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Modelling transpiration of greenhouse gerbera (*Gerbera jamesonii* H. Bolus) grown in substrate with saline water in a Mediterranean climate



Giulia Carmassi ^a, Laura Bacci ^b, Matteo Bronzini ^a, Luca Incrocci ^a, Rita Maggini ^a, Gianni Bellocchi ^c, Daniele Massa ^d, Alberto Pardossi ^{a,*}

^a Department of Agriculture, Food and Environment, University of Pisa, Pisa, Italy

^b Institute of Biometeorology, CNR-IBIMET, Sesto Fiorentino, Firenze, Italy

^c Grassland Ecosystem Research Unit, French National Institute for Agricultural Research, UREP-INRA, Clermont-Ferrand, France

^d Consiglio per la Ricerca e la Sperimentazione in Agricoltura, CRA-VIV, Pescia (PT), Italy

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ABSTRACT

Gerbera plants were grown in semi-closed rockwool culture under greenhouse conditions in different seasons in a Mediterranean climate. The plants were irrigated using either fresh (FW; 1.0 mol m⁻³ NaCl) or moderately saline (SW; 9.0 mol m⁻³ NaCl) water. In autumn, NaCl concentration did not influence significantly plant growth, flower production and transpiration (E), which instead were reduced in spring in the plants irrigated with SW. In both seasons, water salinity did not affect leaf stomatal resistance (r_l), which was determined by the inversion of the Penman–Monteith (PM) equation or measured with a diffusion porometer. The PM formula and two regression equations were calibrated and validated for estimating the hourly rate of daytime transpiration (E_d); a regression model was also fit to nocturnal transpiration (E_n). Regression models predicted E_d as a function of vapour pressure deficit (VPD) and/or the radiation intercepted by the canopy. Leaf area index (LAI), which is required by all the equations, was modelled as function of crop thermal time (i.e. growing degree days). The PM model predicted E_d using a constant value of r_l . Model calibration and validation were performed using independent datasets. The irrigation with FW or SW did not require a different calibration of transpiration models. Both PM formula and regression equations provided accurate estimates of E_d ; fitted equations explained between 80% and 96% of the variance in measured E_d . A linear regression of E_n against (LAI·VPD) accounted for 92% of measured E_n .

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1. Introduction

Greenhouse crops are generally over-irrigated and this results in water loss and environmental degradation due to fertilizers leaching (Vox et al., 2010). A major cause of over-irrigation is inadequate scheduling, which often is based on grower's experience rather than on accurate assessment of crop water requirements (Pardossi and Incrocci, 2011; Thompson et al., 2007).

Leaf transpiration (E) is the primary process affecting plant water uptake (W) and hence its knowledge is necessary to determine crop water needs. In greenhouse crops, particularly in substrate culture, irrigation control requires the determination of E over short time intervals (hourly or less). If E is known as a function of climatic variables, E models can be easily implemented for

automated irrigation control. Modelling E can also provide a soft-sensor in an early warning system for growers (Elings and Voogt, 2007). For instance, a reduction of actual E with respect to the predictions may indicate alterations of plant water status resulting from a technical failure of irrigation system, mistakes in fertilization management and/or the occurrence of root diseases.

The use of the Penman–Monteith (PM) equation (Allen et al., 1998) provides accurate E prediction; however, it requires several input parameters that are difficult to estimate, such as leaf stomatal resistance (r_l). Several authors (e.g. Baille et al., 1994a; Carmassi et al., 2007a; Kittas et al., 1999) proposed simplified forms of the PM formula based on the assumption of constant r_l .

The PM equation and its simplified versions have been used for predicting E in a variety of greenhouse crops, such as cucumber (Medrano et al., 2005), geranium (Montero et al., 2001), lettuce (Pollet et al., 2000), rose (Baille et al., 1994b; Kittas et al., 1999), tomato (Carmassi et al., 2007a; Stanghellini, 1987), zucchini (Rouphael and Colla, 2004) and some pot ornamentals (Bailey et al., 1993; Baille et al., 1994a). However, less attention has been paid

* Corresponding author at: Viale delle Piagge 23, 56124 Pisa, Italy.
Tel.: +39 0502216526; fax: +39 0502216524.

E-mail address: alberto.pardossi@agr.unipi.it (A. Pardossi).

Abbreviation

Symbol or abbreviation

<i>A</i>	empirical coefficient in Eqs. (9) and (12)
<i>B</i>	empirical coefficient in Eqs. (9) and (13) (kg m ⁻² h ⁻¹ kPa ⁻¹)
<i>c_p</i>	specific heat of the air (J kg ⁻¹ K ⁻¹)
<i>d</i>	leaf dimensions (m)
<i>E</i>	transpiration rate (kg m ⁻² h ⁻¹ or kg m ⁻² day ⁻¹)
<i>E_{24h}</i>	crop transpiration in the 24 h period (kg m ⁻² day ⁻¹)
<i>e_a</i>	air vapour pressure (kPa)
<i>e[*]</i>	saturated air vapour pressure (kPa)
<i>EC</i>	electrical conductivity (dS m ⁻¹)
<i>E_d</i>	daytime transpiration rate (kg m ⁻² h ⁻¹)
<i>E_n</i>	nocturnal crop transpiration rate (kg m ⁻² h ⁻¹)
<i>FW</i>	fresh water
<i>g</i>	gravity acceleration (m s ⁻²)
<i>GDD</i>	growing degree days (°C)
<i>Gr</i>	Grashof number
<i>h</i>	heat transfer coefficient (W m ⁻² K ⁻¹)
<i>I</i>	indoor global radiation (MJ m ⁻² ; W m ⁻²)
<i>I_c</i>	global radiation intercepted by crop canopy (MJ m ⁻² ; W m ⁻²)
<i>I_n</i>	net radiation (MJ m ⁻² ; W m ⁻²)
<i>k</i>	light extinction coefficient (dimensionless)
<i>k_c</i>	thermal conductivity of air (W m ⁻¹ K ⁻¹)
<i>l_t</i>	leaf length (m)
<i>LAI</i>	leaf area index
<i>NS</i>	nutrient solution
<i>PM</i>	Penman–Monteith
<i>r_a</i>	aerodynamic resistance of the canopy to vapour transfer (s m ⁻¹)
<i>r_c</i>	canopy resistance (s m ⁻¹)
<i>Re</i>	Reynolds number
<i>r_i</i>	leaf stomatal resistance (s m ⁻¹)
<i>SW</i>	saline water
<i>T_a</i>	air temperature (°C)
<i>T_l</i>	leaf temperature (°C)
<i>u</i>	air velocity (m s ⁻¹)
<i>VPD</i>	vapour pressure deficit (kPa)
<i>v</i>	kinematic viscosity of air (m ² s ⁻¹)
<i>w</i>	leaf width (m)
<i>W</i>	water uptake (kg m ⁻²)
β	thermal expansion coefficient of air (K ⁻¹)
Δ	slope of the relationship of saturation vapour pressure on temperature (kPa °C ⁻¹)
γ	psychrometric constant (kPa °C ⁻¹)
λ	latent heat of water vaporization (J kg ⁻¹)
ρ	air density (kg m ⁻³)
Ω	decoupling coefficient

to cut-flower gerbera (*Gerbera jamesonii* H. Bolus), one of the most important greenhouse ornamental crops (Vidalie, 2007). To the best of our knowledge, only a short paper on modelling *E* in gerbera was published in the proceedings of an international symposium (Marfà et al., 2000).

