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Water availability limits tolerance of apical damage in the Chilean tarweed *Madia sativa*

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ABSTRACT

Plant tolerance is the ability to reduce the negative impact of herbivory on plant fitness. Numerous studies have shown that plant tolerance is affected by nutrient availability, but the effect of soil moisture has received less attention. We evaluated tolerance of apical damage (clipping that mimicked insect damage) under two watering regimes (control watering and drought) in the tarweed *Madia sativa* (Asteraceae). We recorded number of heads with seeds and total number of heads as traits related to fitness. Net photosynthetic rate, water use efficiency, number of branches, shoot biomass, and the root:shoot biomass ratio were measured as traits potentially related to tolerance via compensatory responses to damage. In the drought treatment, damaged plants showed $\approx 43\%$ reduction in reproductive fitness components in comparison with undamaged plants. In contrast, there was no significant difference in reproductive fitness between undamaged and damaged plants in the control watering treatment. Shoot biomass was not affected by apical damage. The number of branches increased after damage in both water treatments but this increase was limited by drought stress. Net photosynthetic rate increased in damaged plants only in the control watering treatment. Water use efficiency increased with drought stress and, in plants regularly watered, also increased after damage. Root:shoot ratio was higher in the low water treatment and damaged plants tended to reduce root:shoot ratio only in this water treatment. It is concluded that water availability limits tolerance to apical damage in *M. sativa*, and that putative compensatory mechanisms are differentially affected by water availability.

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1. Introduction

Herbivory is frequently detrimental to plant fitness (Marquis, 1992) and previous work has shown that plant populations may respond to herbivory pressure by evolving resistance and/or tolerance (Karban and Baldwin, 1997; Strauss and Agrawal, 1999). Traits that reduce the amount of damage experienced by plants, including secondary metabolites, spines and trichomes, are said to confer resistance. Plants may also evolve mechanisms of tolerance which allows a reduction of the fitness impact of damage. The defensive role of resistant traits has been studied extensively (Fritz and Simms, 1992; Karban and Baldwin, 1997). Research on plant tolerance as an evolved response to damage is relatively recent (Strauss and Agrawal, 1999; Stowe et al., 2000; Tiffin, 2000; Pilson and Decker, 2002).

Studies on plant tolerance have generally focused on operationally defined tolerance estimates such as the absolute or proportional reduction in plant performance for a given level of damage (Strauss and Agrawal, 1999; Juenger and Bergelson, 2000; Wise and Abrahamson, 2005, 2007). The mechanisms underlying plant tolerance of herbivory are not completely understood (Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Tiffin, 2000). Some responses to damage have been associated with ratio of plant compensatory ability to increased photosynthetic rate (Dyer et al., 1991; Mabry and Wayne, 1997; Meyer, 1998; Thomson et al., 2003), increased growth rate (Danckwerts, 1993; Houle and Simard, 1996), activation of dormant meristems that increase branching or tillering after release from apical dominance (Lennartsson et al., 1997; Huhta et al., 2000; Lortie and Aarssen, 2000; González-Teuber and Gianoli, 2007) and the capacity to reallocate stored resources (Mabry and Wayne, 1997; Briske et al., 1996). Studies addressing compensatory mechanisms may contribute to understanding potential and constraints in plant defense evolution and the selective role of herbivores on plant physiology and morphology (Haukioja, 1991; Rosenthal and Kotanen, 1994; Tiffin, 2000).

Tolerance may be affected by resource availability (Hilbert et al., 1981; Maschinski and Whitham, 1989; Stowe et al., 2000). Plant compensation, in terms of the regrowth and reproduction following herbivory has been assumed to increase with nutrient availability (Maschinski and Whitham, 1989; Belsky et al., 1993; Irwin and Aarssen, 1996). This follows the reasoning that replacing a given amount of consumed tissue requires a larger fraction of the net production of a plant when it is growing in a resource-poor environment than when it develops in a resource-rich environment (Hawkes and Sullivan, 2001). However, experimental support to this assumption remains inconclusive and different explanatory models have been put forward (Hilbert et al., 1981; Maschinski and Whitham, 1989; Hawkes and Sullivan, 2001; Wise and Abrahamson, 2005, 2007). Although most studies addressing the effects of abiotic factors on plant tolerance have focused in soil nutrients there is also evidence of the regulatory role of water availability (Hawkes and Sullivan, 2001; Wise and Abrahamson, 2007). For instance, some studies suggest that annual variation in plant compensation is associated with rainfall regimes (Maschinski and Whitham, 1989; Lennartsson

