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## Original article

# Induction of glandular and non-glandular trichomes by damage in leaves of *Madia sativa* under contrasting water regimes

Wilfredo L. Gonzáles<sup>a,c,\*</sup>, María A. Negritto<sup>a</sup>, Lorena H. Suárez<sup>b</sup>, Ernesto Gianoli<sup>a</sup>

<sup>a</sup>Departamento de Botánica, Universidad de Concepción, Casilla 160-C, Concepción, Chile

<sup>b</sup>Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

<sup>c</sup>Departamento de Ciencias Biológicas y Fisiológicas, Facultad de Ciencias y Filosofía, Universidad Peruana Cayetano Heredia, Av. Honorio Delgado 430, Urb. Ingeniería, Lima 31, Perú

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## ABSTRACT

Plant traits may play multiple functional roles simultaneously. Leaf trichomes have been related to resistance against herbivores as well as to enhanced water economy in the plant. In a greenhouse study, we evaluated the interactive effect of damage (control vs. mechanical damage) and water availability (control vs. low watering) on the expression of glandular and non-glandular leaf trichomes in the annual Chilean tarweed *Madia sativa* (Asteraceae). We found that the overall trichome density increased both after damage and when plants were grown under water shortage. Interestingly, the type of trichome induced after damage varied with each water environment. While damage induced glandular trichomes only under control watering, non-glandular trichomes were induced by damage only under experimental drought. Results indicate that in *M. sativa* glandular trichomes are equally induced by drought or damage but there is no additive effect of these factors. In both cases glandular trichome density apparently reached a limit, which may be interpreted in terms of constraint or efficacy. On the other hand, the synergistic effect of damage and drought on non-glandular trichomes might suggest that, compared to glandular ones, these trichomes are less responsive to each stress factor separately. Thus, for plants to induce non-glandular trichomes they must be subjected to a degree of stress above a threshold that was not reached for each individual factor in our experimental setting. We did not detect a significant correlation between trichome types. Thus, the contrasting patterns observed likely reflect independent responses of trichomes to the evaluated factors.

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\* Corresponding author. Departamento de Ciencias Biológicas y Fisiológicas, Facultad de Ciencias y Filosofía, Universidad Peruana Cayetano Heredia, Av. Honorio Delgado 430, Urb. Ingeniería, Lima 31, Perú. Tel.: +56 41 203 420; fax: +56 41 246 005.

E-mail addresses: [wgonzales@udec.cl](mailto:wgonzales@udec.cl), [wgonzales@gmail.com](mailto:wgonzales@gmail.com) (W.L. Gonzáles).

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## 1. Introduction

Plants possess chemical and mechanical traits that play a constitutive or induced defensive role against herbivory (Karban and Baldwin, 1997; Wilkens et al., 1996; Gianoli and Niemeyer, 1996; Cipollini and Bergelson, 2002). These defensive traits could be simultaneously involved in other functional roles in the plant. For instance, glucosinolates and their breakdown products can function in herbivore defense and in allelopathy (Siemens et al., 2002), and non-protein aminoacids deter insect herbivores and are involved in plant responses to physical stress (Romeo, 1998). An experimental approach subjecting plants to different environmental stresses simultaneously may allow a better understanding of the functional roles of those plant traits involved in the response to environmental challenges.

Leaf trichomes are described as traits related to both water control and resistance against herbivory in several plant species (Levin, 1973; Ehleringer et al., 1976; Woodman and Fernandes, 1991; Sandquist and Ehleringer, 1997; Körner, 1999; Press, 1999; Molina-Montenegro et al., 2006). Trichomes constitute a mechanical barrier that hinders insect movement and/or feeding (Baur et al., 1991), and chemical compounds in glandular trichomes can be deterrent or toxic to several herbivores (Levin, 1973; Buta et al., 1993). Trichomes also decrease radiation absorbance and hence heat load over leaf surface (Ehleringer et al., 1976; Vogelmann, 1993). This leads to a reduced water loss by transpiration because the relative humidity near the leaf surface is increased and hence the difference in water potential between leaf tissue and the surrounding air layer is reduced (Ehleringer, 1984). Here, we report the interactive effect of damage and water availability on the expression of glandular and non-glandular trichomes in the Chilean tarweed *Madia sativa* (Asteraceae).

