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Effect of grafting on eggplant leaf gas exchanges under mediterranean greenhouse conditions

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Abstract

Grafting is an easier and faster approach than plant breeding to take advantage of both existing resistant plants, especially wild cultivars, and high-bred cultivars. The aim of this study was to investigate the changes in leaf photosynthetic capacity of a hybrid eggplant *Solanum melongena* L., cv. Rima (R), widely used in Greece] when grafted on tomato rootstocks known for their resistance to nematodes and diseases. For this purpose, a hybrid egg-plant has been used as a control and has been self-grafted (grafting of a scion on its own roots used as rootstock) RR and also as a scion on two hybrid tomatoes rootstocks, as follows: Primavera (RP) and Heman (RH). Leaf photosynthetic capacity was estimated by measuring the leaf gas exchanges under several light levels at ambient CO_2 concentration to approximate the leaf light response curve. The measurements performed control plant R and self-grafted eggplants RR show that the leaf respiration per unit leaf area is not altered by the scion/rootstock combination. These elements point out a scion controlled respiration, independent of the rootstock. The leaf photosynthetic capacities of the R and RR treatments were not different, while one of the scion/rootstock combinations (RH) showed a significant change with respect to the control treatments. The rootstock therefore seems to be able to modify the scion leaf photosynthetic capacity, but this may not be true for some scion/rootstock combinations (RP in our case). Leaf stomatal conductance and transpiration were not modified by the grafting, so that the water use efficiency was only altered by the modifications of the net assimilation.

Keywords: Photosynthesis; Transpiration; Respiration; Scion/rootstock; Grafting; Eggplant tomato.

Introduction

Protected cultivation is a widespread technique, especially in the Mediterranean area because it permits a more intensive and an earlier production than in the field. However, this intensification often leads to a reduction of the number of the different crops rotated in a given greenhouse. Common practices are either monoculture, of tomato or eggplant for example in Greece, or the rotation of no more than two cultivars, lettuce and tomato, pepper

or eggplant in southern France. Except for soilless protected cultivation, soil-borne pests (e.g. nematodes) and diseases (Verticilium, Fusarium, Sclerotin) are one of the major problems of these production systems, even more since the withdrawal of the methyl-bromide as a soil fumigant (in 2005 in Europe). Alternative sustainable crop protection techniques like solarisation are currently used with relative success (Yilmaz et al., 2010) while some others are still under development, for example, biofumigation with Allium crop. However, these techniques require use the greenhouse for only a couple of months forbidding any crop during that time. More than that none of the previous approaches offer a complete protection to the cultivated crops. Therefore, the use of plant resistance or tolerance to overcome the soil-borne pests and diseases problems is considered a promising element in the design of sustainable protected cropping systems (Cebolla-Cornejo et al., 2007; Rommens and Kishore, 2000).

Grafting is an easier and faster way than plant breeding to take advantage of both existing resistant plants, especially wild cultivars, and high-bred cultivars. It is a widespread technique used especially in Cucurbitacea and Solanacea vegetables, in protected cultivation (Davis et al., 2008; Minuto et al., 2007; Oda, 2007). Rootstocks are generally selected on because of their high vigour and their tolerance or resistance to bio stress such as pests and diseases (Lockwood et al., 1970; Bletsos et al., 2003). Using vigorous rootstocks generally confers the grafted plant a higher tolerance to abiotic stress such as higher soil temperature and to water and salinity stress (Ahn et al., 1999; Wei et al., 2006; Rivero et al., 2003). This leads to an increased biomass and yield of the scion. These authors, and many others, report an enhanced water use efficiency and, to a less extent, an enhanced light use efficiency. These enhancements are generally attributed to changes in the leaf activity, whether stomatal conductance, photosynthetic capacity or both, in response to grafting. Although some researchers report a reciprocal influence of the rootstock on the scion (Daunay and Malet, 1986; Passam et al., 2005) most studies focus on the changes in the specific scion activity because it determines the productivity of the grafted plant. For grafting to be adopted for vegetable species, improved knowledge of rootstock-scion compatibility as well as different activities in photosynthetic capacity among non grafted and grafted is required. Therefore, in this study, we investigate the change in the leaf photosynthetic capacities of a hybrid eggplant when grafted on tomato rootstocks known for their resistances to nematodes and diseases, in so far that these changes may be a key element in understanding the agronomic behaviour of these grafted plants.

