Plant Growth Regul (2017) 83:361–373
DOI 10.1007/s10725-017-0301-4

ORIGINAL PAPER

The influence of water stress on growth, ecophysiology and ornamental quality of potted *Primula vulgaris* 'Heidy' plants. New insights to increase water use efficiency in plant production

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Received: 23 January 2017 / Accepted: 15 July 2017 / Published online: 20 July 2017

Abstract Efficient irrigation practices are required to reduce the amount of water used. In this study, the effects of different irrigation regimes on changes in growth, ecophysiology and ornamental traits of potted *Primula vulgaris* 'Heidy' plants were investigated. Three experiments were carried out. In the first, the plants were either fully irrigated (100% of container capacity) or not. In the second, plants were watered to full irrigation (control), to 50% of the control (moderate water stress), to 25% of the control (severe water stress), or not irrigated and followed by a rehydration phase. Both experiments were conducted under controlled growth conditions. The third experiment was performed under common nursery conditions in an unheated and shaded greenhouse where plants were either irrigated with common irrigation practices (control), or with 66% of the control amount (moderate water stress), or with 33% of the control (severe water stress). In general, the percentage of senescent plants, the growth index, the number of leaves, and the aerial fresh and the dry weight were not affected by moderate water stress treatments. As expected, increasing water stress resulted in a general decrease in all studied gas exchange parameters. However, stressed plants were more efficient in using water than control plants, suggesting that stomata closed to cope with drought conditions without damaging photosynthesis events. The number of fully opened flowers during the growing season was highest in both control and moderately water stressed plants. In conclusion, moderate, but not severe, water stress could be imposed in *P. vulgaris* 'Heidy' pot production to reduce the water consumption, still maintaining plant ecophysiological performances and ornamental quality.

Keywords Flower · Gas exchange parameters · Instantaneous water use efficiency · Midday leaf water potentials · Plant stress · Primrose

Introduction

Managing global water resources is one of the most pressing challenges of the twenty-first century. In many areas of the world there is a considerable pressure to produce crops more efficiently by reducing the water use (Fulcher et al. 2016). In floriculture, 100–350 L of water are needed to produce 1 kg of plant dry matter, with differences related to species, variety, cultivation system, and plant growing season (Fornes et al. 2007). Surprisingly, irrigation needs of ornamental pot plants have not been much investigated, although they constitute a major part of horticultural production (Henson et al. 2006). In the last decades, the interest in irrigation procedures was mainly centered on fruit and vegetable crops (Goldhamer and Beede 2004; Mo et al. 2016; Pérez-Jiménez et al. 2016).

In flower farming, the irrigation is generally based on personal experience and is rarely managed to match the effective water needs (Grant et al. 2012). Water and nutrients are often applied in excess, resulting in water wastage and environmental pollution due to the leaching of fertilisers and herbicides (ARPAT 2007). The controlled application of the water may be used in potted plants also to improve quality (Cameron

Electronic supplementary material The online version of this article (doi:10.1007/s10725-017-0301-4) contains supplementary material, which is available to authorized users.

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et al. 2006), but precise scheduling is required to minimise the risk of excessive drying of the substrate. In this sense, different works have demonstrated that the plant quality decreases as the severity of water deficit increases (Sánchez-Blanco et al. 2009; Bolla et al. 2010; Bernal et al. 2011; Caser et al. 2012). Plant responses to drought are multiple and interconnected (Efeoğlu et al. 2009; Ali et al. 2017) and their capacities to adapt to this stress may vary considerably within genera and species (Sánchez-Blanco et al. 2002; Torrecillas et al. 2003). Water scarcity can delay and reduce the flowering and the new leaves sizes and the quality (Sánchez-Blanco et al. 2002; Augé et al. 2003) as a physiological consequence to drought (Davies et al. 2002; Zollinger et al. 2006; Álvarez et al. 2009; Caser et al. 2016). Thus, understanding morphological and physiological responses of plants to water management is critical for optimizing a sustainable high-quality production without compromising the economic value of the crop (Cameron et al. 2006; Franco et al. 2006).

Primula vulgaris (primrose, syn. *Primula acaulis* (L.) Hill) is a perennial herbaceous native species of western and southern Europe, northwest Africa, and southwest Asia, frequently cultivated as a garden or potted flowering plant all around the world. Effect of water stress on morphology and physiology of *Primula* species have been reported only in *P. palinuri* (Dietz and Heber 1983) and in *P. veris* (Whale 1984) as high tolerant species. A high tolerance to adverse conditions, namely strong light intensity (photosynthetically active radiation >1500 µmol $m^{-2}s^{-1}$) and heat stress at 38 and 42 °C was assessed within the genus by Liu et al. (2006) and Ceriani et al. (2009) and Hu et al. (2010). Cloned small heat shock proteins (sHSPs) gene, PfHSP17.1, was obtained by *Primula forrestii* plants exposed to thermal stress (42 °C for 2 h) and used to higher resistance to salt and drought in transgenic *Arabidopsis thaliana* plants (Zhang et al. 2013). Moreover, further work is needed to characterize and quantify the responses to water shortage.

The present research investigated the effects of different irrigation regimes on changes in the growth, the physiology and the ornamental traits of *P. vulgaris* 'Heidy', both under controlled growth conditions and common greenhouse practices. Such knowledge might help to optimise water use in primrose production and contribute to develop irrigation protocols for potted ornamental plants.

Materials and methods

Plant material

Plants of *P. vulgaris* 'Heidy' were provided in November 2013 by Planta s.s. (Bressanone, Bolzano, Italy) and immediately potted into vases of 11 cm in diameter, filled with a mixture of peat, conifer bark and clay (Turco Silvestro TS2, Albenga, Italy), and amended with 2 g L^{-1} of Osmocote Plus (14:13:13 N, P, K plus microelements). Their cultivation occurred till April 2014 in an unheated and shaded high tunnel at the Floricoltura Lagomarsino nursery (Genova, Italy) (44°23′06.5″N, 9°02′47.6″E). The weather conditions during greenhouse cultivation are listed in Supplementary Table 1. Plants were used in three different experiments as described below.

