

Running title: Response of geranium to regulated deficit irrigation

Regulated deficit irrigation in different phenological stages of potted geranium plants: Water consumption, water relations and ornamental quality

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Abstract

The irrigation water requirements and sensitivity to water deficits of ornamental plants is of great interest to horticultural producers for plan irrigation strategies. The effect of different deficit irrigation strategies on physiological and morphological parameters in geranium plants was studied in different growth phases to evaluate how such strategies can be safely used and to ascertain whether the flowering phase is sensitive to deficit irrigation. *Pelargonium × hortorum* L.H. Bailey plants, grown in a controlled growth chamber, were subjected to four irrigation treatments: control (100% water field capacity throughout the experiment), sustainable deficit irrigation (75% water field capacity throughout the experiment), and two regulated deficit irrigation treatments that included water stress during the vegetative growth phase or during the flowering development phase. Although the total amount of irrigation water was similar in the three deficit irrigation treatments (around 80% of the control value), the lowest values for both height and flowering were found when deficit irrigation was applied during flowering. This indicates that plant quality does not only depend on the amount of water applied but also on the time when the reduction is applied, and that flowering is the most sensitive phase to water stress. Evapotranspiration was related to the formation of inflorescences and to increased plant height. When the irrigation strategy was changed, plants increased or decreased their water consumption and stomatal conductance to adjust to the new conditions by regulating stomatal opening, although, in general, the values of both parameters remained below those observed in the control plants.

Key words: Evapotranspiration; Gas exchange; Hydraulic conductivity; Osmotic adjustment; Water potential; Water stress

Abbreviations: C, control; C*, chroma; DI, deficit irrigation; EC, electrical conductivity; ET, evapotranspiration; g_s , stomatal conductance; h° , hue angle; L*, lightness; P, significance; PAR, photosynthetic active radiation; PRD, partial root drying; P_n , net photosynthesis; RDI, regulated deficit irrigation; RH, relative humidity; SDI, sustainable deficit irrigation; VPD, vapour pressure deficit; WFC, water at field capacity; Ψ_l , leaf water potential; Ψ_t , leaf turgor potential; Ψ_{100s} , leaf osmotic potential at full turgor.

1. Introduction

1 Regulated deficit irrigation (RDI) is an irrigation tool based on our physical knowledge of plant
2 responses to water stress (Chaves et al. 2007). In RDI, water input is withheld or reduced for specific
3 periods during the crop cycle, sufficiently to reduce vegetative growth but not so much as to reduce the
4 economic value of the crop (Dry et al. 2001; Cameron et al. 2006). The main principle behind RDI is that
5 plant sensitivity to water stress is not constant during the growth season, and that intermittent water stress
6 in specific periods may be beneficial in terms of water saving and improving water use efficiency (Girona
7 et al. 2005; Intrigliolo and Castel 2005; Goldhamer et al. 2006).

8 In the last two decades, interest in irrigation techniques based on RDI procedures has been centred on
9 fruit and nut crops, where it has been applied successfully (Goldhamer and Beede 2004; Ruiz-Sánchez et
10 al. 2000). However, its application to ornamental crops has so far received relatively limited attention
11 (Cameron et al. 2006; Álvarez et al. 2009). Cameron et al. (1999; 2006) demonstrated the feasibility of
12 applying RDI to container-grown ornamental plants and reported that RDI has the potential to improve
13 commercial crop quality in ornamental species by reducing excessive growth and promoting a more
14 compact habit. However, according to Silber et al. (2007), RDI reduces the decorative value of
15 leucadendron, although the response depends on the growth phase when deficit irrigation is applied
16 (stress timing) and the duration of the same during each growth phase. However, periods of water stress
17 during vegetative phases increase flowering intensity in carnation plants (Álvarez et al. 2009).

18 In this sense, differences in sensitivity to deficit irrigation (DI) between different species and cultivars
19 (Savé et al. 2000; Clary et al. 2004; Zollinger et al. 2006) and even between growth stages have been
20 observed in many plants (Sionit et al. 1987; Mingeau et al. 2001). Numerous works in ornamental plants,
21 Hansen and Petersen (2004), Henson et al. (2006), Katsoulas et al. (2006), Chyliński et al. (2007), Silber
22 et al. (2007), De Lucia (2009), Álvarez et al. (2009), Sánchez-Blanco et al. (2009), Bolla et al. (2010),
23 Andersson (2011) and Bernal et al. (2011), have demonstrated that the extent of growth and flowering
24 inhibition increases as the severity of DI increases. It has been suggested that the appropriate scheduling
25 of DI with regard to the stage of development may also determine different growth responses. Therefore,
26 the importance of factors, such as the degree of water stress imposed and the timing and duration of
27 reduced irrigation, have been discussed (Hassanein and Dorion 2006). All these factors are usually related
28 to physiological parameters such as stomatal conductance, photosynthesis, leaf temperature or plant
29 weight, which are indicative of the stress applied (Sharp et al. 2009). Nevertheless, the relationships
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1 between them depend on the growth conditions. Hence, many studies using plants grown in pots revealed
2 that changes in stomatal conductance are the main cause of decreased photosynthesis, while in field
3 conditions using longer-term drying cycles, perturbations in metabolism appeared to be one of major
4 factors for the reduction of photosynthesis (Liang et al. 1997).
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7 Geranium is one of the most widely grown ornamental plants in the world, frequently in potted plant
8 form. *Pelargonium hortorum* has remained very popular with consumers for many years, mainly because
9 of its flowers and drought tolerance (Lang and Trellinger 2001). Its principal characteristic as a potted
10 plant is the presence of a large number of red and scented flowers surrounded by thick green foliage. The
11 leaves are “zoned” with a dark scalloped band halfway down the leaf blade and parallel to the leaf
12 margin, which adds to the plants ornamental value. However, the response of geranium to deficit
13 irrigation has been relatively little studied. In a previous works on *P. hortorum* (Hassanein and Dorion
14 2006; Chyliński et al. 2007), deficit irrigation was applied throughout the whole experiment, although it is
15 plausible to consider that geranium sensitivity to water stress may be related to individual growth phases.
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18 The physiological and morphological response of potted geranium plants to different irrigation levels
19 and during drought recovery was studied by Sánchez-Blanco et al. (2009). The information provided was
20 important for elaborating deficit irrigation strategies that allow irrigation amounts to be changed in
21 accordance with the requirements of successive phenological phases. But it is also necessary to optimize
22 the duration and the timing of water reductions in each species in order to avoid any negative effects on
23 ornamental quality.
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26 The aims of this research were to study the effects of different deficit irrigation strategies, such as
27 sustainable deficit irrigation applied throughout the growth season, and RDI applied in different growth
28 phases (during the flowering phase or outside the flowering phase) on physiological and morphological
29 parameters, to determine the extent to which these strategies can modify water consumption, water
30 relations, growth and quality in potted geranium plants and whether the flowering phase was sensitive to
31 deficit irrigation.
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38 **2. Materials and Methods**