In this work, we used the PM model and two regression equations to predict *E* of gerbera plants grown in semi-closed substrate (rockwool) culture under the typical greenhouse conditions of Mediterranean area. With respect to the paper published by Marfà et al. (2000), different approaches were used to estimate leaf area index (LAI) and *r_i*. Besides, we investigated the effect of NaCl salinity on crop growth and water relations, and its possible influence on modelling *E*. In many regions, particularly in the Mediterranean

area, protected horticulture is increasingly facing the salinization of water resources (Pardossi et al., 2004) and the knowledge of crop response to salinity is important for optimal crop management (Stanghellini et al., 2007). Greenhouse crops cannot be grown with highly saline water for being profitable (Stanghellini et al., 2007). Therefore, in our study a moderately saline water (NaCl concentration of 9.0 mol m⁻³ against 1.0 mol m⁻³ in the fresh or control water) was tested.

2. Materials and methods

2.1. Plant material and growing conditions

Gerbera (cv. Vital) plants were cultivated between 29 May 2004 and 30 November 2005 in a glasshouse at the University of Pisa (Pisa, Italy, latitude 43°43' N, longitude 10°23' E). The glasshouse was equipped with automated side and roof windows (with insect screens) and heating system; ventilation and minimum temperatures were 27 and 15 °C, respectively. The glasshouse was heated sporadically (generally only in the night) and was covered by black plastic net (30% shading rate) from late May to the end of August in both years.

The plants were grown in rockwool slabs at a density of approximately 5 plants m⁻². The glasshouse had six separate growing units, each consisting of two benches with 12 slabs (48 plants in total) and an 80 l mixing tank collecting the drainage NS. The total amount of recirculating NS, including the substrate and the mixing tank, was approximately 150 l (i.e. 15.61 m⁻² expressed per unit of ground area). In order to compensate crop *W*, the mixing tank was automatically refilled with full-strength NS. Drip irrigation was controlled by a timer; the plants were watered 2–6 times a day, depending on growth stage and seasons, with a watering dose of 1.5–2.0 l m⁻² (leaching fraction was roughly 0.30–0.50).

Nutrient solution was made up with either fresh water (FW; 1.0 mol m⁻³ NaCl) or saline water (SW; 9.0 mol m⁻³ NaCl), which were prepared by dissolving appropriate doses of NaCl to rainwater. Each treatment was applied to three separate growing units (replicates). All the plants were initially grown with FW; SW was applied at the beginning of September 2004. The EC of the NS prepared with FW and SW was 1.45 and 2.25 dS m⁻¹, respectively. The nutrient solution also contained 9.1 mol m⁻³ NO₃⁻, 1.0 mol m⁻³ H₂PO₄⁻, 4.3 mol m⁻³ K⁺, 1.1 mol m⁻³ Mg²⁺, 3.0 mol m⁻³ Ca²⁺, plus Hoagland concentration of trace elements. In each growing unit, NS was checked almost daily for EC and pH; the latter was kept between 5.5 and 6.0 by frequent addition of sulphuric acid. Nutrient solution was discharged whenever EC exceeded 3.0 or 4.0 dS m⁻¹ in the FW and SW cultures, respectively.

Older leaves were recurrently removed following growers' practice and in February of 2005 the plants were intensively defoliated in order to stimulate a new flush of growth.

2.2. Determinations

Crop growth, flower production and water relations were monitored in three periods (Table 1): (i) between 22 September 2004 and 9 January 2005 (110 days); (ii) between 11 April and 2 July 2005 (83 days); (iii) between 10 October and 20 November 2005 (42 days). In the third period, only *E* and *W* were measured.

Fresh and recirculating NS was periodically sampled for laboratory analyses of macronutrients and Na, as reported by Massa et al. (2010).

Crop shoot biomass and LAI were determined by sampling six individual plants from each treatment on 9 January and 3 July 2005. The plants were separated in leaves and inflorescences (stem and flower head), which were dried to constant weight at 80 °C

Table 1

Basic information on the experiments conducted for modelling the transpiration of greenhouse gerbera grown in semi-closed substrate culture in different seasons and irrigated with fresh (FW; 1.0 mol m⁻³ NaCl) or saline (SW; 9.0 mol m⁻³ NaCl) water. In autumn 2005, all gerbera plants were irrigated with FW.

Season (start date)	Days of observation	Mean air temperature (°C)	Daily solar radiation (MJ m ⁻²)	Mean VPD (kPa)	EC oscillation (dS m ⁻¹)	
					FW	SW
Autumn 2004 (22 September 2004)	110	17.4	2.27	0.30	2.48–3.42	3.08–4.05
Spring 2005 (11 April 2005)	83	22.6	9.87	1.02	1.97–3.03	2.78–4.21
Autumn 2005 (10 October 2005)	42	16.6	3.97	0.34	2.18–3.02	–

in a ventilated oven. Total biomass accumulation was computed including the leaves and the flowers detached in occasion of pruning and harvesting. Leaf area index was also determined weekly by non-destructive measurements of leaf dimensions (maximum length and width) of individual leaves using the equation reported by Carmassi et al. (2007b).

Daily W was determined by recording with a water meter the amount of NS used to refill the mixing tank. Hourly E was measured by weighing a tray with six plants using an electronic balance. The balance (capacity: 30 kg; resolution: ±0.001 kg) was placed in the centre of a bench with other plants in order to form a continuous canopy. We assumed that weight loss was equal to E as evaporation from substrate was prevented by plastic film. Indoor incident radiation (I), air temperature (T_a), wet and dry bulb air temperature, and calculated vapour pressure deficit (VPD) were recorded with a weather station located in the central part of the glasshouse. Both climate sensors and electronic balance were scanned every minute by a data logger and averages were made over 60 min time periods. Data recorded in occasion of irrigation events (until 20 min after the start of watering, when the drainage from the tray had terminated) and E values below 0.005 kg m⁻² h⁻¹ were discarded. As only one balance was available, crop E was monitored in each salinity treatment every other week. Daytime ($I \geq 25 \text{ W m}^{-2}$) values of E (E_d) were separated from those measured during the night (E_n ; $I < 25 \text{ W m}^{-2}$); actually, for E_d modelling we used the data recorded between 08.00 a.m. and 05.00 p.m. (10 h) in autumn, and between 07.00 a.m. and 07.00 p.m. (13 h) in spring.

On some days in autumn 2004 and in spring 2005, we measured leaf stomatal resistance (r_l) with a diffusion porometer (MK, Delta-T Devices, Cambridge, UK). The measurements were taken between 11.00 a.m. and 01.00 p.m.; in each treatment, 2–3 leaves were sampled from 4 to 6 individual plants.

Leaf temperature (T_l) and air velocity (u , m s⁻¹) were measured discontinuously with a portable infrared thermometer and a hot-wire anemometer.

2.3. Transpiration models

The first model was derived from the PM equation (Allen et al., 1998; Baille et al., 1994b):

$$\lambda \cdot E = \frac{\Delta \cdot I_c}{\Delta + \gamma^*} + \frac{(\rho \cdot c_p / r_a) \cdot (e_a^* - e_a)}{\Delta + \gamma^*} \quad (1)$$

where crop E (kg m⁻² h⁻¹) is based on ground area, λ (J kg⁻¹) is the latent heat of vaporization of water, I_c (W m⁻²) is the radiation intercepted by canopy, ρ (kg m⁻³) is air density, c_p (J kg⁻¹ K⁻¹) is the specific heat of air at constant pressure, e_a (kPa) is the air vapour pressure, e_a^* (kPa) is the saturated air vapour pressure, r_a (s m⁻¹) is the aerodynamic resistance to vapour transfer, Δ (kPa °C⁻¹) is the slope of the relationship of saturation vapour pressure on temperature, $\gamma^* = \gamma(1 + r_c/r_a)$ where γ (kPa °C⁻¹) is the psychrometric constant, and r_c (s m⁻¹) is the mean canopy resistance.

