.28* <i>n</i> = 48	0.25 <sup>NS</sup> <i>n</i> = 52	0.56*** <i>n</i> = 52
Cuticle thickness	0.03 <sup>NS</sup> <i>n</i> = 48	-0.21 <sup>NS</sup> <i>n</i> = 52	-0.30* <i>n</i> = 52
LWC	-0.05 <sup>NS</sup> <i>n</i> = 48	0.42** <i>n</i> = 52	0.09 <sup>NS</sup> <i>n</i> = 48

\*\*\**P* < 0.0005; \*\**P* < 0.005; \**P* < 0.05; NS, *P* > 0.05; *n* indicates the number of points in each correlation. SLA, specific leaf area; LWC, leaf water content.

## RESULTS AND DISCUSSION

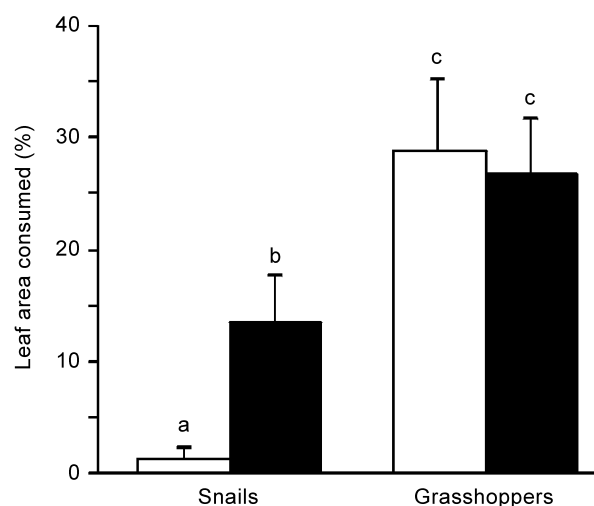
### Is consumption in the field linked to leaf traits?

Leaf area consumed in the field was significantly positively associated with leaf nitrogen content and SLA, and significantly negatively associated to C:N ratio and tensile strength (Table 1). In other words, tender leaves with a higher nutritional quality were preferred by herbivores in the field. Cuticle thickness and leaf water content were not significantly associated with field herbivory ( $P > 0.05$ ), and there was no significant difference in field herbivory among any of the categories of leaf pubescence ( $P > 0.05$ ).

Our results add new evidence to a growing consensus that although herbivory in the field is determined by many factors (Tribe 1959; Grime *et al.* 1970; Grubb 1992), consistent patterns of differential consumption by foliar feeders can be found in leaves differing in nutritional quality and thus in resource-use strategy (Cornelissen *et al.* 1999; Fraser & Grime 1999; Pérez-Harguindeguy *et al.* 2000).

### Is consumption in cafeteria experiments linked to leaf traits?

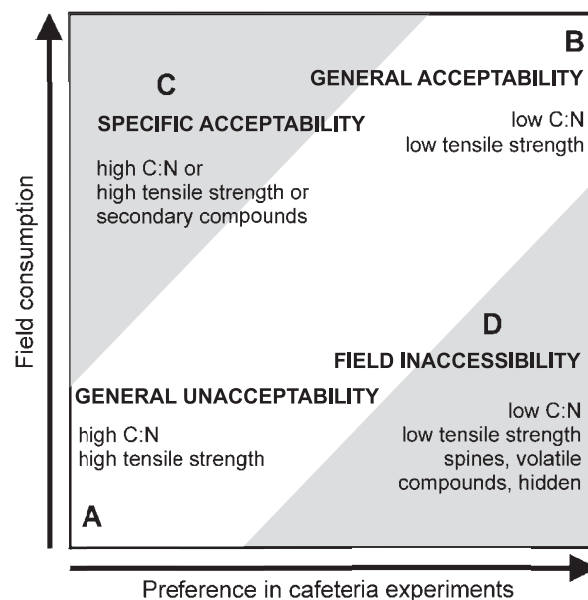
In cafeteria experiments, the preferences of snails and grasshoppers were significantly correlated with leaf N content, C:N ratio, and tensile strength (Table 1). Only grasshopper preference was strongly associated



**Fig. 1.** Leaf area consumed in cafeteria experiments by snails and grasshoppers. Letters indicate significant differences (Kruskal–Wallis test). Grasshoppers have a wider niche amplitude ( $B = 26$  compared to snails, in which  $B = 9$ ; where  $B$  is the Levin Index [ $B = 1/\sum p_j^2$ ], and  $p_j$  is the proportion in the diet that is species  $j$  sensu Krebs, 1989). (□), monocots; (■), dicots.

with SLA and cuticle thickness, whereas only snail preference was associated with LWC. There was a significantly positive correlation between snail preference and grasshopper preference ( $r = 0.31$ ;  $P = 0.03$ ). There was no significant difference in consumption by model herbivores among any of the categories of leaf pubescence ( $P > 0.05$ ).

