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ORIGINAL PAPER

Leaf traits, water stress, and insect herbivory: Is food selection a hierarchical process?

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Abstract Plant water stress can affect selectivity by insect herbivores. Numerous studies have shown greater insect preference for water-stressed plants, but others have reported the opposite response. We evaluated leaf consumption by adults of *Nyctelia circumundata* (a chewing insect) in leaves of *Larrea divaricata* and *Prosopis alpataco*. Three bioassays (two-way choice tests) were performed: two intra-specific comparisons between well-watered (+W) and water-stressed (−W) leaves of each species and one inter-specific comparison between leaves of the two species. Leaf biomass was reduced by water stress in both species. Nitrogen concentration in leaves (N) was reduced by drought in *P. alpataco*. In contrast, total phenolics and specific leaf area (SLA) did not differ between treatments within species. *Nyctelia circumundata* did not show preference by any water supply regimes in intra-specific comparisons. In contrast, in inter-specific choice tests, it showed a marked preference for *P. alpataco*, which is the species with the highest nitrogen concentration and lowest total phenolics concentration. In intra-specific comparisons, maximum leaf consumption was inversely related to SLA in both species. Furthermore, in *P. alpataco*, N concentration was positively related to maximum leaf consumption and negatively related to leaf water content (LWC). In contrast, in inter-specific comparisons, total phenolics was negatively related to maximum leaf consumption, while N concentration exhibited the opposite trend. These results suggest that food selection is a hierarchical process where chemical attributes (i.e., total phenolics and N) are taken into account for species selection, and physical attributes (i.e., SLA and LWC) for choosing individuals inside species.

Keywords *Larrea divaricata* · *Prosopis alpataco* · *Nyctelia circumundata* · Drought · Consumption

Introduction

In plants, leaf tissue quality is affected by growing conditions. Light, nutrients, CO_2, and water availability, among others, can affect primary and secondary metabolisms and, subsequently, leaf chemistry (Koricheva et al. 1998a). As a consequence of predicted climate change, particular attention was paid to the effects of global warming, increased CO_2, and reduced water availability on tissue quality. Moderate plant water stress is frequently associated with reduced growth (e.g., Cella Pizarro and Bisigato 2010) and leaf water content (e.g., Scheirs and De Bruyn 2005), and with increased concentration of secondary compounds (e.g., Wilkens 1997), non-structural carbohydrates (e.g., Meyer et al. 2006), and nitrogen (e.g., White 1984). Since leaf traits such as secondary compound, toughness, and nutrient content have been identified

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to influence the attractiveness of leaves to insects, drought-induced changes can affect selectivity by herbivores (Mattson and Haack 1987; Meyer et al. 2006).

Several hypotheses focusing on the impact of growing condition in the host plant on insect herbivores were proposed. First, the 'plant stress hypothesis' predicts that due to an increased nutritional value, stressed plants will be better hosts for insect herbivores (White 1984). This hypothesis is mainly based on field observations showing positive correlations between insect outbreaks and periods of drought. In contrast, the 'plant vigor hypothesis' predicts that herbivorous insects will prefer and perform better on rapidly growing plants (Price 1991). Both hypotheses were supported by specific studies (e.g., Scheirs and De Bruyn 2005; Meyer et al. 2006; Cornelissen et al. 2008; Ribeiro Neto et al. 2012), and studies including several species frequently reported mixed evidence (Waring and Price 1990; Staley et al. 2006). Because of the inconsistencies among published studies, Larsson (1989) proposed that the effect of stress on insect performance depends on the insect feeding guild. While sucking and mining insects could benefit from moderate stress, performance of chewing and gall-former insects is mostly decreased in that situation. In all guilds, high stress severely decreases insect performance. Other studies (Koricheva et al. 1998b) showed that factors such as plant species, insect species, stress regime, insect feeding guild, life stage of the herbivore, and plant ontogenetic stage may have strong influence on the effects of interactions between insect herbivores and stressed plants. Recently, Huberty and Denno (2004) proposed the 'pulsed stress hypothesis', suggesting that herbivores benefit from host plants that are periodically drought stressed, but performed less well on constantly stressed plants. This hypothesis was also supported by some studies (e.g., Banfield-Zanin and Leather 2014, 2015). More recently, White (2009) proposed that 'plant stress hypothesis' and 'plant vigor hypothesis' are the two ends of a continuum responses, but they deal with quite different kinds of insects. Whereas 'plant vigor hypothesis' was proposed taking flush feeders in mind, White (2009) restricted 'plant stress hypothesis' to senescence feeders.