39 *2.1. Plant material and experimental conditions*

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1 Single rooted cuttings (4-5 cm tall and with 6-7 leaves) of *Pelargonium × hortorum* L.H. Bailey
2 (zonal geranium) were transplanted into 14 x 12 cm pots (1.2 L) filled with a mixture of sphagnum peat,
3 perlite and coconut fibre (6:3:1) and amended with osmocote plus (2 g L⁻¹ substrate) (14:13:13 N, P, K +
4 microelements).
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7 The experiment was conducted in a controlled growth chamber, where the environmental conditions
8 were selected to simulate natural conditions, bearing in mind the conditions necessary for flowering
9 (Armitage et al. 1981; Blanchard and Runkle 2011). The temperature in the canopy was 24 °C during the
10 light phase and 18 °C during darkness. Relative humidity (RH) ranged between 65 and 80%. A mean
11 photosynthetic active radiation (PAR) of 250 μmol m⁻² s⁻¹ at canopy height was supplied during the light
12 phase (08:00-00:00 h). Although the radiation levels in the growth chamber were lower than those
13 applicable in the field, it was assumed that the specific PAR levels used were of secondary importance
14 compared with the contrast in irrigation treatments. All of the plants were watered daily to container
15 capacity prior to starting the treatments, which lasted five weeks.
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28 2.2. Treatments

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30 To determine the maximum water holding capacity of the substrate, all the pots were uniformly mixed
31 and packed to a bulk density of 0.165 g cm⁻³. The substrate surfaces were covered with aluminium foil to
32 prevent water evaporation and the lower parts were submerged, to half the pot's height, in a water bath
33 and then were left to equilibrate overnight. The next day, the pots were removed and left to drain freely
34 until drainage became negligible. The fresh weight was then recorded and calculated for each individual
35 pot and considered as the weight at field capacity (WFC). At the end of the experiment, the substrate was
36 dried in an oven at 105 °C until constant weight in order to obtain the dry weight and calculate the
37 volumetric water content. Later, the difference between the fresh weight and oven-dry weight was
38 measured and the volumetric water content was calculated (61%), which was considered as the substrate's
39 field capacity.
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51 Plants were submitted to four irrigation treatments: container capacity (control) and three deficit
52 irrigation (DI) treatments. Summarised data of the different treatments are presented in Table 1. All plants
53 were irrigated daily and the electrical conductivity of the water applied was 0.8 dS m⁻¹.
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57 Four treatments were considered: control (C), irrigated at 100% WFC throughout the experiment;
58 sustainable deficit irrigation (SDI), irrigated at 75% WFC throughout the experiment; regulated deficit
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1 irrigation I (RDI I), irrigated at 75% throughout the experiment, except during the flowering phase when
2 plants were irrigated at 100%; and regulated deficit irrigation II (RDI II), irrigated at 100% throughout the
3 experiment, except during the flowering phase when plants were irrigated at 75%.
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5 The experimental period lasted 24 weeks. During this period, each individual plant was weighed daily
6 and the volume of irrigation water required to refill the pot to its pre-determined level of WFC (100 or
7 75%) was calculated and added to each plant.
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9 Irrigation was controlled by the decrease in weight of the pot and without compensation for any increase
10 in plant growth, which was disregarded since it was negligible compared with WFC (15-30 g versus 800
11 g). The plants in the experiment were considered to be in the flowering phase when more than 80% of the
12 plants of the control treatment had buds.
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22 *2.3. Growth and plant water measurements*

23 At the end of the experimental period, the substrate was gently washed from the roots of five plants
24 per treatment and the plants were divided into shoots (i.e., leaves and stems) and roots. Leaf number and
25 leaf area (cm²) were determined in the same plants by measuring all mature and recently expanded leaves.
26 Leaf number was directly counted and leaf area was determined using a leaf area meter (AM 200; ADC
27 BioScientific Ltd., Herts, England). Plants were oven-dried at 80 °C immediately after the leaf area
28 measurements until they reached a constant weight to measure the respective dry weights.
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36 Also, the root to shoot ratio was determined in these plants and calculated by dividing root dry weight
37 by the sum of leaf and stem dry weight. Throughout the experiment, plant height, plant width and the
38 number of leaves lost were measured in 24 plants per treatment every week. Plant height was taken as the
39 vertical distance from substrate to the highest inflorescence, plant width was the horizontal distance
40 between the two most distant leaves and the number of leaves lost was calculated by the accumulated sum
41 of fallen or completely dry leaves in each plant.
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48 The number of inflorescences per plant was recorded weekly in 24 plants per treatment and included
49 any buds developed to the point of showing flower colour, and the percentage of plant flowering (with
50 one or more floral buds) was determined in order to schedule the irrigation. The cumulative number of
51 inflorescences was equal to the sum of the total inflorescences in each plant until that moment. Leaf and
52 flower colour was measured with a Minolta CR-10 colorimeter, which provided the colour coordinates
53 lightness (L*), chroma (C*) and hue angle (h°) (McGuire 1992), using three leaves and three flowers for
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1 each plant and five plants per treatment. Leaf colour was measured in the external (darker) and internal
2 zones (lighter).

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4 Evapotranspiration (ET) was measured gravimetrically throughout the experimental period in 24
5 plants per treatment, using the difference in weights (weight after irrigation and weight before irrigating
6 again), using a balance (Analytical Sartorius, Model 5201; capacity 5.2 kg and accuracy of 0.01 g).
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8 Seasonal changes in leaf water potential (Ψ_l), leaf turgor potential (Ψ_t), leaf osmotic potential at full
9 turgor (Ψ_{100s}), stomatal conductance (g_s) and net photosynthesis (P_n) were determined in five plants per
10 treatment during the central hours of illumination. Leaf water potential was estimated according to
11 Scholander et al. (1965), using a pressure chamber (Model 3000; Soil Moisture Equipment Co., Santa
12 Barbara, CA, USA) in which leaves were placed in the chamber within 20 s of collection and pressurised
13 at a rate of 0.02 MPa s⁻¹ (Turner 1988). Leaves from the Ψ_l measurements were frozen in liquid nitrogen
14 (-196 °C) and stored at -30 °C. After thawing, the osmotic potential was measured in the extracted sap
15 using a WESCOR 5520 vapour pressure osmometer (Wescor Inc., Logan, UT, USA), according to Gucci
16 et al. (1991). Leaf turgor potential was estimated as the difference between leaf water potential (Ψ_l) and
17 leaf osmotic potential. Leaf osmotic potential at full turgor (Ψ_{100s}) was estimated as indicated above for
18 leaf osmotic potential, using excised leaves with their petioles placed in distilled water overnight to reach
19 full saturation. Leaf stomatal conductance (g_s) and net photosynthetic rate (P_n) were determined in
20 attached leaves using a gas exchange system (LI-6400; LI-COR Inc., Lincoln, NE, USA). P_n/g_s ratio was
21 used as an estimation of the intrinsic water use efficiency.
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41 *2.4 Statistical analyses of data*