Leaf tensile strength was the best indicator of snail preference, but it was less strongly associated with grasshopper preference. Snails and grasshoppers are both generalist chewers, but snails tend to prefer eudicotyledons and therefore discriminate poorly among monocotyledons. Grasshoppers, however, are more generalist and consume both plant groups (Fig. 1), possibly because their mandibles are more powerful than the radulae of snails. Therefore, snails may not cope with very tough leaves (such as those from graminoids, Pérez-Harguindeguy *et al.* 2000), whereas grasshoppers could be more limited by chemical defences than by physical ones. These findings are consistent with an emerging pattern that molluscs in general differentiate well among eudicotyledons, whereas insects discriminate both among eudicotyledons and monocotyledons (cf. Grime *et al.* 1996; Wardle *et al.* 1998; Cornelissen *et al.* 1999; Fraser & Grime 1999).



**Fig. 2.** Conceptual model for the relationships between leaf quality, field consumption, and preference in cafeteria experiments. Axes  $x$  and  $y$  are preference in cafeteria experiments and field consumption, respectively. The four corners of the proposed model represent four possible plant–herbivore associations (predicted leaf traits in each case are indicated in the appropriate corner). The non-shaded (white) zone, indicating that cafeteria experiments are predictors of consumption in the field, represents the area where leaf quality is the major factor defining plant consumption by herbivores.

### Is consumption in the field linked to preference in cafeteria experiments?

Field herbivory was not significantly associated with preference by generalist herbivores in cafeteria experiments ( $P > 0.1$ ). However, as indicated in the sections on consumption in the field and in the cafeteria linking to leaf traits, above, both were correlated with the same set of leaf traits (N content, C : N ratio and tensile strength). These results illustrate the usefulness of cafeteria experiments in simplifying the general patterns of 'susceptibility to herbivory', but also warn us about the pitfalls in extrapolating preference observed in laboratory tests to consumption in the field (Scheidel & Bruelheide 1999). The different context, including specialized plant-herbivore interactions, can make patterns of herbivory in the field differ from those observed in the laboratory (Tribe 1959; Mattson 1980; Hartley & Jones 1997). However, both types of consumption are linked to leaf quality traits, which in turn are known to be associated with major plant strategies (Aerts & Chapin 2000; Grime 2001; Westoby *et al.* 2002).

### Field consumption and preference in cafeterias: A conceptual model

The relationships between leaf quality, field consumption and preference in cafeteria experiments can be interpreted using a simple conceptual model (Fig. 2). Axes  $x$  and  $y$  are preference in cafeteria experiments and field consumption, respectively, and the four corners of the proposed model represent four possible plant-herbivore associations. At the lower extreme of both axes, situation A is one of 'general unacceptability' (sensu Dirzo 1980). This includes plants that are rarely consumed in either the field or cafeteria experiments, and tend to have low nutritional quality (high C : N, high tensile strength). Examples in our study include the perennial grass *Aristida achalensis* and the xerophytic bromeliad *Bromelia urbaniana*. In fact, we can expect most plant species to fall into category A because, in general, plants are a poor food source (Lawton & McNeill 1979; Hartley & Jones 1997), and even generalist herbivores must attempt to find high-quality food, which is scarce and not easy to differentiate from the poor quality food (Hartley & Jones 1997).

At the upper extreme of both axes, situation B (Fig. 2) is one of 'general acceptability' (sensu Dirzo 1980). This includes plants that are consumed both in the field and in cafeteria experiments, and have high nutritional quality (e.g. the broad-leafed, fast-growing *Eupatorium viscidum*). Within the diagonal area between B and A (Fig. 2, shaded), leaf quality is a major factor defining plant consumption by herbivores.

For plant species falling within this area, cafeteria experiments should be good predictors of consumption in the field.