et al., 1998; Levine and Paige, 2004) and that nurse effects via tolerance of damage may be mediated by amelioration of drought stress (Acuña-Rodríguez et al., 2006). In the present study we evaluated whether experimental drought can limit plant capacity to tolerate herbivore damage.

We studied the effect of water availability on tolerance of apical damage and on some putative compensatory mechanisms in the Chilean tarweed *Madia sativa* (Asteraceae). This native plant species is widely distributed in Chile and is very common in open habitats and disturbed grassland plant communities (Hoffman, 1998; Matthei, 1995). In central Chile, *M. sativa* is frequently attacked by sucking and chewing insects (Artigas, 1994; Delfino and Gonzáles, 2005), especially lepidopterous larvae that commonly produce apical damage (W.L. Gonzáles, personal observation). *M. sativa* is an annual species that grows during spring–summer in central Chile. This area has a Mediterranean-type climate characterized by cool wet winters and dry summers (Di Castri and Hajek, 1976), hence water availability could be a limiting factor for plant populations (Mooney and Dunn, 1970). We specifically addressed the following questions: (1) does *M. sativa* show tolerance of apical damage in terms of growth and reproduction?, (2) does water availability limit plant tolerance?; and (3) which mechanisms are associated with plant tolerance? (i.e. biomass allocation, architecture modification and/or physiological responses).

2. Materials and methods

2.1. Study system

The Chilean tarweed *Madia sativa* Mol. (Asteraceae) is a highly selfing annual plant (Arroyo and Uslar, 1993) that grows in open habitats, disturbed fields and sunny slopes along the entire extension of Chile (20 °S to 50 °S; Matthei, 1995; Hoffman, 1998). The main stems (unbranched or branched) are 20–90 cm tall and cylindrical, and glandular and non-glandular trichomes are found on stems, leaves and involucre (Matthei, 1995; Hoffman, 1998; Gonzáles et al., 2008). We observed plants to be frequently attacked by specialist native aphids (*Uroleucon eumadiae*, Delfino and Gonzáles, 2005) and larvae of Lepidoptera (Noctuidae, Artigas, 1994; W.L. Gonzáles, personal observation). Noctuid caterpillars feed on reproductive buds and inflorescences of *M. sativa* and damage commonly occurs on apical buds of the main stem. This apical damage elicits branching in *M. sativa*, as has been reported for other plants species (Lennartsson et al., 1997; Huhta et al., 2000). Herbivory by mammals was not observed in the study area.

2.2. Experimental procedures

Seeds of *M. sativa* were collected in Farellones (central Chile; 33°21'S, 70°17'W), during late summer 2004 (February–March). We sampled approximately 70 widely spaced plants (approximately 10 m distance among plants), and collected 20–200 seeds per plant. In November 2004, seeds were scarified with sulfuric acid for 2 min and placed on moistened paper in the dark at room temperature to allow germination. Seedlings

were grown in 200 ml pots until they reached the two-leaves stage (20 days), and then were transplanted to 3-L plastic pots at a common garden in the Universidad de Concepción campus (Concepción, central Chile) under natural environmental conditions (PAR radiation at noon ca. $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$; 24°C and 12°C mean maximum and minimum temperatures). Plants were watered every 4 days before treatments were applied.

