Evaluation of some pepper genotypes as rootstocks in water stress conditions

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Abstract

Penella C., Nebauer S.G., López-Galarza S., SanBautista A., Rodríguez-Burruezo A., Calatayud A., 2014. **Evaluation of some pepper genotypes as rootstocks in water stress conditions**. Hort. Sci. (Prague), *41*: 192–200.

Water stress is a major environmental factor that limits crop production and it is important to develop crop varieties with higher yield under water scarcity. Increased pepper tolerance to water stress through grafting onto robust rootstocks could be an optimal alternative in the context of environmentally friendly agriculture. Our work evaluated the behaviour of 18 pepper genotypes during vegetative and reproductive stages under water stress in order to select tolerant genotypes to be used as rootstocks for pepper cultivation. The pepper tolerance screening was based on photosynthetic parameters. The genotypes Atlante, C-40, Serrano, PI-152225, ECU-973, BOL-58 and NuMex Conquistador were revealed as the most tolerant genotypes to water stress because they maintained net photosynthetic rate levels under water stress conditions. The selected genotypes were validated as rootstocks on a pepper cultivar in terms of productivity under severe water stress. Plants grafted onto cvs Atlante, PI-152225 and ECU-973 showed higher marketable yields when compared with ungrafted cultivar.

Keywords: *Capsicum annuum*; chlorophyll fluorescence; graft; photosynthesis; yield

Bell pepper (*Capsicum annuum* L.) is one of the most important crops in the world (Villa-Castonera et al. 2003) and it is one of the most susceptible to water stress, mainly because it has large transpiring leaf surface and high stomatal conductance of water vapour (Alvino et al. 1994; Delfine et al. 2002). In pepper production industry, drought imposes huge reductions in crop yield and quality, with significant economic losses of up to 70% (Delfine et al. 2002; De Pascale et al. 2003; Fernandez et al. 2005). In this regard, irrigation is essential for pepper production as these plants are particularly sensitive to moisture stress at flowering and fruit setting (Bosland, Votava 2000). Thus, reduced yields and smaller fruits are frequently recorded under conditions of moisture stress and, moreover, limiting the water applied to peppers during the period of rapid growth reduces the final yield according to Beese et al. (1982).

In this sense, conventional methods for detecting water stress tolerance in plants, as hydric and osmotic potential (Bajji et al. 2000), relative water content (González et al. 2008), leaf mass per area ra-

Supported by Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Project RTA2010-00038-C03-01-03 and the European Regional Development Fund.

tio (Yadollahi et al. 2011), proline and antioxidant system measurements (Anjum et al. 2012), are frequently laborious and destructive. The development of non-destructive and rapid technologies such as leaf gas exchange or chlorophyll (Chl) *a* fluorescence techniques provides information about photosynthesis during the plant life cycle. Photosynthesis was found to be a very informative indicator for the study of water stress effects because of its extreme sensitiveness to environmental stresses (Massacci et al. 2008). The main effect of water stress is the reduction in carbon fixation associated with stomatal closure and the subsequent increase in resistance to CO_2 diffusion in the leaves (Kaiser 1987). This effect results in a decrease in the rate of leaf photosynthesis and photochemical Chl *a* fluorescence parameters (Lu, Zhang 1998; Calatayud et al. 2006). Moreover, the decrease in carbohydrates synthesis reduces plant growth and, therefore, it has a great impact on crop yield (Stuart et al. 2011).

The need to find pepper plants resistant to water stress has led to several studies and approaches to increase yields and improve quality (Karam et al 2009; Schwarz et al. 2010). Grafting can be an adaptation strategy in integrated or organic agricultural production systems that enable plants to overcome soil borne diseases and environmental stresses (Colla et al. 2010; King et al. 2010; San Bautista et al. 2011). The grafting technique could allow plant breeders to combine desired shoot characteristics with root features that provide tolerance to water stress (Colla et al. 2010). The cultivation of grafted plants has expanded widely (mainly in tomato, melon and watermelon) (Lee et al. 2010), but this practice is still limited in peppers (Miguel et al. 2007; King et al. 2010) and limited information exists regarding water stress tolerant pepper rootstocks.