The term I_c in Eq. (1) was calculated as:

$$I_c = I \cdot (1 - \exp^{-k \cdot LAI}) \quad (2)$$

where k (dimensionless) is the light interception coefficient. This coefficient was determined on the basis of Lambert–Beer's law from the radiation measured with a piranometer placed above and below the crop row (Nobel and Long, 1985).

In Eq. (2), I was used instead of net radiation (I_n) because net radiometer was not available. This was possible because in unheated greenhouses I_n matches I during the light period (Bailey et al., 1993; Baille et al., 1994a). In another experiment conducted in 2006 with gerbera grown in the same glasshouse (unpublished results), a close linear relationship was found between I_n and I ($I_n = 0.981I$; $R^2 = 0.902$; $n = 487$) in the range between 25 and 545 W m⁻².

Leaf area index was estimated as a function of growing degree days (GDD) assuming a base temperature of 8 °C.

Canopy resistance was computed as the ratio between r_l and LAI while r_a was calculated as follows:

$$r_a = \frac{\rho \cdot c_p}{2 \cdot LAI \cdot h} \quad (3)$$

where h (W m⁻² K⁻¹) is the heat transfer coefficient for individual leaves (Bailey et al., 1993).

There is no consensus on how heat is transferred under greenhouse conditions and hence h was calculated according to the free (McAdams, 1954), forced (Gröber and Erk, 1961) or mixed convection (Stanghellini, 1987) using the Grashof (Gr) and Reynolds (Re) numbers (Bailey et al., 1993). In a preliminary data analysis, we found that the best predictions of E were obtained when h was computed assuming a mixed convection, as follows:

$$h = 0.37 \cdot \left(\frac{k_c}{d} \right) \cdot (Gr + 6.92Re^2)^{1/4} \quad (4)$$

where k_c (W m⁻¹ K⁻¹) is the thermal conductivity of air and d (m) is the leaf dimension determined as:

$$d = \frac{2}{(1/l_t) + (1/w)} \quad (5)$$

where l_t (m) and w (m) are, respectively, the length and the width of the leaves.

The numbers of Grashof and Reynolds correspond to the air flow occurring in free and forced convection, respectively.

The Grashof number was computed as a function of the difference between T_l and T_a :

$$Gr = \frac{\beta \cdot g \cdot d^3 \cdot |T_l - T_a|}{\nu^2} \quad (6)$$

where β (K⁻¹) is the thermal expansion coefficient of air, g (m s⁻²) is the acceleration due to gravity and ν (m² s⁻¹) is the kinematic viscosity of air.

The Reynolds number (Re) was obtained from u , d and ν , as follows

$$Re = \frac{u \cdot d}{\nu} \quad (7)$$

Leaves are generally very thin, thus the temperature of the upper and lower leaf surface was assumed equal.

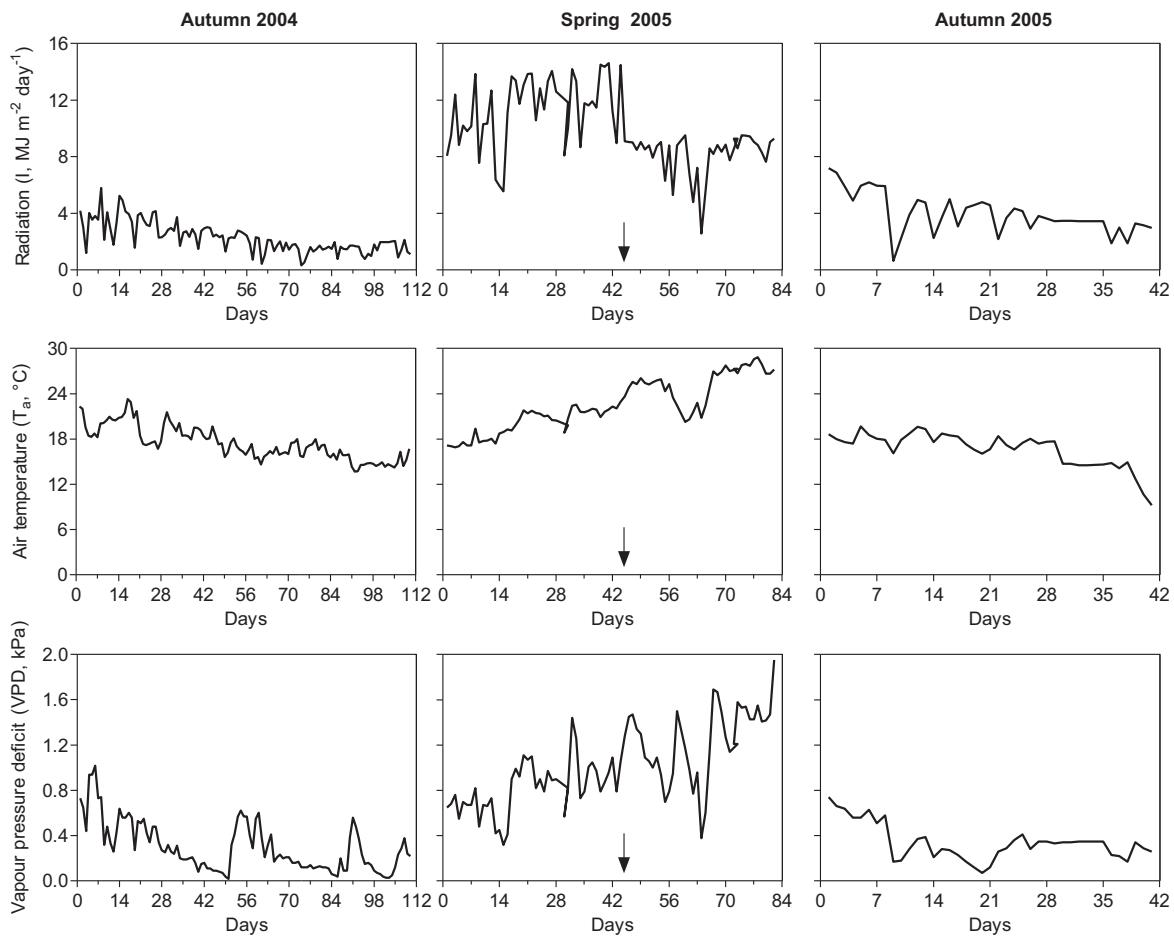


Fig. 1. Daily values of incident radiation and average air temperature and vapour pressure deficit (VPD) in the glasshouse during the experiments conducted with gerbera grown in semi-closed substrate culture in different seasons between 2004 and 2005. Data refer to three periods: (i) 22 September 2004 to 9 January 2005 (110 days); (ii) 11 April to 2 July 2005 (83 days); (iii) 10 October to 20 November 2005 (42 days). Arrows indicate when the greenhouse was shaded with plastic net during the spring of 2005.

The dimensionless decoupling coefficient (Ω) was calculated to analyze the dependence of E_d on atmospheric environment and stomatal opening (Jarvis and McNaughton, 1986), namely:

$$\Omega = \frac{1}{1 + (\gamma/(\Delta + \gamma)) \cdot (r_c/r_a)} \quad (8)$$

Transpiration rate was also modelled using the equation proposed by Baille et al. (1994a):

$$E_d = A \cdot \frac{I_c}{\lambda} + B \cdot LAI \cdot VPD \quad (9)$$

The coefficients A (dimensionless) and B (kg m⁻² h⁻¹ kPa⁻¹) were obtained by regressing measured E against I_c (MJ m⁻² h⁻¹) and (LAI·VPD).