Materials and Methods

Greenhouse facilities and plant material

A hybrid egg-plant (*Solanum melongena* L.) cv. Rima (R) has been used as scion on two hybrid tomatoes rootstocks, *Lycopersicom esculentum* cv. Primavera (RP) and *Lycopersicon hirsutum* cv. Heman (RH). Primavera possesses resistances to *Verticillium* and nematodes, where as Heman is resistant to *Pyrenochaeta lycopersici* and nematodes. Rima plants were used as control (R) and self-grafted i.e. grafting of a scion on its own roots used as rootstock, (RR). Hence the tested combinations were Primavera rootstock with Rima scion (RP), Heman rootstock with Rima scion (RH), Rima rootstock with Rima scion (RR) and non-grafted own-rooted Rima (R).

High quality commercial seed, provided by Geoponiko Spiti Ltd., Athens, were sown in small pots (5 cm × 10 cm) containing commercial, peat-based, compost. Given that the two rootstocks have a known difference in growth vigour, they were sown 10 days after 'Rima' in order to ensure similar stem diameters at the time of grafting. The pots were held in a propagation greenhouse until transplantation. Seedlings were grafted by hand, applying the cleft grafting method when the stem of the scion at the 4-leaf stage and the rootstock at 4 or 5-leaf stage were equal in diameter, as recommended by Oda (1995). Plants were transplanted into an arched roof greenhouse on April 6th, 2005 at the Velestino farm of the University of Thessaly (latitude 39º 22´ N, longitude 22º 44´ E, altitude 85 m). The plants were laid out 0.5 m apart with a row distance of 1.0 m, with a plant density of 1.6 plants per m^2. The experimental was laid out based on Ramdomized Complete Block Design (RCBD) consisted of two blocks with four treatments per block. The plants were grown following the technique that is usually implemented by the local producers that is to keep two stems per plant.

The greenhouse was covered by a double inflated polyethylene film on the roof and by glass on the sidewalls and gables. The geometrical characteristics of the greenhouse were as follows: eaves height 3 m; ridge height 4.65 m; total width 10 m; total length 30 m; ground area 300 m^2 and volume 1237 m^3. The greenhouse was equipped with two side flap vents located at a height of 1.5 m above the ground with a maximum opening area of 13.5 m^2 (30 m length × 0.45 m height) for each and a roof window with a maximum opening area of 18 m^2 (30 m length × 0.60 m height). The vents were controlled automatically and opened in several steps. The ventilation set point temperature was set at 23 ºC. Water and fertilizers were supplied by a drip-system, which was automatically controlled by a fertigation computer.

Measurements

Leaf photosynthetic capacity has been estimated by measuring the leaf gas exchanges under several light levels at ambient CO_2 concentration to approximate the leaf light response curve. The leaf gas exchanges have been measured using a closed chamber LiCor 6200 portable photosynthesis measurement device. The LiCor 6200 CO_2 gas analyser calibration was verified every day against a reference CO_2 gas. At the same time, test of the desiccant and adjustment of the air flow were also performed to ensure proper control of the water vapour pressure in the chamber, a key condition to maintain the stomatal conductance constant during the measurement.

To obtain several light levels ranging from 0 to approximately 1500 μmol photons·m^{-2}·s^{-1}, a lighting system consisting of a high pressure sodium lamp, a cooling filter and shading filters has been built and used. To avoid excess heating of the leaf during the measurement, a cooled water film circulating on a glass was placed between the measurement chamber and the lamp. To reduce the light level for intermediary measurements, shading filters made of shading nets of various shading intensities were also placed between the lamp and the leaf. Total darkness was achieved by placing the measurement chamber in a black and opaque plastic bag.

Leaf gas exchange measurements were carried out during three periods from April to June (period 1: 2005/4/30-2005/5/6, period 2: 2005/5/15-2005/5/18 and period 3: 2005/6/9-

2005/6/23), on three leaves per plant, on two plants per block and on two blocks per treatment, which makes a total of 12 leaves per treatment and measuring period. The leaves selected for measurements were of similar age and were located just below and above the second flower trace of the main stem of each plant. More than 5 measurements per leaf were carried out at several photosynthetic photon flux density (PPFD) levels ranging from 0 to at least 1000 and at most 1500 μmol·photons $m^{-2}·s^{-1}$, depending on the naturally available solar radiation. To maintain a constant CO_2 ambient concentration between every measurement, the chamber was opened after each measurement to flush the content of the chamber. All measurements were performed between 10:00 and 16:00 local time.