The effect of apical damage and water availability on fitness components and on traits related to tolerance (detailed below) was evaluated in a factorial design (30–40 plants per treatment, $N = 145$ plants). Two levels of watering (control and low) and damage (undamaged and apical damage) were assigned to plants randomly. The watering treatments started 70–72 days after plants were transplanted. Plants were watered every 4 days or every 8 days (control and low water availability, respectively). The damage treatment 2 weeks after the start of watering treatment was applied, when all experimental plants had at least one reproductive bud on the main stem. Damage by lepidopterous larvae was mimicked by making multiple (ca 6–8) scissor cuts on the terminal buds of the plant. Part of the damaged tissue was removed. Plants were maintained free from herbivorous insects and pollinators using a transparent plastic mesh and were randomly repositioned every 2 weeks.

2.3. Measured variables

Net photosynthetic rate and transpiration was measured for all plants 20 days after damage was inflicted. Measurements were conducted on one fully expanded leaf per plant located at mid-shoot. A portable infrared gas analyzer with temperature- and light-controlled cuvette (CIRAS-2, PP-Systems, Haverhill, MA, USA) was used. All measurements were carried out between 12:00 and 15:00 h on consecutive sunny days. PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was set at 1000, relative humidity at 70–80%, and CO_2 concentration at the atmospheric level (i.e. 360 ppm). Water use efficiency (WUE) was calculated as photosynthetic rate divided by transpiration ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$).

Plants were harvested 160–165 days after transplanting and were oven-dried for 6 days at 60°C before weighing. The number of branches was recorded with a structure including at least one internodes was considered to be a branch but a leafless pedicel growing from the main stem was not. Reproductive biomass (total biomass of flower heads) and both aboveground and belowground vegetative biomass were determined. Root biomass was harvested by gently washing roots to remove the potting medium. We counted the number of heads showing seeds and the reproductive effort (the total number of heads, including those having and lacking seeds) in each experimental plant as reproductive fitness components. Seed heads were removed before dehiscence and mature seeds were carefully collected.

2.4. Data analysis

Data were log-transformed to meet normality. Photosynthesis, WUE, transpiration, shoot biomass and root:shoot ratio were analyzed using an analysis of variance (ANOVA). Watering and damage were considered fixed factors. Because the number of branches had a non-normal distribution, this

variable was modeled with a Poisson distribution and a log link function using a generalized linear model (Crawley, 1993). Number of heads showing seeds and the reproductive effort were analyzed using an ANOVA with watering and damage as fixed factors.

3. Results

Photosynthesis increased in damaged plants in comparison to undamaged plants, but only in the control water treatment (LSD test, $P < 0.05$) (Table 1, Fig. 1A). Overall, photosynthesis was not affected by watering regime or apical damage (Table 1, Fig. 1). Leaf transpiration ($\text{mmol m}^{-2} \text{s}^{-1}$) was lower in plants under experimental drought (1.43 ± 0.07) than in those under control watering (2.03 ± 0.05) (Table 1). Apical damage did not affect transpiration within each watering treatment (LSD, $P > 0.78$). Under ample water availability, damaged plants showed greater WUE and the expression of this trait was similar for damaged and undamaged plants in the restricted watering treatment (Table 1, Fig. 1B). This result likely explains the overall significant effect of water availability on WUE (Table 1).

Plants growing under experimental drought had smaller shoots (undamaged = 7.34 ± 0.29 g, damaged = 6.91 ± 0.34 g) than those in control watering (undamaged = 13.12 ± 0.47 g, damaged = 13.38 ± 0.45 g) (Table 1). Apical damage did not affect final shoot biomass within each watering treatments (LSD, $P = 0.35$ for each contrast) (Table 1). Experimental drought caused plants to show a greater root:shoot ratio of biomass allocation (Table 1). There were no differences in root:shoot ratio between damaged and intact plants in the control water treatment (LSD, $P = 0.97$) whereas in the low water treatment there was a tendency for damaged plants to show a lower root:shoot ratio than undamaged plants (LSD, $P = 0.088$) (Fig. 2A). While apical damage elicited a three-fold increase in the number of branches in both watering treatments, water shortage slightly reduced branching (Table 1, Fig. 2B).