2.4. Statistics

The influence of growing season and irrigation water salinity on crop growth, flower production and seasonal W was assessed through ANOVA. Calibration and validation of E models was performed using independent datasets. Model accuracy was assessed by regression analysis of predictions against measurements; we computed the slope and the intercept of the linear regression, the determination coefficient (R^2), the standard error of estimates (SEE), the mean percentage error (MPE) and the mean absolute percentage error (MAPE). Statistical analysis was performed with Statgraphics Centurion XV (Statpoint Technologies, Inc., Warrenton, VA, USA).

3. Results and discussion

3.1. Growing conditions

Fig. 1 shows the seasonal variations of daily values of I , T_a and VPD. Daily averages of I , T_a and VPD were, respectively 2.27 MJ m⁻² day⁻¹, 17.4 °C and 0.30 kPa in the autumn of 2004; 9.87 MJ m⁻² day⁻¹, 22.6 °C and 1.02 kPa in the spring of 2005; 3.97 MJ m⁻² day⁻¹, 16.6 °C and 0.34 kPa in the autumn of 2005 (Table 1). Over the daylight period, I , T_a and VPD ranged, respectively; from 0.10 to 0.47 MJ m⁻² h⁻¹, from 17.1 to 23.2 °C and from 0.22 to 0.95 kPa in autumn; from 0.14 to 1.10 MJ m⁻² h⁻¹, from 20.6 to 28.8 °C and from 0.56 to 2.70 kPa in spring. Despite glasshouse shading, in late spring and summer T_a exceeded frequently 30 °C during sunny hours. Significant positive correlations were found between I and T_a ($R^2 = 0.328$; $n = 1374$) or VPD ($R^2 = 0.381$), and between T_a and VPD ($R^2 = 0.738$). In the night, significant correlation ($R^2 = 0.563$; $n = 908$) was found between T_a and VPD.

In the FW culture, the EC of recirculating NS ranged from 2.48 to 3.42 dS m⁻¹ with a mean value of 2.78 dS m⁻¹ in the autumn of 2004, and from 1.97 and 3.03 dS m⁻¹ with a mean value of 2.28 dS m⁻¹ in the spring of 2005; NS solution was discharged on two occasions in autumn and on four occasions in spring. In the SW culture, EC oscillated between 2.78 and 4.21 dS m⁻¹ with a mean value of 3.62 dS m⁻¹ in autumn, when NS was discharged four times, and between 2.78 and 4.21 dS m⁻¹ with a mean value of 3.69 dS m⁻¹ in the spring of 2005, when NS was discharged eight times.

Table 2

Crop water relations, growth and flower production in greenhouse gerbera grown in semi-closed substrate culture in different seasons and irrigated with fresh (FW; 1.0 mol m^{-3} NaCl) or saline (SW; 9.0 mol m^{-3} NaCl) water. Mean values ($\pm \text{SE}$); $n = 3$ or 247–358 E_d observations. Shoot dry biomass includes the older leaves recurrently removed during the cultivation while LAI refers to the values determined at the end of each season. In each column, the means separated by different letters are significantly different ($p < 0.05$) according to ANOVA. The interaction between growing season and water salinity was significant ($p < 0.05$) for all measured quantities.

Season	Water source	Seasonal water uptake (kg m^{-2})	Mean daily water uptake ($\text{kg m}^{-2} \text{ day}^{-1}$)	Mean hourly rate of daytime transpiration (E_d ; $\text{kg m}^{-2} \text{ day}^{-1}$)	Shoot dry biomass (kg m^{-2})	Leaf area index (LAI)	Flower production (stems m^{-2})
Autumn 2004 (110 days)	FW	64.9 \pm 3.7c	0.59 \pm 0.07c	0.053 \pm 0.004c	0.39 \pm 0.02c	1.02 \pm 0.08c	58.2 \pm 5.4c
	SW	56.1 \pm 3.0d	0.51 \pm 0.05c	0.049 \pm 0.004c	0.39 \pm 0.06c	1.04 \pm 0.06c	50.8 \pm 7.8c
Spring 2005 (83 days)	FW	222.4 \pm 8.2a	2.68 \pm 0.10a	0.203 \pm 0.003a	0.71 \pm 0.01a	2.43 \pm 0.19a	104.5 \pm 0.8a
	SW	168.5 \pm 4.6b	2.03 \pm 0.07b	0.136 \pm 0.003b	0.50 \pm 0.05b	1.40 \pm 0.20b	76.3 \pm 9.1b

In all the cultures, salinity build-up in the recirculating NS was principally due to NaCl accumulation (data not shown) as found by other authors in closed-loop soilless cultures (Massa et al., 2010; Savvas et al., 2008). Mean concentrations of both macronutrients and micronutrients in the recirculating NS were generally close to their content in the refill NS (data not shown).

3.2. Crop growth and production

NaCl salinity reduces crop growth and production in sensitive species (Volkmar et al., 1998) due to its negative effects on water and mineral relations, carbon assimilation and biomass partitioning. Crop response to salinity depends on cultivar and growing conditions (e.g. Baas et al., 1995; De Kreij and van Os, 1989; Sonneveld et al., 1999). Gerbera is a crop moderately sensitive to salinity (Baas et al., 1995; Sonneveld et al., 1999). According to these authors, the maximum salinity (expressed as the EC of nutrient solution) without yield reduction in substrate-grown gerbera is $1.5\text{--}2.8 \text{ dS m}^{-1}$; the flower production decreased by 10% for each unit increase of EC above the threshold. In our work, gerbera plants appeared much more sensitive to NaCl salinity, at least in spring, since an increase of 1.41 dS m^{-1} in average EC of the recirculating NS resulted in a reduction of flower production of about 19% (Table 2).

In spring, the use of SW also reduced significantly shoot dry weight and LAI as compared to FW (Table 2). The reduction of LAI was due to an inhibition of both leaf expansion and formation. In fact, at the end of the season the leaves of non-salinized and salinized plants were 26.5 ± 0.50 and 21.50 ± 0.60 , respectively.

Negative effects of salinity on crop growth and/or fruit yield were alleviated in melon (An et al., 2002) and tomato (Li et al., 2001) when the plants were grown under high relative humidity, which reduced E compared to standard conditions.

3.3. Leaf area model

Modelling E requires the determination of LAI, which can be achieved by direct (destructive or non-destructive) measurements or simulation models. In both greenhouse and field crops, LAI development is often modelled as a function of GDD using non-linear (e.g. exponential and sigmoid) equations since crop LAI tends to reach a plateau (Thornley and Johnson, 1990). In our study, LAI increased with time in spring (Fig. 2) whereas it remained fairly constant around 1.0 in autumn, when the formation of new leaves was balanced by the weekly removal of older leaves. Compared to the plants irrigated with SW, those grown with FW showed faster leaf development and reached a maximum LAI around 2.4 within eight weeks from the start of observations (Fig. 2). In the

FW crop, the response of LAI to GDD was adequately described by an exponential function (Eq. (10); $R^2 = 0.986$; $n = 11$):

$$\text{LAI} = (1.043 - 2.448) \cdot \exp^{-0.0066 \cdot \text{GDD}} + 2.448 \quad (10)$$

On the contrary, in salinized plants LAI never reached a plateau during the study period (Fig. 2). A linear model fitted well measured LAI in this culture (Eq. (11); $R^2 = 0.938$; $n = 11$):

$$\text{LAI} = 0.9354 + 0.0006 \cdot \text{GDD} \quad (11)$$

Transpiration model also required to estimate I_c from LAI and k (Eq. (2)). The light extinction coefficient was determined when LAI was 1.03 ± 0.06 and 1.96 ± 0.08 , with similar results. It was 0.60 ± 0.02 ($n = 40$), in agreement with Marfà et al. (2000).