Situation C, with low values along the  $x$  axis and high values along the  $y$  axis, is described as 'specific acceptability' (sensu Dirzo 1980), and includes plants that are consumed in the field, but not preferred in cafeteria experiments, and tend to have low to intermediate nutritional quality. This may be explained by the existence, in the field, of specialized relationships with specific (vertebrate and more commonly invertebrate) herbivores, which can overcome plant defences. Finally, with high values along the  $x$  axis and low values along the  $y$  axis, there is a situation of 'field inaccessibility' (situation D), where species of intermediate nutritional quality are not consumed in the field because physical barriers (such as spines, hairs or plant height) make them inaccessible (Weis & Berenbaum 1989; Westerbergh & Nyberg 1995). However, in cafeteria experiments, where leaves are offered as relatively unprotected fragments of equal accessibility, these species are readily consumed by model herbivores. In situations C and D the results of cafeteria experiments would not be good predictors of consumption in the field.

At a constant level of accessibility (Fig. 2, shaded), consumption by generalist herbivores (such as snails or grasshoppers) is expected to be directly associated with leaf quality. In the field, consumption by specialist herbivores, however, should be only loosely linked to leaf quality as measured in the present study, because specialist herbivores tend to have mechanisms to overcome their host's defences (Crawley 1997; Hartley & Jones 1997) or can thrive on intermediate-quality food resources. For example, the aphyllous shrub *Baccharis articulata* and the vine *Pithecoctenium cynanchoides* were readily consumed in the field but rarely consumed in the cafeteria experiment. In addition, consumption of small amounts of unpalatable species in the field may result from imprecise grazing or browsing by large vertebrate herbivores.

In the field, leaf or plant accessibility can vary between species and between contexts. Some examples include spiny leaf ridges or stems, plant defence by ants, canopy height (relevant to flightless herbivores), herbivore-unfriendly canopy architecture, leaf folding upon plant contact (as in *Mimosa*), induced resistance (Karban *et al.* 1999) and spatial association of palatable plants with unpalatable plants (associational resistance: Olf *et al.* 1999). When a leaf or plant is accessible to generalist herbivores, herbivory is expected to be directly proportional to its nutritional quality. When a plant's foliage is almost inaccessible, herbivory will be extremely low, independent of the plant's nutritional quality. In intermediate cases, the more accessible a plant is, the more the consumption would be related to the leaf nutritional quality.

### Relationships between the conceptual model and empirical results

Figure 3 shows the location of plant species from our study on the extreme quarters of the plane conceptually defined in Fig. 2. Species belonging to the four extreme quarters were assigned to situations A, B, C or D on the basis of herbivory in the field and preference in cafeteria experiments, and by splitting the range of values along each axis into four extreme quarters (A, less than 4.5% field consumption, less than 18% in cafeterias; B, more than 12.5% field consumption, more than 52% in cafeterias; C, more than 12.5% field consumption, less than 18% in cafeterias; D, less than 4.5% in field consumption, more than 52% in cafeterias).

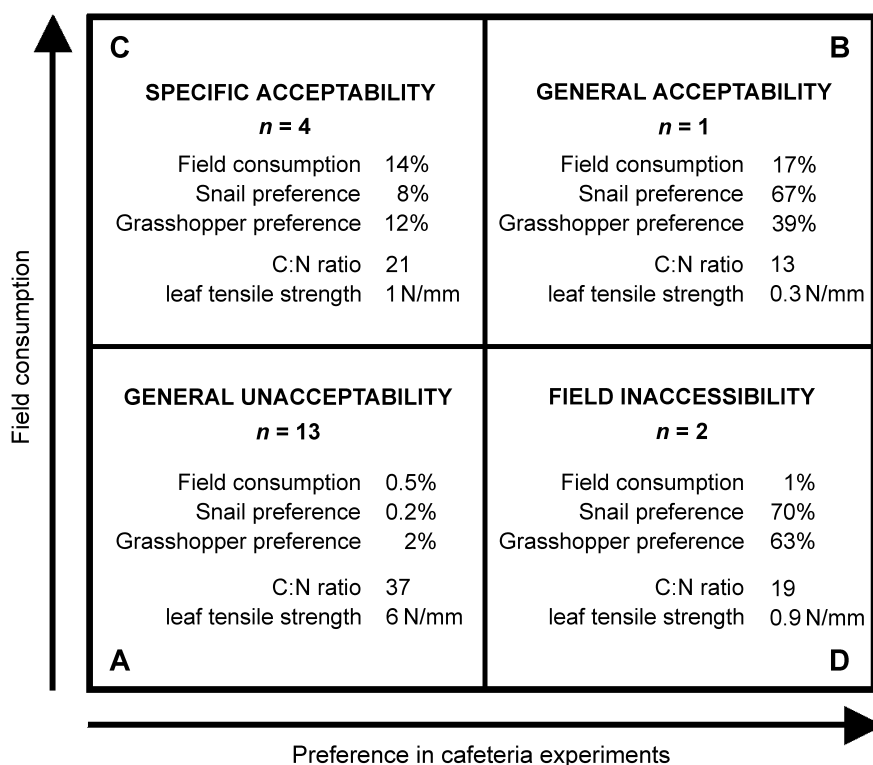
Species located at the extreme of general unacceptability (A) were characterized by high C : N ratios and tough leaves, whereas the species located at the extreme of general acceptability (B) had a low C : N ratio and low leaf toughness values (Fig. 3). Species representing extremes of specific acceptability and inaccessibility in the field (C and D) presented intermediate C : N ratios and leaf toughness values (Fig. 3), but almost all of those in category C were only consumed in the field,