Climate change scenarios for South America predict that northern Patagonia will experience a decrease in summer precipitation by the end of the twenty-first century (Núñez et al. 2009). Although native plant species exhibit drought tolerance, their size, biomass partitioning, and the concentration of different compounds can be affected by drought, at least in juvenile plants (Cella Pizarro and Bisigato 2010). In this study, we performed dual-choice tests including leaves of juvenile plants of *Larrea divaricata* (Cav.) and *Prosopis alpataco* Phil. growing at contrasting levels of water availability. *Larrea divaricata* (Zygophyllaceae) is an evergreen shrub which characterizes Monte Phytogeographical Province in Argentina (Bisigato et al. 2009). Concentration of N and phenolics in green leaves of juvenile plants change with water availability and varied between 1.2–3.2 and 4.6–7.2 %, respectively (Cella Pizarro and Bisigato 2010). *Prosopis alpataco* (Fabaceae) is a deciduous shrub found in Monte and Patagonic Phytogeographical Provinces in Argentina. Concentrations of N and phenolics in green leaves of juvenile plants are affected by water stress and varied between 1.7–3.0 and 2.5–3.6 %, respectively (Cella Pizarro and Bisigato 2010). However, it is not known whether these changes affect insect herbivores feeding on Patagonian plants.

Coleopterans are among the most abundant insects in the ground-dwelling arthropod community of northeastern Patagonia. At the same time, Tenebrionidae (*darkling beetles)* is the most common family (Cheli et al. 2010), and of these, *Nyctelia circumundata* (Lesne) is one of the most frequently observed (Cheli et al. 2009). This species is endemic to Monte Phytogeographical Province (Roig Juñent and Flores 2001). Although most of Tenebrionidae species are scavengers, *N. circummundata* is also a polyphagous leaf chewer, but at the same time, it is highly selective among plant species (Cheli et al. 2009). This species was selected for this study because of their great abundance, as well as because of its large size (3 × 2 cm) and phytophagous habits, which turn this beetle into an excellent candidate to analyze the effect of drought on beetle preference.

The objectives of this study were: (1) to evaluate the relationships between several leaf traits and biomass consumption by adults of *N. circumundata* and (2) to asses whether water stress affects insect consumption through changes in leaf quality in two Patagonian shrubs. To reach these objectives, in this study, we performed dual-choice tests including leaves of juvenile plants of *Larrea divaricata* (Cav.) and *Prosopis alpataco* Phil. growing at contrasting levels of water availability which were offered to adults of the darkling beetle *N. circumundata* (Lesne). We also measured specific leaf area (SLA), leaf water content (LWC), concentration of nitrogen (N), and total phenolics in leaves.

Materials and methods

Plant rearing

Seeds of *P. alpataco* and *L. divaricata* were collected from at least five plants from native populations in Chubut Province, northeastern Patagonia, Argentina (42° 39′S, 65° 23′W). Seeds were carefully sprinkled in 12-cm-diameter Petri dishes with 5 ml distilled water on top of two layers of filter papers (Whatman No. 1) at room temperature.

Immediately after germination, seedlings were transplanted to 2-l pots (one seedling per pot) containing sieved top soil (through a 2-mm mesh sieve) collected from the area where seeds had been collected. Pots were placed randomly within a greenhouse under full sun conditions and were maintained at field capacity for 1 month in order to help the establishment of seedlings.

When plants (*L. divaricata* $n = 24$, *P. alpataco* $n = 34$) were one month old, they were randomly assigned to one of the two water supply regimes (well-watered (+W) = minimum soil water content 13 % and water-stressed (−W) = minimum soil water content 7 %). Soil moisture content was checked daily: Each pot was weighed and watered to achieve soil water content of 15 % (field capacity for this type of soil; Bisigato and Bertiller 1999) whenever its soil moisture had dropped below the lowest level defined for the treatment (Cella Pizarro and Bisigato 2010). Thus, treatments differed in the lowest soil water content reached by pots before re-irrigation took place. Well-watered plants received water every 1–2 days, and water-stressed plants every 6–8 days. In that form, whereas well-watered plants were not stressed, water-stressed plants were subject to intermittent stress, what according to Huberty and Denno (2004) can increase plant attractiveness to herbivores.

Collection of adults of *N. circumundata*

Adult males and females of this darkling beetle were collected in the field 10 days before the bioassays, and they were starved until use.