Experiment 1

Plants at the foliar period were transferred and maintained at the Department of Agriculture, Forest and Food Sciences of the University of Torino (Grugliasco, Italy) (45°03′59.73″N, 7°35′24.72″E) in a growth chamber at 20 °C, 60% of relative humidity and 16 h of photoperiod, with a photosynthetically active radiation (PAR) of 157 µmol m^{-2} s^{-1} at the top of the canopy, provided by high pressure sodium lamps. The experimental design was a split-plot design with two treatments and three replications per treatment. Thirty-six plants were randomly divided in two groups (18 plants each) and subjected to fully irrigation (100% of container capacity), while the others were not irrigated. The water content was kept constant throughout the experiment. Gravimetric determinations of the water content was made by weighing soil samples before and after oven-drying to constant weight at 80 °C for 1 week. These values were used to calibrate all measurements of the moisture content of the substrate in the container. The container capacity was determined 48 h after irrigation and was calculated according to the equation of Paquin and Mehuys (1980). The soil moisture levels were maintained by manual irrigation and checked by weighing individual container every 2 days. This experiment lasted until the not irrigated plants reached the complete leaf turgor loss. These lasts were then recovered by the application of fully irrigation for 1 week.

Experiment 2

Plants at the beginning of the blooming stage were cultivated under the same growth conditions of the Experiment 1 and divided into four lots. The experimental design was a split-plot design with four treatments and three replications per treatment. Seventy-two plants were randomly divided in four groups (18 plants each) and subjected to fully irrigation (100% of container capacity) as control treatment, 50% of the control (moderate water stress), 25% of the control (severe water stress) or no irrigation till the complete leaf turgor loss. To evaluate their recovery attitude, these lasts were irrigated as control after 3 days from the complete leaf turgor loss. The gravimetric determinations of water content was conducted as described in "Experiment 1".

Experiment 3

The experimental design was a split-plot design with three treatments and three replications per treatment. One hundred and eighty plants at the beginning of the foliar period were randomly divided into three lots (60 plants each) and irrigated using a drip irrigation system under common nursery conditions at the Floricoltura Lagomarsino nursery (Genova, Italy). In the common irrigation practice, used as control treatment (100% of container capacity), plants were watered with three emitters per plant for a total of 4.824 L h^{-1} so that 15% (v/v) of the applied water was leached. Plants subjected to moderate water stress were watered with two emitters (66% of the control) and plants subjected to severe water stress with one emitter (33% of the control). The gravimetric determinations of water content was conducted as previously described. This experiment lasted the entire growing season from November 2013 to April 2014.

Measurements

Growth and ornamental quality evaluation

The described parameters were periodically measured over the growing season on the basis of the specific experiment. Height and diameter of each plant per treatment were measured to calculate the growth index (GI; $\Pi \times \{[(D'+D'')/2]/2\}^2 \times H$, where D′ is the widest width, D″ is the perpendicular width and H is the height; Hidalgo and Harkess 2002). The number of leaves per plant and their length and width were measured to assess growth variation leaf area ($k \times$ length $\times$ width; $k = 0.75$; Ruget et al. 1996). The relative quantity of the chlorophyll present in leaf tissue was measured on four leaves of each plant per treatment using the Chlorophyll Meter SPAD-502 (Konica Minolta Sensing Inc., Osaka, Japan). At the end of the experiments, six plants per treatment were harvested and the aerial part was collected. After recording the fresh biomass (FW), the plant aerial parts were oven-dried at 65 °C for 1 week and the dry biomass (DW) was weighted. The DW:FW ratio was then calculated. The root quality was visually evaluated and rated using five classes of roots covering (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100% of vase surface; Larcher et al. 2011).

To assess the ornamental quality, the leaf damage was visually evaluated and rated using five classes (visual damage class: 0 = 0%; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; 4 = 76–100% leaf area; Caser et al. 2013). The number of flowered plants, the number of completely opened flowers per plant and their diameter, and the height of peduncles were determined throughout the experiments. The petal color (L^*, a^*, b^* space) was measured on four flowers of six plants per treatment at the beginning and at the end of the blooming stage using a Spectrophotometer CM-2600 (Konica Minolta Sensing Inc., Osaka, Japan). Chroma (C^*) and hue angle ($h°$) was calculated according to Onozaky et al. (1999) and Scariot et al. (2008).

Ecophysiological measurements

Based on the specific experiment, 1 h before the beginning of the physiological measurements (10–12 a.m.), plants were transferred in the lab for the adaptation to the ambient light intensity, the temperature and the relative humidity. Midday leaf water potentials (MLWP, MPa) were determined in three adult leaves of six plants per treatment using a Scholander-type pressure chamber (Soil Moisture Equipment, Santa Barbara, CA, USA) (Scholander et al. 1965). The measurement of the internal CO_2 concentration (C_i), the transpiration rate (E), the stomatal conductance (GH_20), and the net photosynthetic rate (A) were performed in three adult leaves of six plants per treatment, using a portable infrared gas analyzer ADC-LCPro+ (The Analytical Development Company Ltd, Hoddesdon, UK). The instantaneous water use efficiency (WUE) was calculated as the ratio between A and E. Leaves were clamped in the leaf chamber, where the light source was set at 1200 µmol photons m^{-2} s^{-1} and the temperature (25 °C) kept constant. The environmental concentration of CO_2 (450–470 ppm) and the vapour pressure deficit (about 2.3 kPa) were maintained during the experiments.

Statistical analysis

An arcsine transformation was performed on all percent incidence data before statistical analysis in order to improve homogeneity of variance. All the measured and the derived data were then subjected to the homogeneity of the variances and then post-hoc tested using Ryan–Einot–Gabriel–Welsch–F test (REGW-F). The critical value for statistical significance was $P < 0.05$. All the data were computed by means of the SPSS statistical package (version 21.0; SPSS Inc., Chicago, Illinois).