*M. sativa* has both uniseriate non-glandular and biseriate glandular trichomes on stems, leaves and involucre bracts (Matthei, 1995; Hoffman, 1998; Carlquist, 2003). In central Chile, *M. sativa* is attacked by sucking and chewing insects (Artigas, 1994; Delfino and Gonzáles, 2005), lepidopterous larvae (Noctuidae) commonly producing apical damage (W.L. Gonzáles, personal observations). *M. sativa* grows in open areas during the rather dry spring-summer (Matthei, 1995; Hoffman, 1998), when water availability could be a limiting factor for plant populations in such a Mediterranean-type climate. The present greenhouse study evaluated the effect of apical damage and water availability on the density of both glandular and non-glandular leaf trichomes in *M. sativa*. We specifically addressed the following questions: 1) Does apical damage trigger induction of trichome density?, 2) Does water availability affect the density of both types of trichomes?; and 3) Does each trichome type respond similarly to damage under different water availability regimes?

## 2. Materials and methods

### 2.1. Study system

*Madia sativa* is a highly selfing annual plant (Arroyo and Uslar, 1993). The basal leaves form a rosette and upper leaves are

opposite along the branches. Leaves and stems are covered by biseriolate glandular and uniseriate non-glandular trichomes (see pictures on pages 106 and 109 in Carlquist, 2003). This plant has yellow rayed capitula with hermaphroditic disk florets and fertile female ray florets (Hoffman, 1998). *M. sativa* grows in open habitats, disturbed fields and sunny slopes along Chile (Matthei, 1995; Hoffman, 1998). Central Chile has a Mediterranean-type climate and *M. sativa* grows during the dry season (spring–summer), when drought may be a limiting factor for this and other plant species (Mooney and Dunn, 1970; Di Castri and Hajek, 1976; W.L. Gonzáles, unpublished data). In the study area (Farellones, central Chile; 33°21'S, 70°17'W; at 1970 m altitude) we observed plants frequently attacked by specialist native aphids (*Uroleucon eumadiae*, Delfino and Gonzáles, 2005) and larvae of Lepidoptera (Artigas, 1994; W.L. Gonzáles, personal observations). These caterpillars feed on reproductive buds and inflorescences, and damage commonly occurs on apical buds of the main stem.

### 2.2. Experimental

Seeds of *M. sativa* were collected from Farellones during late summer 2004 (February–March). Approximately 70 plants were harvested in a widely spaced area (range, 20–200 seeds per plant). In November 2004, seeds were pooled and scarified with concentrated sulfuric acid during 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 attained the 2-leaf stage (ca. 20 days), when they were transplanted into 3-l pots filled with potting soil and placed in a greenhouse at the campus of Universidad de Concepción, Concepción, Chile (PAR radiation at noon ca. 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; 24 °C and 12 °C mean maximum and minimum temperatures, respectively). All plants were watered every 4 d before treatments were applied. We evaluated the effect of apical damage and water availability on the density of both glandular and non-glandular trichomes in a factorial design (30–40 plants per treatment, total N = 145 plants). For this purpose we assigned two levels of watering (control and low) crossed with two levels of damage (undamaged and apical damage). The watering treatment started 70–72 d after plants were transferred to the greenhouse. Plants were watered either every 4 d or 8 d (control and low water treatments, respectively). We applied the damage treatment two weeks after the start of watering treatments. Damage was done with scissors on apical parts of the main stem (on the apical flower bud), mimicking damage by lepidopterous larvae. Damage was applied when all experimental plants had a reproductive bud on the main stem. The position of plants in the greenhouse bench was randomized every two weeks. Plants were harvested 160–165 d after transplanting.

Trichome density was measured 11 weeks after experimental damage. We measured the density of glandular and non-glandular trichomes on leaves adjacent to the apical capitula because this is the feeding site of natural insect herbivores (Delfino and Gonzáles, 2005, W.L. Gonzáles, personal observations). Before trichome density assessment, detached leaves were treated with concentrated sodium hypochlorite during 2 min to make leaf tissue diaphanous. Following