Leaf quality and total leaf biomass

Total phenolics concentration in leaves was measured by the Folin–Ciocalteu method which relies on the transfer of electrons in alkaline medium from phenolic compounds to phosphomolybdic/phosphotungstic acid complexes, which are determined spectroscopically at 765 nm (Waterman and Mole 1994). Nitrogen concentration (N) was measured by the micro-Kjeldahl digestion procedure followed by the distillation and titration of the resulting solution (Bremner and Mulvaney 1982). We assessed the specific leaf area (SLA) in seven fully expanded leaves per individual of *L. divaricata* and ten folioles per individual of *P. alpataco* by measuring the leaf area and the leaf dry mass of leaves or folioles. Leaves were weighed to obtain leaf fresh weight and scanned on an EPSON STYLUS TX105 scanner, and the leaf area was measured following the O'Neal et al. (2002) protocol. Subsequently, leaves were oven-dried at 45 °C for 48 h and weighed to assess leaf dry mass.

Leaf water content (LWC) in the leaves and folioles offered in each test was calculated as:

$$\mathrm{LWC} = 1 - \mathrm{dw}(\mathrm{area_i}/\mathrm{area_f})/\mathrm{fw}$$

where fw = leaf fresh weight measured before the trial (mg), dw = leaf dry weight measured after the trial (mg), $\mathrm{area_i}$ = initial leaf area or leaf area before the trial (mm^2), and $\mathrm{area_f}$ = final leaf area or remaining area after the trial (mm^2). The term $\mathrm{area_i}/\mathrm{area_f}$ corrects dw by tissue consumption.

Total leaf biomass was calculated after finishing choice tests (see below), when all remaining fully expanded leaves in each plant were harvested, dried 48 h at 45 °C, and weighed. To obtain an unbiased estimate of total leaf biomass, we added the biomass of leaves employed in the assays to the remaining fully expanded leaf biomass. The biomass of leaves employed in the assays was calculated as:

$$\begin{aligned}\text{Biomass (mg)} = {} & \text{leaf area }(\mathrm{mm}^2)/\mathrm{SLA}\,(\mathrm{mm}^2/\mathrm{g}) \\ & \times 1000\,(\mathrm{mg/g})\end{aligned}$$

Choice tests

We carried out three feeding-preference bioassays using fully expanded leaves of juvenile plants (6 month old) of *L. divaricata* and folioles of *P. alpataco,* and one adult of *N. circumundata.* Each insect was used only once. Bioassays consisted of two-way choice tests, including intra-specific and inter-specific comparisons. All choice tests were performed in cylindrical glass containers (14 cm in diameter). Two intra-specific comparisons were made. In the first one, seven +W and seven −W fresh leaves of *L. divaricata* were offered to an adult. This test was repeated 21 times. In the second test, 27 replications were performed with ten +W and ten −W fresh folioles of *P. alpataco*. Finally, in 14 inter-specific tests, each adult was offered seven fresh leaves of *L. divaricata* and 10 fresh folioles of *P. alpataco*. Seven inter-specific tests included +W leaves/folioles of both species, and the remaining seven tests encompassed −W leaves/folioles of both species. All leaves had been harvested immediately before the tests and had no signs of herbivory. Preference test was fixed-time food choices (Lockwood 1998) and lasted 2 h. Insect consumption was estimated measuring leaf area at the beginning and end of each test. Consumed leaf area was converted into consumed biomass as (Gutbrodt et al. 2012):

$$\begin{aligned}\text{Consumed biomass (mg)} = {} & \text{consumed area }(\mathrm{mm}^2)/ \\ & \mathrm{SLA}\,(\mathrm{mm}^2/\mathrm{mg})\end{aligned}$$

Statistical analysis

Intra-specific differences between +W versus −W leaves as well as inter-specific differences in leaf biomass, SLA, and total phenolics and N concentrations were inspected by one-way ANOVA. When ANOVA assumptions were not fulfilled, the nonparametric Mann–Whitney test was performed. Both analyses were performed using package 'stats' of the R-Project (http://www.r-project.org).

The effect of water supply regimes and species on beetle preference within choice test was assessed with repeated-measures ANOVAs considering each choice test as an independent subject (Gómez and Stuefer 2006). We used repeated-measures ANOVA because measurements on leaves of the same choice test cannot be considered independent of each other (Lockwood 1998; Roa 1992). Since inter-specific tests included +W and −W leaves, the effects of species and water supply regimes were evaluated. Repeated-measures analyses were performed using package 'stats' of the R-Project (http://www.r-project.org).