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43 In the experiment 24 plants were randomly attributed to each treatment. The data were analysed by
44 one-way ANOVA using Statgraphics Plus for Windows 5.1 software. Ratio data were subjected to an
45 arcsine square-root transformation before statistical analysis to ensure homogeneity of variance.
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47 Treatment means were separated with Duncan's Multiple Range Test ($P \leq 0.05$).
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52 **3. Results**

53 *3.1. Plant growth and ornamental parameters*

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1 Water deficit had a significant effect on biomass accumulation (Table 2). Aerial dry weight, the
2 number of leaves and total leaf area decreased with deficit irrigation, regardless of the time when the
3 reduction was applied. However, root dry weight was not modified and the root/shoot ratio increased in
4 the plants grown under deficit irrigation conditions.
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7 Water deficit was seen to significantly alter plant height and width, although the changes differed
8 depending on the time when deficit irrigation was applied (Fig. 1). No pronounced differences in plant
9 height were observed during the experiment between control and RDI I treatment (when deficit irrigation
10 was applied outside the flowering phase) (Fig. 1a). The smallest values of plant height were found in the
11 RDI II treatment (when deficit irrigation was applied during flowering), which shows that this phase is
12 the most sensitive to water stress. Plant height was inhibited a few weeks after application of the deficit
13 irrigation onwards in SDI and, especially, in RDI II (Fig. 1a). The behaviour of plant width was similar to
14 that of plant height, although the differences between treatments were less marked (Fig. 1b). Control
15 plants lost the highest number of leaves per plant during most of the experiment, although the same plants
16 also had the highest number of green leaves (Fig. 1c). Weeks 4-5, 14-15 and, especially, 18-20, when the
17 highest leaf loss was observed, coincided with maximum flowering and the highest number of open
18 inflorescences per plant. Deficit irrigation affected the flowering of geranium plants, with a significant
19 decrease in RDI II compared with the control (Fig. 2). Flowering, as assessed by the evolution of the
20 number of inflorescences, was also affected by the timing of stress (Fig. 2a). During the first flowering
21 phase (weeks 1.5-5.8), plants of the RDI II treatment produced fewer inflorescences than the controls,
22 while there were no significant differences between C, SDI and RDI I, although flowering in the last two
23 treatments lasted less time than in the controls (Fig. 2a). In the second flowering phase (11.8-15.4), plants
24 of the RDI II treatment continued to show a lower flowering intensity and the plants of the SDI and RDI I
25 treatments flowered earlier than the controls. The lowest accumulated number of inflorescences per plant
26 was seen in the plants of RDI II treatment, while in SDI and RDI I no significant differences with respect
27 to the control were observed (Fig. 2b).
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31 In general, no great differences in the leaf and flower colour parameters were observed in the deficit
32 irrigation treatments compared with the control (Online Resource 1). The leaf external zone remained
33 darker (lower L* value) and less vivid green (lower C*) compared with leaf internal zone throughout the
34 experimental period (Online Resource 1a, 1b). The hue angle values recorded in both zones confirmed the
35 green colour of the foliage and suggested the absence of chlorosis and necrosis (Online Resource 1c).
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Plants maintained their differences in h^o values between leaves and flowers during the experimental period. Deficit irrigation did not affect the colour contrast between green leaves and red flowers.

3.2 Water consumption

The average amount of water added to each pot during the whole experimental period was 7.89 L for the control and 6.26, 6.25 and 6.32 L for SDI, RDI I and RDI II plants, respectively (Fig. 3a). The total irrigation amount was similar in the three deficit irrigation treatments, approximately 80% of the amount of water supplied in the control treatment. However, the timing of deficit irrigation varied and depended on the phase of the plants.

The daily evapotranspiration is shown in several figures (Fig. 3b; all treatments), (Fig. 3c; C and SDI), (Fig. 3d; C, SDI and RDI I), (Fig. 3e; C, SDI and RDI II). Water consumption varied during the experiment (Fig. 3b). During the four weeks following the beginning of the treatments, the daily ET in all treatments reached its maximum value, even though environmental conditions (temperature, RH, light and VPD) were constant throughout the experiment. Evapotranspiration was higher in control plants than in plants of the SDI treatment (Fig. 3c). However, these differences were not constant during the whole experiment. At the beginning of the experiment, differences between treatments were greater and during some specific periods (weeks 7-8 and from week 15 onwards) the consumption of SDI plants was similar to that of control plants, despite the lower levels of water in the substrate.

In the RDI treatments, when the irrigation pattern was changed, the plants increased or decreased their water consumption (ET) and adjusted to the new conditions, but with some particular characteristics (Fig. 3d and 3e). When plants were exposed to deficit irrigation after normal irrigation conditions (striped area), humidity readjustment took several days, although plants of both RDI treatments restricted their ET the day after the change in irrigation and their ET matched that of plants that had been exposed to deficit irrigation since the beginning of the experiment. During this phase, the ET of RDI plants (I and II) was equal to, and even though lower than the ET of SDI plants. This was particularly marked after the first change of irrigation. Once well watered conditions were restored (shaded area), the humidity in the substrate immediately recovered. In contrast, ET values in the RDI plants increased more slowly and were still significantly lower than in control plants.