3.4. Crop water relations

The reliability of the electronic balance used for measuring E was assessed by comparing daily-cumulated E (E_{24h}) of the six test-plants to the daily W of the whole growing unit (48 plants). A significant ($R^2 = 0.885$; $n = 176$) linear relationship was found between E_{24h} and W with a slope close to 1 (0.986) and a negligible intercept ($0.064 \text{ kg m}^{-2} \text{ day}^{-1}$).

Crop water uptake was not affected by NaCl salinity in autumn (Table 2); daily W was as high as $1.78 \text{ kg m}^{-2} \text{ day}^{-1}$ and averaged $0.55 \text{ kg m}^{-2} \text{ day}^{-1}$. In spring, daily W was significantly higher when the plants were irrigated with FW ($2.68 \text{ kg m}^{-2} \text{ day}^{-1}$) instead of SW ($2.03 \text{ kg m}^{-2} \text{ day}^{-1}$); this resulted in large difference in seasonal W (222.4 versus 168.5 kg m^{-2}).

In the autumn of 2004, the salinity of irrigation water did not influence E_d , which ranged between 0.009 and $0.139 \text{ kg m}^{-2} \text{ h}^{-1}$.

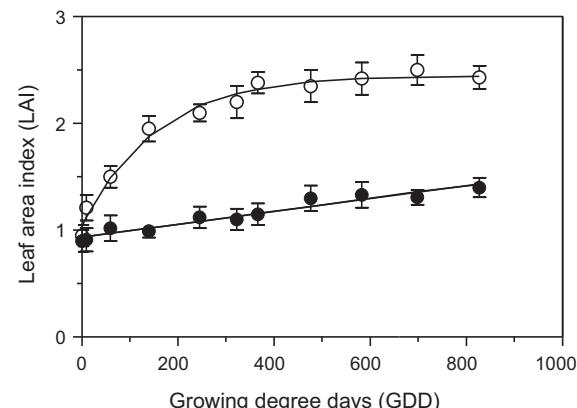


Fig. 2. Relationships between leaf area index (LAI) and growing degree days (GDD) in greenhouse gerbera grown in semi-closed substrate culture in the spring of 2005. The plants were irrigated with fresh (FW; 1.0 mol m^{-3} NaCl) or saline (SW; 9.0 mol m^{-3} NaCl) water. Solid lines represent fits to the data ($n = 3$; $\pm \text{SE}$) with a linear (SW, filled symbols) or non-linear (FW, empty symbols) function.

with an average of $0.050 \text{ kg m}^{-2} \text{ h}^{-1}$ (Table 2). On the contrary, in the following spring, the use of SW significantly reduced E_d , which ranged between 0.020 and $0.354 \text{ kg m}^{-2} \text{ h}^{-1}$ in non-salinized plants (average was $0.203 \text{ kg m}^{-2} \text{ h}^{-1}$) and between 0.015 and $0.270 \text{ kg m}^{-2} \text{ h}^{-1}$ in salinized plant (average was $0.136 \text{ kg m}^{-2} \text{ h}^{-1}$; Table 2). Approximately, 75% of cumulative E_d occurred between 10.00 a.m. and 03.00 p.m. in autumn, and between 09.00 and 04.00 p.m. in spring (data not shown).

Night transpiration did not exceed $0.013 \text{ kg m}^{-2} \text{ h}^{-1}$ in autumn and 0.061 (FW) or 0.045 (SW) $\text{kg m}^{-2} \text{ h}^{-1}$ in spring and it accounted for about 12% and 8% of E_{24h} in autumn and in spring, respectively, in agreement with previous findings in greenhouse cucumber grown in a Mediterranean area (Medrano et al., 2005). In contrast, E_n contributed up to 36% of E_{24h} in rose plants grown in rockwool during winter in a heated greenhouse (Baille et al., 1994b).

In the light period, T_l was $0.2\text{--}1.5^\circ\text{C}$ lower than T_a . In other greenhouse crops such as *Ficus benjamina* (Bailey et al., 1993), geranium (Montero et al., 2001) and zucchini (Rouphael and Colla, 2004), the $T_l - T_a$ difference was up to 5°C .

Calculated r_l , ranged from 80 and 198 s m^{-1} ; these values are among the typical values reported for standard greenhouse conditions (e.g. Stanghellini, 1987; Baille et al., 1994b).

The analysis of daytime r_l , as calculated by the inversion of the PM formula, did not disclose any important effect of NaCl salinity on stomatal behaviour, although on average r_l was slightly lower in non-salinized plants than in salinized plants both in autumn ($265.1 \pm 17.8 \text{ s m}^{-1}$ against $300.5 \pm 18.4 \text{ s m}^{-1}$) and in spring ($439.9 \pm 14.8 \text{ s m}^{-1}$ against $475.4 \pm 15.9 \text{ s m}^{-1}$). This result was corroborated by the measurements with a leaf porometer; we never found significant differences in r_l between the plants irrigated with FW and those irrigated with SW. The values of r_l determined with a porometer ranged between 185 and 367 s m^{-1} .

In our work, minimum values of r_l were higher than those reported for gerbera (Issa et al., 2001) and other greenhouse crops (e.g. Baille et al., 1994b; Rouphael and Colla, 2004); however, they were in the range determined by Tsirogiannis et al. (2010) in greenhouse gerbera grown in pumice.

The absence of a salinity effect on stomata was in contrast with the reduction of leaf growth observed in salinized plants in the spring of 2005 (Table 2 and Fig. 2). Leaf growth and stomata may show different sensitivity to the water availability in the growing medium (Mohd et al., 2002). It has been reported that leaf growth was more sensitive to moderate salinity (Plaut et al., 2000) or drought (Saab and Sharp, 1989) than transpiration and stomatal conductance.

During daytime r_l responded to changes in light conditions and tended to decrease with increasing I . However, the large day-to-day variability in stomata behaviour resulted in poor correlation between r_l and climatic variables (data not shown). Mean hourly values of r_l changed little in the central hours of the day and were consistently higher in spring than in autumn (Fig. 3, top). This difference was likely due to a reduction of r_l induced by higher VPD in spring than in autumn (Figs. 1 and 3, bottom). Stomata are very sensitive to VPD and tend to close in dry atmosphere in order to reduce leaf water loss (Bunce, 1996; Kirkham, 2011). Saturation deficit higher than $1.5\text{--}2.0 \text{ kPa}$ reduced E in tomato (Boulard et al., 1991) and in rose (Baille et al., 1995).

Crop W and E_d were also monitored for six weeks in the autumn of 2005, when indoor climate conditions were similar to those recorded in the autumn of 2004 (Table 1 and Fig. 1). In this season, the plants were irrigated with FW and half of them were defoliated in order to compare different LAI (1.95 ± 0.17 vs. 1.10 ± 0.10). Daily W and E_d averaged, respectively, $1.22 \pm 0.13 \text{ kg m}^{-2} \text{ day}^{-1}$ and $0.146 \pm 0.068 \text{ kg m}^{-2} \text{ h}^{-1}$ in intact plants, and $0.79 \pm 0.09 \text{ kg m}^{-2} \text{ day}^{-1}$ and $0.086 \pm 0.038 \text{ kg m}^{-2} \text{ h}^{-1}$ in defoliated plants.