Plants in the drought stress treatment had fewer heads with seeds (Table 2, Fig. 3). Apical damage reduced the number of heads with seeds in the low water treatment (LSD, $P < 0.001$) but not in the control water treatment (LSD, $P = 0.61$). Damaged plants grown under drought conditions had a $\approx 43\%$ reduction in this fitness component in relation to undamaged plants. The same pattern was found for reproductive effort and number of heads with seeds (Table 2). Consequently the number of heads with seeds was highly correlated with both the reproductive effort (Pearson correlation moment; $r = 0.94$, $P < 0.0001$, $N = 137$) and reproductive biomass ($r = 0.90$, $P < 0.0001$, $N = 137$).

4. Discussion

Tolerance of apical damage in *M. sativa* was limited by water availability. This supports broad predictions by Maschinski and Whitham (1989) and Wise and Abrahamson (2005) that compensation varies with resource availability. Earlier work has shown that some plant populations are tolerant of apical-meristem damage only in environments with high nutrient availability or low competition (Maschinski and

Table 1 – Two-way analysis of variance (ANOVA) of the effect of apical damage and water availability on ecophysiological and allocation traits of *Madia sativa*. $F_{(1,143)}$ values are shown (for Branches, Wald $_{(1,143)}$ values are listed instead)

Source	Photosynthetic rate	Water use efficiency	Transpiration	Number of branches	Shoot biomass	Root:shoot biomass ratio
Damage	1.89	0.67	0.001	64.67***	0.20	1.92
Water	0.02	29.89***	96.77***	4.67*	150.09***	4.58*
Damage × Water	4.24*	3.78*	0.149	0.02	1.04	1.84

*P ≤ 0.05; ***P < 0.001.

Whitham, 1989; Fay et al., 1996; Juenger and Bergelson, 1997; Lennartsson et al., 1997; Huhta et al., 2000). There is however contrasting evidence regarding the impact of water limitation on plant tolerance of damage. On one hand, field work with *Gentianella campestris* (Lennartsson et al., 1998) and *Ipomopsis arizonica* (Maschinski and Whitham, 1989) showed that tolerance was positively associated with rainfall and experimental water supply during a severe drought year increased compensatory ability of *I. aggregata* (Levine and Paige, 2004). On the other hand, additional water did not affect tolerance of damage by *I. arizonica* during years in which water presumably

was not a limiting resource (Maschinski and Whitham, 1989). Similarly, some genotypes of *Amaranthus hybridus* showed enhanced tolerance to damage under drought in greenhouse conditions (Gassmann, 2004). These contrasting results can be explained by the limiting resource model (Wise and Abrahamson, 2007). To predict the effect of variation in resource availability on the impact of herbivory on plant fitness, this model considers which resource is limiting plant fitness and which resource is primarily affected by