Data analysis

Leaf gas exchange measurements were first checked for the temperature, the humidity and CO_2 level at which they had been made. The estimated stomatal conductance has also been checked and measurements corresponding to low values eliminated. The remaining measurements were used to calibrate a leaf photosynthesis model (Farquhar et al., 1980; Harley and Tenhunen, 1991). The calibration has been performed in two steps. The first one used the measurements realised without light to estimate the leaf dark respiration (R_d) and its dependence to temperature (T_l), for each block, within each treatment, within each period:

$$R_d(T_l) = R_{25} \cdot Q_{10}^{\frac{T_l - 25}{10}} \quad (1)$$

Where R_{25} is the dark respiration at a leaf temperature of 25 ºC and Q_{10} is the exponential rate of increase of the respiration with the leaf temperature. Leaf temperature varied sufficiently during the different repetitions of the measurements to allow a proper estimation of these parameters. Model comparisons were performed to verify that the leaves and blocks of one treatment at a given period did not differ significantly, before calibrating equation (1) again on all the data of one treatment at a given period. The second step of the calibration used estimated gross photosynthesis (P_g) values: for each treatment, and for each measurement of a treatment at a given period, the measured leaf temperature was used to estimate a leaf dark respiration using the calibrated equation (1) and the net photosynthesis measurement (P_n): $P_g=P_n-R_d$. The leaf gross photosynthesis model used is the model proposed by Farquhar et al. (1980), in the form presented by Harley and Tenhunen (1991), respiration and nitrate limitation excluded. The parameters subjected to calibration and used to represent the leaf photosynthetic capacity were the maximum velocity of the carboxylase (V_{cmax}), the maximum rate of electron transport (J_{max}) and the efficiency of light energy conversion (α). Model comparisons were carried out to verify that the leaves and blocks within one treatment and one measurement period did not differ significantly.

Model comparisons were performed to assess whether two sets of parameters, obtained on two sets of measurements, differ significantly or not (Morris, 2010). The method used for the comparison requires calibrating the model twice, first with common parameters for the two data sets (reduced model), and then with different parameters for each of these two

data sets (full model). An ANOVA is then used to determine whether the full model differs significantly from the reduced one (Venables and Ripley, 1997). As an example,

Figure **1** shows the measurements obtained on one treatment, for the two experimental blocks used here. It also shows the resulting leaf light response curves for each block and common to these two blocks, the latter being legitimate since the model comparison yields no significant difference between the two blocks.

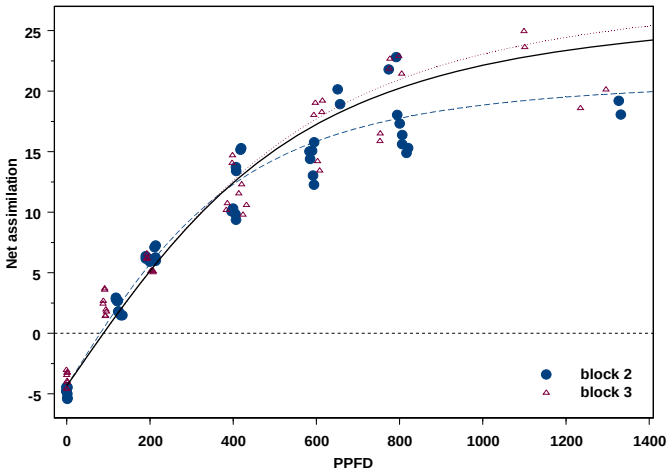

Figure 1. Net photosynthesis measurements on the RP treatment during the first period, for block 2 (filled circles) and 3 (empty triangles). PPFD in µmol electron. m^{-2} s^{-1}, net assimilation rate in µmol CO_2 m^{-2} leaf s^{-1}. The dashed line represent the fitted Farquhar model on block 2 data, the dotted line on block 3 data and the continuous one on blocks 2 and 3 together.

Results

Greenhouse and leaf microclimate

The average values of the greenhouse and leaf microclimate characteristics, during three periods of measurements are shown in Table 1. It can be seen that period 1 and 2 were similar but that period 3 was warmer, both in terms of greenhouse air temperature and leaf temperature during the measurements. It must be noticed that CO_2 concentration in the chamber during all the measurement of the three periods was successfully kept constant, close to 36.5 kPa partial pressure (365 ppm).

Effect of grafting on leaf gas exchanges

The leaf dark respiration is characterised by two parameters, the respiration at 25 ºC (R_{25}) and the Q_{10} temperature dependence factor. Table 2a shows the values of the parameters and the standard error of estimation. Respiration rates at 25 ºC lay between -1.55 and -3.2 µmol CO_2 m^{-2} s^{-1}, while the Q_{10} values are between 0.75 and 2.9.

