

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

3

4 Giulia Carmassi¹, Laura Bacci², Matteo Bronzini¹, Luca Incrocci¹, Rita Maggini¹, Gianni
5 Bellocchi³, Daniele Massa⁴, Alberto Pardossi^{1*}

6

7 ¹Department of Agriculture, Food and Environment, University of Pisa, Pisa, Italy

8 ²Institute of Biometeorology, CNR-IBIMET, Sesto Fiorentino, Firenze, Italy

9 ³Grassland Ecosystem Research Unit, French National Institute for Agricultural Research,
10 UREP-INRA, Clermont-Ferrand, France

11 ⁴Consiglio per la Ricerca e la Sperimentazione in Agricoltura, CRA-VIV, Pescia (PT), Italy

12

13

14 * Corresponding author:

15 Address: Viale delle Piagge 23, 56124 Pisa, Italy

16 Tel. +39 0502216526; Fax +39 0502216524

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

18

19

20 **ABSTRACT**

21 Gerbera plants were grown in semi-closed rockwool culture under greenhouse conditions in
22 different seasons in a Mediterranean climate. The plants were irrigated using either fresh
23 (FW; $1.0 \text{ mol m}^{-3} \text{ NaCl}$) or moderately saline (SW; $9.0 \text{ mol m}^{-3} \text{ NaCl}$) water. In autumn, NaCl
24 concentration did not influence significantly plant growth, flower production and transpiration
25 (E), which instead were reduced in spring in the plants irrigated with SW. In both seasons,
26 water salinity did not affect leaf stomatal resistance (r_l), which was determined by the
27 inversion of the Penman-Monteith (PM) equation or measured with a diffusion porometer.
28 The PM formula and two regression equations were calibrated and validated for estimating
29 the hourly rate of daytime transpiration (E_d); a regression model was also fit to nocturnal
30 transpiration (E_n). Regression models predicted E_d as a function of vapour pressure deficit
31 (VPD) and/or the radiation intercepted by the canopy. Leaf area index (LAI), which is
32 required by all the equations, was modelled as function of crop thermal time (i.e. growing
33 degree days). The PM model predicted E_d using a constant value of r_l . Model calibration and
34 validation were performed using independent datasets. The irrigation with FW or SW did not
35 require a different calibration of transpiration models. Both PM formula and regression
36 equations provided accurate estimates of E_d ; fitted equations explained between 80% and 96%
37 of the variance in measured E_d . A linear regression of E_n against (LAI · VPD) accounted for
38 92% of measured E_n .

39

40 **KEYWORDS**

41 Gerbera, greenhouse crops, model, NaCl salinity, Penman-Monteith equation, transpiration.

42

43

44 **HIGHLIGHTS**

- 45 • Greenhouse soilless gerbera was grown in autumn and spring with fresh or moderately
46 saline water.
- 47 • The Penman-Monteith model and two regression equations, which responded to vapour
48 pressure deficit and/or radiation, were used to predict the hourly transpiration rate.
- 49 • Water salinity affected crop growth and production only in spring, but it influenced
50 neither stomatal resistance nor model calibration.
- 51 • The models explained 80% to 96% of the variability of measured transpiration.

52

53

54 **ABBREVIATIONS**

Symbol or abbreviation	Description (unit)
A	empirical coefficient in Eqs. 9 and 12 (dimensionless)
B	empirical coefficient in Eqs. 9 and 13 ($\text{kg m}^{-2} \text{h}^{-1} \text{kPa}^{-1}$)
c_p	specific heat of the air ($\text{J kg}^{-1} \text{K}^{-1}$)
d	leaf dimensions (m)
E	transpiration rate ($\text{kg m}^{-2} \text{h}^{-1}$ or $\text{kg m}^{-2} \text{day}^{-1}$)
$E_{24\text{h}}$	crop transpiration in the 24 h period ($\text{kg m}^{-2} \text{day}^{-1}$)
e_a	air vapour pressure (kPa)
e_a^*	saturated air vapour pressure (kPa)
EC	electrical conductivity (dS m^{-1})
E_d	daytime transpiration rate ($\text{kg m}^{-2} \text{h}^{-1}$)
E_n	nocturnal crop transpiration rate ($\text{kg m}^{-2} \text{h}^{-1}$)
FW	fresh water
g	gravity acceleration (m s^{-2})
GDD	growing degree days ($^{\circ}\text{C}$)
Gr	Grashof number
h	heat transfer coefficient ($\text{W m}^{-2} \text{K}^{-1}$)
I	indoor global radiation (MJ m^{-2} ; W m^{-2})
I_c	global radiation intercepted by crop canopy (MJ m^{-2} ; W m^{-2})
I_n	net radiation (MJ m^{-2} ; W m^{-2})
k	light extinction coefficient (dimensionless)
k_c	thermal conductivity of air ($\text{W m}^{-1} \text{K}^{-1}$)
lt	leaf length (m)

LAI	leaf area index (dimensionless)
NS	nutrient solution
PM	Penman-Monteith
r_a	aerodynamic resistance of the canopy to vapour transfer ($s\ m^{-1}$)
r_c	canopy resistance ($s\ m^{-1}$)
Re	Reynolds number
r_l	leaf stomatal resistance ($s\ m^{-1}$)
SW	saline water
T_a	air temperature ($^{\circ}C$)
T_l	leaf temperature ($^{\circ}C$)
u	air velocity ($m\ s^{-1}$)
VPD	vapour pressure deficit (kPa)
ν	kinematic viscosity of air ($m^2\ s^{-1}$).
w	leaf width (m)
W	water uptake ($kg\ m^{-2}$)
β	thermal expansion coefficient of air (K^{-1})
Δ	slope of the relationship of saturation vapour pressure on temperature ($kPa\ ^{\circ}C^{-1}$)
γ	psychrometric constant ($kPa\ ^{\circ}C^{-1}$)
λ	latent heat of water vaporization ($J\ kg^{-1}$)
ρ	air density ($kg\ m^{-3}$)
Ω	decoupling coefficient

55

56

57

58 1. INTRODUCTION

59

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

64 Leaf transpiration (E) is the primary process affecting plant water uptake (W) and hence its
65 knowledge is necessary to determine crop water needs. In greenhouse crops, particularly in
66 substrate culture, irrigation control requires the determination of E over short time intervals
67 (hourly or less). If E is known as a function of climatic variables, E models can be easily
68 implemented for automated irrigation control. Modelling E can also provide a soft-sensor in an
69 early warning system for growers (Elings and Voogt, 2007). For instance, a reduction of actual
70 E with respect to the predictions may indicate alterations of plant water status resulting from a
71 technical failure of irrigation system, mistakes in fertigation management and/or the
72 occurrence of root diseases.

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

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

83 gerbera (*Gerbera jamesonii* H. Bolus), one of the most important greenhouse ornamental crops
84 (Vidalie, 2007). To our knowledge, only a short paper on modelling E in gerbera was
85 published in the proceedings of an international symposium (Marfà et al., 2000).
86 In this work, we used the PM model and two regression equations to predict E of gerbera
87 plants grown in semi-closed substrate (rockwool) culture under the typical greenhouse
88 conditions of Mediterranean area. With respect to the paper published by Marfà et al. (2000),
89 different approaches were used to estimate leaf area index (LAI) and r_1 . Besides, we
90 investigated the effect of NaCl salinity on crop growth and water relations, and its possible
91 influence on modelling E. In many regions, particularly in the Mediterranean area, protected
92 horticulture is increasingly facing the salinization of water resources (Pardossi et al., 2004) and
93 the knowledge of crop response to salinity is important for optimal crop management
94 (Stanghellini et al., 2007). Greenhouse crops cannot be grown with highly saline water for
95 being profitable (Stanghellini et al., 2007). Therefore, in our study a moderately saline water
96 (NaCl concentration of 9.0 mol m^{-3} against 1.0 mol m^{-3} in the fresh or control water) was
97 tested.