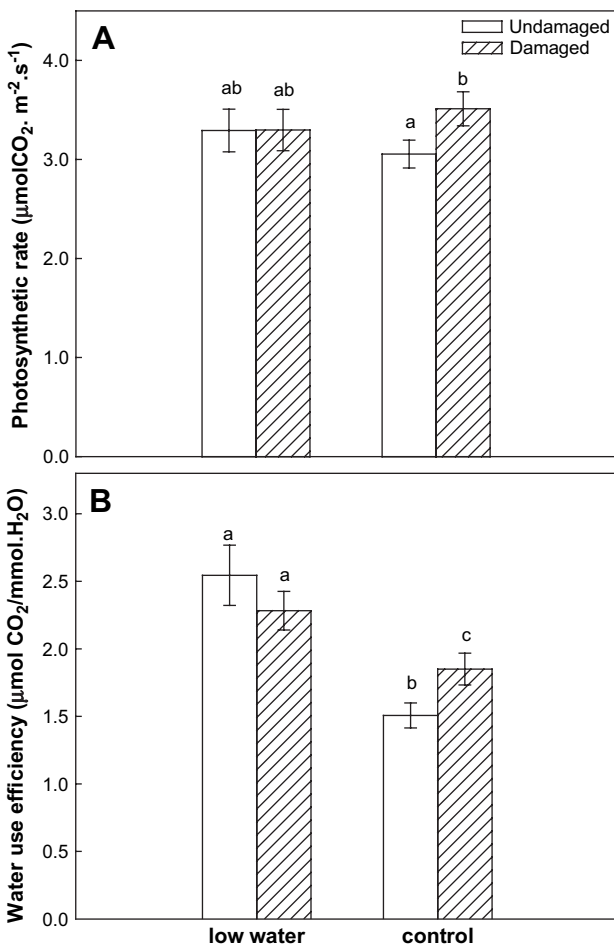


Fig. 1 – (A) Photosynthetic rate and (B) water use efficiency in undamaged and damaged plants of *Madia sativa* under two levels of water availability. Bars represent ±1 standard error. In each figure, different letters above bars are significantly different (a posteriori LSD test, P < 0.05).

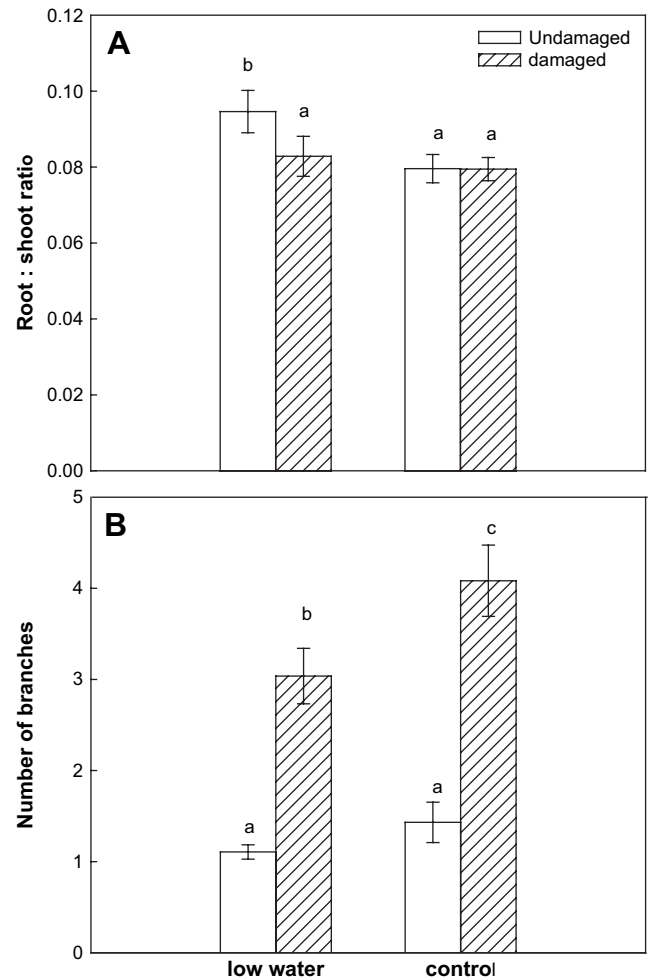


Fig. 2 – (A) The ratio of root to shoot biomass and (B) number of branches in undamaged and damaged plants of *Madia sativa* under two levels of water availability. Bars represent ±1 standard error. In each figure, different letters above bars are significantly different (a posteriori LSD test, P < 0.05).

Table 2 – Two-way analysis of variance (ANOVA) of the effect of apical damage and water availability on the number of heads with seeds and the total number of heads in *Madia sativa*

Source	Number of heads with seeds	Total number of heads
	$F_{(1,143)}$	$F_{(1,143)}$
Damage	5.03*	5.30*
Water	64.92***	65.07***
Damage × Water	5.94*	6.40*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

herbivory. In the case of *M. sativa*, water, the focal resource, limits plant fitness in a low focal resource environment (experimental drought). Considering that we found the prediction of the model of Wise and Abrahamson (2007) would be that higher tolerance in the low-stress environment, would be that apical damage primarily affected use or acquisition of water in *M. sativa*. This inference is somewhat supported when the variation in trait expression in the different experimental treatments is taken into account (see below).