Results and discussion

Experiment 1

The changes in physiological traits and growth were investigated in fully or not irrigated plants to characterize the responses to water stress and to determine the minimal water needs of *P. vulgaris* 'Heidy'. Significant differences in midday leaf water potential between treatments were observed starting from the day 2 in not irrigated plants with a constant decrease till day 8, followed by a strong decline to the complete loss of the leaf turgor which occurred at day 10 (MLWP = −0.71 MPa in not irrigated plants, Fig. 1a). Similarly, a general decrease was observed in all the studied gas exchange traits (Fig. 1b–e). Stomatal limitation is the first major event that occurs in response to the drought stress (Grassi and Magnani 2005). In fact, the stomatal conductance is extremely sensitive to physiological and environmental factors (e.g. leaf water status). In drought conditions, water deficit stress leads to a progressive limitation of photosynthesis, which is a consequence of an alteration in carbon assimilation (Siddique et al. 2016). The opening and closing of stomata is regulated by changes in turgor pressure in the guard cells that are present in epidermis and, hence, this process protects plants from the dehydration and death during fluctuating environmental conditions. Hence, a complex set of factors is involved in stomatal response to drought stress (Lawlor 2002). Here, a stomatal limitation to photosynthesis occurred. In fact, as stomatal conductance (Fig. 1b) closes starting from day 2, the amount of carbon dioxide (Fig. 1c) present in mesophyll spaces in leaves also decreases which results in the decline of carbon dioxide to oxygen ratio and to a constant decrease in photorespiration rate (Fig. 1d) during mid-time period (from day 2 to day 8) of applied water stress with a mean value of *E* equal to 1.30 mmol m^{-2} s^{-1}. In the same period, net assimilation rate (Fig. 1e) kept constant values (mean $A = 6.04$ μmol m^{-2} s^{-1}), perhaps because internal CO_2 concentration was utilized in photosynthesis (Faußer et al. 2016). Later stomatal close completely during severe drought at days 9 and 10, which causes both photosynthesis and photorespiration rates to lower (Athar and Ashraf 2005). However, midday leaf water potential equal to

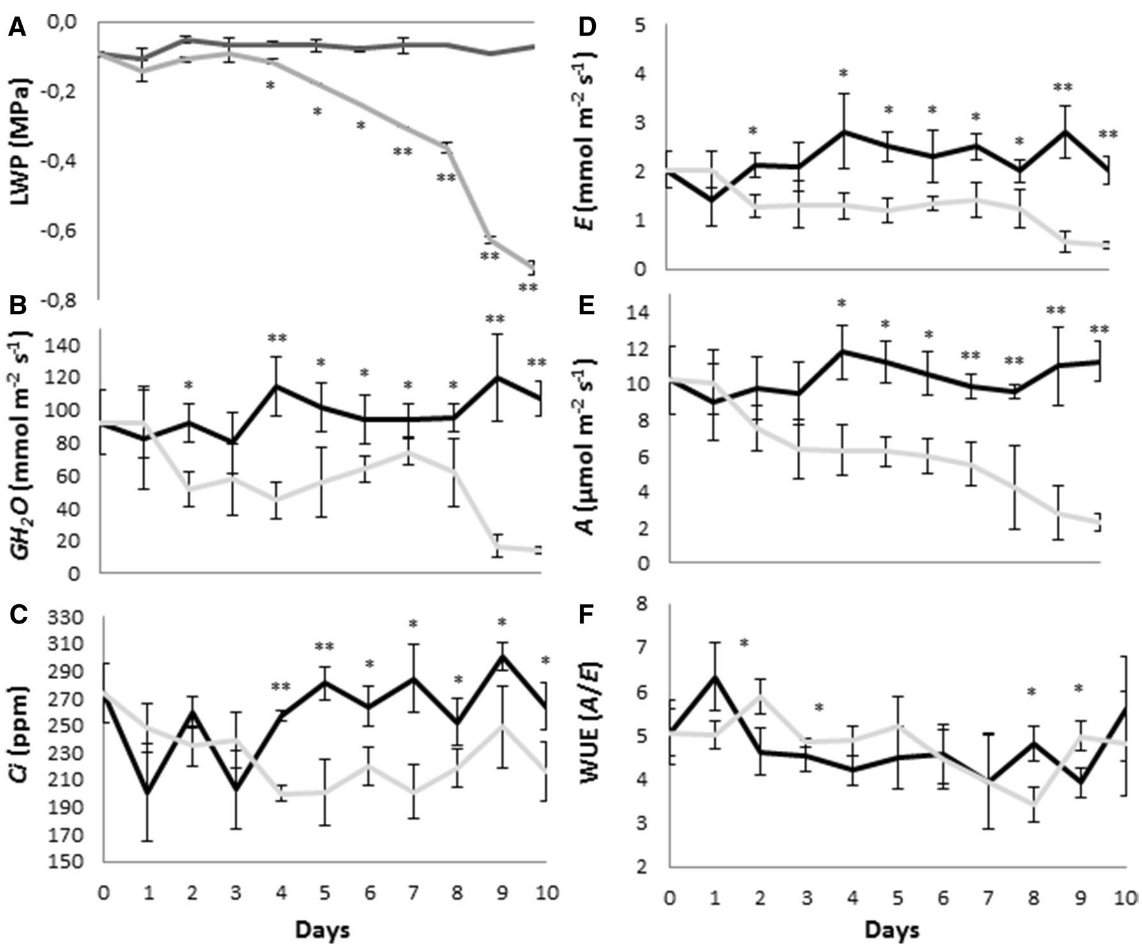


Fig. 1 Dynamics of midday leaf water potential (MLWP, MPa) (**a**), stomatal conductance (*GH_2O*) (**b**), internal CO_2 concentration (C_i) (**c**), transpiration rate (*E*) (**d**), net photosynthetic rate (*A*) (**e**), and instantaneous water use efficiency (WUE, *A*/*E*) (**f**) in *Primula vulgaris* 'Heidy' plants subjected to full irrigation (100% of container capacity, control, *solid black line*) or no irrigation (*solid grey line*) during the Experiment 1. Each time point represents the mean values of six replicas and the *vertical bars* indicate standard errors. The statistical relevance of 'Between-Subjects Effects' tests (*$P \leq 0.05$, ** ≤ 0.001) was evaluated

−0.40 MPa (day 8) could represent the minimum threshold to maintain the ornamental quality of the studied cultivar. Figure 1f shows how instantaneous water use efficiency (*A*/*E*) changed during the experiment. In general, stressed plants resulted equally efficient in using water than control plants, with the exception at days 1, 2, 8 and 9. In the lasts time points, in particular, we hypothesize that plants start to dissipate energy and to close the stomata to survive under severe drought conditions, inducing a consequent increase of WUE at the end of the experiment. Drought-stressed plants with higher WUE are more efficient in utilizing energy captured by photosynthesis per unit of water transpired. Similar trends were observed in *Callistemon laevis* (Álvarez et al. 2011), *Hybanthus floribundus* (Kachenko et al. 2011), *Rosa* × *hybrida* 'RADrazz' (Cai et al. 2012), and in *Zea mays* (Zhang et al. 2015). An experiment carried out on *Erica multiflora* and *Globularia alypum* confirmed that plants exposed to drought conditions show low gas exchange rates compared to plants grown in normal environmental conditions (Llorens et al. 2004).