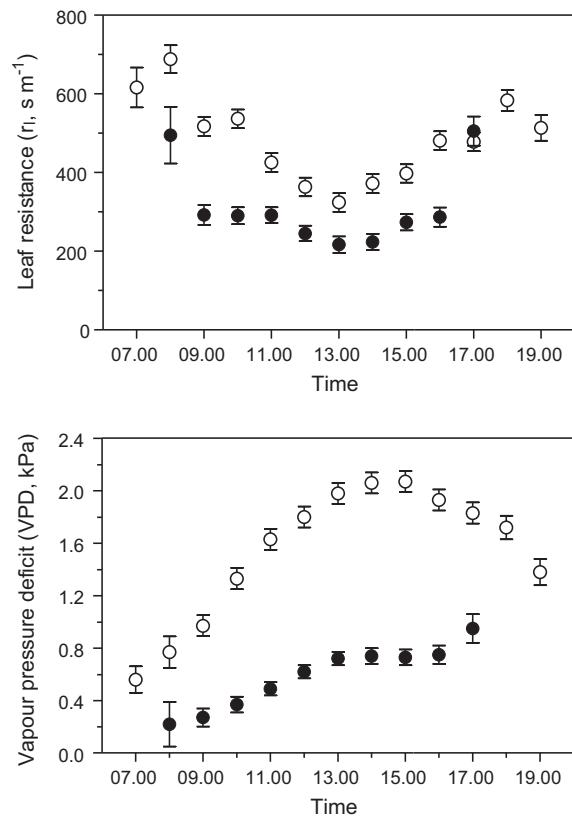


Fig. 3. Mean values of leaf stomatal resistance (as calculated with the Penman-Monteith equation, Eq. (1)) and vapour pressure deficit (VPD) in greenhouse gerbera grown in substrate culture in the autumn of 2004 (filled symbols) and in the spring of 2005 (empty symbols). Each point is the mean ($\pm \text{SE}$) of 15–76 values.

3.5. PM model

The PM equation was run using a value of 0.10 m s^{-1} for u and a difference of 1.0°C between T_a and T_l . For each day of the study period in the spring of 2005, LAI was interpolated from the measurements on the basis of GDD using Eq. (10) (FW) or (11) (SW). Instead, a constant LAI was used for autumn crops: 0.98 in 2004 and 1.95 or 1.10 in 2005 (see previous section).

The calibration dataset ($n=593$), which included the measurements taken in the autumn of 2004 ($n=257$) and in the spring of 2005 ($n=336$), was used to develop empirical relations of r_l against VPD, I , I_c and T_a . Several functions were tested, including the multiplicative models reported by Jarvis (1976) and by Baille et al. (1994b). The latter authors modelled r_l in a variety of greenhouse pot ornamentals as a function of I and/or VPD. In most cases, the models explained more than 50% of the variability of r_l with the exception of poinsettia; R^2 was much lower (0.29) for this species.

Unfortunately, none of the tested equations acceptably described the relationship between r_l and climatic variables (the values of R^2 were 0.30 or lower). Therefore, the PM model predicted E_d using a constant value of r_l . Other authors estimated daytime E in greenhouse crops with the assumption of a constant r_l (200 s m^{-1} ; Aikman and Houter, 1990; Chalabi and Bailey, 1989).

The PM model was validated using an independent dataset ($n=781$), which included the data collected in the autumn of 2005. The validation was performed using separate values of r_l for autumn (282 s m^{-1}) and spring (458 s m^{-1}), or their average (370 s m^{-1}); these values were calculated using the calibration dataset.

The PM equation accurately predicted E_d in both seasons, with the slopes of the regression equations about to 1, negligible intercepts and R^2 values close to 0.90 or higher (Table 3). Accurate

Table 3

Validation of the Penman–Monteith equation (Eq. (1) in the text) used to estimate the hourly rate of daytime transpiration (E_d) of greenhouse gerbera grown in semi-closed substrate culture in different seasons: the slope and the intercept of the linear regression between predicted and measured E_d ; standard error of the estimates (SSE); coefficient of determination (R^2); mean absolute percentage error (MAPE); mean percentage error (PME).

Season	Slope	Intercept ($\text{kg m}^{-2} \text{h}^{-1}$)	R^2	SEE ($\text{kg m}^{-2} \text{h}^{-1}$)	MAPE (%)	MPE (%)	n
Autumn	0.872 ± 0.009	0.005 ± 0.001	0.953	0.012	16.4	2.4	457
Spring	0.903 ± 0.017	0.013 ± 0.003	0.899	0.026	13.7	-1.4	324
Autumn + spring	0.985 ± 0.010	-0.001 ± 0.001	0.926	0.024	17.2	2.7	781

Table 4

Calibration of the regression models (Eqs. (9) and (12) in the text) of the hourly rate of daytime transpiration (E_d) of greenhouse gerbera grown in semi-closed substrate culture in different seasons: regression coefficients (A and B), coefficient of determination (R^2) and number of observations (n).

Season	$A (\pm \text{SE})$	$B (\pm \text{SE}) (\text{kg m}^{-2} \text{h}^{-1} \text{kPa}^{-1})$	R^2	n
Eq. (9)				
Autumn	0.626 ± 0.016	0.024 ± 0.001	0.974	257
Spring	0.553 ± 0.020	0.019 ± 0.001	0.974	336
Autumn + spring	0.547 ± 0.011	0.019 ± 0.001	0.972	593
Eq. (12)				
Autumn	0.847 ± 0.012	–	0.947	257
Spring	0.770 ± 0.010	–	0.942	336
Autumn + spring	0.774 ± 0.0080	–	0.942	593

estimates of E_d were also obtained using the average r_1 (Table 3 and Fig. 4).

3.6. Regression models

Eq. (9) was initially parameterized separating, for each growing season, the FW culture from the SW culture. Water salinity influenced the coefficient A much less than the growing season, although this coefficient was higher for the FW culture than for the SW culture, both in autumn (0.639 ± 0.020 against 0.609 ± 0.027) and in spring (0.559 ± 0.019 against 0.495 ± 0.001). Both water salinity and growing season had no important effect on the coefficient B , which ranged from 0.019 to $0.024 \text{ kg m}^{-2} \text{h}^{-1} \text{kPa}^{-1}$ (Table 4).

When data collected in FW and SW crops were pooled in each season, the coefficients A and B were, respectively: 0.626 and $0.024 \text{ kg m}^{-2} \text{h}^{-1} \text{kPa}^{-1}$ in autumn; 0.553 and $0.019 \text{ kg m}^{-2} \text{h}^{-1} \text{kPa}^{-1}$ in spring (Table 4). Higher A in autumn is consistent with lower r_1 in this season compared to spring (Fig. 3, top). Using the validation datasets, we found a good agreement between predicted and measured E_d (Table 5), although the models tended to overestimate E_d (MPEs were negative) with MAPE ranging from 15.4% to 17.7%.

A joint regression analysis of data from different seasons produced the following results (Table 4): A was 0.547 and B was $0.019 \text{ kg m}^{-2} \text{h}^{-1} \text{kPa}^{-1}$. With these coefficients, Eq. (9) predicted accurately measured E_d ; the slope was close to 1 (0.949) and the intercept ($0.002 \text{ kg m}^{-2} \text{h}^{-1}$) was negligible (Table 5 and Fig. 5).