98

99 **2. MATERIALS AND METHODS**

100

101 **2.1. Plant material and growing conditions**

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

108 The plants were grown in rockwool slabs at a density of approximately 5 plants m⁻². The
109 glasshouse had six separate growing units, each consisting of two benches with 12 slabs (48
110 plants in total) and an 80 l mixing tank collecting the drainage NS. The total amount of
111 recirculating NS, including the substrate and the mixing tank, was approximately 150 l (i.e.
112 15.6 l m⁻² expressed per unit of ground area). In order to compensate crop W, the mixing tank
113 was automatically refilled with full-strength NS. Drip irrigation was controlled by a timer; the
114 plants were watered 2-6 times a day, depending on **growth stage** and seasons, with a watering
115 dose of 1.5-2.0 l m⁻² (leaching fraction was roughly 0.30 to 0.50).

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

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

128

129 **2.2. Determinations**

130 Crop growth, flower production and water relations were monitored in three periods (Table 1):
131 i) between 22 September 2004 and 9 January 2005 (110 days); ii) between 11 April and 2 July
132 2005 (83 days); iii) between 10 October and 20 November 2005 (42 days). In the third period,

133 only E and W were measured.

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

136 Crop shoot biomass and LAI were determined by sampling six individual plants from each
137 treatment on 9 January and 3 July 2005. The plants were separated in leaves and inflorescences
138 (stem and flower head), which were dried to constant weight at 80°C in a ventilated oven.
139 Total biomass accumulation was computed including the leaves and the flowers detached in
140 occasion of pruning and harvesting. Leaf area index was also determined weekly by non-
141 destructive measurements of leaf dimensions (maximum length and width) of individual leaves
142 using the equation reported by Carmassi et al. (2007b).

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

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

162 Leaf temperature (T_l) and air velocity (u , $m\ s^{-1}$) were measured discontinuously with a portable
 163 infrared thermometer and a hot-wire anemometer.

164

165 **2.3. Transpiration models**

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

$$167 \quad \lambda \cdot E = \frac{\Delta \cdot I_c}{\Delta + \gamma^*} + \frac{\left(\frac{\rho \cdot c_p}{r_a} \right) \cdot (e_a^* - e_a)}{\Delta + \gamma^*} \quad \text{Eq. 1}$$

168 where crop E ($kg\ m^{-2}\ h^{-1}$) is based on ground area, I_c ($W\ m^{-2}$) is the radiation intercepted by
 169 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
 170 (kPa) is the air vapour pressure, e_a^* (kPa) is the saturated air vapour pressure, r_c ($s\ m^{-1}$) is the
 171 mean canopy resistance, r_a ($s\ m^{-1}$) is the aerodynamic resistance to vapour transfer, Δ ($kPa\ ^\circ C^{-1}$)
 172 is the slope of the relationship of saturation vapour pressure on temperature, $\gamma^* = \gamma (1+r_c/r_a)$
 173 where γ ($kPa\ ^\circ C^{-1}$) is the psychrometric constant, and λ ($J\ kg^{-1}$) is the latent heat of
 174 vaporization of water.

175 The term I_c in Eq. 1 was calculated as:

$$176 \quad I_c = I \cdot (1 - \exp^{-k \cdot LAI}) \quad \text{Eq. 2}$$

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

180 In Eq. 2, I was used instead of net radiation (I_n) because net radiometer was not available. This

181 was possible because in unheated greenhouses I_n matches I during the light period (Bailey et
182 al., 1993; Baille et al., 1994a). In another experiment conducted in 2006 with gerbera grown in
183 the same glasshouse (unpublished results), a close linear relationship was found between I_n and
184 I ($I_n = 0.981 I$; $R^2 = 0.902$; $n = 487$) in the range between 25 and 545 $W m^{-2}$.

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

187 Canopy resistance was computed as the ratio between r_1 and LAI while r_a was calculated as
188 follows:

$$189 \quad r_a = \frac{\rho \cdot c_p}{2 \cdot LAI \cdot h} \quad \text{Eq. 3}$$

190 where h ($W m^{-2} K^{-1}$) is the heat transfer coefficient for individual leaves (Bailey et al., 1993).

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

$$196 \quad h = 0.37 \cdot \left(\frac{k_c}{d} \right) \cdot (Gr + 6.92Re^2)^{1/4} \quad \text{Eq. 4}$$

197 where k_c ($W m^{-1} K^{-1}$) is the thermal conductivity of air and d (m) is the leaf dimension
198 determined as:

$$199 \quad d = \frac{2}{(1/l_t) + (1/w)} \quad \text{Eq. 5}$$

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

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

203 The Grashof number was computed as a function of the difference between T_1 and T_a :

204
$$Gr = \frac{\beta \cdot g \cdot d^3 \cdot |T_l - T_a|}{\nu^2}$$
 Eq. 6

205 where β (K^{-1}) is the thermal expansion coefficient of air, g ($m\ s^{-2}$) is the acceleration due to
 206 gravity and ν ($m^2\ s^{-1}$) is the kinematic viscosity of air.

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

208
$$Re = \frac{u \cdot d}{\nu}$$
 Eq. 7

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

211 The dimensionless decoupling coefficient (Ω) was calculated to analyze the dependence of E_d
 212 on atmospheric environment and **stomatal opening** (Jarvis and McNaughton, 1985), namely:

213
$$\Omega = \frac{1}{1 + \frac{\gamma}{\Delta + \gamma} \cdot \frac{r_c}{r_a}}$$
 Eq. 8

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

215
$$E_d = A \cdot \frac{I_c}{\lambda} + B \cdot LAI \cdot VPD$$
 Eq. 9

216 The coefficients A (dimensionless) and B ($kg\ m^{-2}\ h^{-1}\ kPa^{-1}$) were obtained by regressing
 217 measured E against I_c ($MJ\ m^{-2}\ h^{-1}$) and $(LAI \cdot VPD)$.

218

219 **2.4. Statistics**

220 The influence of growing season and irrigation water salinity on crop growth, flower
 221 production and seasonal W was assessed through ANOVA. Calibration and validation of E
 222 models was performed using independent datasets. Model accuracy was assessed by regression
 223 analysis of predictions against measurements; we computed the slope and the intercept of the
 224 linear regression, the determination coefficient (R^2), the standard error of estimates (SEE), the
 225 mean percentage error (MPE) and the mean absolute percentage error (MAPE). Statistical

226 analysis was performed with Statgraphics Centurion XV (Statpoint Technologies, Inc.,
227 Warrenton, Virginia USA).