Regarding morphological changes, the growth index, the leaf area and SPAD values were measured at the end of the experiment (day 10) and after 1 week of recovery (Table 1). At day 10, fully irrigated plants were bigger and showed wider leaves than not irrigated plants (1004.80 and 207.63 cm^3 G.I.; 35.19 and 30.75 cm^2 in full irrigation and no irrigation, respectively). While, no differences in SPAD values were recorded (data not shown). Similar results were observed by Álvarez et al. (2009) in *Dianthus caryophyllus* and by Caser et al. (2012) in *Salvia dolomitica* subjected to severe water stress conditions. This is in agreement with the common plant responses to water stressed conditions leading to the decrease in cell enlargement and leaf size due to the low turgor pressure (Martinez et al. 2007). After 1 week of recovery, no more differences were observed with the exception for the leaf area with 38.10 and 32.15 cm^2 in full irrigated and not irrigated plants, respectively. Similar trend was observed in *Echinacea purpurea, Gaillardia aristata, Lavandula angustifolia, Leucanthemum* × *superbum, Penstemon barbatus* and *Penstemon* × *mexicali* irrigated every 4 weeks (Zollinger et al. 2006).

Table 1 Values of the growth index (G.I., cm^3) and the leaf area (cm^2) in potted *P. vulgaris* 'Heidy' plants subjected to full irrigation (100% of container capacity) or no irrigation at day 10 and after the recovery phase during Experiment 1

Treatments	G.I. (cm^3)		Leaf area (cm^2)	
	Day 10	Recovery	Day 10	Recovery
Full irrigation	1004.80	1140.12	35.19	38.10
No irrigation	207.63	930.74	30.75	32.15
P	**	ns	*	*

The statistical relevance of 'Between-Subjects Effects' tests (*P ≤ 0.05, ** ≤ 0.001, ns = not significant) was evaluated

Experiment 2

The morphological responses to the imposed water stress and consequently the ornamental quality of *P. vulgaris* 'Heidy' were characterized by the application of four different irrigation regimes under controlled growth conditions. Water stress significantly affected leaf damage values, SPAD values, leaf area, growth index, number of fully opened flowers and flower damages as reported in Fig. 2. Only few damages (dead leaves or yellowing and wilted leaves) appeared starting from 21 days of cultivation (leaf damage = 1.0) in fully irrigated plants. Starting from this time point, moderate and severe stressed plants presented always superior leaf damage values than control. These achieved the complete leaf damage (class = 4.0) at day 42. Not irrigated plants reached the complete leaf damage after 11 days of cultivation. But imposed re-watering of them after 3 days (day 14) lead to the restoration of their morphological traits. The application of the recovery reduced the leaf damage of these plants already after 3 days (day 21 = 2.0) but, it could not reinstate as the control and, at day 49, resulted in the highest leaf damage values as well as half irrigated plants. Zollinger et al. (2006) explained that the excellent visual quality of *Penstemon barbatus* after severe drought may be related to the ability to regulate the water loss by stomata closure.

Regarding SPAD values, here, no differences were counted between control and moderate stressed plants, showing that a half irrigation not affected the health plant status. On the opposite, the application of severe water stress and no irrigation treatments significantly reduced this parameter. Several studies reported that water stress leads to a decreased level of chlorophylls in plant leaves (Reddy et al. 2004; Kaminska-Rozek and Pukacki 2004; Guerfel et al. 2009). Here, the reduction in SPAD value could be identified as a drought response mechanism in order to minimize the light absorption by chloroplasts (Pastenes et al. 2005). The application of the recovery induced an increase in SPAD values similarly to control and moderate water stress treatments already from day 14 till the end of the experiment with the exception at day 35, showing that *P. vulgaris* 'Heidy' has an excellent desiccation tolerance of their pigment apparatus (Netto et al. 2005).

Plant can adapt to environmental change usually by morphological and anatomical modifications. In the present study, fully irrigated plants showed the widest leaves and the highest growth index. While, surprisingly plants subjected to moderate water stress showed more narrow leaves, starting from day 8, and reduced growth, after 21 days of cultivation, as well as severe water stressed plants.