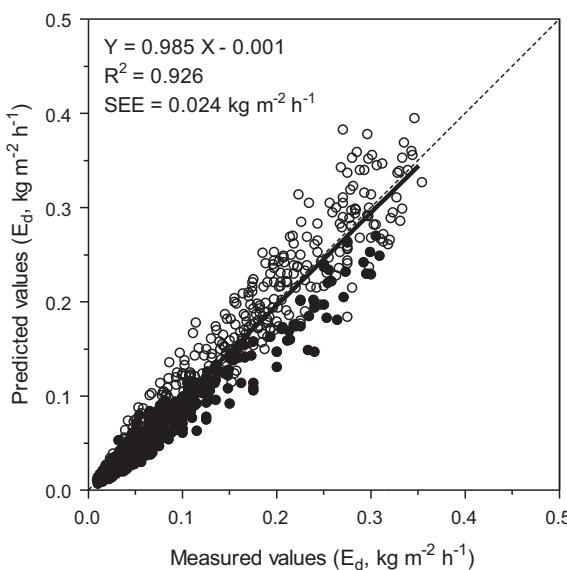


Fig. 4. Relationship between predicted and measured values of daytime transpiration (E_d) in greenhouse gerbera grown in substrate culture in different seasons (autumn, filled symbols; spring, empty symbols). Transpiration was predicted using the Penman–Monteith equation (Eq. (1) in the text) and assuming a constant value of leaf stomatal resistance (370 s m^{-1}). Solid line represents the linear regression (the equation is reported inside the graph) between predicted and measured E_d while dotted line is the 1:1 relationship. The slope and the intercept of the linear regression were not significantly different from 1 and 0, respectively.

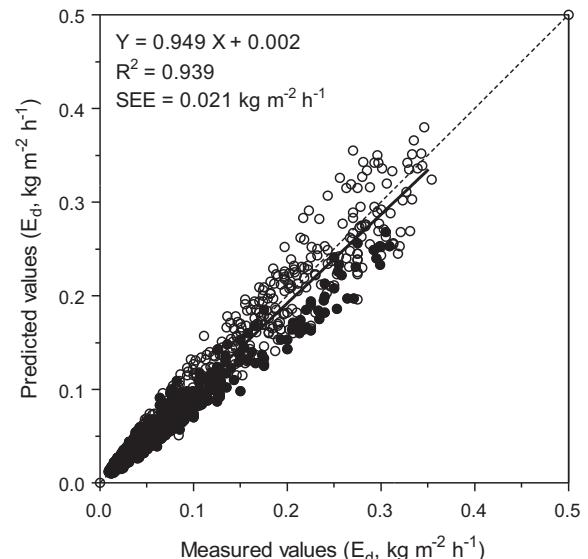


Fig. 5. Relationship between predicted and measured values of daytime transpiration (E_d) in greenhouse gerbera grown in substrate culture in different seasons (autumn, filled symbols; spring, empty symbols). Transpiration was predicted using an empirical function (Eq. (9) in the text) of E_d against intercepted radiation and vapour pressure deficit. Solid line represents the linear regression (the equation is reported inside the graph) between predicted and measured E_d while dotted line is the 1:1 relationship. The intercept of the linear regression was not significantly different from 0.

Table 5

Validation of the regression models (Eqs. (9) and (12) in the text) of the hourly rate of daytime transpiration (E_d) of greenhouse gerbera grown in semi-closed substrate culture in different seasons: the slope and the intercept of the linear regression between predicted and measured E_d ; standard error of the estimates (SEE); coefficient of determination (R^2); mean absolute percentage error (MAPE); mean percentage error (MPE).

Season	Slope	Intercept ($\text{kg m}^{-2} \text{h}^{-1}$)	R^2	SEE ($\text{kg m}^{-2} \text{h}^{-1}$)	MAPE (%)	MPE (%)	n
Eq. (9)							
Autumn	0.950 ± 0.009	0.007 ± 0.001	0.960	0.012	17.7	-10.9	457
Spring	0.945 ± 0.016	0.014 ± 0.003	0.910	0.026	14.6	-6.0	324
Autumn + spring	0.949 ± 0.009	0.002 ± 0.001	0.939	0.021	15.4	1.1	781
Eq. (12)							
Autumn	0.944 ± 0.015	0.007 ± 0.001	0.900	0.020	24.3	-10.8	457
Spring	0.951 ± 0.027	0.003 ± 0.005	0.793	0.043	22.6	2.7	324
Autumn + spring	0.939 ± 0.013	0.0031 ± 0.002	0.875	0.031	22.0	0.2	781

A linear regression (forced through the origin) of E_d against I_c was also evaluated:

$$E_d = A \cdot \frac{I_c}{\lambda} \quad (12)$$

The calibration yielded a slope of 0.847 in autumn and 0.770 in spring; the slope was 0.774 when data for autumn and spring were pooled (Table 4). Therefore, gerbera plants converted around 80% of the incident energy into latent heat in agreement with previous findings in greenhouse crops (e.g. Baille et al., 1994a; Carmassi et al., 2007a; Teitel et al., 2008). Eq. (12) predicted satisfactorily E_d , although model accuracy was lower compared to the PM model and Eq. (9), as indicated by the differences in R^2 , SEE and MAPE (Tables 3 and 5).

In substrate cultures of tomato in unheated greenhouse, Massa et al. (2011) found that a linear regression with I_c explained 81–93% of the variation in daily W , which was dominated by E (it corresponded to more than 93% of W). According to Stanghellini (1987), in most climates the E of greenhouse crops can be better estimated as a function of measured radiation than of VPD.

A simple model that predicts E as a function of radiation can be easily applied in low-technology greenhouses that may have only a simple solarimeter or gather meteorological data from local weather station. In modern greenhouses, indoor climate is automatically monitored and E models responding to changes of both radiation and air humidity can be easily implemented in algorithms for irrigation and climate control.

A linear regression was also fitted to E_n using the whole calibration dataset ($n=338$), with VPD ranging from approximately 0.1 to 1.0 kPa:

$$E_n = B \cdot \text{LAI} \cdot \text{VPD} \quad (13)$$

The calibration yielded a slope of $0.015 \text{ kg m}^{-2} \text{ h}^{-1} \text{ kPa}^{-1}$ ($R^2=0.876$; $n=338$). There was a good correspondence between predicted and measured E_n ($R^2=0.918$; $n=569$) with a slope close to 1 (0.929) and a negligible intercept ($0.0005 \text{ kg m}^{-2} \text{ h}^{-1}$); SEE, MPE and MAPE were $0.002 \text{ kg m}^{-2} \text{ h}^{-1}$, -0.1% and 13.9%, respectively.

The same linear regression (with $B=0.026 \text{ kg m}^{-2} \text{ h}^{-1} \text{ kPa}^{-1}$) accounted for 80% of measured E_n in greenhouse cucumber (Medrano et al., 2005).

3.7. Radiative and aerodynamic components of transpiration

The first term on the right-hand side of Eq. (1) is referred to as the “radiation term” while the second as the “aerodynamic term” (Seginer, 2002); they correspond to the coefficients A and B of Eq. (9) (Baille et al., 1994a; Seginer, 2002).

Baille et al. (1994a) reported that the contribution of the two PM terms was similar in some ornamental species (e.g. begonia, cyclamen and gloxinia) grown under greenhouse in a Mediterranean climate while the radiation term was the main component in other species (e.g. gardenia, impatiens, pelargonium and schefflera). In

our work, the radiative component of gerbera E_d (calculated using Eq. (9)) averaged 76% in autumn and 66% in spring.

From a practical point of view, the estimation of radiative and aerodynamic components can suggest the efficacy of climate control devices, such as shading net and fog system, for E reduction, which may be necessary during plant recovery from root disease or salinity stress, for instance. For crops with high values of A (like gerbera, for instance) shading screen will be much more effective in reducing E_d than fog system.