whereas almost all in category D were only in cafeterias.

It should be noted, however, that most of the species in our dataset are tough and poor in nitrogen compared with species from temperate floras without major drought stress (Cornelissen *et al.* 1999; Diaz *et al.* 2001), and thus fall into the 'general unacceptability' corner of the conceptual model (A in Fig. 2). This may explain why the correlations between herbivore preference in cafeteria experiments and leaf quality traits (Table 1) were not as strong as those found for other floras (Grime *et al.* 1996). The fact that leaf C : N ratio and leaf tensile strength are only two of the many aspects of leaf nutritional quality may also explain these weak correlations.

### Final considerations

Despite the complications discussed above that affect plant-herbivore relationships, tender leaves with higher nutritional value are consumed more by herbivores, both in the field and in cafeteria experiments, over a wide range of plant taxa and functional types from a



**Fig. 3.** Relationships between leaf quality, field consumption, and preference in cafeteria experiments according to our empirical data. Species belonging to the four extreme quarters were assigned to situations A, B, C or D on the basis of their values of field consumption and preference in cafeteria experiments and by splitting the range of values along each axis into 4 extreme quarters. A, less than 4.5% field consumption, less than 18% in cafeterias; B, more than 12.5% field consumption, more than 52% in cafeterias; C, more than 12.5% field consumption, less than 18% in cafeterias; D, less than 4.5% in field consumption, more than 52% in cafeterias. Mean values of field consumption, preference in cafeteria experiments and leaf quality of species representing the extreme situations of possible plant-herbivore associations mentioned in the conceptual model of Fig. 2.

variety of habitats of origin. Simple leaf nutritional quality components, such as C:N ratio, and even tensile strength proved to be good indicators of general patterns of herbivore preference. This agrees with previous findings by other authors (Mattson 1980; Coley *et al.* 1985; Chapin *et al.* 1993; Choat & Clements 1998; Cornelissen *et al.* 1999; Poorter & Garnier 1999), and adds new evidence to the generality of these trends, expanding their applicability to a much wider functional and taxonomic range of plants. However, herbivory is very complex and depends on the interplay of many factors, of which leaf nutritional quality is only one component (Dirzo 1980; Huntly 1991; Grubb 1992). For this reason, we suggest that direct extrapolation from cafeteria experiment results to herbivory in the field should be done with caution and should depend on the aims of the study. Cafeteria experiments can be extremely useful when broad patterns of herbivory by generalists are the focus of the study, or when species with similar accessibility in the field are compared.

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## APPENDIX I

**Table A1.** List of the dominant species, families, plant functional types (modified from Díaz & Cabido 1997) from the flora of central Argentina, included in the herbivory screening, and results of the herbivory screening (field herbivory and preference in cafeteria experiments [% of leaf area consumed in both cases])