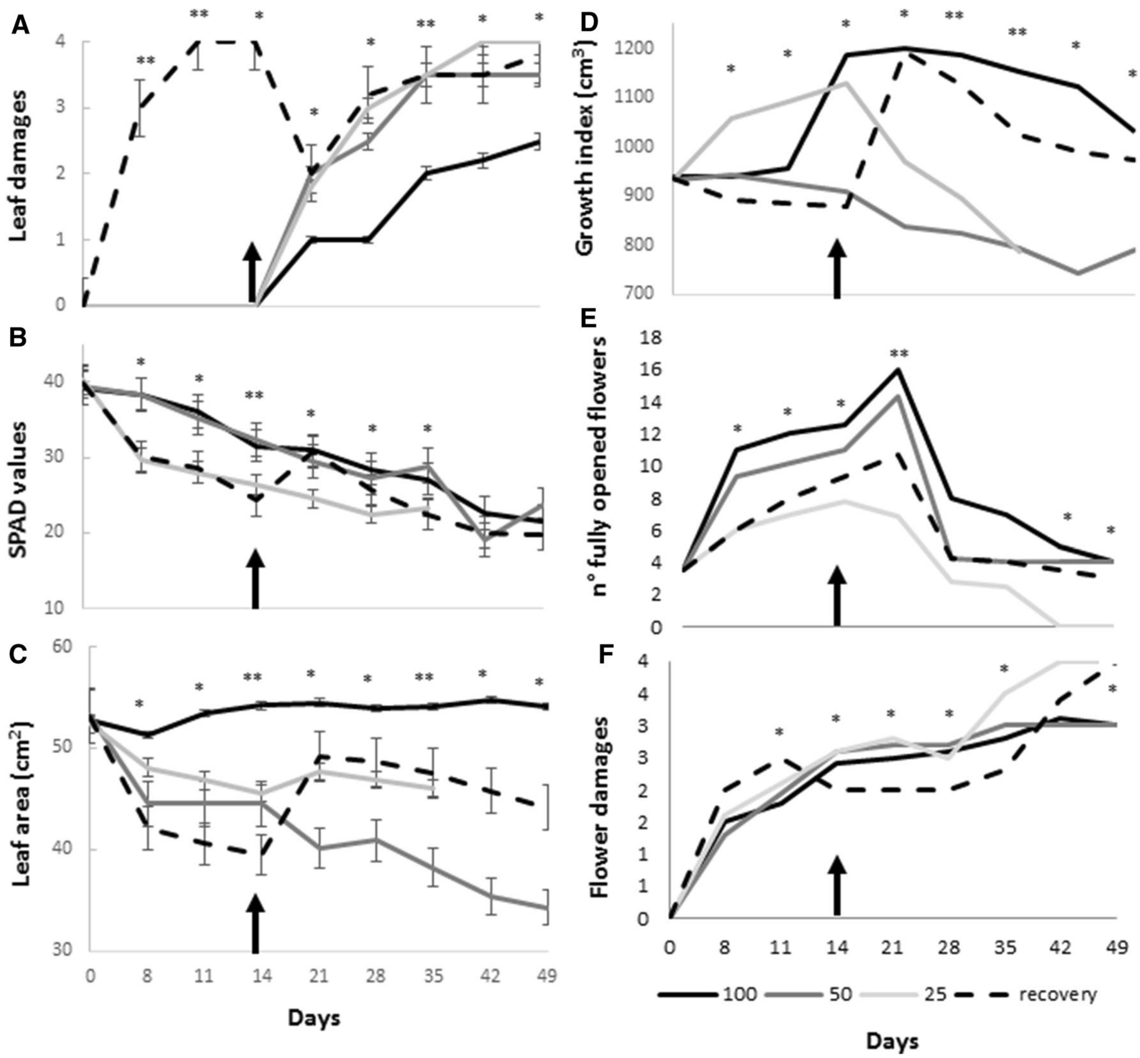


Fig. 2 Effect of irrigation treatments (100% of container capacity, control, *solid black line*), 50% of the control (moderate water stress, *solid dark grey line*), 25% of the control (severe water stress, *solid light grey line*), or no irrigation followed by recovery phase at day 14 (*dotted black line*) on leaf damage (class values) (**a**), SPAD values (**b**), leaf area (cm^2) (**c**), growth index (G.I., cm^3) (**d**), number of opened flowers (**e**), and flower damages (**f**) based on five class of flower withered (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100% of flower area) of *P. vulgaris* 'Heidy' plants during the Experiment 2. The *arrow* indicate the begin of the recovery phase. Means were subjected to Ryan–Einot–Gabriel–Welsch (F) post hoc test (*$P \leq 0.05$, **≤ 0.001)

Not irrigated plants showed the lowest values for both traits at day 11. The recovery phase was effective to increase the studied traits starting from the day 14 onward. The effect of water stress on plant growth reduction has been described in several crops species such as *Cistus albidus, Cistus monspeliensis, Petunia* × *hybrida, Pelargonium* × *hortorum* and *Callistemon citrinus* (Sánchez-Blanco et al. 2002; Niu et al. 2006; Vernieri et al. 2006; Álvarez and Sanchez-Blanco 2013). During severe water stress, the total leaf area and the stem length commonly significantly decreased in many ornamentals such as potted *Dianthus caryophyllus* and *Petunia* × *hybrida* (Álvarez et al. 2009; Van Iersel et al. 2010), resulting from the decline in the cell enlargement and the leaves senescence (Bañón et al. 2004).

The present experiment was conducted at the beginning of the blooming stage and is known that flowering is the most sensitive phase to water stress in ornamental plants such as in potted geranium (Álvarez et al. 2013). Here, significant differences between treatments in the number of fully opened flowers were observed (Fig. 2e). At day 8, fully irrigated plants presented more opened flowers (11 flowers per plant) than the others. At day 21, plants subjected to control, moderate water stress, and recovery treatments had more flowers than severe water stressed plants (16, 14, 11 and 7, respectively). In fact, these lasts anticipated the flowering peak at day 14. Later, a general decrease in all the treated plants was observed. As indicated in the previous experiment, *P. vulgaris* 'Heidy' subjected to drought stress maintain active photosynthesis, suggesting that no metabolic impairment occurred in this cultivar. In fact, in this experiment we can observe a flower production strictly related to the severity of imposed water stress and not a flowering peak induction caused by severe water stress. Figure 2f shows the evolution of flower damage (wilted flowers) during the experiment. In general no significant differences were observed, even if, fully and half irrigated plants had a similar dynamic. The recovered plants showed a restoration already after the first week of recovery, showing the lowest damages from day 14 till day 35. Later, a strong increase occurred, reaching the highest class of flower damage (4.0) at the end of the experiment as well as for severe water stressed plants. As reported by different authors, water stress application may increase flower damages and reduce flowering intensity such as in *Antirhinum majus* (Asrar et al. 2012) and in *Callistemon citrinus* (Álvarez and Sanchez-Blanco 2013, 2015).

Table 2 Influence of water stress (full irrigation, control, 100% of container capacity; 50% of the control, moderate water stress, MWS; 25% of the control, severe water stress, SWS; no irrigation water followed by recovery at day 14) on flower diameter (cm), dry weight/fresh weight rate (DW:FW), and midday leaf water potential (MLWP, MPa) on *P. vulgaris* 'Heidy' plants at the end of the Experiment 2

Treatments	Flower diameter	DW:FW	MLWP
Control	3.2a§	0.29c	−0.07a
MWS	3.0a	0.50b	−0.15b
SWS	1.9b	0.98a	−0.46c
No water + r	3.0a	0.28c	−0.27b
P	**	**	**

§Different letter indicates significant differences at the 0.05 level, Ryan–Einot–Gabriel–Welsch (F) post hoc test (*P ≤ 0.05, ** ≤ 0.001, *ns* not significant)

At the end of the experiment the mean flower diameter, dry weight and fresh weight ratio, and the midday leaf water potential were evaluated (Table 2). Fully irrigated plants showed the highest values in flower diameter, without significant differences with half irrigated and recovered plants, and in MLWP. No differences with recovered plants were observed also in DW:FW ratio. On the opposite, plants subjected to severe water stress showed the lowest values in all the traits (1.9 cm, and −0.46 MPa, respectively) with exception for DW:FW ratio (0.98). These results confirmed that controlled irrigation practices could be possible and can be a useful tool to affect ornamental and morphological characteristics.