228

229 3. RESULTS AND DISCUSSION

230

231 3.1. Growing conditions

232 Fig. 1 shows the seasonal variations of daily values of I, T_a and VPD. Daily averages of I, T_a
233 and VPD were, respectively 2.27 MJ m⁻² day⁻¹, 17.4°C and 0.30 kPa in the autumn of 2004;
234 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
235 0.34 kPa in the autumn of 2005 (Table 1). Over the daylight period, I, T_a and VPD ranged,
236 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
237 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.
238 Despite glasshouse shading, in late spring and summer T_a exceeded frequently 30°C during
239 sunny hours. Significant positive correlations were found between I and T_a (R² = 0.328; n =
240 1374) or VPD (R² = 0.381), and between T_a and VPD (R² = 0.738). In the night, significant
241 correlation (R² = 0.563; n = 908) was found between T_a and VPD.

242 In the FW culture, the EC of recirculating NS ranged from 2.48 to 3.42 dS m⁻¹ with a mean
243 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
244 of 2.28 dS m⁻¹ in the spring of 2005; NS solution was discharged **on** two occasions in autumn
245 and **on** four occasions in spring. In the SW culture, EC oscillated between 2.78 to 4.21 dS m⁻¹
246 with a mean value of 3.62 dS m⁻¹ in autumn, when NS was discharged four times, and between
247 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
248 discharged eight times.

249 In all the cultures, salinity build-up in the recirculating NS was principally due to NaCl
250 accumulation (data not shown) as found by other authors in closed-loop soilless cultures

251 (Massa et al., 2010; Savvas et al., 2008). Mean concentrations of both macronutrients and
252 micronutrients in the recirculating NS were generally close to their content in the refill NS
253 (data not shown).

254

255 **3.2. Crop growth and production**

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

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

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

273

274 **3.3. Leaf area model**

275 Modelling E requires the determination of LAI, which can be achieved by direct (destructive

276 or non-destructive) measurements or simulation models. In both greenhouse and field crops,
277 LAI development is often modelled as a function of GDD using non-linear (e.g. exponential,
278 sigmoid, etc.) equations since crop LAI tends to reach a plateau (Thornley and Johnson,
279 1990). In our study, LAI increased with time (Fig. 2) in spring whereas it remained fairly
280 constant around 1.0 in autumn, when the formation of new leaves was balanced by the weekly
281 removal of older leaves. Compared to the plants irrigated with SW, those grown with FW
282 showed faster leaf development and reached a maximum LAI around 2.4 within eight weeks
283 from the start of observations (Fig. 2). In the FW crop, the response of LAI to GDD was
284 adequately described by an exponential function (Eq. 10; $R^2 = 0.986$; $n = 11$):

$$285 \quad \text{LAI} = (1.043 - 2.448) \cdot \exp^{-0.0066\text{GDD}} + 2.448 \quad \text{Eq. 10}$$

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

$$288 \quad \text{LAI} = 0.9354 + 0.0006 \cdot \text{GDD} \quad \text{Eq. 11}$$

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

292

293 **3.5. Crop water relations**

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

298 Crop water uptake was not affected by NaCl salinity in autumn (Table 2); daily W was as high
299 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
300 higher when the plants were irrigated with FW ($2.68 \text{ kg m}^{-2} \text{ day}^{-1}$) instead of SW (2.03 kg m^{-2}

301 day⁻¹); this resulted in large difference in seasonal W (222.4 versus 168.5 kg m⁻²).

302 In the autumn of 2004, the salinity of irrigation water did not influence E_d, which ranged
303 between 0.009 and 0.139 kg m⁻² h⁻¹ with an average of 0.050 kg m⁻² h⁻¹ (Table 2). On the
304 contrary, in the following spring, the use of SW significantly reduced E_d, which ranged
305 between 0.020 and 0.354 kg m⁻² h⁻¹ in non-salinized plants (average was 0.203 kg m⁻² h⁻¹) and
306 between 0.015 and 0.270 kg m⁻² h⁻¹ in salinized plant (average was 0.136 kg m⁻² h⁻¹; Table 2).

307 Approximately, 75% of cumulative E_d occurred between 10.00 a.m and 03.00 p.m. in autumn,
308 and between 09.00 and 04.00 p.m. in spring (data not shown).

309 Night transpiration did not exceed 0.013 kg m⁻² h⁻¹ in autumn and 0.061 (FW) or 0.045 (SW)
310 kg m⁻² h⁻¹ in spring and it accounted for about 12% and 8% of E_{24h} in autumn and in spring,
311 respectively, in agreement with previous findings in greenhouse cucumber grown in a
312 Mediterranean area (Medrano et al., 2005). In contrast, E_n contributed up to 36% of E_{24h}, as
313 found for rose plants grown in rockwool during winter in a heated greenhouse (Baille et al.,
314 1994b).

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

318 Calculated r_a, ranged from 80 and 198 s m⁻¹; these values are among the typical values reported
319 for standard greenhouse conditions (e.g. Stanghellini, 1987; Baille et al., 1994b).

320 The analysis of daytime r_l, as calculated by the inversion of the PM formula, did not disclose
321 any important effect of NaCl salinity on stomatal behaviour, although on average r_l was
322 slightly lower in non-salinized plants than in salinized plants both in autumn (265.1 ± 17.8 s m⁻¹
323 ¹ against 300.5 ± 18.4 s m⁻¹) and in spring (439.9 s m⁻¹ ± 14.8 against 475.4 ± 15.9 s m⁻¹). This
324 result was corroborated by the measurements with a leaf porometer; we never found significant
325 differences in r_l between the plants irrigated with FW and those irrigated with SW. The values

326 of r_i determined with a porometer ranged between 185 and 367 s m⁻¹.

327 In our work, minimum values of r_i were higher than those reported for gerbera (Issa et al.,
328 2001) and other greenhouse crops (e.g. Baille et al., 1994b; Rouphael and Colla 2004);
329 however, they were in the range determined by Tsirogiannis et al. (2010) in greenhouse
330 gerbera grown in pumice.

331 The absence of a salinity effect on stomata was in contrast with the reduction of leaf growth
332 observed in salinized plants in the spring of 2005 (Table 2; Fig. 2). Leaf growth and stomata
333 may show different sensitivity to the water availability in the growing medium (Mohd et al.,
334 2002). It has been reported that leaf growth was more sensitive to moderate salinity (Plaut et
335 al., 2000) or drought (Saab and Sharp, 1989) than transpiration and stomatal conductance.

336 During daytime r_i responded to changes in light conditions and tended to decrease with
337 increasing I. However, the large day-to-day variability in stomata behaviour resulted in poor
338 correlation between r_i and climatic variables (data not shown). **Mean hourly values** of r_i
339 changed little in the central hours of the day and were consistently higher in spring than in
340 autumn (Fig. 3, top). This difference was likely due to a reduction of r_i induced by higher VPD
341 in spring than in autumn (Fig. 1 and Fig. 3, bottom). Stomata are very sensitive to VPD and
342 tend to close in dry atmosphere in order to reduce leaf water loss (Bunce, 1996; Kirkham,
343 2011). Saturation deficit higher than 1.5 - 2.0 kPa reduced E in tomato (Boulard et al., 1991)
344 and in rose (Baille et al., 1995).

345 Crop W and E_d were also monitored for six weeks in the autumn of 2005, when indoor climate
346 conditions were similar to those recorded in the autumn of 2004 (Table 1 and Fig. 1). In this
347 season, the plants were irrigated with FW and half of them were defoliated in order to compare
348 different LAI (1.95 ± 0.17 vs. 1.10 ± 0.10). Daily W and E_d averaged, respectively, 1.22 ± 0.13
349 kg m⁻² day⁻¹ and 0.146 ± 0.068 kg m⁻² h⁻¹ in intact plants, and 0.79 ± 0.09 kg m⁻² day⁻¹ and
350 0.086 ± 0.038 kg m⁻² h⁻¹ in defoliated plants.