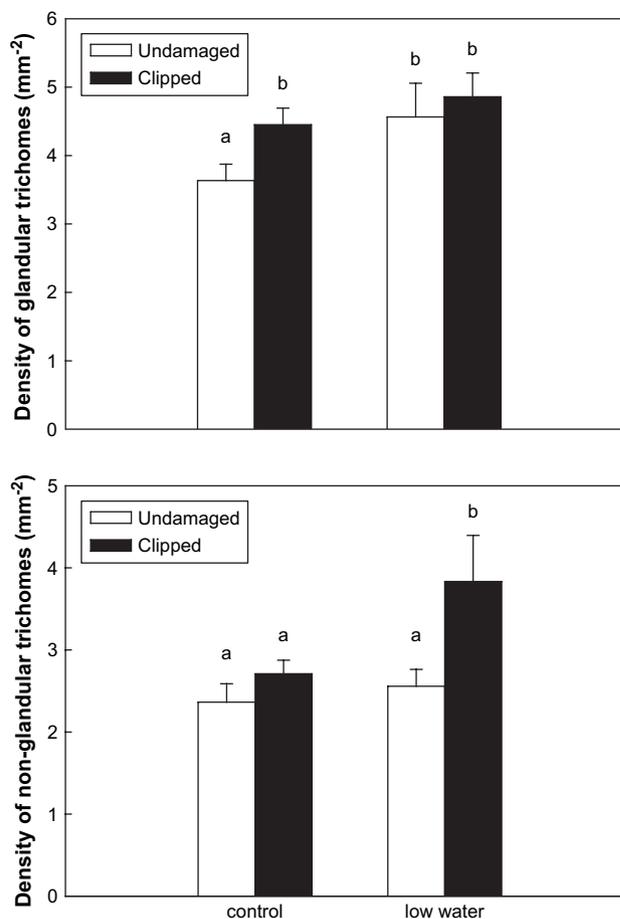
anatomical criteria particular to the subtribe Madiinae (Carlquist, 2003), biseriate and uniseriate trichomes correspond to glandular and non-glandular trichomes, respectively (Carlquist, 2003). We counted the total number of each type of trichome on the abaxial leaf surface using a compound microscope (100 $\times$ ; Nikon Eclipse E200). Leaf area was measured from digital images. All images were analyzed in UTHCSA ImageTool for Windows, version 2.0 (University of Texas Health Science Center, San Antonio, TX, USA). Density was calculated dividing the number of trichomes by the leaf area (trichomes mm<sup>-2</sup>).

### 2.3. Data analysis

Densities of glandular and non-glandular trichomes were analyzed using analysis of variance (ANOVA, Statistica 6.0, StatSoft Inc., Tulsa, OK, USA), where watering, damage and type of trichome were considered fixed factors. Least Significant Difference (LSD) tests were used to compare all treatments within each type of trichome. The correlation between both types of trichomes in each experimental treatment was also evaluated (Pearson product-moment correlation). This was done because leaf epidermal cells may differentiate into either glandular or non-glandular trichomes (Glover, 2000).

## 3. Results

The three-way ANOVA results showed that the factors damage, watering and type of trichome had significant effects on density of trichomes (Table 1), while the all two-way interactions (damage  $\times$  water, damage  $\times$  type of trichome, and water  $\times$  type of trichome) did not have any significant effect. The interaction water  $\times$  damage  $\times$  type of trichome was marginally not significant ( $P = 0.09$ , see Table 1). Drought and damage increased the overall trichome density. For the glandular trichomes, experimental damage triggered an increase of density under control watering ( $P = 0.028$ , LSD test), but not under low watering ( $P = 0.542$ , LSD test) (Fig. 1a). In contrast with the results of glandular trichomes, the density of non-glandular trichomes was induced by experimental damage under low watering ( $P = 0.009$ , LSD test), but not under



**Fig. 1 – Effect of water availability and mechanical damage on the density of glandular trichomes (a); and non-glandular trichomes (b) of *Madia sativa* leaves. Bars indicate Mean  $\pm$  1 S.E. Bars with different letters represent significant differences (Fisher LSD test a posteriori,  $P < 0.05$ ).**

control watering ( $P = 0.352$ , LSD test) (Fig. 1b). We did not detect a significant correlation between trichome types within any experimental treatment ( $r$ -coefficient range from  $-0.07$  to  $0.017$ , and  $P \geq 0.72$  for all correlations).

**Table 1 – Analysis of variance of the density of trichomes on the leaf surface of *Madia sativa* considering the effect of mechanical damage, water availability and type of trichome (glandular and non-glandular)**

	df	MS	F	P
Damage	1	31.22	10.08	0.001
Water	1	29.47	9.44	0.002
Type of trichome	1	152.56	48.90	0.0001
Damage $\times$ water	1	0.70	0.22	0.635
Damage $\times$ type of trichome	1	1.08	0.34	0.556
Water $\times$ type of trichome	1	0.002	0.001	0.981
Damage $\times$ water $\times$ type of trichome	1	8.78	2.87	0.094
Error	280	3.12		

## 4. Discussion

Overall, water shortage increased the density of trichomes in *M. sativa*. Several studies have shown that reduced water availability is associated with an increase in leaf pubescence (Ehleringer, 1982; Cano-Santana and Oyama, 1992; Sandquist and Ehleringer, 1997; Pérez-Estrada et al., 2000, but see Wilkens et al., 1996). In resource-limited environments, the selection of increased expression of resistance traits may be the result of both direct selection from herbivores and the benefits conferred by these resistance traits in other functional roles for the plant (Langenheim, 1994; Press, 1999; Close and McArthur, 2002).