The relationships between plant consumption of each item in every choice test and SLA, LWC, total phenolics, and N concentration of that item were inspected by quantile regression using the Blossom statistical package (http://www.fort.usgs.gov/products/software/blossom/blossom.asp). Since plant consumption in a particular item depends not only on its quality but also on the quality of the other item involved in that comparison as well as on the insect employed in the assay, quantile regression is preferred to least-squared regression. Quantile regression is based on least absolute values, and the model is fit by minimizing the sum of the absolute values of the residuals; the technique is very resistant to outliers and permits for the exploration of relationships from the boundaries of the diagrams by estimating quantiles of the dependent variable ranging from 0 to 100 % (Scharf et al. 1998). Using high percentiles instead of the median (i.e., the 50th percentile) provides a statistical solution to the examination of ecological limiting factors (Cade and Noon 2003). As we are interested in knowing whether plant traits restrict maximum plant consumption, we used 0.85–0.99 conditional quantiles to obtain estimates near the upper boundary of the tissue consumption as it changes with plant traits, which better reflects the process of plant traits limiting maximum tissue consumption than does mean regression (Cade and Noon 2003). When more than one of these quantiles were statistical significant, we showed that with the best fit. In contrast to the repeated-measures ANOVA mentioned in the previous paragraph, which evaluated whether mean plant consumption differs between water supply regimes and/or species, quantile regression as employed here indicates whether maximum leaf consumption is related to plant traits regardless of water supply regimes.

Results

Drought effects on leaf biomass and leaf quality

Drought reduced leaf biomass in both *L. divaricata* ($F_{(1,22)} = 8.891$, $p < 0.01$, Fig. 1a; ANOVA) and