Table 1. Average values of climate data measured in the greenhouse and the LiCor measuring chamber, during the three periods of measurements.

Period	T_g	T_c	T_l	RH_c	CO_2
1 (30/4-6/5)	29.2 (2.3)	30.5 (2.7)	29.7 (2.4)	55.9 (12.2)	36.3 (1.8)
2 (15-18/5)	28.4 (2.2)	29.5 (2.4)	28.9 (2.4)	59.9 (10.0)	36.6 (1.1)
3 (9-23/6)	32.1 (2.1)	34.2 (2.2)	33.1 (2.2)	69.7 (12.2)	36.8 (1.1)

T_g: mean greenhouse air temperature, T_c: mean air temperature inside the measuring chamber, T_l: mean leaf temperature during the measurements (temperatures in Celsius), RH_c: mean air relative humidity inside the measuring chamber (%), CO_2: mean CO_2 concentration in the chamber during the measurements (kPa).

Table 2. A: Leaf dark respiration parameters (values in parenthesis represent the standard deviation of the estimation). ANOVA test results for model comparisons, B: comparisons of grafting treatments within the same measurement period; C: comparisons of measurements periods within the same grafting treatment. Treatments are: non grafted egg plants of Rima (R), self-grafted Rima (RR) and the grafted on tomato resistance rootstock of Heman (RH) and Primavera (RP).

A

Period	Treatment	R_{25} μmol CO_2 m^{-2} s^{-1}		Q_{10}-	
1 (4/30-5/6)	*R*	-1.88	(0.23)	2.88	(0.70)
	RR	-1.55	(0.35)	2.76	(1.05)
	RH	-2.03	(0.35)	0.75	(0.48)
	RP	-1.84	(0.25)	2.07	(0.42)
2 (5/15-5/18)	*R*	-2.45	(0.45)	2.35	(0.76)
	RR	-2.88	(0.29)	1.86	(0.49)
	RH	-2.25	(0.23)	2.57	(0.44)
	RP	-2.48	(0.20)	2.86	(0.77)
3 (6/9-6/23)	*R*	-1.77	(0.41)	2.57	(0.76)
	RR	-1.98	(0.38)	2.74	(0.64)
	RH	-3.19	(0.41)	1.36	(0.19)
	RP	-2.81	(0.48)	1.66	(0.33)

B

	1(4/30-5/6)	2(5/15-5/18)	3(6/9-6/23)
R	a	A	a
RR	abc	A	a
RH	b	A	a
RP	c	A	a

C

	R	RR	RH	RP
1(4/30-5/6)	a	a	a	a
2 (5/15-5/18)	b	b	b	b
3(6/9-6/23)	a	ab	c	b

Identical letters in a column indicate a non-statistically significant difference for 99% confidence interval.

The R and RR treatments are not significantly different for each of the three measurement period, as can be seen on Table 2B and on Figure 2. Measurements in period 2 lead to significantly lower parameter values than in the other two periods (Table 2C). Also, RH and RP treatments differ from each other and from R for the first period (Table 2B). For the second and third period, they do not differ significantly from each other, nor do they differ from RR and R. Moreover, RH measurements differ significantly across the

measurement periods. RP measurements for the first period are significantly different from the second and third period (Table 3).

Figure 2 also shows that R and RR treatments share the same trend along the three measurement periods (lower values for the second than for the two others) and that the RH and RP treatments also share a common trend (higher values for the second period), but different, and opposite, from that of R and RR.

Respiration models are therefore could be affected by the grafting treatment during the first measurement period, not during the other two. They are affected by the measurement period, within each treatment.

Effect on photosynthesis

The results found for all the treatments for each measurement period are shown in Table 3A. It can be seen that the standard errors of the estimation of the parameters are fairly stable and low (less than 5% of the value for V_{cmax}, 10% for J_{max}, 5 to 10% for α) indicating a rather good fit of the model in all cases. V_{cmax} varies from 78.5 to 135.5 µmol $CO_2.m^{-2}.s^{-1}$, J_{max} from 104.3 to 162 µmol electrons.$m^{-2}.s^{-1}$ and α from 0.15 to 0.20 mol electrons.mol^{-1} photons.