Plant traits potentially related to tolerance of damage in *M. sativa* were differentially affected by water availability. Apical meristem damage releases a plant from apical dominance and increases branching via the activation of dormant meristems (Benner, 1988; Lennartsson et al., 1997, 1998; Huhta et al., 2000). The ability of *M. sativa* to enhance branching in response to damage was limited by drought. Branching results from the cessation of bud inhibition by auxins produced by shoot apex and/or the release of axillary buds from resource competition with the terminal bud (Sachs and Hassidim, 1996; Cline, 1997; Novoplansky, 2003). Our results suggest that even though damage-induced branching, presumably through release of apical inhibition, water shortage did constrain branching. The latter might be due to competition for limited resources between axillary buds in damaged plants.

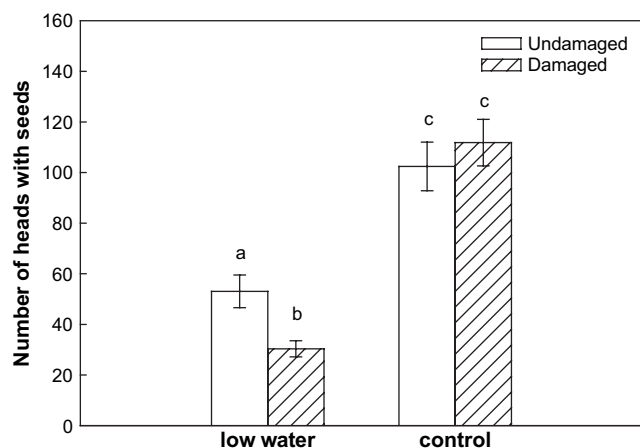


Fig. 3 – Number of heads showing seeds in undamaged and damaged plants of *Madia sativa* under two levels of water availability. Bars represent ± 1 standard error. In each figure, different letters above bars are significantly different (a posteriori LSD test, $P < 0.05$).

Damage induced an increase in photosynthetic rate, i.e., compensatory photosynthesis, only under regular watering. Together with enhanced branching, increased photosynthesis following damage is the most cited mechanism of tolerance (McNaughton, 1979; Strauss and Agrawal, 1999; Tiffin, 2000). This response mitigates the negative effect of damage on fitness mainly through the enhancement of plant growth (Arntz et al., 1998, 2000). Compensatory photosynthesis could be due to increased assimilate demand by previously existing or new sinks such as new branches and floral meristems (Hartt et al., 1964; Daley and McNeil, 1987; Trumble et al., 1993). Under low water supply *M. sativa* did not increase photosynthesis after damage. Previous work has shown that water stress can constrain compensatory photosynthesis, mostly through stomatal closure effects on carbon assimilation (Hsiao, 1973; Cox and McEvoy, 1983; McGraw et al., 1990). Thus, leaves conserve water and control whole-plant water potentials by varying stomatal conductance, but in this process CO_2 uptake is also affected (Ehleringer and Monson, 1993).

Damaged plants were able to compensate shoot biomass within both watering treatments. Compensatory shoot growth may involve different pathways depending on water availability. Under sufficient water supply, shoot biomass compensation could be due to enhanced photosynthesis and branching. These responses, however, were limited under water stress as discussed above. Therefore, the maintenance of aboveground biomass in damaged plants under drought was probably the result of reallocation of resources from belowground organs, as it is suggested from the observed reduction in root:shoot ratio in damaged plants of *M. sativa* under water shortage. Plants under drought stress typically increase relative allocation to roots in order to maximize water uptake (Hsiao, 1973). Consequently, it has been shown that low water availability can affect compensatory shoot growth by opposing the mobilization of stored carbon from roots following damage (Hsiao, 1973; Danckwerts and Gordon, 1987; Morvan-Bertrand et al., 1999; Lawson et al., 2000).

In summary, water availability constrained tolerance of apical damage and differentially affected the putative compensatory mechanisms in *M. sativa*. It is suggested that plant responses to drought could explain variation in compensatory responses to herbivory. Further work should assess the genetic variation of the compensatory responses for which expression was limited by water shortage and thus presumably explain the constrained tolerance of apical damage in *M. sativa* under drought conditions. This would provide evidence of their evolutionary potential and of the possible selective role of herbivores in plant physiology and morphology under environments differing in resource availability.

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