

# Boron deficiency effects on growth, photosynthesis and relative concentrations of phenolics of *Dittrichia viscosa* (Asteraceae)

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## Abstract

*Dittrichia viscosa* (Asteraceae) is an invading ruderal plant species of the Mediterranean region, bearing abundant glandular hairs on its aerial surfaces. The exudates of the glandular hairs show allelopathic and antimicrobial properties. We investigated the effects of boron deficiency on growth, photosynthesis, as well as on the relative concentration of phenolic compounds in exudates ('external' phenolics) and those of the leaf lamina or the root ('internal' phenolics). Boron deficiency caused a dramatic restriction of growth, but did not have any negative effect on parameters related to photosynthesis (such as stomatal density, chlorophyll concentration, photosynthetic capacity and intrinsic photochemical efficiency of PS II). In addition, boron deficiency significantly affected neither the density of glandular hairs on neither leaf surfaces, nor the quantitative or qualitative composition of the 'external' leaf phenolics (obtained by immersing leaves in chloroform). On the other hand, boron deficiency caused a notable increase in the relative concentration of 'internal' leaf and root phenolic compounds. The lack of effects of boron deficiency on certain traits of the glandular hairs suggest that metabolic compartmentation and autonomy of different structures must be taken into account in studies dealing with the effects of various stress factors on plant structure and function.

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**Keywords:** Boron deficiency; *Dittrichia viscosa*; Epicuticular materials; Glandular hairs; Phenolics; Photosynthesis

## 1. Introduction

Plants have the ability to synthesize a plethora of phenolic compounds that participate in significant ecophysiological phenomena, such as interactions between them and the biotic or abiotic environment (Harborne, 1988; Seigler, 1998). In many plants, a significant part of their phenolic pool is secreted on the leaf surface by specialized tissues (either secretory glands or glandular hairs). These secretion materials (exudates) usually take the form of a complex, resinous mixture of secondary metabolites, consisting mainly of terpenoids, flavonoid aglycones and simple phenolics, frequently embedded in a hydrophobic matrix (Wollenweber and Dietz, 1981; Wagner, 1991; Gibson, 1996; Fahn, 2000). The occurrence of phenolic compounds (and other secondary metabolites) in these mixtures has been related to their defen-

sive roles against biotic attacks. Secreted phenolics can protect leaf surfaces against phytopathogenic micro-organisms (Kelsey et al., 1984; Karamanoli, 2002) and have allelopathic properties by inhibiting or stimulating the growth of neighbouring plants if leached to the soil (Inderjit and Duke, 2003).

The leaves of *Dittrichia viscosa* (L.) W. Greuter (syn. *Inula viscosa* (L.) Aiton), an invading ruderal species of the Asteraceae family, bear sessile and stalked glandular hairs, which secrete a resinous mixture of secondary metabolites throughout the leaf life span (Werker and Fahn, 1981, see also Fig. 1). These exudates consist of several flavonoid aglycones (Wollenweber et al., 1991), as well as numerous terpenoids (Ceccherelli et al., 1985; Grande et al., 1992; Abu Zarga et al., 1998). They show strong allelopathic activity (Stephanou and Manetas, 1995, 1997; Stavrianiakou et al., 2001, 2004) as well as inhibitory effect against phytopathogenic micro-organisms (Stavrianiakou et al., 2001).

The phenolic content of plant tissues varies according to the environmental conditions and is also affected by the

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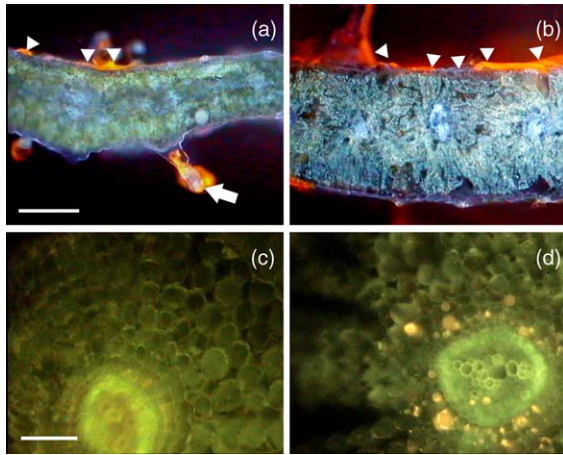