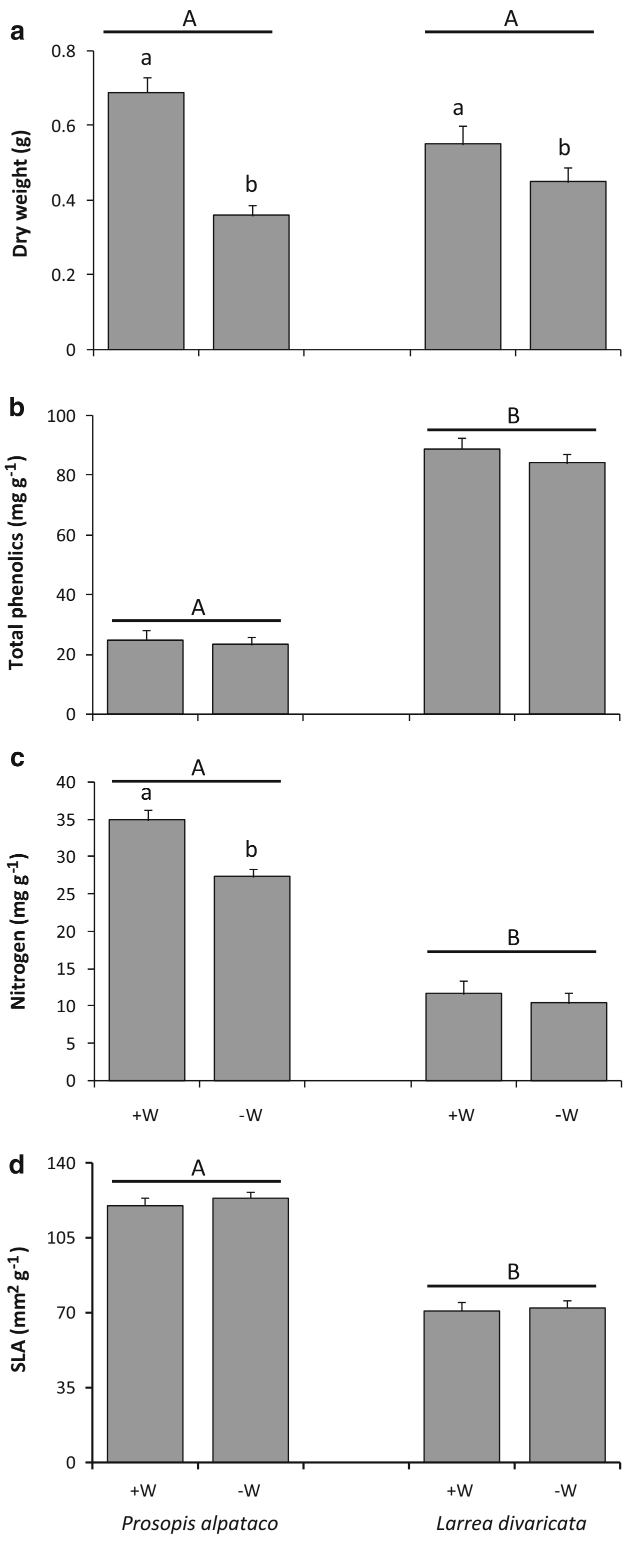

Fig. 1 Mean ± 1 standard error leaf biomass (**a**), total phenolics (**b**), nitrogen (**c**), and SLA (**d**) in well-watered (+W) and water-stressed (−W) treatments. *Different lowercase letters* indicate significant differences between treatments within species. *Different uppercase letters* denote significant differences between species

P. alpataco ($Z = 3.48$, $p < 0.01$, Fig. 1a; Mann–Whitney test). Total phenolics (Fig. 1b) and SLA (Fig. 1d) did not differ between treatments within species. In contrast, nitrogen concentration in leaves was reduced by drought in *P. alpataco* ($Z = 2.77$, $p < 0.01$, Fig. 1c; Mann–Whitney test). Thus, leaf quality did not differ between treatments in *L. divaricata*, while in *P. alpataco*, drought was associated with a reduction in nitrogen concentration in leaves.

Plant species did not differ in leaf biomass (Fig. 1a). However, total phenolics concentration was significantly lower in *P. alpataco* than in *L. divaricata* ($Z = 6.48$, $p < 0.01$, Fig. 1b; Mann–Whitney test), while nitrogen concentration and SLA were higher ($Z = 6.42, p < 0.01$, Fig. 1c; and $Z = 6.44$, $p < 0.01$, Fig. 1d; Mann–Whitney tests).

Choice test

Nyctelia circumundata did not show preference by any water supply regimes in intra-specific comparisons; mean leaf consumption did not differ between water supply regimes (*Larrea divaricata:* $F_{(1,38)} = 0.153$, $p = 0.697$, Fig. 2a, repeated-measures ANOVA; *Prosopis alpataco:* $F_{(1,50)} = 0.790$, $p = 0.378$, Fig. 2b, repeated-measures ANOVA). However, in most cases, the insect consumed one of the offered items, ignoring almost completely the other (most dots in Fig. 2a, b are near the axes). In contrast, in choice tests involving both plant species, *N. circumundata* showed a marked preference for *P. alpataco* ($F_{(1,20)} = 5.774, p < 0.05$, Fig. 2c, repeated-measures ANOVA) irrespective of the water supply regime ($F_{(1,20)} = 0.380$, $p = 0.544$, filled and empty symbols in Fig. 2c, repeated-measures ANOVA). On average, 80 % of consumed tissue belonged to *P. alpataco* in inter-specific comparisons.

Relationship between leaf consumption and leaf quality

In intra-specific comparisons, maximum leaf consumption was inversely related to SLA in both species (Fig. 3c, g). In addition, in *P. alpataco*, N concentration was positively related to maximum leaf consumption, whereas LWC showed the opposite tendency (Fig. 3f, h). Total phenolics was not related to maximum leaf consumption in any species (Fig. 3a, e). These results indicate that although beetles did not discriminate between +W and −W plants in intra-specific tests (see previous section), maximum leaf consumption is related to leaf traits in both species.

In contrast, in inter-specific comparisons, total phenolics was negatively related to maximum leaf consumption, while N concentration exhibited the opposite trend (Fig. 3i, j). SLA and LWC were not related to maximum leaf consumption in choice tests including leaves of both species (Fig. 3k, l).

