



## Original article

# Leaf damage decreases fitness and constrains phenotypic plasticity to drought of a perennial herb

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## ABSTRACT

Mediterranean-type ecosystems are increasingly prone to drought stress. Herbivory might limit plant functional responses to water shortage. This may occur as a result of plant resource depletion or due to the fact that leaf damage and drought may elicit opposite phenotypic responses. We evaluated the impact of herbivory on plant fitness in the field, and the effects of leaf damage on phenotypic plasticity to reduced soil moisture in a greenhouse. The study species was *Convolvulus demissus*, a perennial herb endemic to central Chile, which has a Mediterranean-type climate. Controlled herbivory by chrysomelid beetles (natural herbivores) in the field had a negative impact on plant fitness, estimated as number of fruits. Whereas reduced soil moisture alone did not affect seedling survival, damaged seedlings (simulated herbivory) had greater mortality when growing under water shortage. The hypothesis that herbivory would constrain phenotypic plasticity was supported by significant statistical interactions between leaf damage and soil moisture, followed by inspections of reaction norms. This was verified both overall (all phenotypic traits taken together, MANOVA) and in four of the six traits evaluated (ANOVAs). When plants were damaged, the reaction norms in response to low soil moisture of water use efficiency, root:shoot ratio and xylem water potential showed reduced slopes. While undamaged plants increased root biomass in response to low moisture, the opposite trend was found for damaged plants. The simultaneous occurrence of herbivory and drought events might curtail recruitment in plant populations of central Chile and other Mediterranean-type ecosystems due to the inability of damaged seedlings to show functional responses to low soil moisture. This finding is of ecological significance in view of current and projected trends of increased aridity in these ecosystems.

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## 1. Introduction

Environmental stress and herbivory may have additive and even synergistic detrimental effects on plant performance (Hawkes and Sullivan, 2001). Plants have evolved responses to these ecological factors and consequently show, in an ecological timescale, phenotypic adjustments that ameliorate their negative impact (Karban and Baldwin, 1997; Strauss and Agrawal, 1999; Schulze et al., 2005). Considerable research has addressed the interactive effects of herbivory and resource limitation on plant survival or reproductive output (reviewed in Gurevitch et al., 2000; Hawkes and Sullivan, 2001; Wise and Abrahamson, 2007). Less attention has been devoted to the mechanistic basis of such patterns. For instance,

comparatively little research has addressed whether herbivory may limit plant functional responses to the environment (but see Cipollini, 2004; Kurashige and Agrawal, 2005; Gianoli et al., 2007; Valladares et al., 2007).

Plants display phenotypic plasticity in response to environmental changes, and plasticity is often described using reaction norms (the plot of phenotypic trait expression against environmental variation) (Schlichting and Pigliucci, 1998). Adaptive phenotypic plasticity occurs when reaction norms are positively associated with plant fitness (Sultan, 1995; van Kleunen and Fischer, 2005). This may result from either correlated responses of plant phenotype and plant fitness, when there is enhanced exploitation of the environment, or phenotypic responses that allow fitness homeostasis (flat fitness reaction norms) when plants face challenging environments (Alpert and Simms, 2002). If damage by herbivores causes maladaptive modifications of plant reaction norms to the environment, then we will gain insights into proximate explanations for fitness losses due to herbivory. Plants exhibit phenotypic plasticity to drought that allows

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them to minimize water loss by transpiration and/or maximize water uptake. Typical phenotypic responses of plants to reduced soil moisture include an increase in the relative allocation of biomass to roots, a reduction in leaf area and number of leaves, enhanced water use efficiency (the ratio between carbon gain and water loss through stomata), and a decrease in the internal osmotic potential (Schulze, 1986; Sultan and Bazzaz, 1993; Grace, 1997; Chaves et al., 2002).

The perennial herb *Convolvulus demissus* (Convolvulaceae) is endemic to Andean slopes in central Chile and Argentina. This is a region with temperate, Mediterranean-type climate, where plant populations often experience drought during the dry season (spring–summer) (Di Castri and Hajek, 1976; Arroyo et al., 1981). There is evidence of a trend of increased aridity in Central Chile (Pezoa, 2003). In general, likely scenarios of global climate change indicate that Mediterranean-type ecosystems would experience increased aridity (Valladares, 2004), and in the case of central Chile climate change projections consider a 20–30% decrease in precipitations during plant growth season (IPCC, 2007). Populations of *C. demissus* suffer herbivory mainly by leaf beetles (Chrysomelidae, Cassidinae) and occasionally by livestock, with common field levels of herbivory in the range of 20–60% defoliation (Gianoli et al., unpublished data). The occurrence of drought and leaf damage may be particularly critical for seedlings of *C. demissus*, which lack belowground reserves that might confer tolerance to herbivory and environmental stress. Seedlings of *C. demissus* have shown phenotypic plasticity to experimental variations in soil moisture (Quezada and Gianoli, 2006) and light intensity (González and Gianoli, 2004). In the present study with *C. demissus*, we first determined whether herbivory by chrysomelid beetles reduces plant fitness in the field. Secondly, we addressed the effect of leaf damage and soil moisture on seedling survival, and evaluated the effect of leaf damage on plant phenotypic plasticity to reduced soil moisture. We aimed at determining whether herbivory may constrain plant reaction norms of potential adaptive value in a stressful environment. This may be of increased importance given the expected accentuation of aridity in the study ecosystem.