First, traits minimizing herbivory in resource-limited environments are important because of the relative inability of plants in these environments to show compensatory growth

after herbivory (Maschinski and Whitham, 1989; Herms and Mattson, 1992). Field work with *Gentianella campestris* (Lennartsson et al., 1998) and *Ipomopsis arizonica* (Maschinski and Whitham, 1989) found that tolerance to herbivory in plant populations was positively associated with water availability (rainfall). Levine and Paige, 2004 showed experimentally that compensatory ability of *Ipomopsis aggregata* was drastically reduced by drought under field conditions. In our system, there is evidence that experimental drought reduces the tolerance capacity of *M. sativa* estimated as number of capitula with mature seeds after suffering herbivory (González, Suárez, Molina-Montenegro and Gianoli, unpublished data). Thus, if tolerance to herbivory is limited by drought in *M. sativa* then an increase in the expression of resistance traits in such environmental conditions should be advantageous. Second, leaf trichomes have multiple functions in the plant (Press, 1999). In addition to its defensive role against herbivores (Levin, 1973; Baur et al., 1991; Woodman and Fernandes, 1991), leaf pubescence protects plants in arid environments from excessive water loss by decreasing radiation absorbance and hence heat load over leaf surface (Ehleringer et al., 1976; Vogelmann, 1993; Körner, 1999). Few studies have simultaneously addressed more than one of the putative functional roles of leaf pubescence. Work on *Phyllyrea latifolia* suggests that glandular trichomes could be considered facultative "salt glands" and that they may be part of the mechanism of diffusion of excessive radiation (Tattini and Gucci, 1999; Tattini et al., 2000). Woodman and Fernandes (1991) showed that pubescence in *Verbascum thapsus* provides some protection against leaf chewing insects and helps in reducing transpiration water loss in young leaves.

Our results suggest the occurrence of differential induction of trichomes after damage depending on water availability and trichome type. Damage increased the density of glandular trichomes only under control watering, and the density of non-glandular trichomes was induced under water shortage only. The lack of correlation between trichome types in *M. sativa* suggests that the pattern observed reflects independent responses to the evaluated factors. We did not find previous studies reporting a similar pattern. Rautio et al. (2002) reported that defoliation caused a shift from glandular to non-glandular trichomes on leaves of *Betula pubescens*, but the study did not address the role of the environment.

A useful approach to interpret differential trichome induction is to consider costs and efficacy issues regarding each trichome type. On one hand, the relatively low cost of building the cellulose walls of non-glandular trichomes contrasts with the cost of building glandular trichomes, which is probably higher due to the secondary metabolites -such as flavonoids and terpenes-produced by excretory cells in glands (Bohm et al., 1992; Bohm and Yang, 2003). On the other hand, both trichome types may enhance water economy and interfere with insect movement and feeding, but glandular trichomes may confer additional resistance through their exudates, which may contain toxins, feeding deterrents, or sticky compounds (Thurston, 1970; Levin, 1973; Kennedy and Yamamoto, 1979; Buta et al., 1993). It has been suggested that water may be a limiting resource for plants that produce glandular trichomes because the production of exudates can divert a fraction of the water resources (Elle et al., 1999),

especially under drought conditions (Lauter and Munns, 1986). However, given that in *M. sativa* resource shortage (experimental drought) increased trichome density instead of limiting it, cost-related arguments seem to be not suitable in this case. Glandular trichomes are equally induced by drought or damage but there is no additive effect of these factors. It seems that in both cases glandular trichome density reached a limit, which can be interpreted in terms of constraint or efficacy (such density is enough to deter herbivores). These alternatives can be tested by including more levels of experimental drought and conducting bioassays with herbivores, respectively. Non-glandular trichomes were only induced by damage in the low water treatment. The same pattern has been found in other plant species (*Ipomoea purpurea*, E. Gianoli & C. Atala, unpublished data). The synergistic effect of damage and drought on non-glandular trichomes might suggest that, compared to glandular ones, these trichomes are less responsive to each stress factor separately. Thus, for plants to induce non-glandular trichomes they must be subjected to a degree of stress above a threshold that was not reached for each individual factor in our experimental setting. This idea may be tested by the inclusion of further levels of experimental drought and damage, both separately and simultaneously. Further research should also experimentally test the fitness cost of inducing each type of trichome in *M. sativa* under contrasting water environments, and the actual effect of these traits on the performance of its herbivores under field conditions.