Fig. 1. (a and b) Hand-cut cross-sections of mature leaves of *D. viscosa* under B sufficient (a) or B deficient conditions (b), as they appeared under the epifluorescent microscope. Glandular secreting hairs are abundant on both surfaces of the lamina. Bright yellow–orange fluorescence is emitted by the trichome head (arrow), indicating the presence of flavonoids or related compounds. The exudates leak out from the head and form a continuous layer covering a significant part of the leaf surface (arrowheads). (c and d) Hand-cut cross-sections of roots of *D. viscosa* under B sufficient (c) or B deficient conditions (d), as they appeared under the epifluorescent microscope. Cortex parenchyma cells adjacent to endodermis of the B deficient roots emitted a bright yellow fluorescence, indicating the probable accumulation of flavonoids or related compounds within these cells. All samples were observed at plant harvest. Scale bar 100  $\mu\text{m}$ . For details on staining procedure and optical filters used, see in Section 2.

nutritional status of the plant (Gershenzon, 1984; Dixon and Paiva, 1995). In general, when growth is restricted due to resource limitation, more carbon can be diverted to defensive structures and to the production of carbon-based secondary metabolites such as phenolics (Herms and Mattson, 1992). Boron nutrition strongly affects phenylpropanoid metabolism (Brown et al., 2002). The accumulation of these compounds characterizes B deficient tissues, probably due to a combination of increased synthesis and restricted utilization of phenolics for cell wall construction (Marschner, 1995; Cakmak and Römheld, 1997). Since boron starvation does not directly affect photosynthetic production (Dell and Huang, 1997), the well-documented inhibitory effect of boron deficiency on growth rates (Blevins and Lukaszewski, 1998) would result in a build-up of surplus carbon skeletons. This could facilitate an enhanced accumulation of carbon-based secondary metabolites.

Despite the fact that the effects of boron deficiency on plant tissues are well documented, there is no evidence for an implication of B on the structure and function of glandular hairs, as well as on the secretion of secondary metabolites, such as phenolic compounds. Any information related to the possible effects of the plant nutritional status on the production of the effective substances is essential for the elaborate understanding of the defensive and allelopathic functions (Inderjit and Duke, 2003).

The aim of the present study was to investigate the effect of B deficiency on certain morphological, anatomical and physiological parameters of *D. viscosa* plants, including growth, photosynthesis and the production of exudate ('external') and laminar ('internal') phenolics. The choice of the particular plant concerning the study of phenolics was based on the following criteria: (a) the separation between the 'external' and 'internal' phenolics is easy and rapid, (b) 'external' phenolics are secreted by specialized tissues (glandular hairs) spatially separated from the rest of the leaf and (c) the exudates represent an effective chemical layer with ecophysiological significance.

## 2. Materials and methods

### 2.1. Plant material

Seeds of *D. viscosa* were collected from naturally grown individuals at the foot of mount Parnis, Greece (500 m above sea level). Seeds were stratificated at 4 °C for 1 week using moist filter paper and afterwards the seedlings were kept in a growth chamber to acclimate to the experimental conditions until the length of the epicotyls was ca. 2 cm.

### 2.2. Plant culture

Plants were grown semi-hydroponically in a growth chamber using 21 plastic containers, filled with quartz sand (7–15 mesh). Sand had been previously purified using tap water followed by a solution of 5% (w/v) HCl and 1% (w/v) oxalic acid (sand:solution, 1:1, v/v), and finally, leached with deionized water until the leachate reached a pH value of 5.0 or above. Plants were assigned in two treatments (B+ (control plants) and B– (deficient plants)) in an alternating plan (12 plants per treatment). Nutrient solution contained (in  $\mu\text{M}$ ):  $\text{KNO}_3$  3000;  $\text{Ca}(\text{NO}_3)_2$  2000;  $\text{MgSO}_4$  1000;  $\text{NH}_4\text{H}_2\text{PO}_4$  500;  $\text{FeNaEDTA}$  50;  $\text{H}_3\text{BO}_3$  23 (B+ plants only);  $\text{MnCl}_2$  4.60;  $\text{ZnSO}_4$  0.43;  $\text{CuSO}_4$  0.16;  $\text{Na}_2\text{MoO}_4$  0.06; pH adjusted to 6.5 using KOH. Each plant received 12 irrigations  $\text{day}^{-1}$  (67 ml/irrigation). The leaching solution was discarded. The plants were grown under controlled environmental conditions with a photoperiod of 15/9 h (day/night), air temperature 24/19 °C, air relative humidity 70–80%, photon flux density 450–550  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (PAR) at plant height, provided by sodium vapour lamps (VIALOX NAV-T 400 4Y; OSRAM, GmbH, Munich, Germany). PAR intensity was measured using a portable photometer (LI-188B; Li-COR, Lincoln, NE, USA).

### 2.3. Samplings and measurements

Experimental period lasted 30 days during which B– plants were continuously subjected to boron starvation. Growth and photosynthesis-related parameters were mea-

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