3.3. Water relations

1 Leaf water potential values were always higher in the control than in the SDI treatment (Fig. 4a),
2 while the Ψ_1 values changed in the RDI treatments according to the irrigation applied in each phase. Leaf
3 turgor potential (Ψ_t) was similar to Ψ_1 and decreased slightly when plants received less water (Fig. 4c).
4 However, no differences in Ψ_{100s} between treatments during the experimental period were observed (Fig.
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10 The values of the stomatal conductance and photosynthesis net rate during the period can be seen in
11 fig. 5. In general, g_s values were higher in control plants and lower in plants submitted to deficit irrigation
12 (Fig. 5a). In the plants of both RDI treatments, when the change in irrigation involved a reduction in the
13 amount of water, g_s decreased as a result of stomatal opening regulation. When irrigation was increased,
14 g_s increased, although the plants did not reach the values of the control plants. Such reductions with
15 respect to the control plants were also observed in the photosynthesis levels, although the differences
16 were less pronounced (Fig. 5b). In general, the plants of SDI and RDI I treatments showed higher P_n/g_s
17 ratios (intrinsic water use efficiency) than control plants throughout the experimental period (Fig. 5c).
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28 **4. Discussion**

29 Plant growth is usually decreased when soil water availability is limited. In our experiment, deficit
30 irrigation, regardless of the time of application, decreased aerial dry weight, the number of leaves per
31 plant and total leaf area, which may be an adaptive role, restricting the evaporative surface area (Sharp
32 1996). In contrast, the root/shoot ratio increased as a result of DI treatments largely because the
33 reductions in shoot growth were not matched by an equivalent loss of root development (Sánchez-Blanco
34 et al. 2004). This response could speed up the establishment of ornamental plants in gardening or
35 landscaping projects (Franco et al. 2006; 2011). The same responses were found by Jaleel et al. (2008) in
36 *C. roseus*, by Henson et al. (2006) and by Hassanenin and Dorion (2006) in *P. hortorum*, by Andersson
37 (2001) in *P. zonale*, by Álvarez et al. (2011) in *C. citrinus* and by Andersson (2011) in *I. walleriana* and
38 *Petunia x hybrid*. The reduction in growth was not accompanied by colour modifications or a greater loss
39 of leaves. The last parameter was not related with deficit irrigation, since the leaf loss was greatest during
40 the last weeks in all treatments, even in the controls which had received enough irrigation water to
41 prevent wilting, and was probably due to the increased number of inflorescences in conjunction with
42 other factors such as ontogeny (Brawner 2003). According to Hassanein and Dorion (2006), leaf area is
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1 affected by deficit irrigation levels of -40 kPa before than wilting and leaf loss, which only begin to be
2 affected when water stress is severe (Bargali and Tewari 2004).

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4 The colorimetric values measured suggest that deficit irrigation levels had little effect on leaf and
5 flower colour, and so did not reduce the quality of geranium as an ornamental plant. In a previous study
6 Sánchez-Blanco et al. (2009) suggested that geranium plants can cope with water shortages without losing
7 their ornamental value.
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11 In geranium, as other ornamental plants, there is a tendency for the first shoots to grow so long that
12 the flowers extend a long way from the foliage, which lowers the commercial value of plants. In general,
13 deficit irrigation decreases plant height more than width, representing a greater reducing effect on vertical
14 than on horizontal growth, so flowers are closer to the foliage. Aesthetically and commercially, an
15 increase in foliage size in relation to plant height gives the plant a compactness and architectural
16 equilibrium that are much appreciated by customers. Also, this is one the positive aspects of deficit
17 irrigation, since height reduction makes plant management and later transplantation easier (Lang and
18 Trellinger 2001; Van Iersel and Nemali 2004).
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27 The application of water deficit saves water and reduces excessive growth in ornamental plants
28 (Álvarez et al. 2009). However, plants subjected to water deficit may reduce flowering intensity, bring
29 forward, or delay flowering and shorten the same (Cuevas et al. 2009; Bernal et al. 2011; Álvarez et al.
30 2012). However, in our experiment, plant quality or flowering did not only depend on the amount of
31 applied water, but also on the time when the reduction was applied. Similar responses have been cited by
32 Sharp et al. (2009) in *Rhododendron*, when responses depended on the phases during which the deficit
33 irrigation was applied.
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42 The floriculture market appreciates plants with leaves and flowers with intense colour, a high root to
43 shoot ratio and a certain relationship between plant height and width. However, the attractiveness and
44 commercial value of *P. hortorum* is primarily associated with flowering, so that the fewer flowers per
45 plant and the shorter flowering of the RDC II plants must be considered to be negative aspects.
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50 Plants are able to adapt to a reduced moisture level within the growing medium and, as a result,
51 transpiration is reduced. In our conditions, daily evapotranspiration varied during the experiment and
52 depended mainly on the available water content. Several works have studied the evolution of water
53 consumption in ornamental plants under different environmental conditions, levels of water stress or
54 substrates. For example, Montero et al. (2001) found that transpiration in zonal geranium was closely
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1 related to radiation. Nevertheless, a relation between ET and both temperature and vapour pressure deficit
2 (VPD) has been described in other studies (Bakker 1991; Álvarez et al. 2009). In our case, other
3 parameters, including the formation of inflorescences and increase in plant height, had an effect on the
4 behaviour of ET, since environmental conditions (temperature, RH, light and VPD) were constant
5 throughout the experiment.
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10 Reductions in water consumption under deficit irrigation have been attributed to the reduction in leaf
11 area (Atkinson and Crisp 1983) and to lower stomatal conductance (Pinhero et al. 1997; Bolla et al.
12 2010). In our experiment, the control showed higher daily ET values than SDI, which may be explained
13 by greater plant growth (larger transpiration area), the higher levels of stomata conductance and greater
14 amount of water available in the control compared with SDI. The differences between the ET values
15 obtained in the control and SDI varied throughout the experiment and might also be explained by
16 differences in the date of flowering. Maximum ET values were found during the time when
17 inflorescences were forming because the plants were physiologically more active (Lorenzo et al. 1996;
18 Bañón et al. 2009).
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22 All the ornamental species studied by García-Navarro et al. (2004) responded to water stress by
23 reducing daily water consumption, although the time before this response was observed and the intensity
24 of the same varied between species. When these authors compared average daily ET in relation to leaf
25 area rather than ET per plant, they found that while all species reduced ET per plant, some species did so
26 in relation to leaf area, but others did not. At the beginning of our experiment, geranium plants of the DI
27 treatments reduced the ET values in relation to leaf area compared with control plants, but such
28 differences were less marked as the experiment progressed. The same observation was made for the
29 evolution of the stomatal conductance values. Maximum g_s values were found at the beginning of the
30 experiment in all treatments, when ET was also highest. In this case, evapotranspiration was practically
31 equivalent to transpiration, as evaporation from the soil was very low. Moreover, at the beginning of the
32 experiment, leaf area was much lower, so transpiration values in relation to leaf area were much higher
33 than during the rest of the experiment. This behaviour explains the lower water potential values measured
34 at that time. The close relationship found between g_s , ET and Ψ_h at the beginning of the experiment
35 continued during the rest of the experimental period, as was observed by Colom and Vazzana (2003),
36 Jaleel et al. (2008), Lenzi et al. (2009) and Bolla et al. (2010).
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1 Plants from the RDI treatments modified stomatal conductance to adjust to irrigation changes,
2 although, in general, g_s remained below that of the control plants. This could be due to acclimation to the
3 previous water deficit situations (Leskovar 1998; Liptay et al. 1998; Franco et al. 2001; Vilagrosa et al.
4 2003; Bruce et al. 2007; Cameron et al. 2008; Walter et al. 2011).