Species	Family	Plant functional type	Field	Preference in cafeterias	
			herbivory	Snails	Grasshoppers
<i>Acacia aroma</i>	Fabaceae	Woody deciduous	8	0	13
<i>Acacia caven</i>	Fabaceae	Woody deciduous	14	0	22
<i>Acalypha communis</i> var. <i>guaranitica</i> .	Euphorbiaceae	Woody deciduous	3	12	59
<i>Alchemilla pinnata</i>	Rosaceae	Herbaceous dicots	0	0	95
<i>Allenrolfea patagonica</i>	Chenopodiaceae	Leaf and stem succulents	0	0	0
<i>Alternanthera pungens</i>	Amaranthaceae	Herbaceous dicots	4	26	33
<i>Aristida achalensis</i> var. <i>achalensis</i>	Poaceae	Graminoids	0	0	0
<i>Aspidosperma quebracho-blanco</i>	Apocynaceae	Woody evergreen	0	0	0
<i>Baccharis articulata</i>	Asteraceae	Aphyllous shrubs	15	0	3
<i>Bouteloua aristidoides</i>	Poaceae	Graminoids	8	0	51
<i>Bromelia urbaniana</i>	Bromeliaceae	Bromeliads	0	0	0
<i>Buddleja brasiliensis</i>	Buddlejaceae	Woody deciduous	1	0	11
<i>Capparis atamisquea</i>	Capparaceae	Woody evergreen	0	1	4
<i>Carduus thoermeri</i>	Asteraceae	Herbaceous dicots	0	77	77
<i>Carex fuscata</i> var. <i>distenta</i>	Cyperaceae	Graminoids	6	0	36
<i>Celtis pallida</i>	Celtidaceae	Woody deciduous	7	0	3
<i>Celtis tala</i>	Celtidaceae	Woody deciduous	6	6	6
<i>Cortaderia rudiusscula</i>	Poaceae	Graminoids	0	0	19
<i>Croton sarcopetalus</i>	Euphorbiaceae	Woody deciduous	7	30	94
<i>Eryngium agavifolium</i>	Apiaceae	Herbaceous dicots	0	6	17
<i>Eupatorium viscidum</i>	Asteraceae	Woody deciduous	17	67	39
<i>Festuca tucumanica</i>	Poaceae	Graminoids	0	0	1
<i>Flourensia campestris</i>	Asteraceae	Woody deciduous	7	26	11
<i>Gentianella parviflora</i>	Gentianaceae	Herbaceous dicots	0	2	23
<i>Gomphrena pulchella</i>	Amaranthaceae	Herbaceous dicots	4	71	11
<i>Heterothalamus alienus</i>	Asteraceae	Woody evergreen	4	1	10
<i>Juncus uruguensis</i>	Juncaceae	Graminoids	0	0	80
<i>Larrea divaricata</i>	Zygophyllaceae	Woody evergreen	3	17	73
<i>Lithraea molleoides</i>	Anacardiaceae	Woody evergreen	3	0	6
<i>Maytenus vitis-idea</i>	Celastraceae	Leaf and steam succulents	10	0	13
<i>Mimozyanthus carinatus</i>	Fabaceae	Woody deciduous	5	0	33
<i>Monanthochloë acerosa</i>	Poaceae	Graminoids	0	0	26
<i>Muhlenbergia peruviana</i>	Poaceae	Graminoids	0	0	73
<i>Neobouteloua lophostachya</i>	Poaceae	Graminoids	0	0	46
<i>Nothoscordum gracile</i>	Liliaceae	Graminoids	ND	21	87
<i>Opuntia sulphurea</i>	Cactaceae	Leaf and steam succulents	2	62	49
<i>Pappophorum caespitosum</i>	Poaceae	Graminoids	4	0	23
<i>Paspalum quadrifarium</i>	Poaceae	Graminoids	9	0	0
<i>Pithecoctenium cynanchoides</i>	Bignoniaceae	Herbaceous dicots	14	31	1
<i>Poa stuckertii</i>	Poaceae	Graminoids	ND	0	8
<i>Polylepis australis</i>	Rosaceae	Woody deciduous	2	0	57
<i>Prosopis flexuosa</i> var. <i>flexuosa</i>	Fabaceae	Woody deciduous	14	0	23
<i>Schinopsis haenkeana</i>	Anacardiaceae	Woody deciduous	ND	0	30
<i>Schizachyrium condensatum</i>	Poaceae	Graminoids	2	0	8
<i>Senna aphylla</i>	Fabaceae	Aphyllous shrubs	0	0	1
<i>Setaria pampeana</i>	Poaceae	Graminoids	7	0	55
<i>Sorghum halepense</i>	Poaceae	Graminoids	ND	0	38
<i>Tephrocactus articulatus</i> var. <i>articulatus</i>	Cactaceae	Steam succulents	0	0	0
<i>Tillandsia capillaris</i>	Bromeliaceae	Bromeliads	0	3	2
<i>Tillandsia duratii</i>	Bromeliaceae	Bromeliads	0	0	1
<i>Trichloris crinita</i>	Poaceae	Graminoids	1	0	26
<i>Zizyphus mistol</i>	Rhamnaceae	Woody deciduous	4	0	45

ND, no data available.