351

352 **3.6. PM model**

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

357 The calibration dataset ($n = 593$), which included the measurements taken in the autumn of
358 2004 ($n = 257$) and in the spring of 2005 ($n = 336$), was used to develop empirical relations of
359 r_l against VPD, I , I_c and T_a . Several functions were tested, including the multiplicative models
360 reported by Jarvis (1976) and by Baille et al. (1994b). The latter authors modelled r_l in a
361 variety of greenhouse pot ornamentals as a function of I and/or VPD. In most cases, the models
362 explained more than 50% of the variability of r_l with the exception of poinsettia; R^2 was much
363 lower (0.29) for this species.

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

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

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

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

376

377 **3.7. Regression models**

378 Equation 9 was initially parameterized separating, for each growing season, the FW culture
379 from the SW culture. Water salinity influenced the coefficient A much less than the growing
380 season, although this coefficient was higher for the FW culture than for the SW culture, both
381 in autumn (0.639 ± 0.020 against 0.609 ± 0.027) and in spring (0.559 ± 0.019 against $0.495 \pm$
382 0.001 ; Table 4). Both water salinity and growing season had no important effect on the
383 coefficient B, which ranged from 0.019 to 0.024 $\text{kg m}^{-2} \text{h}^{-1} \text{kPa}^{-1}$ (Table 4).

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

390 A joint regression analysis of data from different seasons produced the following results
391 (Table 4): A was 0.546 and B was 0.019 $\text{kg m}^{-2} \text{h}^{-1} \text{kPa}^{-1}$. With these coefficients, Eq. 9
392 predicted accurately measured E_d ; the slope was close to 1 (0.949) and the intercept (0.002 kg
393 $\text{m}^{-2} \text{h}^{-1}$) was negligible (Table 5 and Fig. 5).

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

$$395 \quad E_d = A \cdot \frac{I_c}{\lambda} \quad \text{Eq.12}$$

396 The calibration yielded a slope of 0.847 in autumn and 0.770 in spring; the slope was 0.774
397 when data for autumn and spring were pooled (Table 4). Therefore, gerbera plants converted
398 around 80% of the incident energy into latent heat in agreement with previous findings in
399 greenhouse crops (e.g. Baille et al., 1994a; Carmassi et al., 2007a; Teitel et al. 2008). Equation
400 12 predicted satisfactorily E_d , although model accuracy was lower compared to the PM model

401 and Eq. 9, as indicated by the differences in R^2 , SEE and MAPE (Tables 3 and 5).
402 In substrate cultures of tomato in unheated greenhouse, Massa et al. (2011) found that a linear
403 regression with I_c explained 81% to 93% of the variation in daily W , which was dominated by
404 E (it corresponded to more than 93% of W). According to Stanghellini (1987), in most climates
405 the E of greenhouse crops can be better estimated as a function of measured radiation than of
406 VPD.

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

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

$$414 \quad E_n = B \cdot LAI \cdot VPD \quad \text{Eq. 13}$$

415 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
416 good correspondence between predicted and measured E_n ($R^2 = 0.918$; $n = 569$) with a slope
417 close to 1 (0.929) and a negligible intercept ($0.0005 \text{ kg m}^{-2} \text{ h}^{-1}$); SEE, MPE and MAPE were
418 $0.002 \text{ kg m}^{-2} \text{ h}^{-1}$, - 0.1% and 13.9%, respectively

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

421

422 **3.6. Radiative and aerodynamic components of transpiration**

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

426 Baille et al. (1994a) reported that the contribution of the two PM terms was similar in some
427 ornamental species (e.g. begonia, cyclamen and gloxinia) grown under greenhouse in a
428 Mediterranean climate while the radiation term was the main component in other species (e.g.
429 gardenia, impatiens, pelargonium and schefflera). In our work, the radiative component of
430 gerbera E_d (calculated using Eq. 9) averaged 76% in autumn and 66% in spring.

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

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

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

450 The relationship between A and B and its significance for greenhouse ventilation design has

451 been analyzed by Seginer (2002). According to this author, two reasons may account for
452 negative correlation between A and B:

453 i) a difference in greenhouse (reference) temperature. As Δ increases with temperature, the first
454 and the second term of Eq. 1 are functions of temperature, if r_c and r_a do not change; however,
455 A augments with temperature while B decreases when the temperature increases.

456 ii) The decoupling of greenhouse from the atmospheric air as a result of poor ventilation, as
457 previously discussed.

458 Several authors calculated the Jarvis and McNaughton's (1986) decoupling coefficient Ω (Eq.
459 8) to analyze the influence of physical and physiological factors on canopy E both in natural
460 vegetation (e.g. Magnani et al., 1998) and in crop plantations in open field or under cover (e.g.
461 Dayan et al., 2000; Nicolas et al, 2008). The coefficient Ω describes the degree to which E is
462 controlled by radiation rather than by stomata (Jarvis and McNaughton, 1985; Polhamus et al.,
463 2013). It ranges from 0 (strong influence of stomata on E, because VPD at canopy surface is
464 coupled to air VPD) to 1 (decoupled canopy; E is controlled by radiation and independent on
465 stomata behaviour).

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

473 Therefore, in our experiment gerbera crop was poorly coupled to the ambient air and this
474 explains why E_d was accurately predicted either using the PM equation (Table 3) with the
475 assumption of a constant r_1 (this assumption is also implicit in the regression models) or as a

476 function of the sole radiation (Eq. 12), although the accuracy of E_d predictions increased when
477 VPD was also considered (Eq. 9; Table 5).

478

479 **4. CONCLUSIONS**

480 In greenhouse gerbera grown in substrate in different seasons, moderate NaCl salinity of
481 irrigation water reduced plant growth, flower production and E in spring while no significant
482 effects on all measured quantities were observed in autumn.

483 NaCl salinity affected E through an inhibition of leaf area development and not through
484 stomatal closure, as r_1 did not differ significantly in salinized and non-salinized plants both in
485 autumn and in spring. This avoided the necessity of a different calibration of E models for the
486 crop irrigated with FW or SW. However, it required the use of different sub-models of leaf
487 area development depending on water salinity.

488 The PM model was run using a constant value of r_1 . Both the PM formula and the regression
489 equations predicted satisfactorily E_d in both seasons. Our findings are consistent with the
490 concept of greenhouse **crop** decoupling from the atmosphere.

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

494

495 **ACKNOWLEDGEMENTS**

496

497 This work was supported by Ministry of University and Research (MIUR-PRIN 2004-2005)
498 and by the European Commission, Directorate General for Research (7th Framework RTD
499 Programme, Project EUPHOROS, 2008-2012). We are grateful to two anonymous referees
500 for their constructive comments to the manuscript.

501 **REFERENCES**

502

503 Aikman, D.P., Houter, G., 1990. Influence of radiation and humidity on transpiration -
504 Implications for calcium levels in tomato leaves. J. Hortic. Sci 65, 245-253.

505 Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop evapotranspiration: guidelines for
506 computing crop water requirements. Irrigation Drainage Paper 56, FAO, Rome. Available
507 at: <http://www.fao.org/docrep/X0490E/x0490e00.htm> (accessed January 31, 2013).

508 An, P., Inanaga, S., Lux A., Li, X.J., Ali, M.E.K., Matsui, T., Sugimoto, Y., 2002. Effects of
509 salinity and relative humidity on two melon cultivars differing in salt tolerance. Biol.
510 Plantarum 45, 409-41.