## 2. Methods

*C. demissus* (Convolvulaceae) is a perennial prostrate herb distributed between 1200 m and 2700 m a.s.l. on the Andean slopes of Central Chile and Argentina (O'Donnell, 1957; Herbarium Universidad de Concepción [CONC]). Stems are numerous and short (0.1–0.5 m long). Leaves are ovate to triangular and of small size (0.5–2.5 cm long). Flowers are hermaphroditic and solitary, with light pink funnel-like corollas (1–2 cm diameter). The fruit is a capsule with one to four seeds (4–7 mm long) (O'Donnell, 1957). This species blooms throughout November, December and January. The plant dies back during February–March and remains dormant until the first rains of the next season (April–May). The dry season extends from October to March. In the study population (see below) we determined water availability in the soil at the start (October) and at the end (February) of the growing season. Soil matric water potential was measured with tensiometers (2725 Series Jet Fill, Soil Moisture, CO, USA) in bare ground adjacent to each of four plants of *C. demissus* randomly chosen. Measurements were made at a depth of 15 cm.

The field experiment was carried out in a population of *C. demissus* located at 2380 m a.s.l. in the Andes close to Santiago, Chile (33°21'S, 70°18' W). The climate in this site is Mediterranean, with a cold and rainy winter and a dry and warm summer (Di Castri and Hajek, 1976; Arroyo et al., 1981). In October 2005 we located 80 plants of *C. demissus* at the vegetative stage. Selected plants had between one and three stems, and between six and ten leaves per stem. We randomly chose 40 plants to receive herbivory by larvae of *Chelymophra varians* (Chrysomelidae, Cassidinae). In each of these

plants two or three third-instar larvae were placed on leaves and the whole stem was immediately enclosed with a nylon mesh bag. This was done in such a way that approximately half of the leaves were exposed to beetles. A similar number of empty nylon mesh bags were put on each of the other 40 plants. We periodically checked for larval survival in order to replace them, and manually excluded other larvae naturally colonizing exposed stems of experimental plants. A wire cage covered each of the 80 plants in order to exclude herbivory by mammals. We withdrew beetles two weeks later and estimated the actual defoliation level of each plant, which ranged between 30% and 50%. Four months after the start of the experiment, we recorded the number of fruits and the number of seeds per fruit, and determined seed mass in the laboratory. Differences between damaged and undamaged plants were determined by a one-way ANOVA or by a Mann–Whitney *U* test, depending on whether data met parametric analysis assumptions or not.

Seedlings of *C. demissus* used in the greenhouse experiment were grown from seeds collected in the Andes close to Santiago at approximately 2400 m, in a population close to that described above. Seeds were collected from more than 30 widely spaced mother plants and pooled thereafter. In the lab, 300 seeds were subjected to acid scarification and then kept in the dark at 20 °C on wet papers to allow germination. On November 2005, we selected 120 seedlings of vigorous appearance. Seedlings were planted singly in 2 l plastic bags filled with potting soil and placed on benches of a greenhouse at Universidad de Concepción (central Chile). After four weeks, when seedlings had 10 leaves on average, the experimental treatments were applied. Experiments were performed during summer time, under approximately 1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PAR at noon, and maximum and minimum temperatures (daily ranges) of 22–29 °C and 10–14 °C, respectively.

Four groups of 30 plants were arranged in a factorial design, crossing two levels of herbivory (undamaged vs. leaf damage) and two levels of soil moisture (regular watering vs. restricted watering). The resulting experimental groups were: control, drought, damage, and drought + damage. Plants from the control and damage groups were watered to field capacity every 3 days. Plants from the drought and the drought + damage treatments were watered to field capacity every 10 days. A simulated herbivory treatment was applied to plants of the damage and drought + damage treatments, which consisted in clipping with scissors half of the leaves along the mid vein (50% defoliation), simulating defoliation caused by herbivores. Simulated herbivory is a common practice in this kind of experiments (Tiffin and Inouye, 2000). We used it to standardize the defoliation level, avoiding deviations such as those observed in the field experiment. Plants of the four experimental groups were placed alternately on greenhouse benches in a systematic design in order to minimize micro-environmental biases, and were relocated over the benches every 10 d.

Two months after the onset of treatments, we recorded seedling mortality in each experimental group and the following traits were measured for each plant: main stem length, leaf area, instantaneous water use efficiency (WUE, the ratio of CO<sub>2</sub> assimilation and evapotranspiration), root biomass (dry weight), root:shoot biomass ratio, and xylem water potential. Leaf area was estimated from digital images of detached leaves using SigmaScan® (SPSS Inc., Illinois, USA). We sampled three leaves per plant to obtain the average leaf area of the individual. Xylem water potential was recorded using a Scholander pressure chamber (PMS 600, PMS Instruments, Corvallis, USA). In order to obtain the individual value of WUE, it was measured on three attached leaves per plant with a portable gas exchange system (LCi, ADC Bioscientific Ltd., Hertfordshire, UK) between 10:00 and 12:00. At the time of measurements PAR varied between 800 and 1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , which were assumed to be saturating light levels.

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