Our work evaluated the performance of 18 pepper genotypes during vegetative and reproductive stages under water stress in order to select tolerant genotypes to be used as rootstocks for pepper cultivation. The pepper tolerance screening was based on photosynthetic parameters. The tolerant genotypes were validated as rootstocks on a pepper cultivar in terms of a productivity parameter under severe water stress.

MATERIAL AND METHODS

Experiment 1. Screening pepper genotypes to be used as rootstocks under water stress conditions during vegetative and reproductive stages. In this study, many different genotypes were used and a numerical code for each cultivar is indicated in brackets: the commercial rootstock cvs Atlante (Ramiro Arnedo (1)), C40 (Ramiro Arnedo (2)), Tresor (Nunhems (3)); the accessions of *Capsicum annuum* Serrano Criollo de Morelos-334 (4), Serrano (5), Pasilla Bajío (6), Pimiento de Bola (7), Piquillo de Lodosa (8), Guindilla (9), Habanero (10), and NuMex Conquistador (17); the accessions of *Capsicum chinense* Jacq. PI-152225 (11), ECU-973 (12) and the accessions of *Capsicum baccatum* L. var. *pendulum* BOL-134 (13) and BOL-58 (14); the accessions of *Capsicum pubescens* R.&P. BOL 60 amarillo (15) and BOL 60 rojo (16) and the accession of *Capsicum frutescens* L. BOL-144 (18). All the accessions used for the present study belong to the collection of the Institute for Conservation and Improvement of Valencian Agrodiversity (Universitat Politècnica de València, Valencia, Spain). Seeds were germinated in moistened perlite under greenhouse conditions at 28 ± 2°C and 80% of relative humidity. The seedlings with 8 mature leaves were transferred to 15 l pots containing dust substrate as coir in a heated polyethylene greenhouse on the January 15, 2011 at the Instituto Valenciano de Investigaciones Agrarias (Valencia, Spain). Plants were drip-irrigated with Hoagland's No. 2 nutrient solution containing (all in mM): 14 NO_3^-, 1.0 $H_2PO_4^-$, 2.0 SO_4^{2-}, 1.0 NH_4^+, 16.0 K^+, 4.0 Ca^{2+} and 2.0 Mg^{2+}. Micronutrients were also provided (all in μM): 15 Fe^{2+}, 10 Mn^{2+}, 5 Zn^{2+}, 30 B^{3+}, 0.75 Cu^{2+} and 0.6 Mo^{6+}) (Maynard, Hochmuth 2007). The EC of the nutrient solution was 1.9 dS/m and pH 6.1. The greenhouse conditions in this period were 16–22°C and 50–70% of relative humidity

After 15 days in the pots, 16 plants were divided in two groups (8 plants each) for control and water deficit treatments. Water deficit treatment was initiated by reducing the amount of irrigation water to 60% of the control, the latter being based on estimations of the weekly crop evapotranspiration (ETc). The volume of each irrigation and the number of irrigation were scheduled to maintain drainage between 10% and 20% (depending on solar radiation).

Eight plants per cultivar were used in each treatment. Plants were grown for six months in pots. During the measurements the environmental parameter ranges in the greenhouse were: temperature (21–24°C); relative humidity (52–72%); and solar radiation (750–1,150 μmol/m^2·s).