511 Baas, R., Nijssen, H.M.C., Van Den Berg, T.J.M., Warmenhoven, M.G., 1995. Yield and
512 quality of carnation (*Dianthus caryophyllus* L.) and gerbera (*Gerbera jamesonii* L.) in a
513 closed nutrient system as affected by sodium chloride. Sci. Hortic. 61, 273-284.

514 Bailey, B.J., Montero, J.I., Blel, C., Wilkinson, D.J., Anton, A., Jolhet, O., 1993. Transpiration
515 of *Ficus benjamina*: comparison of measurements with predictions of the Penman-
516 Monteith model and a simplified version. Agric. and Forest Meteorol. 65, 229-243.

517 Baille, K., Baille, A., Delmon, D., 1995. Microclimate and transpiration of greenhouse rose
518 crops. Agric. Forest Meteor., 71, 83-97.

519 Baille, M., Baille, A., Laury, J.C., 1994a. A simplified model for predicting evapotranspiration
520 rate of nine ornamental species vs climate factors and leaf area. Sci. Hortic. 59, 217-232.

521 Baille, M., Baille, A., Laury, J.C., 1994b. Canopy surface resistances to water vapour transfer
522 for nine greenhouse pot plant crops. Sci. Hortic. 57, 143-155.

523 Bakker, J.C., 1991. Leaf conductance of four glasshouse vegetable crops as affected by air
524 humidity. Agric. For. Meteor. 55, 23-36.

525 Boulard, T., 1996. Caractérisation et modélisation du climat des serres. Application à la

526 climatisation estivale. PhD. thesis. ENSA Montpellier, France. 121 pp.

527 Boulard, T., Baille, A., Le Gall, F., 1991. Etude de différentes méthodes de refroidissement sur
528 le climat et la transpiration de tomates de serre. *Agronomie* 11, 543-53.

529 Bunce, J.A., 1996. Growth at elevated carbon dioxide concentration reduces hydraulic
530 conductance in alfalfa and soybean. *Glob. Change Biol.* 2, 155-158.

531 Carmassi, G., Incrocci, L., Maggini, R., Malorgio, F., Tognoni, F., Pardossi, A., 2007a. An
532 aggregated model for water requirements of greenhouse tomato grown in closed
533 rockwool culture with saline water. *Agr. Water Manage.* 88, 73-82.

534 Carmassi, G., Incrocci, L., Incrocci, G., Pardossi, A., 2007b. Non-destructive estimation of
535 leaf area in (*Solanum lycopersicum* L.) and gerbera (*Gerbera jamesonii* H. Bolus). *Agric.*
536 *Mediterr.* 137, 172-176.

537 Chalabi, Z.S., Bailey, B.J., 1989. Simulation of the energy balance in a greenhouse. Divisional
538 note 1516/AFRC, Institute of Engineering Research.

539 **Dayan, E., Fuchs, M., Plaut, Z., Presnov, E., Grava, A., Matan, E., Solphoy, A., Mugira, U.,**
540 **Pines, N., 2000. Transpiration of roses in greenhouses. *Acta Hortic.* 554, 239-249.**

541 De Kreijl, C., van Os, P.C., 1989. Production and quality of gerbera in rockwool as affected by
542 electrical conductivity of the nutrient solution. *Proc. 7th Int. Cong. Soilless Culture*, 225-
543 264.

544 Elings, A., Voogt, W., 2007. Management of greenhouse crop transpiration: the way forward.
545 *Acta Hortic.* 801, 1221-1228.

546 Gonzalez-Real, M.M., 1994. Estudio y modelización de intercambios gaseosos en el cultivo de
547 rosas bajo invernadero. Universidad Politecnica de Valencia, Valencia.

548 Gröber, H., Erk, S., 1961. *Fundamentals of heat transfer*, 3^d ed. McGraw-Hill, New York.

549 Issa, M., Ouzounidou, G., Maloupa, H., Constantinidou, H.I.A., 2001. Seasonal and diurnal
550 photosynthetic responses of two gerbera cultivars to different substrates and heating

551 systems. *Sci. Hortic.* 88, 215-234.

552 Jarvis, P.G., 1976. Interpretation of Variations in Leaf Water Potential and Stomatal
553 Conductance Found in Canopies in Field. *Philos. T. Roy. Soc. B.* 273, 593-610.

554 Jarvis, P.G., McNaughton, K.G., 1986. Stomatal control of transpiration: scaling up from leaf
555 to region. *Adv. Ecol. Res.* 15, 3-50.

556 Jones, H.G, Tardieu, F., 1999. Modelling water relations of horticultural crops: A review. *Sci.*
557 *Hortic.* 74, 21-46.

558 Kirkham, M.B., 2011. Elevated atmospheric carbon dioxide: transpiration and
559 evapotranspiration. In: Kirkham, M.B., (Ed.), *Elevated Carbon Dioxide: Impacts on Soil*
560 *and Plant Water Relations*. CRC Press, Boca Raton, FL, pp 197-224.

561 Kittas, C., Katsoulas, N., Baille, A., 1999. Transpiration and canopy resistance of greenhouse
562 soilless roses: measurements and modelling. *Acta Hortic.* 507, 61-68.

563 Li, Y., Stanghellini, C., Challa, H., 2001. Effect of electrical conductivity and transpiration on
564 production of greenhouse tomato (*Lycopersicon esculentum* L.). *Sci. Hortic.* 88, 11-29.

565 Magnani, F., Leonardi, S., Tognetti, R., Grace, J., Borghetti, M., 1998. Modelling the surface
566 conductance of a broad-leaf canopy: effects of partial decoupling from the atmosphere.
567 *Plant Cell Envir.* 21, 867-879.

568 Marfà, O., Biel, C., Blanch, F., Montero, J.I., 2000. Water consumption of a closed soilless
569 culture of gerbera: usefulness of model to estimate evapotranspiration. *Acta Hortic.* 534,
570 147-153.

571 Massa, D., Incrocci, L., Maggini, R., Bibbiani, C., Carmassi, G., Malorgio, F., Pardossi, A.,
572 2011. Simulation of crop water and mineral relations in greenhouse soilless culture.
573 *Environ. Modell. Softw.* 26, 711-722.

574 Massa, D., Incrocci, L., Maggini, R., Carmassi, G., Campiotti, C.A., Pardossi, A., 2010.
575 Strategies to decrease water drainage and nitrate emission from soilless cultures of

576 greenhouse tomato. *Agr. Water Manage.* 97, 971-980.

577 McAdams, W.H., 1954. *Heat transmission*, 3^d ed. McGraw-Hill, New York.

578 Medrano, E., Lorenzo, P., Sánchez-Guerrero, M.C., García, M.L., Caparrós, I, Giménez, M.,
579 2004. Influence of an external greenhouse mobile shading on tomato crop transpiration.
580 *Acta Hortic.* 659, 195-199

581 Medrano, E., Lorenzo, P., Sanchez-Guerrero, M.C., Montero, J.I., 2005. Evaluation and
582 modelling of greenhouse cucumber-crop transpiration under high and low radiation
583 conditions. *Sci. Hortic.* 105, 163-175.

584 Mohd, R.I., Davies, W.J., Mohamad, H.A., 2002. Leaf growth and stomatal sensitivity to ABA
585 in droughted pepper plants. *Sci. Hortic.* 96, 313-327.