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## REFERENCES

- Arroyo, M.T.K., Usler, P., 1993. Breeding systems in a temperate Mediterranean-type climate montane sclerophyllous forest in central Chile. *Bot. J. Linn. Soc.* 111, 83-102.
- Artigas, J.N., 1994. *Entomología económica*. Vol. I. Ediciones Universidad de Concepción. Concepción, Chile.
- Baur, R., Binder, S., Benz, G., 1991. Nonglandular leaf trichomes as short-term inducible defense of the gray alder, *Alnus Incana* (L), against the chrysomelid beetle, *Agelastica Alni* L. *Oecologia* 87, 219-226.
- Bohm, B.A., Yang, J.Y., 2003. Secondary metabolites of Madiinae, the tarweeds. In: Carlquist, S., Baldwin, B.G., Carr, G.D. (Eds.), *Tarweeds and Silverswords. Evolution of the Madiinae (Asteraceae)*. Missouri Botanical Garden Press, pp. 105-114.
- Bohm, B.A., Fong, C., Hiebert, M., et al., 1992. Nonpolar flavonoids of *Calycadenia*, *Lagophylla* and *Madia*. *phytochemistry* 3, 1261-1263.
- Buta, J.G., Lusby, W.R., Neal, J.W., et al., 1993. Sucrose esters from *Nicotianan gossei* active against the greenhouse whitefly *Trialeurodes vaporariorum*. *phytochemistry* 32, 859-864.
- Cano-Santana, Z., Oyama, K., 1992. Variation in leaf trichomes and nutrients of *Wigandia urens* (Hydrophyllaceae) and its implications for herbivory. *Oecologia* 92, 405-409.