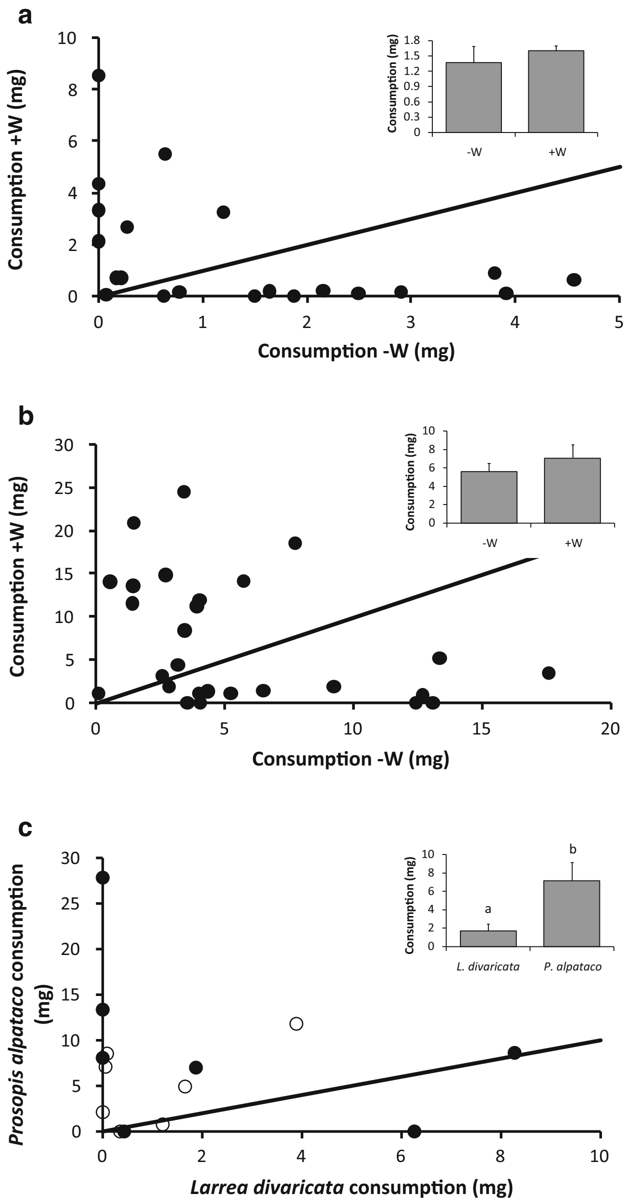

Fig. 2 Leaf consumption in every choice test involving well-watered (+W) and water-stressed (−W) leaves of *L. divaricata* (**a**), and well-watered (+W) and water-stressed (−W) folioles of *P. alpataco* (**b**). Leaf consumption in every choice test involving *L. divaricata* leaves and *P. alpataco* folioles (**c**). Diagonals are equal-consumption lines. *One point* denotes one choice test. **c** *Filled symbols* indicate tests involving +W pairs, and *empty symbols* tests containing −W pairs. Mean ± 1 standard error consumptions are shown in the *top-right corner* of the corresponding panel. *Different lowercase letters* indicate significant differences in mean leaf consumption between items

Discussion

Although water-stress treatments were efficiently reducing total leaf biomass (Fig. 1a), most plant traits were not affected by drought. Only nitrogen concentration in folioles of *P. alpataco* was decreased in the −W treatment. This