5
6
7 Plants under irrigation deficit exhibited moderate water stress levels as indicated by the leaf potential
8 and turgor values. Also, the degree to which deficit irrigation was imposed did not point to any osmotic
9 adjustment. In a previous experiment, limited osmotic adjustment was observed only in geranium plants
10 that received 60% less water than the control (Sánchez-Blanco et al. 2009). However, deficit irrigation
11 caused a decrease in stomatal conductance, which suggests that geranium has very sensitive stomata
12 (Arora et al. 1998). A reduction in stomatal opening could lead to a lower photosynthetic rate at some
13 moments during the experimental period. However, differences in stomatal conductance between
14 treatments did not seem to be followed by similar changes in photosynthetic rate. In this sense, plants
15 submitted to SDI and RDI I treatments are able to increase their intrinsic water use efficiency, i. e., plants
16 maintain acceptable photosynthetic rates despite reduced stomatal opening respect to the control. CO_2
17 assimilation remains proportionally higher than water vapour loss from the stomata as an additional
18 drought acclimatation mechanism. Previous studies in a variety of ornamental species indicated that P_n/g_s
19 can be modified under deficit irrigation (increasing or decreasing) (Rasoul Sharifi and Rundel 1993;
20 Mugnai et al. 2005; Jaleel et al. 2008; Álvarez et al. 2009; Bolla et al. 2010).

37 38 **Conclusion**

39
40 Despite the fact that the amounts of water provided to *P. hortorum* plants in the deficit treatments
41 were similar, their behaviour differed, depending on the phase when deficit irrigation was applied, even
42 though deficit irrigation was moderate. Deficit irrigation applied outside the flowering phase brought this
43 phase forward, but did not decrease flowering intensity; it also increased the root/shoot ratio and the
44 width to height ratio, providing a better plant, besides saving 20% water. Deficit irrigation during the
45 flowering phase is not to be recommended because the intensity and duration of flowering are reduced.
46 This finding should be borne in mind when deciding irrigation strategies for use in this kind of plant.

56 **Author Contribution**

1 S Álvarez performed the experiment, carried out statistical analysis and wrote the article. MJ Sánchez-
2 Blanco and S Bañón designed and instructed the research work. MJ Sánchez-Blanco also coordinated the
3 study and provided study material and facilities for the experiments. The three authors were involved in
4 data interpretation and paper preparing. All authors have read and approved the final manuscript. The
5 authors declare that they have no conflict of interest.
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Figure captions

1
2 **Fig. 1** Evolution of plant height (a), plant width (b) and leaf loss (c) in *P. hortorum* plants subjected to
3 different irrigation treatments during the experimental period. Values are means (n =24) and the vertical
4 bars indicate standard errors. Symbols represent the different treatments: Control (filled circles), SDI
5 (open circles), RDI I (filled triangles) and RDI II (open triangles). Vertical lines indicate irrigation
6 changes and numbers at the top of the figure indicate threshold levels of WFC after irrigation in the plants
7 of both RDI treatments. Asterisks indicate significant differences between treatments
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16 **Fig. 2** Evolution of number of inflorescences (a) and cumulative number of inflorescences per plant (b) in
17 *P. hortorum* plants subjected to different irrigation treatments during the experimental period. Values are
18 means (n =24) and the vertical bars indicate standard errors. Symbols represent the different treatments:
19 Control (filled circles), SDI (open circles), RDI I (filled triangles) and RDI II (open triangles). Vertical
20 lines indicate irrigation changes and numbers at the top of the figure indicate threshold levels of WFC
21 after irrigation in the plants of both RDI treatments. Asterisks indicate significant differences between
22 treatments
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32 **Fig. 3** Evolution of daily evapotranspiration (ET) in *P. hortorum* plants subjected to different irrigation
33 treatments during the experimental period. Values are means (n =24) and the vertical bars indicate
34 standard errors. Symbols represent the different treatments: Control (filled circles), SDI (open circles),
35 RDI I (filled triangles) and RDI II (open triangles). Vertical lines indicate irrigation changes in the plants
36 and numbers at the top of the figure indicate threshold levels of WFC after irrigation in the plants of both
37 RDI treatments
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46 **Fig. 4** Evolution of leaf water potential (Ψ_l , a), leaf turgor potential (Ψ_t , b) and leaf osmotic potential at
47 full turgor (Ψ_{100s} , c) in *P. hortorum* plants subjected to different irrigation treatments during the
48 experimental period. Values are means of 5 plants per treatments and the vertical bars indicate standard
49 errors. Symbols represent the different treatments: Control (filled circles), SDI (open circles), RDI I
50 (filled triangles) and RDI II (open triangles). Vertical lines indicate irrigation changes and numbers at the
51 top of the figure indicate threshold levels of WFC after irrigation in RDI treatments. Asterisks indicate
52 significant differences between treatments
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1 **Fig. 5** Evolution of stomatal conductance (g_s ; a), net photosynthetic rate (P_n ; b) and intrinsic water use
2 efficiency (P_n/g_s ; c) in *P. hortorum* plants subjected to different irrigation treatments during the
3 experimental period. Values are means of 5 plants per treatments and the vertical bars indicate standard
4 errors. Symbols represent the different treatments: Control (filled circles), SDI (open circles), RDI I
5 (filled triangles) and RDI II (open triangles). Vertical lines indicate irrigation changes and numbers at the
6 top of the figure indicates threshold levels of WFC after irrigation in the plants of both RDI treatments.
7 Asterisks indicate significant differences between treatments
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18 **ESM 1** Evolution of colour parameters measured in external leaf zone (i), internal leaf zone (ii) and
19 flowers (iii), in *P. hortorum* plants subjected to different irrigation treatments during the experimental
20 period. Values are means ($n = 5$) and the vertical bars indicate standard errors
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- 1 **Table 1.** Scheme of phenological phases of *P. hortorum* plants and irrigation threshold
- 2 levels in the different treatments during the experimental period.

	Not flowering	Flowering	Not flowering	Flowering	Not flowering
Time elapsing since beginning of treatments (weeks)	0-1.5	1.5-5.8	5.8-11.8	11.8-15.4	15.4-24
TREATMENT	WEIGHT AFTER IRRIGATION/ WEIGHT AT FIELD CAPACITY (%)				
C	100	100	100	100	100
SDI	75	75	75	75	75
RDI I	75	100	75	100	75
RDI II	100	75	100	75	100

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Table 2 Growth and biomass traits at the end of the experimental period in *P. hortorum* plants subjected to different irrigation treatments. Values are the mean of 5 plants.