Experiment 3

Plant growth and ornamental traits

Water use in the nursery is an increasingly important factor due to limited water supply and drought is one of the main adverse factors for seasonal plants, especially for plants grown in pots (Álvarez et al. 2013). In the present experiment three irrigation regimes were applied during the common growing cycle of potted *P. vulgaris* 'Heidy' in nursery conditions.

The percentage of senescent plants, the aerial dry and fresh weight ratio, the growth index, the number of leaves and the SPAD values were not affected by control and moderate water stress treatments (Table 3; Fig. 3). At the opposite, severe water stress significantly increased the percentage of senescent plants starting from day 29 (21.7%) until the end of the experiment, when the 83% of plants were completely senescent. While the application of the same irrigation regime resulted in the lower values in the G.I., starting from day 29, in the leaf area, from day 46, and in the number of leaves from day 85. A significant increase in SPAD values occurred at day 163 (32.7) in comparison with control and moderate water stress (20.0 and 21.1,

Table 3 Effect of different irrigation regimes (full irrigation, control, 100% of container capacity; 66% of the control, moderate water stress, MWS; 33% of the control, severe water stress, SWS) on the mean percentage (%) of senescent plants of *P. vulgaris* 'Heidy' during the pot cultivation and the aerial dry weight/fresh weight ratio (DW:FW) calculated at the end of the Experiment 3

Treatments	Senescence (%)							
	Days							
	29	46	71	85	113	142	163	DW:FW
Control	0b§	0b	0b	0b	0b	0b	0b	0.19b
MWS	0b	1.7b	3.3b	3.5b	3.8b	4.0b	5.3b	0.19b
SWS	21.7a	36.7a	38.6a	41.7a	59a	66.7a	83a	0.29a
P	*	*	*	*	**	**	**	*

§Different letter indicates significant differences at the 0.05 level, Ryan–Einot–Gabriel–Welsch (F) post hoc test (*P ≤ 0.05, ** ≤ 0.001, ns = not significant)