- Carlquist, S., 2003. Diversity of trichomes and glandular structures of Madiinae. In: Carlquist, S., Baldwin, B.G., Carr, G.D. (Eds.), *Tarweeds and Silverswords. Evolution of the Madiinae (Asteraceae)*. Missouri Botanical Garden Press, pp. 105-114.
- Cipollini, D.F., Bergelson, J., 2002. Plant density and nutrient availability constrain constitutive and wound-induced expression of trypsin inhibitors in *Brassica napus*. *J. Chem. Ecol.* 27, 593-610.
- Close, D.C., McArthur, C., 2002. Rethinking the role of many plant phenolics – protection from photodamage not herbivores? *Oikos* 99, 166-172.
- Delfino, M.A., Gonzáles, W.L., 2005. A new species of *Uroleucon* (Hemiptera: Aphididae) on *Madia* (Asteraceae) in Chile. *Neotrop. Entomol.* 34, 221-225.
- Di Castri, F., Hajek, E.R., 1976. *Bioclimatología de Chile*. Editorial Universidad Católica de Chile. Chile, Santiago.
- Ehleringer, J.R., 1982. The influence of water stress and temperature on leaf pubescence development in *Encelia farinosa*. *Am. J. Bot.* 69, 670-675.
- Ehleringer, J.R., 1984. Ecology and ecophysiology of leaf pubescence in North American desert plants. In: Rodriguez, E., Healy, P.L., Mehta, I. (Eds.), *Biology and Chemistry of Plant Trichomes*. Plenum Press, New York, pp. 113-132.
- Ehleringer, J.R., Björkman, O., Mooney, H.A., 1976. Leaf pubescence: effects on absorbance and photosynthesis in a desert shrub. *Science* 192, 376-377.
- Elle, E., Van Dam, N.M., Hare, J.D., 1999. Cost of glandular trichomes, a “resistance” character in *Datura wrightii* regel (Solanaceae). *Evolution* 53, 22-35.
- Gianoli, E., Niemeyer, H.M., 1996. Environmental effects on the induction of wheat chemical defences by aphid infestation. *Oecologia* 107, 549-552.
- Glover, B.J., 2000. Differentiation in plant epidermal cells. *J. Exp. Bot.* 51, 497-505.
- Harms, D.A., Mattson, W.J., 1992. The dilemma of the plants: to grow or defend. *Quart. Rev. Biol.* 67, 283-335.
- Hoffman, A.J., 1998. *Flora silvestre de Chile*. Zona Central. Ediciones Fundación Claudio Gay, fourth ed. Chile, Santiago, 254 pp.
- Karban, R., Baldwin, I.T., 1997. *Induced Responses to Herbivory*. University of Chicago Press, Chicago, USA.
- Kennedy, G.G., Yamamoto, R.T., 1979. A toxic factor causing resistance in a wild tomato to the tobacco hornworm and some other insects. *Entomol. Exp. Appl.* 26, 121-126.
- Körner, C., 1999. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer.
- Langenheim, J.H., 1994. Higher plant terpenoids: a phytocentric overview of their ecological roles. *J. Chem. Ecol.* 20, 1223-1280.
- Lauter, D.J., Munns, D.N., 1986. Water loss via the glandular trichomes of chickpea (*Cicer arietinum* L.). *J. Exp. Bot.* 37, 640-649.
- Lennartsson, T., Nilsson, P., Tuomi, J., 1998. Induction of overcompensation in the field gentian, *Gentianella campestris*. *Ecology* 79, 1061-1072.
- Levin, D.A., 1973. The role of trichomes in plant defense. *Quart. Rev. Biol.* 48, 3-15.
- Levine, M.T., Paige, K.N., 2004. Direct and indirect effects of drought on compensation following herbivory in scarlet gilia. *Ecology* 85, 3185-3191.
- Maschinski, J., Whitham, T.G., 1989. The continuum of plant-responses to herbivory – the influence of plant-association, nutrient availability, and timing. *Am. Nat.* 134, 1-19.
- Matthei, O.J., 1995. *Manual de las malezas que crecen en Chile*. Alfabeta impresores, Santiago.
- Molina-Montenegro, M.A., Ávila, P., Hurtado, et al., 2006. Leaf trichome density may explain herbivory patterns of *Actinote* sp. (Lepidoptera: Acraeidae) on *Liabum mandonii* (Asteraceae) in a montane humid forest (Nor Yungas, Bolivia). *Act. Oecol.* 30, 147-150.
- Mooney, H.A., Dunn, E.L., 1970. Photosynthetic systems of mediterranean-climate shrubs and trees of California and Chile. *Am. Nat.* 104, 447-453.
- Pérez-Estrada, L.B., Cano-Santana, Z., Oyama, K., 2000. Variation in leaf trichomes of *Wigandia urens*: environmental factors and physiological consequences. *Tree Physiol.* 20, 629-632.
- Press, M.C., 1999. The functional significance of leaf structure: a search for generalizations. *New Phytol.* 143, 213-219.
- Rautio, P., Markkola, A., Martel, J., et al., 2002. Developmental plasticity in birch leaves: defoliation causes a shift from glandular to nonglandular trichomes. *Oikos* 98, 437-446.
- Romeo, J.T., 1998. Functional multiplicity among non protein amino acids in mimosoid legumes: a case against redundancy. *Ecoscience* 5, 287-294.
- Sandquist, D.R., Ehleringer, J.R., 1997. Intraspecific variation of leaf pubescence and drought response in *Encelia farinosa* associated with contrasting desert environments. *New Phytol.* 135, 635-644.
- Siemens, D.H., Garner, S.H., Mitchell-Olds, T., et al., 2002. Cost of defense in the context of plant competition: *Brassica rapa* may grow and defend. *Ecology* 83, 505-517.
- Tattini, M., Gucci, R., 1999. Ionic relations of *Phillyrea latifolia* L. plants during NaCl stress and relief from stress. *Can. J. Bot.* 77, 969-975.
- Tattini, M., Gravano, E., Pinelli, P., et al., 2000. Flavonoids accumulate in leaves and glandular trichomes of *Phillyrea latifolia* exposed to excess solar radiation. *New Phytol.* 148, 69-77.
- Thurston, R., 1970. Toxicity of trichomes exudates of *Nicotiana* and *Petunia* species to tobacco hornworm larvae. *J. Econ. Entomol.* 63, 272-274.
- Vogelmann, T.C., 1993. Plant-tissue optics. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 44, 231-251.
- Wilkens, R.T., Shea, G.O., Halbreich, S., et al., 1996. Resource availability and the trichome defenses of tomato plants. *Oecologia* 106, 181-191.
- Woodman, R.L., Fernandes, G.W., 1991. Differential mechanical defense: herbivory, evapotranspiration, and leaf hairs. *Oikos* 60, 11-19.