Parameters	Treatments				P
	C	SDI	RDI I	RDI II	
Aerial dry weight (g pl ⁻¹)	5.33 ± 0.37 b	3.44 ± 0.40 a	3.22 ± 0.26 a	2.65 ± 0.31 a	***
Root dry weight (g pl ⁻¹)	2.25 ± 0.24	2.06 ± 0.41	1.94 ± 0.07	1.65 ± 0.10	ns
Root/shoot ratio	0.42 ± 0.04 a	0.59 ± 0.07 b	0.62 ± 0.05 b	0.68 ± 0.04 b	*
Number of leaves per plant	68 ± 4.10 b	51 ± 4.43 a	45 ± 2.44 a	45 ± 6.36 a	**
Total leaf area (cm ²)	446 ± 35 b	273 ± 42 a	279 ± 28 a	284 ± 27 a	**

Means within a row without a common letter are significantly different by Duncan _{0.05} test. (P: probability

level, ns: not significant, *P<0.05, ** P ≤ 0.01, *** P ≤ 0.001).

Figure 11
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	75%	100%	75%	100%	75%
RDI II	100%	75%	100%	75%	100%

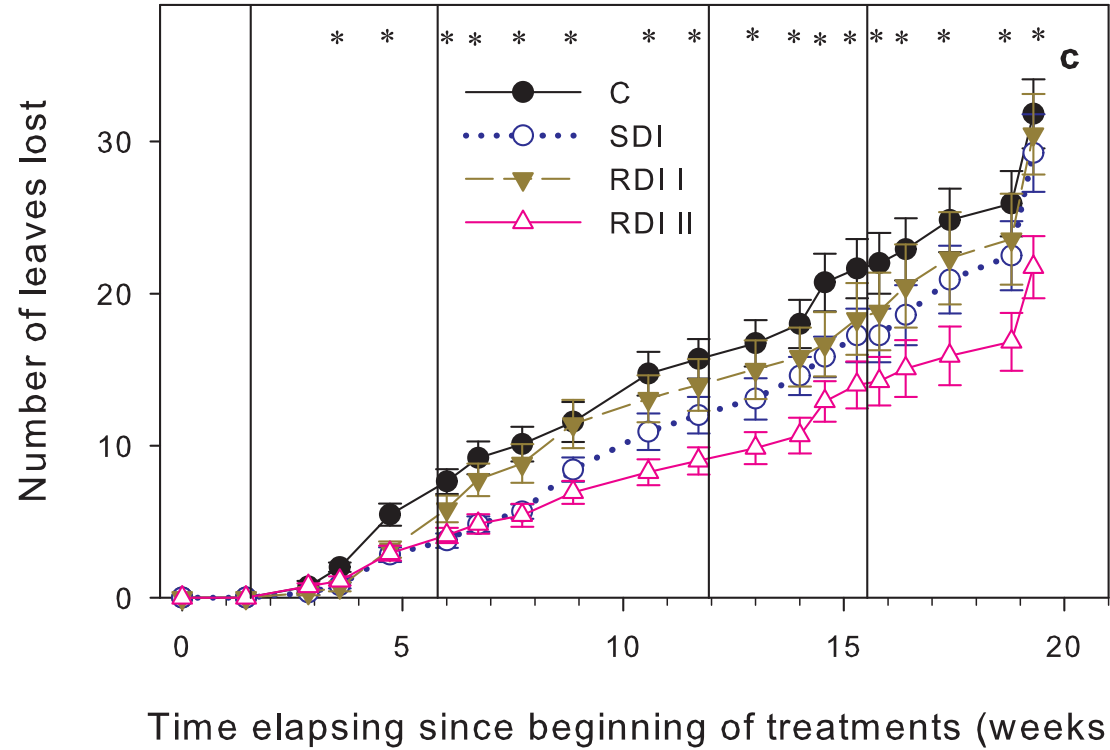
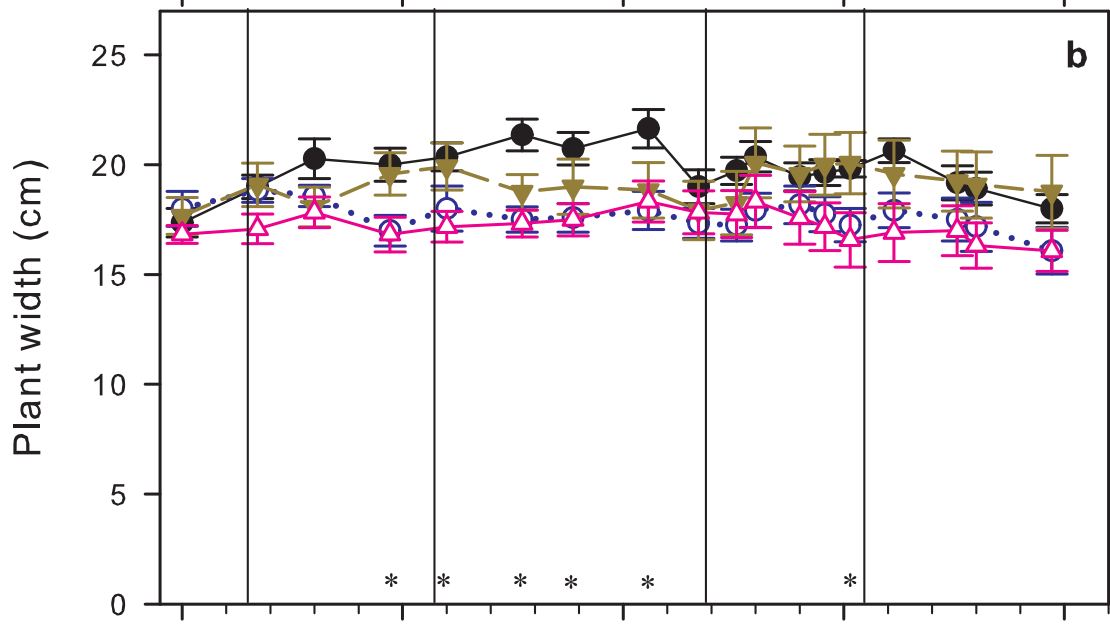
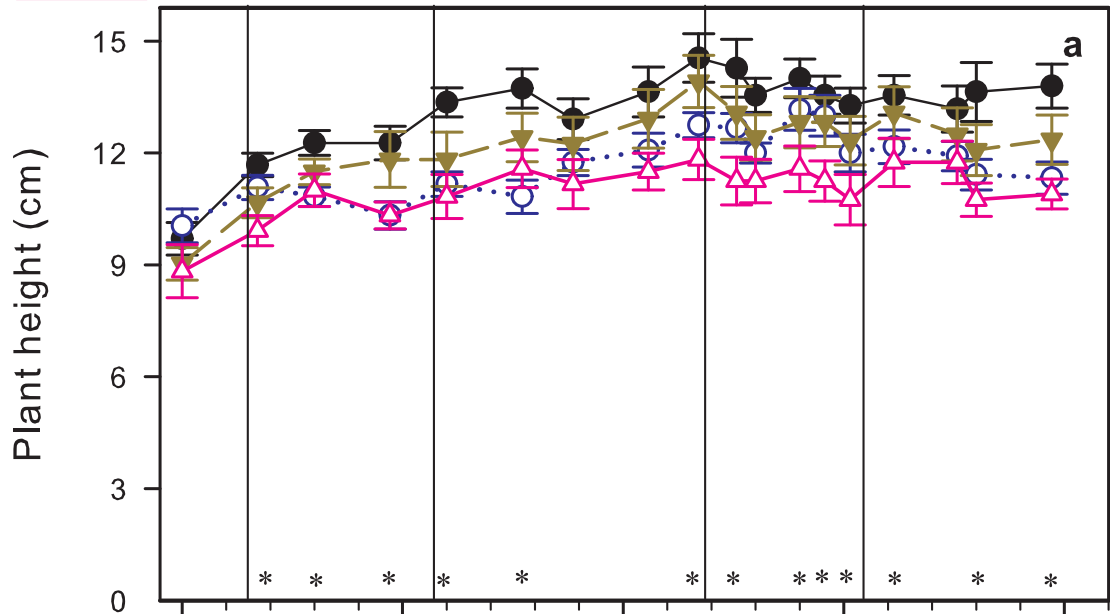