According to Jones and Tardieu (1999), the aerodynamic term may be not necessary to predict E in greenhouse crops, since greenhouses are generally scantly ventilated, unlike the open field, and thus ‘decoupled’ from the atmospheric air. In a ‘decoupled’ greenhouse, VPD is positively correlated to I , as it was found in our work, and there is large uncertainty of partitioning between the radiative and aerodynamic components of E . On the other hand, I and VPD could become uncorrelated under greenhouse conditions (Bakker, 1991) due to strong climate conditioning (Baille et al., 1994a).

The values of the coefficients A and B determined for gerbera in our work were within those reported for other greenhouse crops in Mediterranean regions (Table 6). The pairs (A, B) reported in Table 6 and those determined for gerbera in our study using the complete calibration dataset (Table 4) are shown in Fig. 6; the pair with zero B (Eq. (12)) was also included. The divergence among the crops could be ascribed to differences in plant habit, stomatal resistance and growing conditions. In spite of scatter, there is an apparent negative correlation between A and B , with a significant R^2 (0.366).

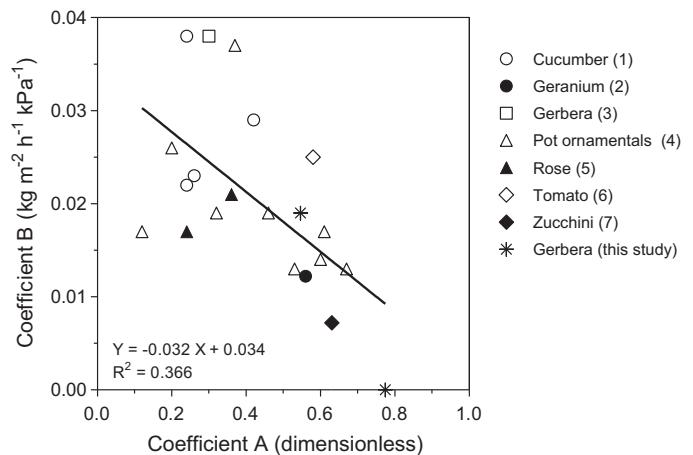


Fig. 6. Relationship between the values of A and B coefficients of Eq. (9) in the text as computed for gerbera in this study or reported in the literature for other greenhouse crops. Solid line represents the linear regression (the equation is reported inside the graph). References: (1) cucumber: Medrano et al. (2005); (2) geranium: Montero et al. (2001); (3) gerbera: Marfa et al. (2000); (4) pot ornamentals: Baille et al. (1994a,b); (5) rose: Kittas et al. (1999) and Gonzalez-Real (1994); (6) tomato: Medrano et al. (2004); (7) zucchini: Rouphael and Colla (2004).

Table 6

Values of coefficients A and B of Eq. (9) in the text for some greenhouse crops.

Crop	Growing conditions ^a	A	B ($\text{kg m}^{-2} \text{h}^{-1} \text{kPa}^{-1}$)	Reference
Begonia		0.20	0.026	
Cyclamen		0.32	0.019	
Gardenia		0.46	0.019	
Gardenia		0.53	0.013	
Hibiscus	Angers, France; spring, summer or autumn; 10–20 plants m^{-2} ; peat-rockwool (pot plants).	0.37	0.037	Baille et al. (1994a)
Impatiens		0.67	0.013	
Pelargonium		0.61	0.017	
Poinsettia		0.12	0.017	
Schefflera		0.60	0.014	
Cucumber	Almeria, Spain; autumn (2 plants m^{-2}) and spring (1.33 plants m^{-2}); perlite	0.24–0.42	0.022–0.038	Medrano et al. (2005)
Geranium	Barcelona, Spain; May–July; pot plants (unknown crop density and substrate)	0.56	0.012 ^b	Montero et al. (2001)
Gerbera	Barcelona, Spain; July–March; 5.7 plants m^{-2} ; perlite	0.30	0.038 ^b	Marfà et al. (2000)
Rose	Volos, Greece; winter; 6 plants m^{-2} ; perlite	0.24	0.017	Kittas et al. (1999)
Rose	Valencia, Spain; summer; 7 plants m^{-2} ; rockwool	0.36	0.021	Gonzalez-Real (1994)
Tomato	Almeria, Spain; autumn and spring; 7 plants m^{-2} ; perlite bag	0.58	0.025	Medrano et al. (2004)
Zucchini	Viterbo, Italy; autumn and spring; 2.1 plants m^{-2} ; pumice	0.63	0.007 ^b	Rouphael and Colla (2004)

^a Location, season, crop density and type of substrate.^b The original data were converted to B ($\text{kg m}^{-2} \text{h}^{-1} \text{kPa}^{-1}$) of this paper.

The relationship between A and B and its significance for greenhouse ventilation design have been analyzed by Seginer (2002). According to this author, two reasons may account for negative correlation between A and B:

- (i) a difference in greenhouse (reference) temperature. As Δ increases with temperature, the first and the second term of Eq. (1) are functions of temperature, if r_c and r_a do not change; however, A augments with temperature while B decreases when the temperature increases.
- (ii) The decoupling of greenhouse from the atmospheric air as a result of poor ventilation, as previously discussed.

Several authors calculated the Jarvis and McNaughton's (1986) decoupling coefficient Ω (Eq. (8)) to analyze the influence of physical and physiological factors on canopy E both in natural vegetation (e.g. Magnani et al., 1998) and in crop plantations in open field or under cover (e.g. Dayan et al., 2000; Nicolàs et al., 2008). The coefficient Ω describes the degree to which E is controlled by radiation rather than by stomata (Jarvis and McNaughton, 1986; Polhamus et al., 2013). It ranges from 0 (strong influence of stomata on E, because VPD at canopy surface is coupled to air VPD) to 1 (decoupled canopy; E is controlled by radiation and independent on stomata behaviour).

Under greenhouse, the degree of coupling between the crop and the ambient air depends on ventilation (Boulard, 1996). Our experiments were conducted in a greenhouse that was poorly ventilated (discontinuous measurements of u never exceeded 0.2 m s^{-1}) due to its urban location and, more notably, to the presence of insect screens and, in late spring and summer, shading net. The coefficient Ω averaged 0.69 ± 0.11 in autumn and 0.65 ± 0.11 in spring. Gerbera vegetation is short and compact and this seemingly contributed to canopy decoupling (Jones and Tardieu, 1999).

Therefore, in our experiment gerbera crop was poorly coupled to the ambient air and this explains why E_d was accurately predicted either using the PM equation (Table 3) with the assumption of a constant r_l (this assumption is also implicit in the regression models) or as a function of the sole radiation (Eq. (12)), although the accuracy of E_d predictions increased when VPD was also considered (Eq. (9); Table 5).

4. Conclusions

In greenhouse gerbera grown in substrate in different seasons, moderate NaCl salinity of irrigation water reduced plant growth,

flower production and E in spring while no significant effects on all measured quantities were observed in autumn.

NaCl salinity affected E through an inhibition of leaf area development and not through stomatal closure, as r_l did not differ significantly in salinized and non-salinized plants both in autumn and in spring. This avoided the necessity of a different calibration of E models for the crop irrigated with FW or SW. However, it required the use of different sub-models of leaf area development depending on water salinity.

The PM model was run using a constant value of r_l . Both the PM formula and the regression equations predicted satisfactorily E_d in both seasons. Our findings are consistent with the concept of greenhouse crop decoupling from the atmosphere.

The models could be easily implemented for irrigation and climate control. All the equations require LAI, which can be estimated either from recurrent, non-destructive measurements of leaf dimensions or as a function of crop thermal time.

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