Net CO_2 fixation rate (A_N, μmol CO_2/m^2·s), stomatal conductance of water vapor (g_s, mol H_2O/m^2·s)

and substomatal CO_2 concentration (C_i, μmol CO_2/mol (air)) were measured at steady-state under conditions of saturating light (1,200 μmol/m^2·s) and 400 ppm CO_2 with a LI-6400 (LI-COR, Nebraska, USA). To evaluate the presence of chronic photoinhibitory processes, the max. quantum yield of PSII (F_v/F_m; where $F_v = F_m - F_o$) was measured on leaves after 30 min of dark adaptation using a portable pulse amplitude modulation fluorometer (MINI PAM; Walz, Effeltrich, Germany). The background fluorescence signal for dark adapted leaves (F_o) was determined with a 0.5 μmol photon/m^2·s measuring light at a frequency of 600 Hz. The application of a saturating flash of 10,000 μmol photon/m^2·s enabled estimations of the max. fluorescence (F_m).

Gas exchange and fluorescence measurements (n = 8 per treatment) were performed on the third or fourth leaf from the shoot apex. Measurements were performed at two months (T1, vegetative stage) and five months (T2, reproductive stage) after starting the water deficit treatment.

At the end of experiment (T2), Chl *a* fluorescence imaging under water stress was measured in one genotype tolerant to water stress (ECU-973, code 12) and one genotype sensitive to water stress (Piquillo de Lodosa, code 8) based on the photosynthesis rate measurements. Chlorophyll *a* fluorescence imaging was used for providing more detailed information on the spatial heterogeneity of photosynthetic activity under water stress in two genotypes that differ in their photosynthetic rate behaviour. Six different plants were used for each genotype and measurements were performed at the third or fourth leaf from the apex with an Imaging-PAM fluorometer (Walz, Effeltrich, Germany). Pepper leaves were darkened for 10 min prior to the F_v/F_m measure. Actinic illumination (204 μmol photons/m^2·s) was then turned on and saturating pulses were applied at 20 s intervals for 5 min in order to determine the max. fluorescence (F_m'), and the Chl fluorescence yield during the actinic illumination (F_s). The quantum efficiency of PSII photochemistry, ϕ_{PSII}, was calculated according to Genty et al. (1989) using the formula: $(F`_m - F_s)/F'_m$. The coefficient of photochemical quenching, q_p, is a measurement of the fraction of open centres calculated as $(F'_m - F_s)/(F'_m - F'_o)$ (Schreiber 1986). Calculation of quenching due to the non-photochemical dissipation of the absorbed light energy (NPQ) was determined at each saturating pulse, according to the equation NPQ = $(F_m - F'_m)/F'_m$ (Bilger, Björkman 1991). The measured value of NPQ was divided by four (NPQ/4) for the display of values < 1.000. Images of the fluorescence parameters were displayed by means of a false colour code ranging from 0.00 (black) to 1.00 (purple). The three small circles in each image are the areas of interest (AOI) and are accompanied by a small red box displaying the averaged values of the selected fluorescence parameters within this AOI. Three AOI were selected in the central part of the leaf. For more details about Chl *a* fluorescence measurements see Calatayud et al. (2006).

Data were analysed by ANOVA type III and means were compared using the Fisher's least significance difference (LSD) test at $P \leq 0.05$ (Statgraphics Centurion for Windows; Statistical Graphics Corp., Warrenton, USA).

Experiment 2. Yield responses to water stress conditions of the commercial cv. Verset grafted onto the selected genotypes of Experiment 1. The experiment was performed during 2012 in a sweet pepper producing area in Alicante, Spain, and the cv. Verset F_1 was used as scion (California type; Rijk Zwaan, the Netherlands). The genotypes 1, 2, 5, 11, 12, 14 and 17, selected as tolerant in Experiment 1, and genotype 3 (a commercial rootstock used by growers), selected as sensitive, were used as rootstocks. Ungrafted cv. Verset plants were used as controls. Pepper seeds were sown in a series of steps to obtain the appropriate diameter for grafting. The graft was performed at the middle of February using the tube grafting method (cutting the growing tip of the rootstock at a 45° angle below the cotyledons, attaching the scion, previously cut at a 45° angle above the cotyledons, and fixing the rootstock and scion with a clip). The plants were transplanted to 104-cell trays. They were maintained in a chamber where the relative humidity was above 95% and the air temperature around 28–29°C for a 4–6 days period. The grafted plants were then placed outside of this humidity chamber in a greenhouse until being transplanted.