586 Montero, J.I., Antón, A., Muñoz, P., Lorenzo, P., 2001. Transpiration from geranium grown
587 under high temperatures and low humidities in greenhouses. *Agri. Forest Meteorol.* 107,
588 323-332.

589 Nicolàs, E., Barradas, V.L., Ortuño, M.F., Navarro, A., Torrecillas, A.A., Alarcón, J.J., , 2008.
590 *Environmental and stomatal control of transpiration, canopy conductance and decoupling*
591 *coefficient in young lemon trees under shading net. Envir. Exp. Bot.* 63, 200–206.

592 Nobel, P.S., Long, S.P., 1985. Canopy structure and light interception techniques, in: Coombs,
593 J., Hall, D.O., Long, S.P., Scurlock, J.M.O. (Eds.), *Bioproductivity and Photosynthesis*.
594 Pergamon Press, Oxford, pp. 41-49.

595 Pardossi, A., Incrocci, L., 2011. Traditional and new approaches to irrigation scheduling in
596 vegetable crops. *HortTechnology* 21, 309-313.

597 Pardossi, A., Tognoni, F, Incrocci, L., 2004. *Mediterranean Greenhouse Technology*. *Chronica*
598 *Hortic.* 44, 28-34.

599 Plaut, Z., Meinzer, F.C., Federman, E., 2000. Leaf development, transpiration and ion uptake
600 and distribution in sugarcane cultivars grown under salinity. *Plant Soil* 218, 59–69.

601 Polhamus, A., Joshua, B. Fisher, J.B., Kevin P., Tu, K.P., 2013. What controls the error
602 structure in evapotranspiration models? *Agric. For. Meteor.* 169, 12-24.

603 Pollet, S., Bleyaert, P., Lemeur, R., 2000. Application of the Penman-Monteith model to
604 calculate the evapotranspiration of head lettuce (*Lactuca sativa* L. var. *capitata*) in
605 glasshouse conditions. *Acta Hortic.* 519, 151-162.

606 Roupshael, Y., Colla, G., 2004. Modelling the transpiration of a greenhouse zucchini crop
607 grown under a Mediterranean climate using the Penman-Monteith equation and its
608 simplified version. *Aust. J. Agr. Res.* 55, 931-937.

609 Saab, I.N., Sharp, R.E., 1989. Non-hydraulic signals from maize roots in drying soil: inhibition
610 of leaf elongation but not stomatal conductance. *Planta* 179, 466-474.

611 Savvas, D., Chatzieustratiou, E., Pervolaraki, G., Gizas, G., Sigrimis, N., 2008. Modelling Na
612 and Cl concentrations in the recycling nutrient solution of a closed-cycle pepper
613 cultivation. *Biosyst. Eng.* 99, 282-291

614 Seginer, I., 2002. The Penman-Monteith evapotranspiration equation as an element in
615 greenhouse ventilation design. *Biosyst. Eng.* 82, 423-439.

616 Sonneveld, C., Baas, R., Nijssen, H.M.C., de Hoog, J., 1999. Salt tolerance of flower crops
617 grown in soilless culture. *J. Plant Nutr.* 22, 1033-1048.

618 Stanghellini, C., 1987. Transpiration of greenhouse crops. An aid to climate management. PhD
619 Thesis. Wageningen Agricultural University, The Netherlands, 150 pp.

620 Stanghellini, C., Pardossi, A., Sigrimis, N., 2007. What limits the application of wastewater
621 and/or closed cycle in horticulture? *Acta Hortic.* 747, 323-330.

622 Teitel, M., Liran, O., Tanny, J., Barak, B., 2008. Wind driven ventilation of a mono-span
623 greenhouse with a rose crop and continuous screened side vents and its effect on flow
624 patterns and microclimate. *Biosyst. Eng.* 101, 111-122.

625 Thompson, R.B., Martínez-Gaitan, C., Gallardo, M., Giménez, C., Fernández, M.D., 2007.

626 Identification of irrigation and N management practices that contribute to nitrate leaching
627 loss from an intensive vegetable production system by use of a comprehensive survey.
628 *Agr. Water Manage.* 89, 261–274.

629 Thornley, J.H.M., Johnson, I.R., 1990. *Plant and Crop Modelling. A Mathematical Approach*
630 *to Plant and Crop Physiology.* Clarendon Press, Oxford.

631 Tsirogiannis, I., Katsoulas, N., Kittas, C., 2010. Effect of irrigation scheduling on gerbera
632 flower yield and quality. *HortScience* 45, 265-270.

633 Vidalie, H., 2007. Varietal richness and technology for gerbera. *PHM Rev. Hortic.*, 497, 33-41.

634 Volkmar, K. M., Hu, Y., Steppuhn, H., 1998. Réponse physiologique des plantes à la salinité:
635 Mise au point bibliographique. *Can. J. Plant Sci.* 78, 19–27.

636 Vox, G., Teitel, M., Pardossi, A., Minuto, A., Tinivella, F., Schettini, E., 2010. Sustainable
637 greenhouse systems. In: Salazar A., Rios I. (Eds.), *Agriculture: technology, planning and*
638 *management.* Nova Sci Publishers, New York, pp. 1-79.

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; $1.0 \text{ mol m}^{-3} \text{ NaCl}$) or saline (SW; $9.0 \text{ mol m}^{-3} \text{ NaCl}$) 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	-

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 SE); n = 3 or 247-358) of three replicates 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 (kg m ⁻² day ⁻¹)	Mean hourly rate of daytime transpiration (E _d ; kg m ⁻² 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 3.7 c	0.59 \pm 0.07 c	0.053 \pm 0.004 c	0.39 \pm 0.02 c	1.02 \pm 0.08 c	58.2 \pm 5.4 a
	SW	56.1 \pm 3.0 d	0.51 \pm 0.05 c	0.049 \pm 0.004 c	0.39 \pm 0.06 a	1.04 \pm 0.06 c	50.8 \pm 7.8 a
Spring 2005 (83 days)	FW	222.4 \pm 8.2 a	2.68 \pm 0.10 a	0.203 \pm 0.003 a	0.71 \pm 0.01 a	2.43 \pm 0.19 a	104.5 \pm 0.8 a
	SW	168.5 \pm 4.6 b	2.03 \pm 0.07 b	0.136 \pm 0.003 b	0.50 \pm 0.05 b	1.40 \pm 0.20 b	76.3 \pm 9.1 b

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 (dimensionless)	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

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

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 (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
Equation 9							
Autumn	0.950 \pm 0.009	0.007 \pm 0.001	0.960	0.012	17.7	-10.9	457
Spring	0.945 \pm 0.016	0.014 \pm 0.003	0.910	0.026	14.6	-6.0	324
Autumn + spring	0.949 \pm 0.009	0.002 \pm 0.001	0.939	0.021	15.4	1.1	781
Equation 12							
Autumn	0.944 \pm 0.015	0.007 \pm 0.001	0.900	0.020	24.3	-10.8	457
Spring	0.951 \pm 0.027	0.003 \pm 0.005	0.793	0.043	22.6	2.7	324
Autumn + spring	0.939 \pm 0.013	0.0031 \pm 0.002	0.875	0.031	22.0	0.2	781

Table 6. Values of coefficients A and B of Eq. 9 in the text for some greenhouse crops.