Figure 2
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RDI I	75%	100%	75%	100%	75%
RDI II	100%	75%	100%	75%	100%

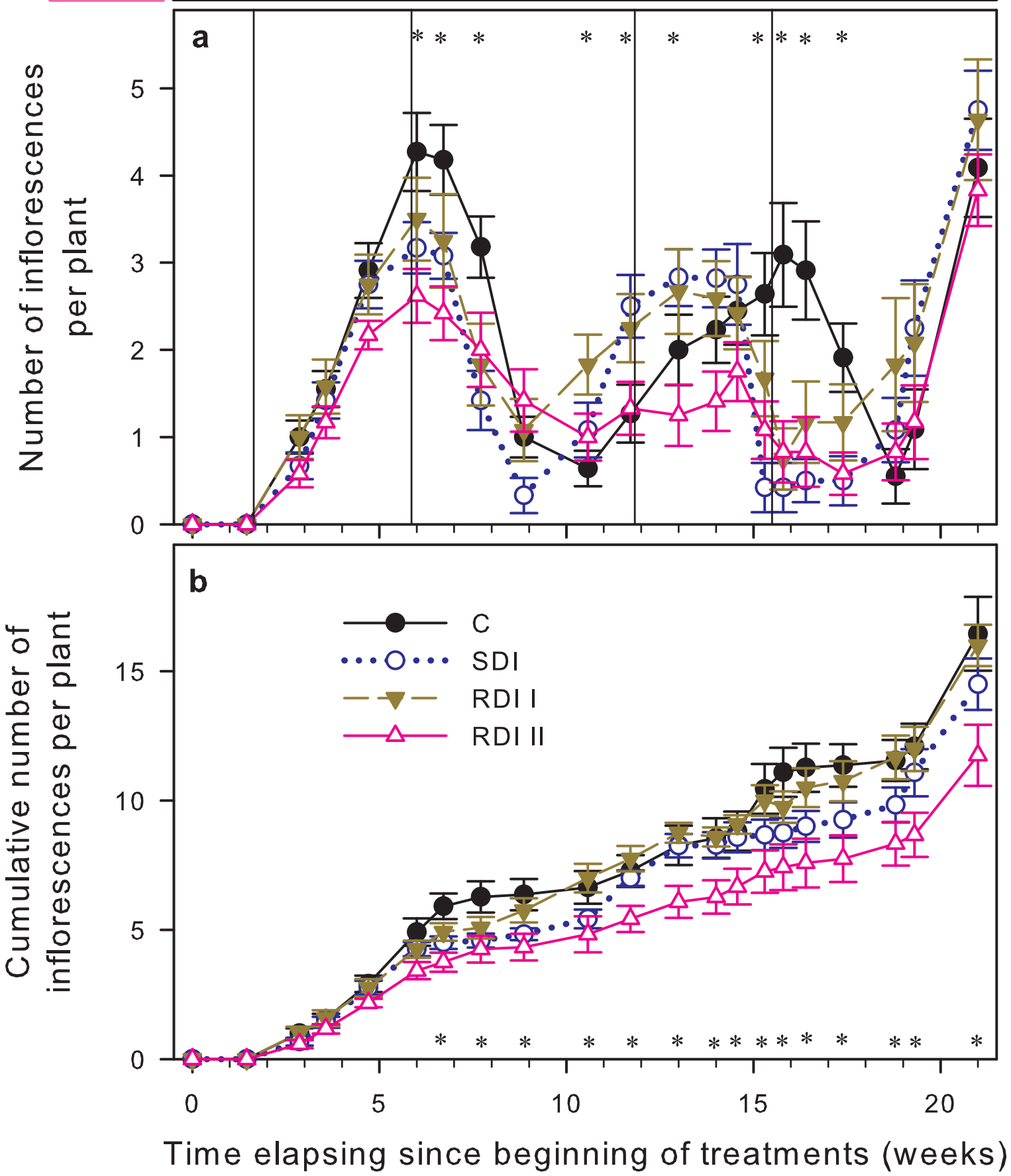


Figure 3

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