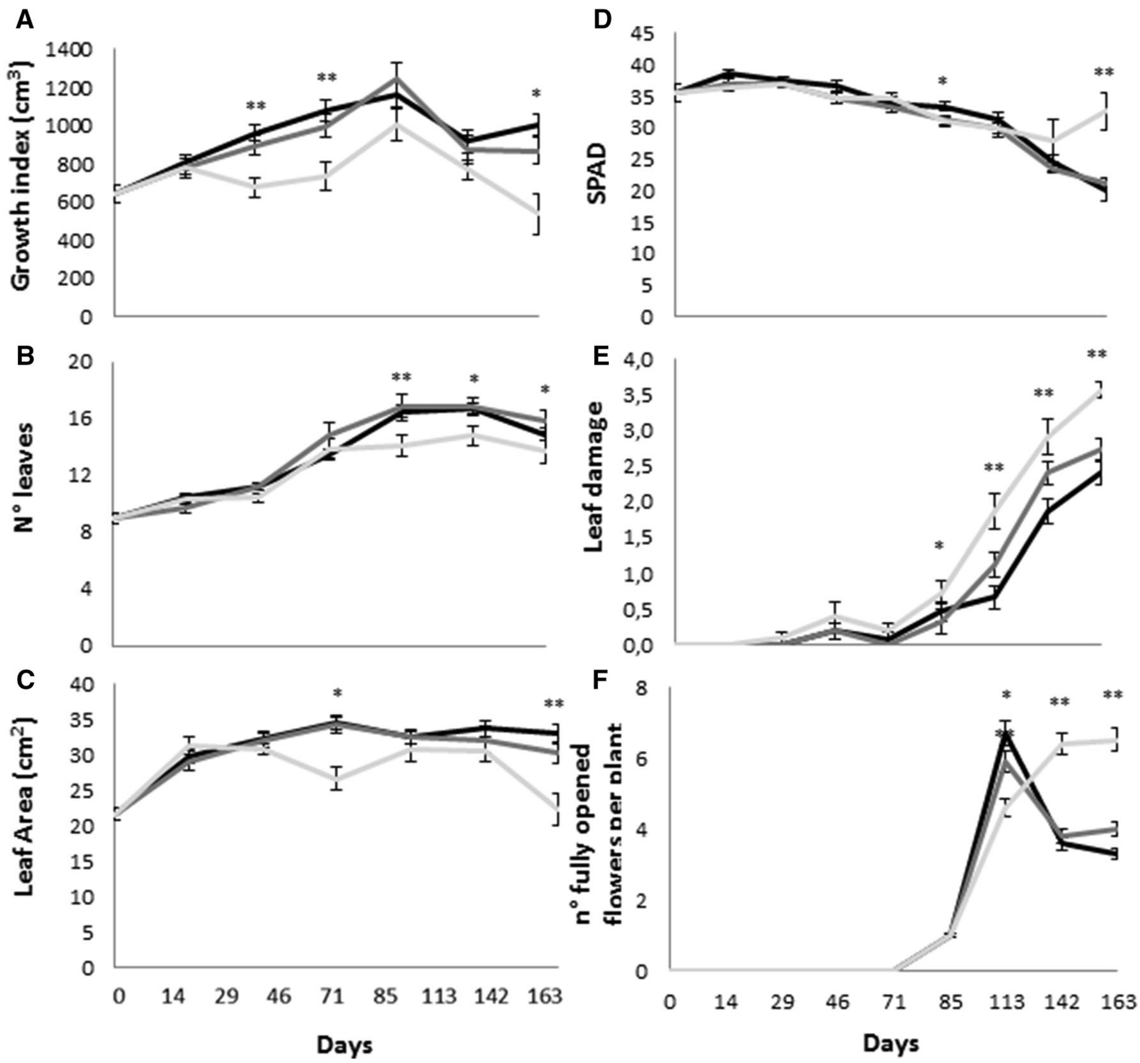


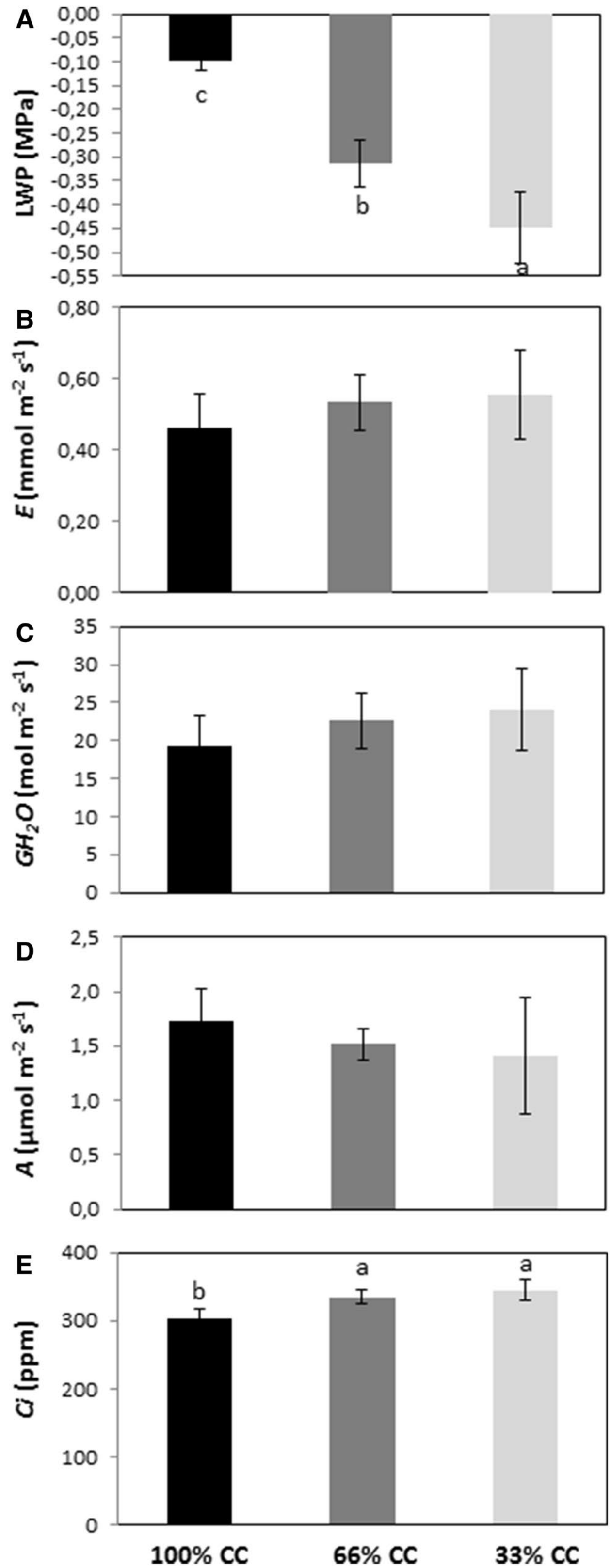
Fig. 3 Growth index (cm^3) (**a**), number of leaves (**b**), leaf area (cm^2) (**c**), SPAD values (**d**), leaf damages based on five classes of wilted damages (0 = 0%; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; 4 = 76–100% leaf area) (**e**), and number of opened flowers (**f**) variation in potted *P. vulgaris* 'Heidy' plants under full irrigation (100% of container capacity, control, *solid black line*), moderate water stress (66% of the control, *solid dark grey line*), or severe water stress (33% of the control, *solid light grey line*). Each time point represents the mean values and the *vertical bars* indicate standard errors. Means were subjected to Ryan–Einot–Gabriel–Welsch (F) post hoc test (*P ≤ 0.05, ** ≤ 0.001)

respectively). A peak in SPAD values in plants close to the full senescence was observed also in aromatic plants such as *Salvia sinaloensis, S. dolomitica* and *Helicrhysum petiolare* treated with 20% of container capacity as showed by Caser et al. (2012). This result could be explained by the fact that the leaf water status of a plant may interfere with the SPAD 502 Chlorophyll Meter measurements. Martinez and Guiamet (2004) also described that SPAD values increased as leaf water content decreased in wheat leaves. Taken together these data highlighted the possibility of water safe of ca. 35% without compromise the survival of plants. With the same purpose to reduce water irrigation, similar results were observed also in other nursery potted species such as *D. caryophyllus* and *Pelargonium* × *hortorum* subjected to 35 and 40% of control irrigation as described by Álvarez et al. (2009) and Sánchez-Blanco et al. (2009), respectively. Moreover, as shown in Table 3, the irrigation with 33% of the control induced significant higher aerial dry/fresh weight ratio. While, no differences in the root quality (data not shown) was observed between treatments, indicating that shoots and roots react differently to drought (Bacelar et al. 2007). The effect of water stress is usually greater on aerial growth than on root growth as indicated by Navarro et al. (2009). As reported by Bradford and Hsiao (1982) and by Sánchez-Blanco et al. (2009), this is probably due to the plants need to maintain root surface area under drought conditions in order to absorb water from the substrate. This criterion can be considered as a plant adaptation to drought conditions and could promote a quicker establishment in gardening (Franco et al. 2011). Within the genus *Primula*, also Noda et al. (2004) found out that water stress increased the root weight in *Primula sieboldii*. Thus, the application of controlled deficit irrigation during nursery production can be used as a technique to save water without reducing morphological traits (Morvant et al. 1998). However, plants may lose their ornamental characteristics and reduce and delay flowering to save assimilates (Augé et al. 2003; Cameron et al. 2006; Álvarez et al. 2009). Flower colour parameters (lightness, chroma and hue angle) variation during the blooming stage were not affected by imposed treatments (data not shown). This suggested that the petal colour was not modified by the applied water stress conditions and meaning that plants can cope with water shortage without losing their ornamental value (Brawner 2003). Similar results were observed in potted *Pelargonium* × *hortorum* (Sánchez-Blanco et al. 2009; Álvarez et al. 2013), *Dianthus caryophyllus* (Álvarez et al. 2009) and in *Callistemon citrinus* (Álvarez and Sanchez-Blanco 2013) plants in which deficit irrigation treatments did not affected flower colour parameters. Instead, plant quality in terms of percentage of leaf damage (wilted leaves) was significantly affected by moderate and severe water stress starting from day 113 onward (Fig. 3e). Only at the end of the experiment moderate water stressed plants showed a similar leaf damage to the controlled (2.73 and 2.40, respectively). Concerning the number of fully opened flowers during the growing season, control and moderate water stressed plants showed a similar trend (Fig. 3f). The blooming peak was observed at day 113 with 6.7 and 5.9 flowers per plants, respectively. On the opposite, at day 142 and 163 the highest number of flowers per plants was observed in severe stressed plants (6.4 and 6.5 flowers, respectively). These results highlighted that this condition extend and delay the flowering period in *P. vulgaris* 'Heidy'. Unlike the Experiment 2, here, in common growing condition, we observed that severe water stress significantly influenced a delay of flowering in the studied plants, implying that the different growing conditions may influence the flower development. Several studies further indicate that drought delays the onset of flowering and shortens the length of flowering (Prieto et al. 2008; Jentsch et al. 2009) such as in *Genista tinctoria* and *Calluna vulgaris* subjected to recurring weather extremes (Nagy et al. 2013). Control and moderate water stress induced also the highest peduncles and the largest flowers in comparison with the severe water stress conditions (5.9, 6.1 and 4.4 cm and 5.1, 5.2 and 3.7 cm, respectively). These data suggested that *P. vulgaris* 'Heidy' requires at least 66% of control irrigation to maintain acceptable plant and flower quality. Similarly, another season plant such as potted geranium, cultivated in nursery, needs at least 75% of control irrigation as reported by Henson et al. (2006) and Sánchez-Blanco et al. (2009). Nevertheless, further research is required to determine the most appropriate degree of water stress in order to optimise the growth and health of the plants and flower development. Similarly, Ma and Gu (2012) successfully applied severe water stress to extend flowering in *Bougainvillea spectabilis* 'Raspberry ice'.