Table 3B shows that R and RR treatments differ for the first measurement period, but not for the second or the third. RH is consistently different from the other treatments for each measurement period. RP does not differ from R for the first period, from RR for the third. Control plants R treatment measurements differ for each measurement period, while in all grafted plants measurements were different in first period comparing with second and third period, with exception of RH which was different in third period only (Table 3).

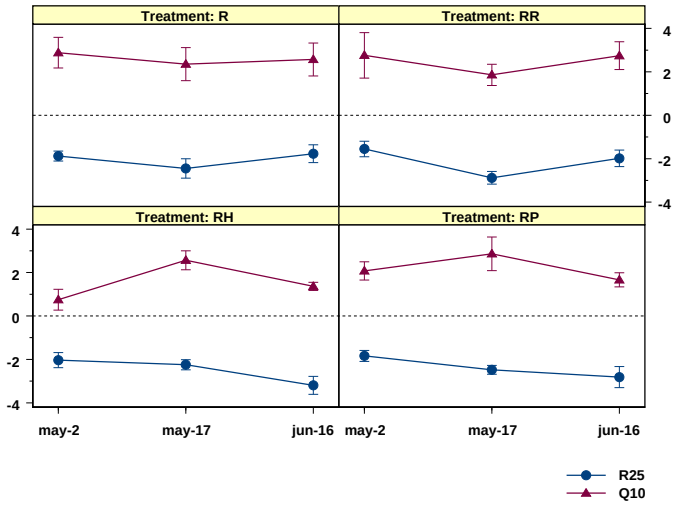

Figure 2. Respiration model parameters evolution between non grafted egg plants of Rima (R) and self-grafted Rima (RR) and the grafted on tomato resistance rootstock of Heman (RH) and Primavera (RP) along the three measurement periods, for each treatment. Measurement periods are referred by their middle date: may-2=(april-30-may-6), may-17=(may-15-may-18), jun-16=(jun-9-jun-23).Vertical bars represent the standard error of the estimated parameter values.

Table 3. A: Calculated parameters of the photosynthesis model during the three periods of measurements (values in parenthesis represent the standard deviation of the estimation). ANOVA test results for model comparisons; B: comparisons of grafting treatments within the same measurement period; C: comparisons of measurements periods within the same grafting treatment. Treatments are: non grafted egg plants of Rima (R), self-grafted Rima (RR) and the grafted on tomato resistance rootstock of Heman (RH) and Primavera (RP).

A

period	Treatment	Vcmax μmol $CO_2.m^{-2}.s^{-1}$		Jmax μmol electron.$m^{-2}.s^{-1}$		Alpha mol $CO_2.mol^{-1}$ electron	
4/30-5/6	R	93.85	(3.88)	127.07	(10.39)	0.16	(0.007)
	RR	105.65	(2.90)	162.05	(15.73)	0.15	(0.005)
	RH	80.64	(1.91)	135.99	(12.51)	0.20	(0.012)
	RP	110.77	(4.63)	139.83	(11.83)	0.16	(0.008)
5/15-5/18	R	103.74	(2.44)	136.25	(8.13)	0.19	(0.008)
	RR	78.46	(1.63)	155.93	(15.21)	0.20	(0.007)
	RH	124.10	(6.99)	119.45	(5.52)	0.21	(0.008)
	RP	69.77	(2.72)	104.26	(3.67)	0.22	(0.010)
6/9-6/23	R	101.64	(2.05)	158.71	(18.88)	0.16	(0.010)
	RR	135.44	(7.62)	131.10	(4.57)	0.19	(0.008)
	RH	115.03	(4.67)	124.83	(12.54)	0.17	(0.010)
	RP	110.13	(2.36)	125.19	(5.36)	0.20	(0.008)

B

	4/30-5/6	5/15-5/18	6/9-6/23
R	a	a	ab
RR	b	a	ac
RH	c	b	b
RP	ab	c	c

C

	R	RR	RH	RP
4/30-5/6	a	a	a	a
5/15-5/18	b	b	a	b
6/9-6/23	c	b	b	b

Identical letters in a column indicate a non-statistically significant difference for 99% confidence interval.

From Figure 3 and Figure 4, it can be noticed that no specific ordering of the treatments emerges from the values of these parameters. Therefore, in order to have a simpler representation of the leaf photosynthetic capacities, we have used the fitted models to estimate a reference gross assimilation rate at 500 μmol m^{-2} s^{-1} PPFD, 30 kPa internal CO_2 partial pressure and 25 ºC leaf temperature. These results are presented on Figure 5 which shows that the self-grafted RR always have a higher assimilation rate than R and RH treatment keeps a high assimilation rate during the first two measurements while the RP reaches a high level starting at the third period.