The water stress treatment plants were irrigated to satisfy 50% of the ETc by modifying the number of irrigations and maintaining the volume constant for each irrigation, while the irrigation of control plants satisfied 100% of ETc.

The seedlings were transplanted on the April, 23 at a density of 2.1 plants/m^2 in a loam soil in a polyethylene greenhouse that featured a complete randomised block design with three replicates, each consisting of 25 seedlings with 8–10 mature leaves. The electrical conductivity of the irrigation water was 1.03 dS/m. Fertilizers were applied at a rate of

200 N, 50 P_2O_5, 250 K_2O, 110 CaO, and 35 MgO all in kg/ha, as recommended by Maroto (2005).

Harvest was staggered from the beginning of July to the end of September. The marketable fruits were counted and weighed for each genotype and treatment.

Data were subjected to ANOVA type III and means were compared using the Fisher's least significance difference (LSD) test at $P \leq 0.05$ (Statgraphics Centurion for Windows; Statistical Graphics Corp., Warrenton, USA).

RESULTS AND DISCUSSION

Experiment 1

In this work, 18 pepper genotypes were evaluated under water stress conditions in a greenhouse. Photosynthesis measurements were used as a quick and sensitive method that could help to identify plants tolerant to water stress (Fig. 1). Screening for specific tolerance traits under controlled greenhouse environment is often necessary to reduce the complexity of interactions between genetic and environmental effects on plants. Since tolerance to abiotic stress was described as a developmental stage-specific phenomenon (Ashraf 2004), it has been evaluated at different stages in the present study.

One of the earliest responses to water stress is a decrease in stomatal aperture (Munns, Tester 2008; Chaves et al. 2009). This abiotic stress may restrict net photosynthesis either due to diffusional limitation in CO_2 supply arising from a partial closure and/or mesophyll conductance restriction, or by impairing the CO_2 fixation reactions (Niu et al. 2010). In our results, photosynthesis and stomatal conductance were negatively affected by water stress in vegetative (Fig. 1a,b) and reproductive stages (Fig. 1c,d) in some genotypes. A logarithmic correlation between net CO_2 photosynthetic rate (A_N) and stomatal conductance (g_s) was observed (A_N = 6.14ln g_s + 25.6; R^2 = 0.68). Moreover, stomatal conductance was related to substomatal CO_2 concentration (C_i), (C_i = 75.5ln g_s + 365; R^2 = 0.84). These relations indicate that lowered g_s values are responsible for the diminishing intercellular CO_2 concentration, so suggesting stomatal constraints. Only genotypes 1, 5, 12, 14 and 17 maintained A_N and g_s parameters with values that did not significantly differ during growth in comparison to the controls (Fig. 1). Genotype 11 at T1 (Fig. 1b) and genotype 2 at T2 (Fig. 1c) showed significant differences for g_s parameter with respect to their controls without effect on A_N. This can be explained by the fact that only very critically low levels of g_s, described as lower than 0.1 mol H_2O/m·s (Flexas et al. 2004), in these genotypes affect photosynthesis. Since limitation by CO_2 was the main factor responsible for the decrease in net photosynthetic carbon uptake rates (Chaves, Oliveira 2004), we have selected A_N as the indicator parameter for plant tolerance to stress. In this context, the net photosynthesis rates of the genotypes Atlante (1), C-40 (2), Serrano (5), PI-152225 (11), ECU-973 (12), BOL-58 (14) and NuMex Conquistador (17) were unaffected by water stress. No differences were observed when compared with their controls in the measured periods (Fig. 1).

The Chl *a* fluorescence parameter F_v/F_m is the max. quantum yield of PSII photochemistry and is frequently used as an indicator of damage photoinhibition. In our study, F_v/F_m measured at T1 and T2 did not show significant differences between control and stress treatments (data not shown). Other studies showed little or no effect on F_v/F_m (Lee et al. 2004; Naumann et al. 2007; Niu et al. 2010;) even when leaf growth and gas exchange were reduced.