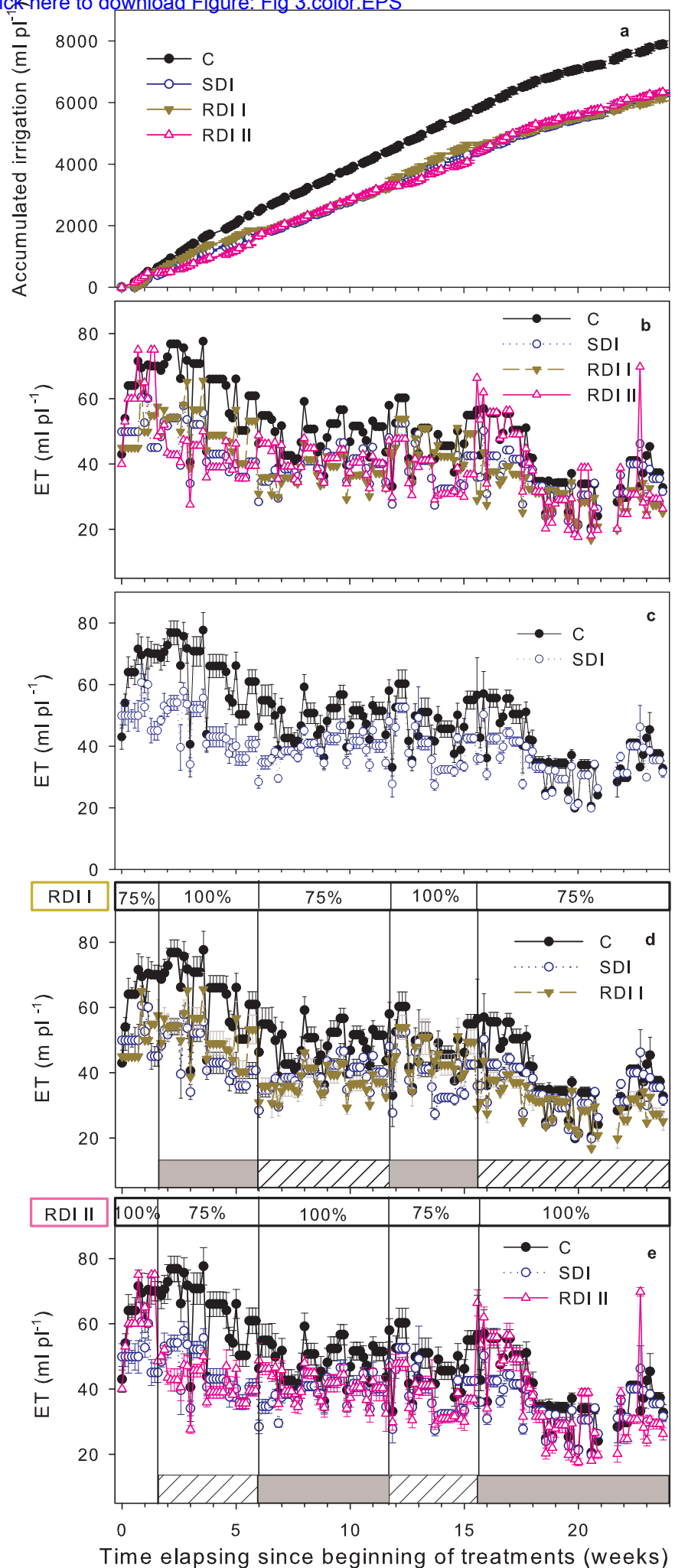
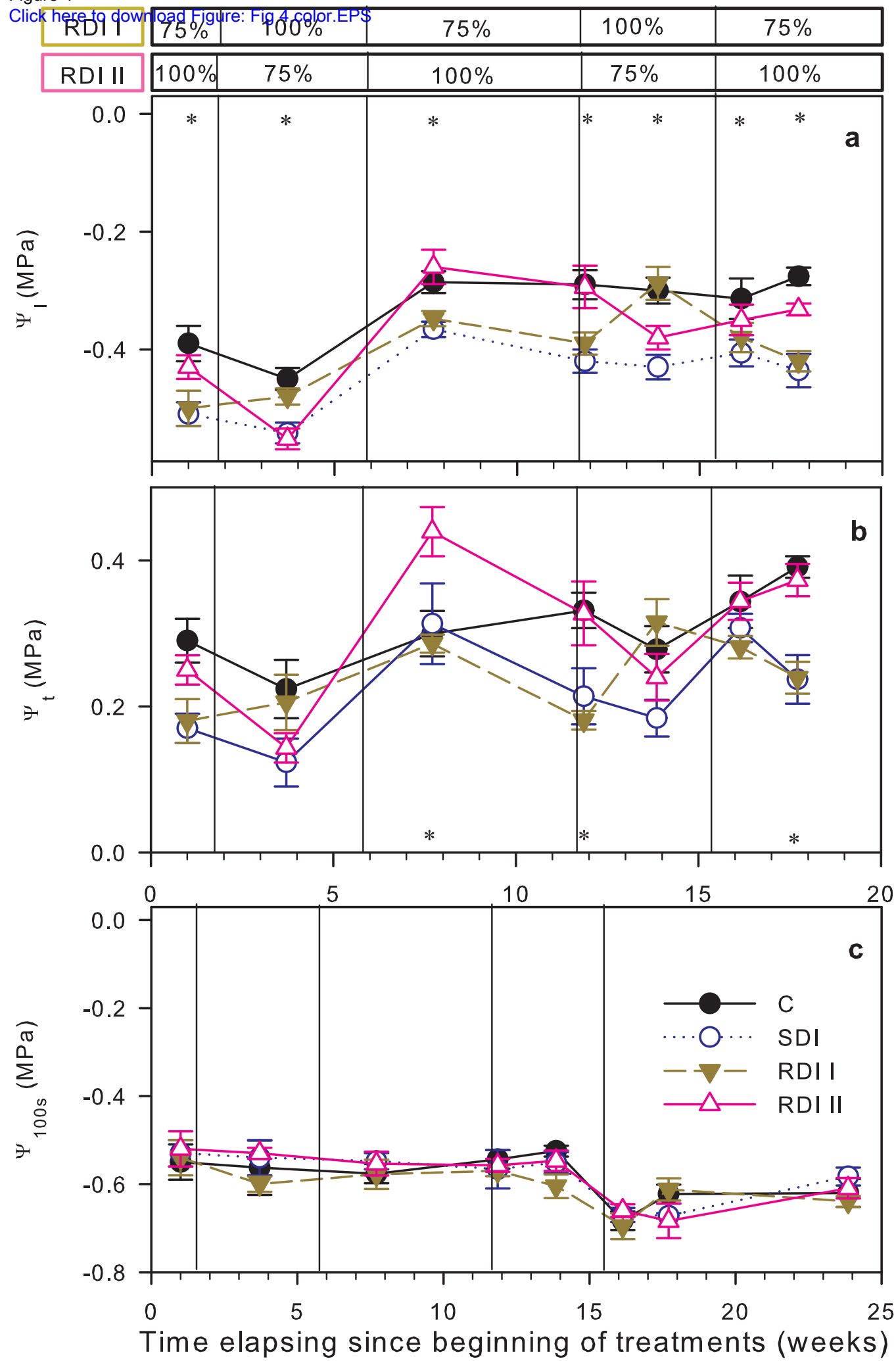


Figure 4

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RDII	75%	100%	75%	100%	75%
RDII	100%	75%	100%	75%	100%