Effect on transpiration and stomatal conductance

Leaf transpiration rate (E) and stomatal conductance (g_s) were also measured during the three periods of measurements by the LI-COR 6200 as part of the measurements necessary

for the estimation of the photosynthesis (Table 4). These measurements were divided according to the PPFD level at which they were obtained to exclude the response of E and g_s to PPFD. An ANOVA shows that the measurement period has a significant effect on E and g_s while the treatment has no significant effect (Table 4 shows the results for the data obtained between 400 and 600 µmol m^{-2} s^{-1} PPFD).

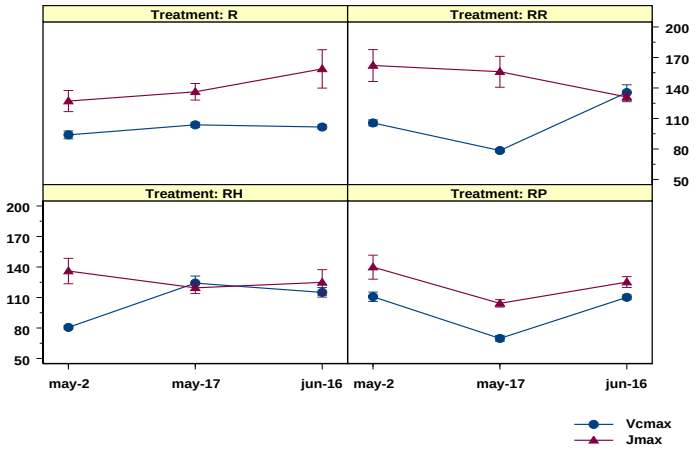

Figure 3. Photosynthesis model parameter (J_{max} and V_{cmax}) evolutions between non grafted egg plants of Rima (R) and self-grafted Rima (RR) and the grafted on tomato resistance rootstock of Heman (RH) and Primavera (RP) along the three measurement periods, for each treatment. Measurement periods are referred by their middle date: may-2=(april-30-may-6), may-17=(may-15-may-18), jun-16=(jun-9-jun-23).

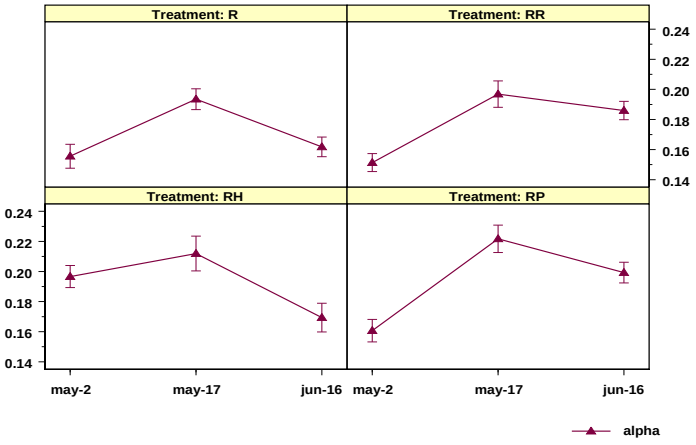

Figure 4. Photosynthesis model parameter (α) evolutions between non grafted egg plants of Rima (R) and self-grafted Rima (RR) and the grafted on tomato resistance rootstock of Heman (RH) and Primavera (RP) along the three measurement periods, for each treatment. Measurement periods are referred by their middle date: may-2= (april-30-may-6), may-17=(may-15-may-18), jun-16=(jun-9-jun-23).

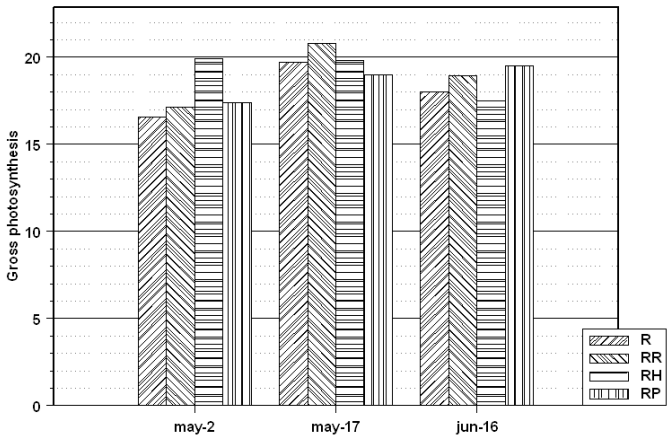

Figure 5. Estimated gross photosynthesis (µmol CO_2 m^{-2} s^{-1}) at 500 µmol m^{-2} s^{-1} PPFD, 30 kPa internal CO_2 partial pressure and 25 °C leaf temperature between non grafted egg plants of Rima (R) and self-grafted Rima (RR) and the grafted on tomato resistance rootstock of Heman (RH) and Primavera (RP) in the greenhouse. Measurement periods are referred by their middle date: may-2=(april-30-may-6), may-17=(may-15-may-18), jun-16=(jun-9-jun-23).