Fig. 2 shows Chl *a* fluorescence imaging of F_v/F_m after dark adaptation and Chl *a* fluorescence parameters at steady-state kinetics for a single representative leaf in both stress tolerant (12) and stress sensitive genotypes (8) at T2 under water stress. When both genotypes were compared, the ratio F_v/F_m (0.746 and 0.725 mean values for three AOI for genotype 12 and 8, respectively) and the parameter q_P (0.791 and 0.746 mean values, respectively) were unaffected, indicating that the photochemistry of PSII and its ability to reduce the primary acceptor electron Q_A was also unaltered by water stress. The ϕ_{PSII} related to the quantum yield of non-cyclic electron transport at any given light intensity (Genty et al. 1989) decreased in genotype 8 (0.412; Fig. 2) with respect to genotype 12 (0.536; Fig. 2). Since the q_P parameter was unaffected, the decrease in the rate of non-cyclic electron transport may be caused by factors beyond the Q_A acceptor. Considering the adverse effects of water stress on the electron transport rate, the decrease of photosynthesis could be partially responsible for a decreased availability of ATP and reduced power in genotype 8. However, the possibility of damage on Calvin cycle enzymes after six months of water stress must also be considered (Calatayud et al. 2004; Guidi et al. 2001). The Chl *a* fluorescence image in ϕ_{PSII} showed the heterogeneous distribution of light utilization and photosynthetic