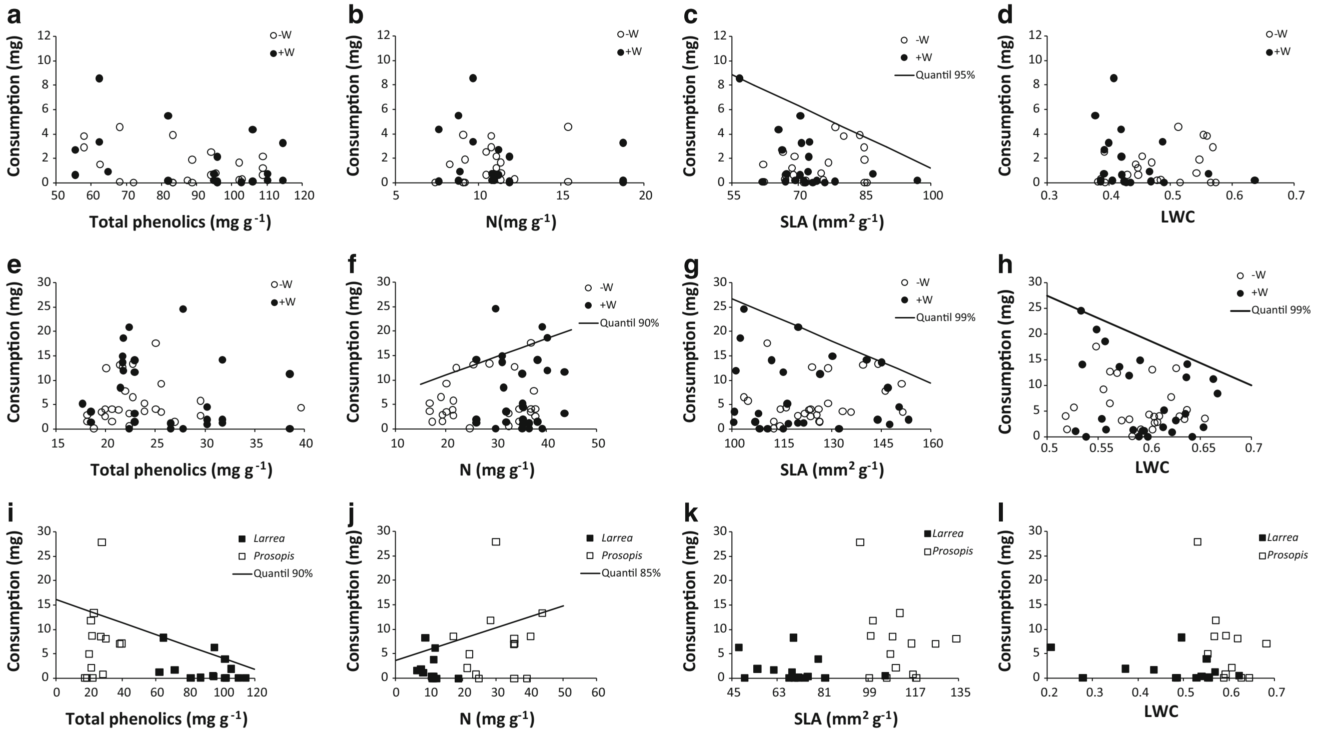

Fig. 3 Relationships between leaf consumption of *L. divaricata* and total phenolics (**a**), nitrogen (N) (**b**), specific leaf area (SLA) (**c**), and leaf water content (LWC) (**d**) in choice tests involving well-watered (+W) and water-stressed (−W) plants. Relationships between consumption of folioles of *P. alpataco* and total phenolics (**e**), N (**f**), SLA (**g**), and LWC (**h**) in choice tests involving well-watered (+W) and water-stressed (−W) plants. Relationships between folioles/leaf consumption of *P. alpataco*/*L. divaricata* and total phenolics (**i**), N (**j**), SLA (**k**), and LWC (**l**) in choice tests involving both species. Lines are quantile regressions. The significant quantile greater than 0.85 exhibiting the best fit is shown

result is opposite to the increase in nitrogen concentration as a consequence of drought supposed by White (1984) when proposing the plant stress hypothesis. Indeed, several studies have reported decreased nitrogen concentration in water-stressed plants (e.g., Inbar et al. 2001; Staley et al. 2006), while others found no differences in nitrogen concentration between water-stressed and control plants (Björkman 2000; De Bruyn et al. 2002). This discrepancy among studies was attributed to nonlinear effects of drought on plant chemistry (Scheirs and De Bruyn 2005; Staley et al. 2006). In contrast, total phenolics concentration in leaves was not affected by water stress in our study. As in the case of nitrogen, a curvilinear relationship was also proposed between water stress and concentration of secondary metabolites (growth–differentiation balance hypothesis, Herms and Mattson 1992).

In intra-specific comparisons, *N. circumundata* showed no preference between water-stressed or well-watered leaves. This may be a consequence of high variability in leaf traits (*x* axes on Fig. 3a–h), what prevented us to detect significant differences between treatments in most traits (Fig. 1). Although most published studies to date have reported changes in plant traits and palatability as consequence of drought, there are also studies reporting no effects of drought on these variables (Backhaus et al. 2014). However, in our study, leaf water content was inversely related to maximum leaf consumption in *P. alpataco* (Fig. 3h). This result insinuates that although we did not find differences in mean leaf consumption between water-stress treatments, leaves with lower water content may be subject to higher consumption than well-hydrated leaves. This may be related to the fact that most plants lower their osmotic potential during drought by accumulating inorganic ions, amino acids, sugars, sugar alcohols, and organic acids in the aboveground tissues (Mattson and Haack 1987). Similar results were found by Meyer et al. (2006) in a study where a leaf cutting ant (Attini: *Atta colombica*) selectively feed on drought-stressed plants, which showed lower water content and a higher concentration of osmolytes. Dry matter content (the ratio of dry mass to wet mass) could be used to predict variations in palatability, especially at the intra-specific level (Elger and Willby 2003). The fact that leaf water content was inversely related to maximum leaf consumption in *P. alpataco* (Fig. 3h) strongly suggests that besides being affected by permanent changes in leaf chemical and/or physical properties (i.e., nitrogen and total phenolics concentrations, SLA), insect consumption can be affected by rapidly changing variables such as leaf water content.