Table 4. Summary of transpiration and stomatal conductance measured between 400 and 600 µmol.m^{-2}.s^{-1} PPFD and ANOVA results with treatment and period as factors. Values in parenthesis are the standard deviations. Treatments are: non grafted egg plants of Rima (R), self-grafted Rima (RR) and the grafted on tomato resistance rootstock of Heman (RH) and Primavera (RP).

Period	Treatment	E mol.m^{-2}.s^{-1}		g_s mol.m^{-2}.s^{-1}	
4/30-5/6	R	0.0061	(0.0028)	0.851	(0.392)
	RR	0.0074	(0.0015)	1.632	(0.613)
	RH	0.0058	(0.0006)	1.137	(0.239)
	RP	0.0051	(0.0010)	0.788	(0.243)
5/15-5/18	R	0.0061	(0.0017)	1.234	(0.266)
	RR	0.0044	(0.0015)	0.610	(0.181)
	RH	0.0072	(0.0016)	1.309	(0.373)
	RP	0.0049	(0.0014)	0.861	(0.356)
6/9-6/23	R	0.0087	(0.0008)	3.608	(1.890)
	RR	0.0076	(0.0014)	2.022	(0.655)
	RH	0.0077	(0.0054)	1.835	(1.214)
	RP	0.0103	(0.0033)	3.201	(2.602)

ANOVA results for the transpiration *E*.

	Df	Sum of Sq	Mean Sq	F Value	Pr (F)
Treatment	3	0.00000628	0.00000209	0.361	0.780
Period	2	0.000248	0.000124	21.44	<0.0001
Residuals	155	0.000898	0.00000579		

ANOVA results for the stomatal conductance g_s.

	Df	Sum of Sq	Mean Sq	F Value	Pr (F)
Treatment	3	2.958	0.986	0.772	0.511
Period	2	79.87	39.93	31.26	<0.0001
Residuals	155	198.01	1.277		

Discussion

Leaf respiration rate

The R and the RR have similar respiration rates at 25 ºC for each measurement period. These values are comparable to those reported by Bunce (2001) who found, for non grafted eggplants, respiration rates between -1.5 and -2.8 μmol CO_2 m^{-2} s^{-1}. Respiration is classically divided into maintenance and growth components, the maintenance component being proportional to the dry weight of the plant and the growth component to the available assimilates (McCree, 1970; Amthor, 2000). The R and RR treatments had comparable yield and dry matter (data not shown), which may explain the absence of significant difference for their respiration rates. The introduction of the graft between the rootstock and the scion seems to be of no consequence on the respiration which may advocates for an independence of the scion respiration on the rootstock. The measurement period, for each of the treatments, has a significant effect. The periods differ both by the plant and leaf ages and by the greenhouse climate. Plant and leaf age increased from period 1 to period 3, while period 1 and 2 had similar environmental conditions, period 3 being warmer. Leaf respiration generally increases with the age of the leaf, and with temperature. However, if respiration increases from period 1 to period 2, which may be attributed to ageing, it decreases from period 2 to period 3, although leaf age and temperature increase. The Q_{10} values for the R and RR treatments at each measurement period remain above 1.8, almost always above 2.5. Although no Q_{10} values could be found in the literature for eggplant, values for tomato and another *Solanacea* are generally range around 2 (Jones et al., 1991).

The RH and RP grafted treatment respiration rates at 25 ºC are not different from each other for the second and third periods, nor are they different from those of the references and RR treatments. However, they display a regular increase of the respiration rate at 25 ºC with the measurement period, that is with plant and leaf age, which is more consistent than what is observed on R and RR. Contrarily to R and RR, the Q_{10} values of the RH and RP treatments vary in time, with high values at period 2 and surprisingly low values for period 3, showing a relative independence of the leaf respiration to temperature.