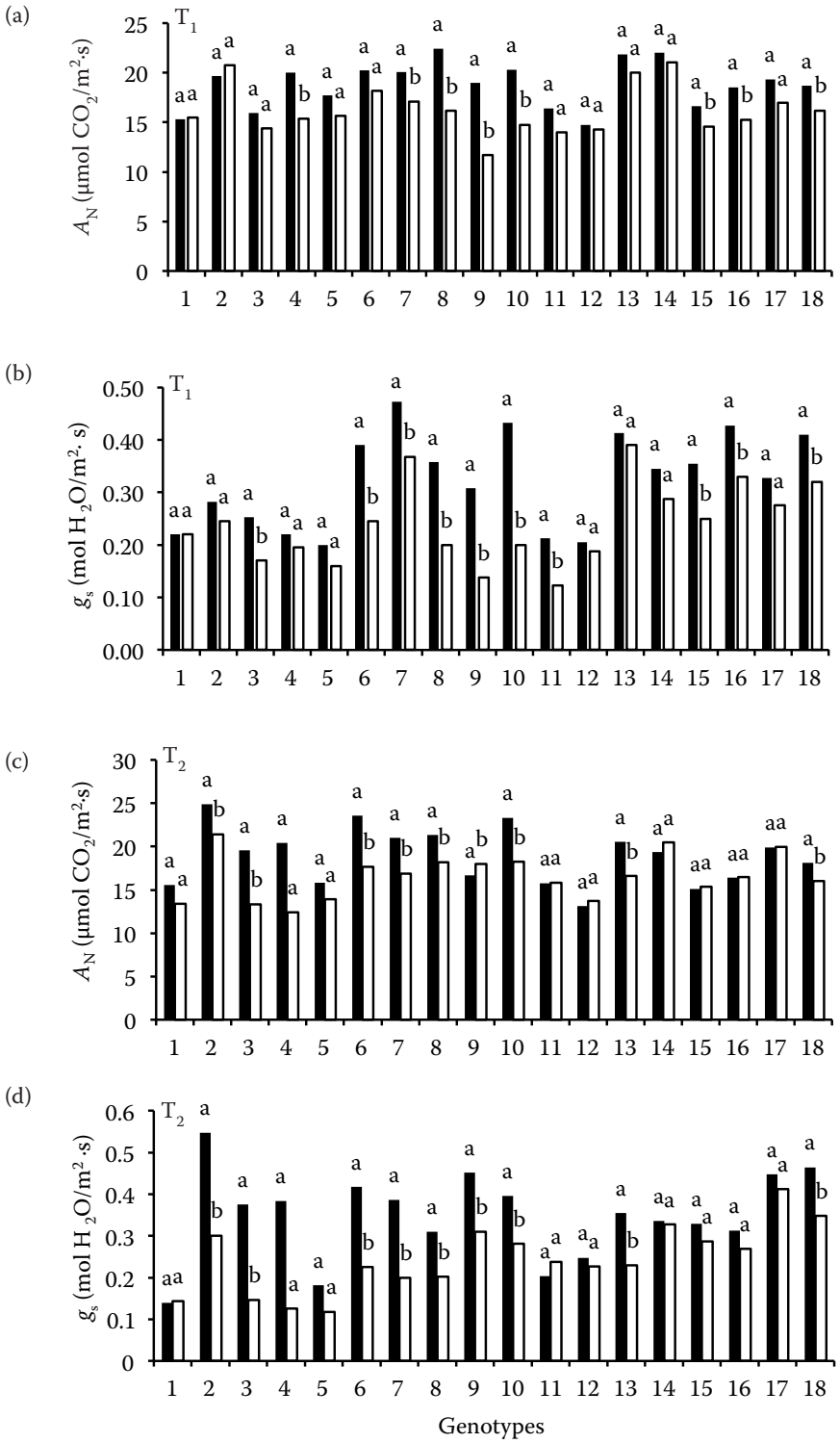

Fig. 1. Gas exchange parameters in pepper genotypes measured after (a, b) 2 months (T1 – vegetative stage) and (c, d) 5 months (T2 – reproductive stage) in the control (100% of ETc) and water stress (60% of ETc)

A_N – assimilation rate of CO_2 fixation; g_s – stomatal conductance to water vapour; values are means of 8 samples; for comparison of means, analysis of variance (ANOVA) followed by the least significant difference (LSD) test were performed and calculated at $P \leq 0.05$ confidence level; values followed by different letters (on the top of the bars) indicate significant differences between control and water stress treatment