Crop	Growing conditions ¹	A (dimensionless)	B (kg m ⁻² h ⁻¹ kPa ⁻¹)	Reference
Begonia		0.20	0.026	
Cyclamen		0.32	0.019	
Gardenia		0.46	0.019	
Gardenia	Angers, France; spring, summer or autumn; 10-20 plants m ⁻² ; peat-rockwool (pot plants).	0.53	0.013	Baille et al., 1994a
Hibiscus		0.37	0.037	
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 ²	Montero et al., 2001
Gerbera	Barcelona, Spain; July-March; 5.7 plants m ⁻² ; perlite	0.30	0.038 ²	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 ²	Rouphael and Colla 2004

¹ Location, season, crop density and type of substrate. ² The original data were converted to B (kg m⁻² h⁻¹ kPa⁻¹) of this paper.

FIGURE CAPTIONS

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) 19 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.

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; $1.0 \text{ mol m}^{-3} \text{ NaCl}$) or saline (SW; $9.0 \text{ mol m}^{-3} \text{ NaCl}$) 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.

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.

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 (317 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.

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: Marfà et al., 2000; 4) Pot ornamentals: Baille et al., 1994; 5) rose: Kittas et al., 1999; Gonzalez-Real, 1994; 6) tomato: Medrano et al, 2004; 7) zucchini: Rouphael and Colla 2004.

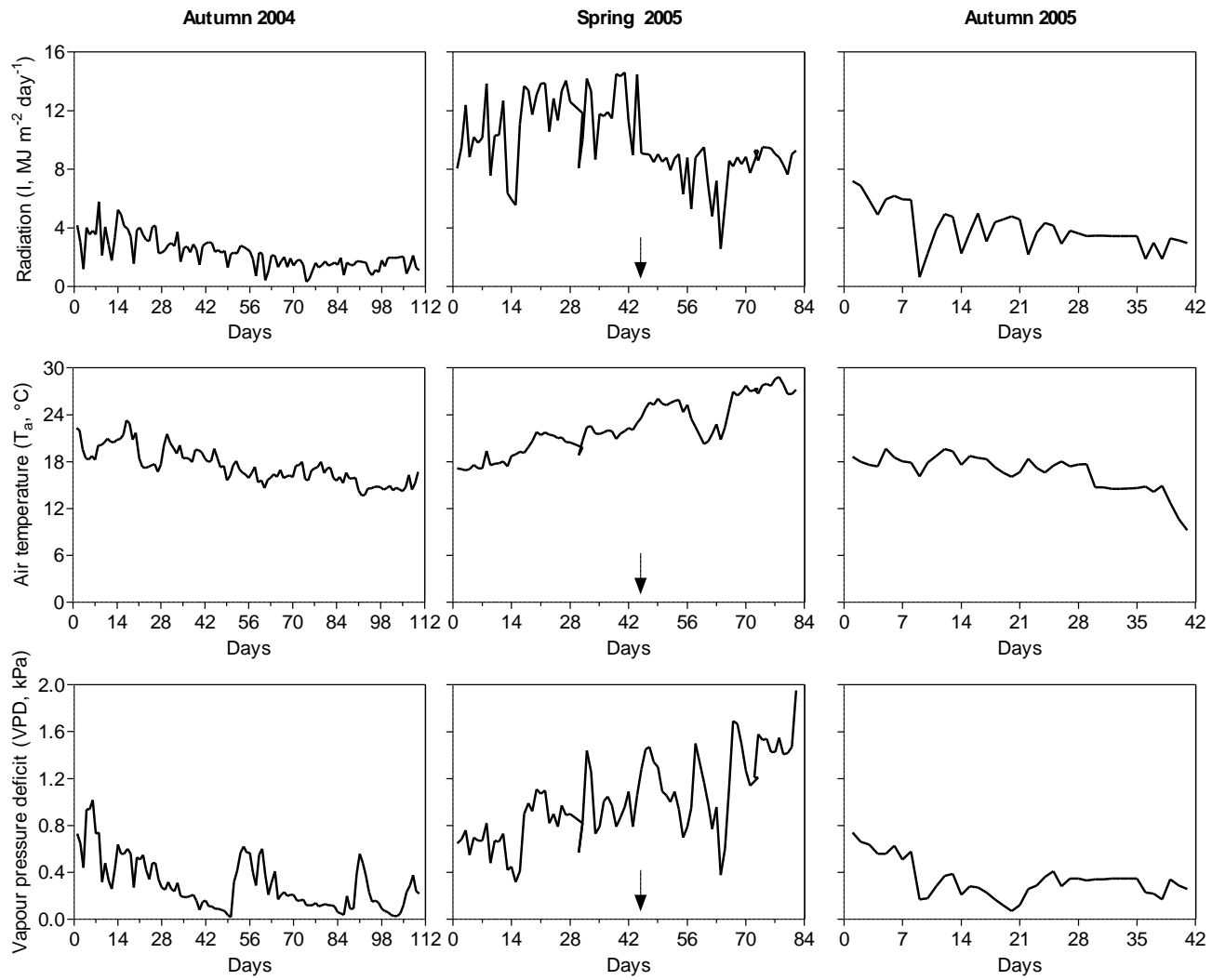


Fig. 1.

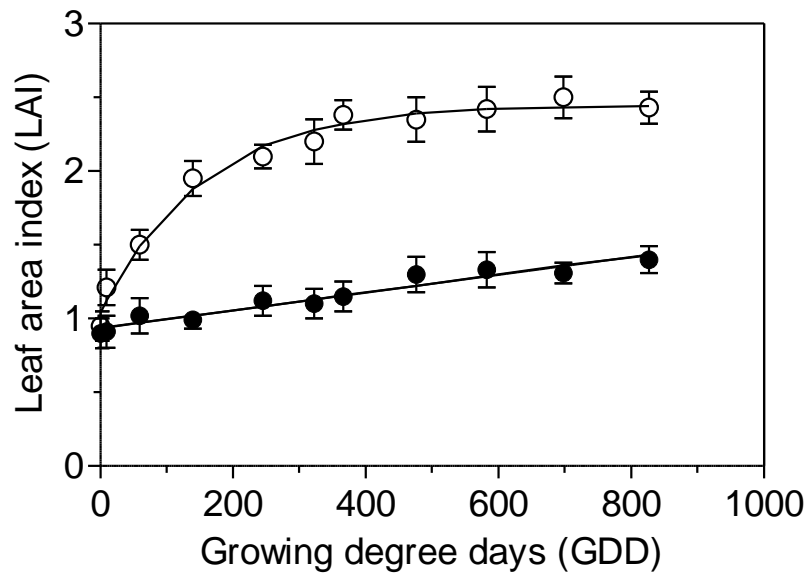


Fig. 2.