Leaf gross photosynthesis and stomatal conductance

The R and RR treatments have similar photosynthetic parameters except for period 1. For the first period, the difference between these two models is due to the estimated value of J_{max}, the values of V_{cmax} and α being close. However, an ANOVA performed on measurements for these treatments, during the first period, and under high PPFD values (above 1000 μmol.m^{-2}.s^{-1}) shows no effect of the treatment, indicating comparable light saturated assimilation rates. The grafted treatment RH was generally different from the other treatments. Figure 5 shows that this treatment established high assimilation rates during the first two periods, while R, RR and RP treatments reached an equivalent level at the second measurement period only.

The effects of grafting on the photosynthetic capabilities of the leaves of the scion are obviously not clearly established. On eggplants, Brandao Filho et al. (2003) report that the grafting did not modify the photosynthetic capabilities of the grafted hybrids, which points

to a control of the photosynthetic capacities by the scion, not by the rootstock. However, on eggplant too (Shu et al., 2006) on netted melons (Wei et al., 2006), on watermelon (Yetisir et al., 2006) and on vines (Düring, 1994), the common report is that the grafted plants have higher photosynthetic capacities and that these modifications depend on the rootstock. In our case, the differences between the RH (or RP) treatment and the R and RR treatments may be attributed to an effect of the rootstock. The fact that the R and RR treatments, which share a common rootstock are more consistently comparable to each other than they are to the other two treatments is also pointing towards this conclusion. Ruiz et al. (1997) found that on melon grafted onto three different Cucurbitacea rootstocks and point out that the leaf macronutrient content of the leaves of grafted plants, and especially the N content, was not affected by the rootstock. The grafting effect of the rootstock may therefore not be linked to differences in the leaf concentration in chlorophyll, but to a faster assimilate translocation from the leaves to the plant.

Many authors observe an increased water use efficiency, either because of an increased net assimilation rate (Düring, 1994; Wei et al., 2006) or because of a reduction of the transpiration and stomatal conductance (Brandao Filho et al., 2003) or because of both (Yetisir et al., 2006). In our results, the stomatal conductance was only affected by the measurement period, not by the grafting treatment, in agreement with observations of Daunay et al. (1986) who found that the rootstock has little influence on the stomatal conductance of eggplants. The transpiration rate follows the same trend as the conductance. The increased assimilation rate of the RH treatment therefore leads to an increased water use efficiency of this scion/rootstock combination in comparison to the other treatments. It must be noted, moreover, that our measurements of transpiration and stomatal conductance were taken during the photosynthesis measurement, during a stressed period for the leaf. Indeed, the leaf was submitted to high air speed due to the ventilation within the chamber, to increasing PPFD and temperature levels and to the mechanical stress linked to the pinching when closing the chamber.

Measurements of the agronomic behaviour of the grafted and non grafted eggplant show a clear advantage to the RH scion/rootstock combination, with a significantly higher yield (20.5 kg/plant for RH against an average 14 kg/plant for RP, 235 days after transplantation, DAT). The yield difference was built up about 170 days after transplant (our measurements took place between 24 and 30 DAT for period 1, 39 and 41 DAT for period 2 and 64 and 78 DAT for period 3, before the first harvest in all cases). Previously reported that leaf dry weight and leaf area were similar between all the treatments (Khah, 2005). The increased photosynthetic capability of the RH treatment might be one of the reasons of its increased yield.

Conclusion

The measurements performed on own-rooted and self-grafted eggplants show that the leaf respiration per unit leaf area is not altered by the scion/rootstock combination. Khah (2005) reported on the same experiment that leaf area and leaf dry weight per plant were also not different between the grafting treatments, implying a comparable specific leaf area. These elements pointed a scion controlled respiration, independent of the rootstock. The leaf photosynthetic capacities of the own-rooted and of the self-grafted treatment were not different, while one of the scion/rootstock combinations (RH) showed a clear change with

respect those two control treatments. The rootstock therefore might be able to modify the scion leaf photosynthetic capacity, but this may not be true for some scion/rootstock combinations (RP in our case), for reasons possibly due to the negative incompatibility between scion/rootstock combinations. The leaf stomatal conductance and the leaf transpiration were not modified by the grafting, so that the water use efficiency was only altered by the modifications of the net assimilation.

To better understand the processes leading to a change in the leaf photosynthetic capacities, further studies should focus on the leaf chlorophyll content and on nutrient translocation from and to the leaf, in order to determine whether the rootstock effect is due to a change in the leaf photosynthetic apparatus or to a change in the water, nutrient and assimilate flows which would prevent the inhibition of photosynthesis due to a high leaf content in carbohydrates.

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