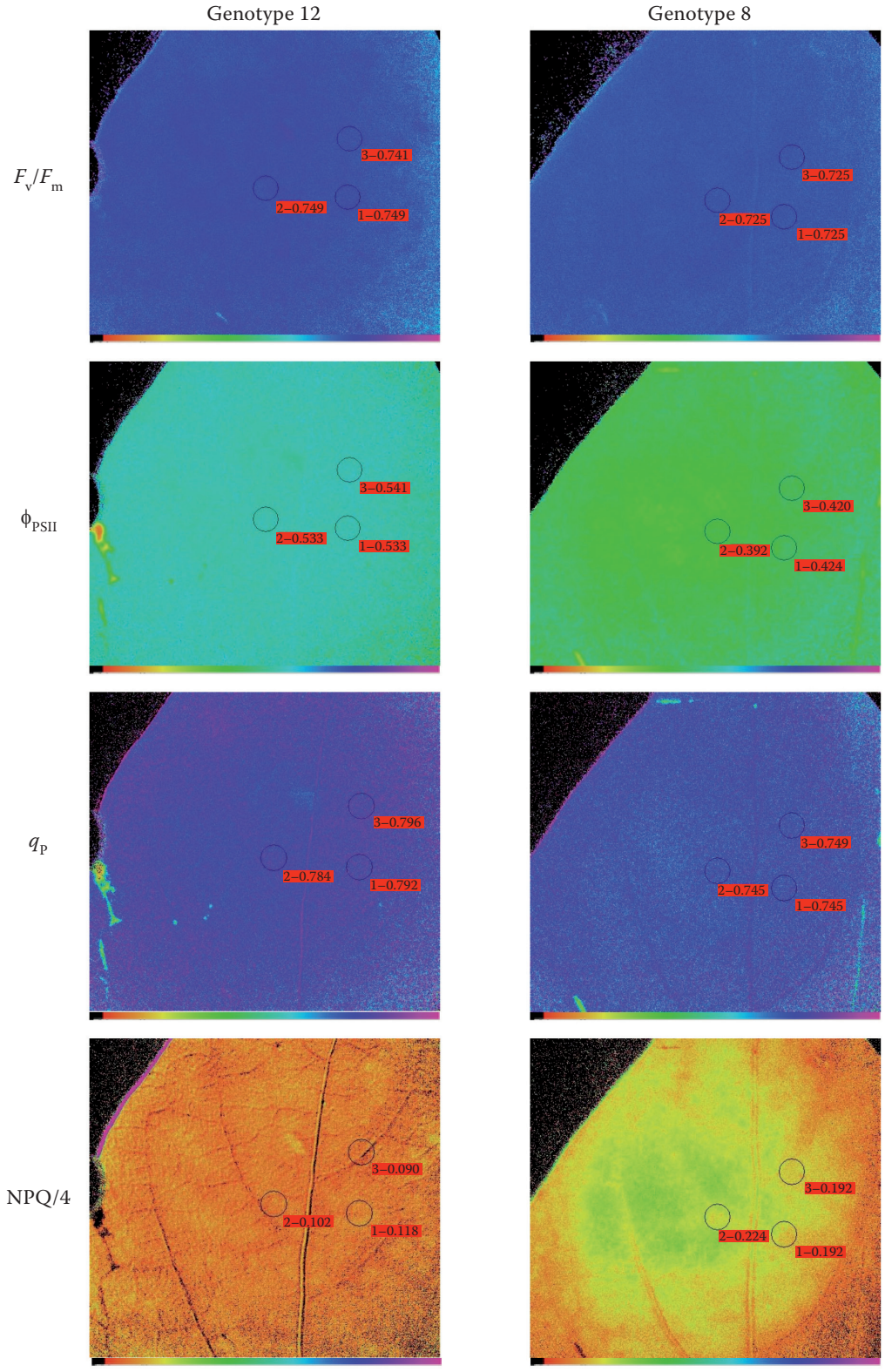

Fig. 2. Chlorophyll fluorescence images of F_v/F_m, ϕ_{PSII}, q_P and NPQ/4 at steady-state with actinic illumination of 204 µmol photons/m^2·s at the end of water stress period (5 months) in tolerant (12, ECU-973) and sensitive (8, Piquillo de Lodosa) genotypes in terms of photosynthesis rate

mean values for three areas of interest in each image – F_v/F_m: 0.746 and 0.725; ϕ_{PSII}: 0.536 and 0.412; q_P: 0.791 and 0.746 and NPQ/4: 0.103 and 0.202, the first value for each parameter being of genotype 12 and second value of genotype 8; AOI are defined using the PAM software (V0.55; Walz, Effeltrich, Germany)

activity over the leaf surface in the genotype 8. The ϕ_{PSII} values in genotype 8 were lower in the upper-left leaf part (0.392) compared to the values in the middle of the leaf (0.422). The heterogeneity of images suggests that pigment composition and concentration, water potential, and stomatal function differ in cells between different regions of the leaf, contributing to spatial differences in photochemical activity under water stress in this sensitive genotype. A decrease in photosynthetic quantum conversion (ϕ_{PSII}) favoured the development of non-photochemical quenching (NPQ) in genotype 8 (0.203) compared with genotype 12 (0.103). The NPQ constitutes an important protective response that could dissipate excitation energy in light-harvesting antenna complex (Müller et al. 2001) and avoid photoinhibition damage (Calatayud et al. 2006) as indicated by the unchanged F_v/F_m ratios. An increase of NPQ on the left of the leaf (0.224) (heterogeneity) in genotype 8 was associated with a decrease of ϕ_{PSII} in this area.