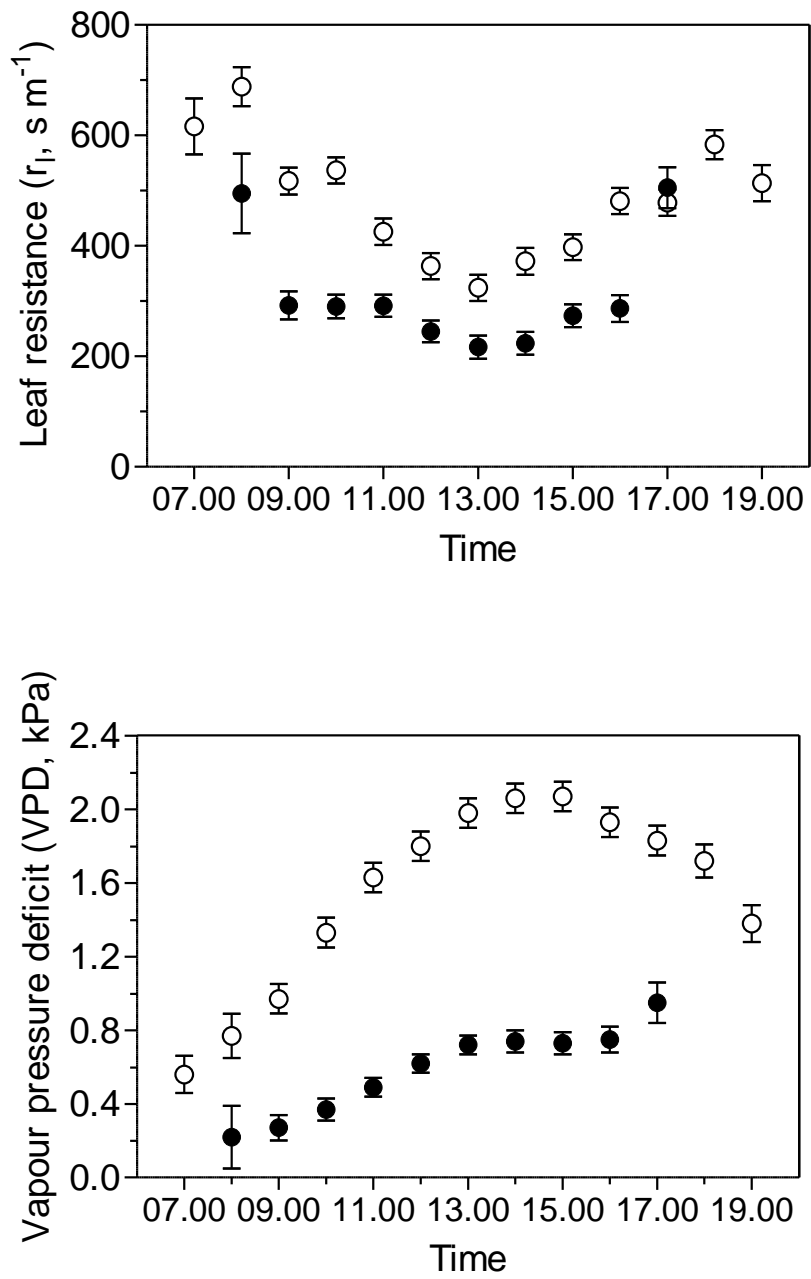


Fig. 3.

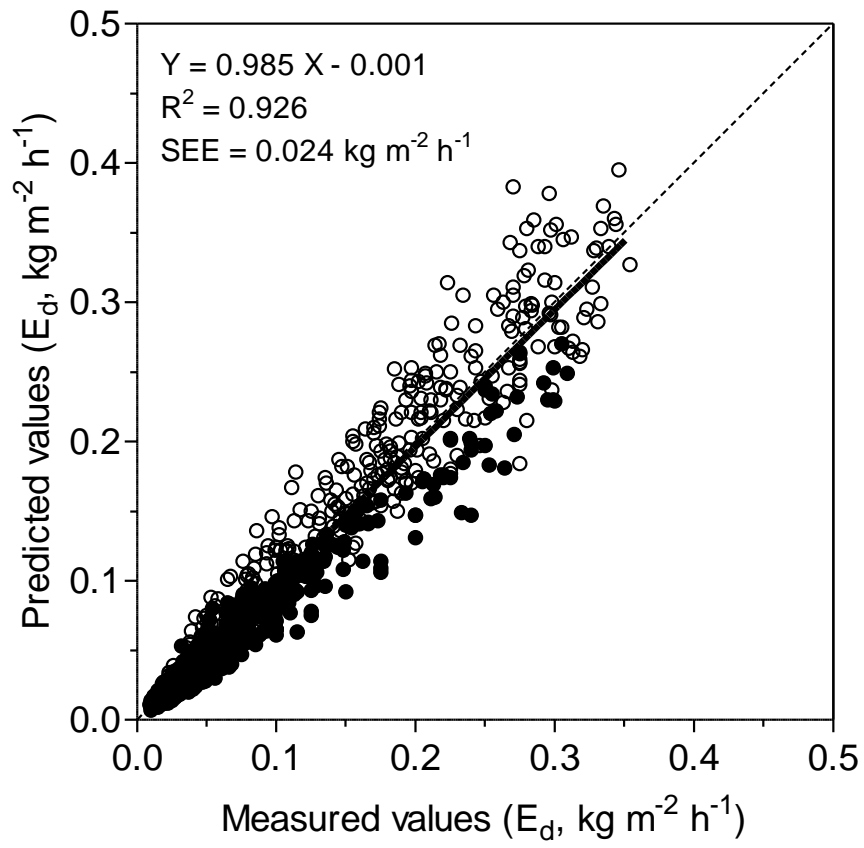


Fig. 4.

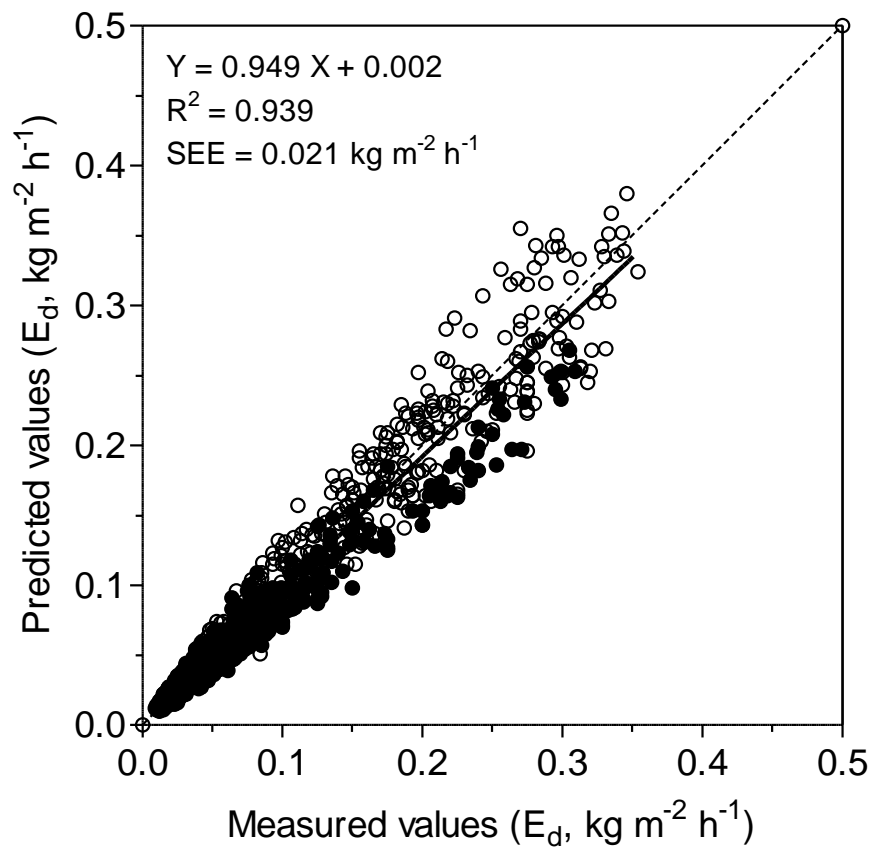


Fig. 5.