Only specific leaf area (SLA) affected maximum consumption in both species (Fig. 3c, g). In both cases, SLA was negatively related to leaf consumption expressed in mg. At first glance, it may seem counterintuitive, since leaf consumption was lower in thinner leaves. We believe that our experimental design (two-way choice tests lasting for 2 h) can be the cause of this result, because most invertebrate herbivory involves the gradual removal of small amounts of tissue over a long period (Hanley et al. 2007).

Nitrogen concentration in leaves was positively related to maximum foliole consumption in *P. alpataco* (Fig. 3f). This result suggests that the leaf quality is important on the food selection by *N. circumundata* and agrees with several studies which have found a positive relationship between foliage quality to herbivores and insect consumption (Mattson and Haack 1987; Staley et al. 2006). However, total phenolics were not related to maximum consumption in intra-specific comparisons. It could be due to the fact that in intra-specific preference tests, variation in secondary compounds due to water-stress treatments is small compared to the drastically altered plant physiology for osmoregulation (Ribeiro Neto et al. 2012).

On the other hand, in inter-specific comparisons, adults of *N. circumundata* showed a marked preference against *L. divaricata*. This result is similar to that of Cheli et al. (2009), who evaluated the relative preference of *N. circumundata* by 10 Patagonian plant species. In our inter-specific comparisons, maximum consumption was negatively related to total phenolics but positively related to nitrogen concentration. As proposed in several articles (Mattson and Haack 1987; Alonso and Herrera 1990; Lower and Orians 2003; Pérez-Harguindeguy et al. 2003; Campanella and Bisigato 2010), herbivores prefer species with low total phenolics and high nitrogen concentrations.

This is the first study evaluating drought effects on insect consumption including *L. divaricata* and *P. alpataco* as host plants. However, several studies were performed in *L. tridentata*, the dominant species in most of southwestern North American deserts. For example, Greenfield et al. (1987, 1989) found that the desert clicker grasshopper, *Ligurotettix coquilletti* (Orthoptera: Acrididae), prefers leaves with lower content of nordihydroguaiaretic acid (NDGA), a phenolic resin coating *Larrea* foliage which reduces conversion rates of digested food. However, NDGA not only reduced plant consumption by insects, but this pattern is also present among vertebrates; Meyer and Karasov (1989) found that woodrats (*Neotoma lepida*, Rodentia: Muridae) consistently select plant parts of low NDGA content.

In general, in intra-specific comparisons, physical traits (i.e., SLA and LWC, Fig. 3c, g, h) were more relevant to determine maximum consumption than chemical attributes (i.e., total phenolics and N, Fig. 3a, b, e). However, in inter-specific comparisons, physical traits were not related to maximum leaf consumption (Fig. 3k, l), whereas chemical attributes were significantly related to that variable (Fig. 3i, j). This result suggests that food selection is a hierarchical process where chemical attributes are taken into account for species selection, and physical attributes for choosing individuals inside species. Frequently, insects use different physical and chemical cues when selecting patches and food items inside patches (Hassell and Southwood 1978).

We have to remain cautious to extrapolate our results to plants growing in the field since cultivated greenhouse plants may respond in a very different way to stress that their wild counterparts, as they are free from other insects, pathogens, and competition from other plant species (Staley et al. 2006). In addition, factors like plant species, insect species, stress regime, insect feeding guild, life stage of the herbivore, insect starvation status, and plant ontogenetic stage may have strong influence on the effects of interactions between insect herbivores and stressed plants (Koricheva et al. 1998b). However, our results suggest that future reductions in summer precipitation could affect plant–herbivore relationships in northeastern Patagonia. Although we did not find differences in mean consumption between well-watered and water-stressed plants, some traits, which are frequently affected by drought in the bibliography, were related to maximum consumption. Particularly, thicker and drier leaves were subjected to highest consumption. So, it is possible that leaves of plants exposed to extended summer droughts will be thicker and drier and consequently suffer high herbivore rates.

Conclusions

We concluded that in inter-specific comparisons, *N. circumundata* showed a marked preference for *P. alpataco*, which present higher N and lower total phenolics concentrations than *L. divaricata*. In contrast, water supply regimes did not affect mean leaf consumption in intra-specific comparisons. Nonetheless, in intra-specific tests, maximum consumption of *L. divaricata* was related to SLA, whereas maximum consumption of *P. alpataco* was affected by N, SLA, and LWC. Our results suggest that food selection is a hierarchical process where different leaf attributes are taken into account for inter- and intra-species selection.

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