Experiment 2

A significant genotype × irrigation interaction schedule was found in marketable yields ($P \leq 0.01$) (Fig. 3). In general terms, under severe water stress, the grafted cv. Verset achieved higher marketable yields when compared with the ungrafted plants (Fig. 3).

Grafted plants usually show an increased uptake of water and minerals when compared with ungrafted plants, as a consequence of a vigorous root system in the rootstock (Martínez-Ballesta et al. 2010). These favourable effects could be due to a correct callus connection between rootstock and scion. A low or incorrect callus formation could lead to defoliation, reduction of scion growth, and a low survival of grafted plants (Martínez-Ballesta et al. 2010). In our results, although genotype 5 appeared to be tolerant in terms of photosynthesis rate (Experiment 1), it provided lower fruit yields when used as rootstock by the grafted cultivar in control conditions. Furthermore, we observed that plants grafted onto genotype 5 showed a lower growth (1 m mean height) than other grafted plants (2 m mean height) and their stem diameter at the graft union was approximately three-fold than those observed in other plant combinations. These responses are characteristic of graft incompatibility and are due to a poor connection of vascular bundles between rootstock and scion (Oda et al. 1996). Moreover, similar results were obtained for this genotype under saline conditions (Penella et al. 2013).

Under severe water stress, the grafted plants of our selected tolerant genotypes showed higher marketable yields (mainly in genotypes 1, 11 and 12) than ungrafted plants; by contrast grafting did not increase yield in control condition. The main reason to use graft is enhance of tolerance to the abiotic and biotic stresses conferred by robust rootstocks (Lee et al. 2010). Genotype 3 was identified as sensitive to water stress in terms of photosynthesis rate and showed lower yields under water stress conditions in the field. The behaviour of this sensitive genotype in terms of A_N during the vegetative and reproductive stages in Experiment 1 was certainly in accordance with the yield decrease in the field under severe water stress when genotype 3 was used as rootstock.

CONCLUSION

The results confirm that some of the selected accessions in this work provide a yield comparable to commercial rootstocks (genotypes 1 and 2) commonly used in pepper crops. Nevertheless, improvements in management should be made

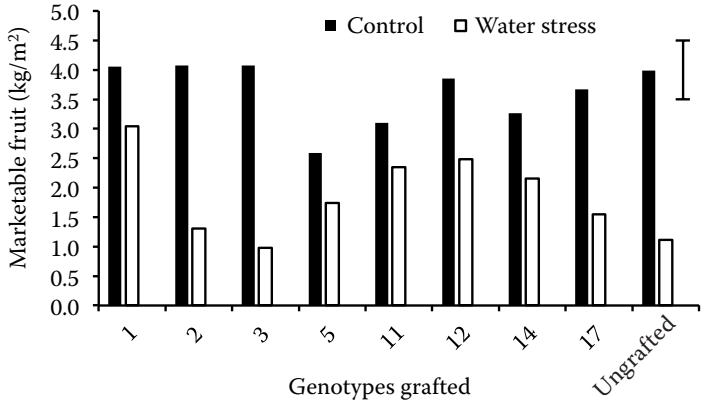

Fig. 3. Interaction of genotype × irrigation for marketable fruits of cv. Verset ungrafted or grafted onto genotypes 1, 2, 3, 5, 11, 12, 14 and 17 under control (100% of ETc) or water stress (60% of ETc)

values are means of 75 plants; the vertical bar indicates the LSD value ($P \leq 0.05$) for comparisons between treatments and genotypes

to obtain higher yields of these accessions under stressed and non-stressed conditions, and/or to satisfy higher values of water use efficiency to compensate for the extra cost of grafting. In addition, these results suggest that photosynthesis rate measurements could be considered a useful parameter to screen large collections of genotypes to drought tolerance to be used as rootstocks with satisfactory yields in a water stress condition.

Acknowledgement

The authors are thankful to the Surinver Co. (San Javier, Spain) for their help in field experiments.

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Received for publication March 24, 2014
Accepted after corrections July 25, 2014

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