Water relations

Midday leaf water potential and gas exchange traits were measured at the beginning of the blooming stage (Fig. 4). Moderate and severe water stressed plants showed significant lower MLWP (−0.31 and −0.45 MPa, respectively) than control (−0.10 MPa; Fig. 4a). The data on MLWP are in agreement with the previous experiments conducted under controlled growth conditions. In particular, under severe water stress the decrease in the leaf water potential could be the cause of morphological adaptations previously described such as lower growth index, number of leaves, leaf area, and dry weight, which could contribute to reduce the total water consumption (Kang et al. 2000). Moreover, we can confirm that a MLWP equal to −0.40 MPa could be considered as a critic threshold for the survival of the studied plants. On the opposite, differences with the previous experiment were highlighted on gas exchange traits. We observed that after about 80 days of cultivation under common nursery conditions, no differences between treatments were measured, and the levels of transpiration rate (*E*), stomatal conductance (GH_2O), and net photosynthetic rate (*A*) were lower than at the end of the Experiment 1 (almost 1/5 in *E* and GH_2O and 1/10 in *A*). This fact could be explained by the completely different growing conditions and by the longest cultivation period in comparison to the previous experiment. While, both moderate and severe water stress induced significant higher content of internal CO_2 concentration (C_i). Within the genus *Primula*, Dietz and Heber (1983) reported that water stressed *P. palinuri* in field showed a complete wilting with MLWP equal to −4.0 MPa, much lower than in our study and that the complete stomatal closure was reach with at least a water loss of the 20% of turgid leaves. Here, a shift from stomatal limitation to non-stomatal limitation was observed as described by Siddique et al. (2016). We can hypothesize that studied plants impaired carbon assimilation to cope with drought by conserving the internal CO_2 and blocking photosynthesis. Hasibeder et al. (2015) demonstrated that in plants under severe drought regimes the usage of fresh photosynthates is transferred from metabolic activity to osmotic adjustment and storage compounds. Taken together all these results

Fig. 4 Values of midday leaf water potential (MLWP, MPa) (**a**), transpiration rate (*E*) (**b**), stomatal conductance (*GH_2O*) (**c**), net photosynthetic rate (*A*) (**d**), and internal CO_2 concentration (C_i) (**e**) at the beginning of the blooming phase (day 85) of *P. vulgaris* 'Heidy' plants. *Black histograms* referred to full irrigation (100% of container capacity, control), *dark grey histograms* to moderate water stress (66% of the control), and *light grey histograms* to severe water stress (33% of the control). Each histogram represents the mean values, the *vertical bars* indicate standard errors and *similar letters* indicate not significant differences ($P \leq 0.05$) according to Ryan–Einot–Gabriel–Welsch (F) post hoc test



suggested that there is variability within *Primula* species and that *P. vulgaris* 'Heidy' is a not a drought tolerant cultivar under severe water stress.

Conclusions

In controlled growth conditions, the mechanism of drought tolerance of *P. vulgaris* 'Heidy' was described by the physiological dynamics, that show a long-term decline in stomatal conductance and transpiration rate also under extreme drought condition. The application of recovery resulted in a restoration of all the morphological and ornamental traits and in the leaf water potential, thus the decrease in leaf water potential during the water stress could be reversed by the application of control irrigation.

Under common nursery cultivation practices, moderate water stress could be successfully applied in potted *P. vulgaris* 'Heidy' production, allowing a reduction of ca. 40% (ca. 1.64 L h^{-1} per plant) of irrigation water and in the meanwhile maintaining plant health and ornamental quality comparable with common irrigation practice. Also severe deficit irrigation did not affect ornamental quality in terms of flower colour, number and size, but it deeply compromised plant survival. Overall, the studied cultivar appears to be a not drought tolerant cultivar reacting to deficit irrigation by reducing leaf water potential and stomata, activating photosynthesis and maintaining the water use efficiency similarly to control plants. In both growth conditions, the parameters that best allow determining the water use of the studied species were leaf water potential, gas exchanges, leaves traits, growth index, and the percentage of senescent plants.

In conclusion, the degree of the imposed water stress is critical to reveal the responses of the different species at the different phenological stages. The knowledge of physiological dynamics and morphological responses to water stress of a potted seasonal ornamental plant along the cultivation cycle could allow floriculture companies to schedule a sustainable irrigation plan, which match the effective species water needs.

Acknowledgements This work has been supported by "PSR 2007-2013-Misura 1.1.1. - Progetti dimostrativi semplici - Risparmio Idrico in Floricoltura (R.ID.inFlor.)" project. The authors gratefully acknowledge Alessia Aru, Eugenio Lagomarsino and Andrea Sampietro for providing plant material and practical help.

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