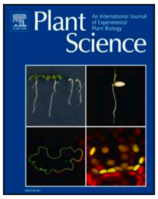
Plant Science 295 (2020) 110250

Contents lists available at ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci



Review article

The influence of grafting on crops' photosynthetic performance

Mateu Fullana-Pericàs[a], Miquel À. Conesa[a], Francisco Pérez-Alfocea[b], Jeroni Galmés[a,*]

[a] *Research Group on Plant Biology under Mediterranean Conditions-INAGEA, Universitat de les Illes Balears, Balearic Islands, Spain*
[b] *Centro de Edafología y Biología Aplicada del Segura (CEBAS-CSIC), Department of Plant Nutrition, Campus Universitario de Espinardo, E-30100, Murcia, Spain*

ARTICLE INFO

Keywords:
Drought
Photosynthesis
Rootstock
Salinity
Scion
Water use efficiency

ABSTRACT

In a near scenario of climate change where stress-derived limitations on crops' yield by affecting plant gas-exchange are expected, grafting may become a cheap and easy technique to improve crops photosynthetic performance and water-use efficiency. Inconsistent data of the effect of rootstocks over gas-exchange can be found in literature, being necessary an integrative analysis of the effect of grafting over photosynthetic parameters. With this aim, we present a compilation of the effect of graft on the net CO_2 assimilation rate (A_N) and other photosynthetic parameters across different species with agronomic interest. No differences were observed in any photosynthetic parameter between non-grafted and self-grafted plants under non-stress conditions. However, differences were found depending on the used rootstock, particularly for the intrinsic water-use efficiency (WUE_i). We observed that variations in A_N induced by rootstocks were related to changes in both diffusive and biochemical parameters. Under drought or salt stress, different photosynthetic performances were observed depending on the rootstock, although the high variability among studies promted to remarkable results. Overall, we observed that grafting can be a useful technique to improve plant photosynthetic performance, and therefore, crop yield and WUE, and that the rootstock selection for a target environment is determinant for the variations in photosynthesis.

1. Introduction

Grafting is a very ancient technique, consisting in the union of a plant shoot (scion) and a root system (rootstock). For centuries, grafting has been used in woody fruit trees and forestry as a clonal propagation system [1,2], and more recently extended to horticultural crops, mainly in cucurbits and solanaceous species [3]. Nowadays, it is a widely used technique in orchards and greenhouses, overcoming the use of graft for clonal propagation purposes, and focusing the target of rootstocks selection in improving agronomic and physiologic traits [4].

Grafting induces a dramatic stress for plants, since water and nutrient flow from roots to shoots is interrupted until the new xylem is re-established. Different biological steps need to occur during graft union formation, involving differential gene expression and hormonal signaling [5–9]. After adhesion of both graft partners and callus cell proliferation at the graft interface, it takes 3–4 days after grafting to reconnect phloem for most of the vegetables, while xylem reconnects after 6–7 days [10,11].

Not only graft compatibility, but also the rootstock traits determine scion performance. Rootstocks are mainly used to increase biotic [12] and abiotic [13,14] stress tolerance and scion vigour [15,16]. Despite the mechanisms through which rootstocks affect scion are not fully understood yet, there are some evidences of higher root hydraulic conductance [17–19] and extended soil exploration [20,21] of scions grafted onto vigorous rootstocks. Furthermore, the growth promotion of particular rootstocks has been related with an increased nutrient acquisition capacity, which was translated in higher leaf chlorophyll content or fluorescence [22–26]. Another described effect of grafting is the alteration of the hormonal balance between rootstock-scion (detailed review in [27,28]). Changes in the xylem sap concentration of ABA, cytokinins and ethylene precursor aminocyclopropane-1-carboxylic acid (ACC) have been reported when using high-vigorous rootstocks as compared to low-vigorous ones or non-grafted plants, interacting with leaf size, stomatal closure and water loss [29–33]. Also, the enhancement of proteomic and metabolic activities involved in Calvin cycle, amino acids biosynthesis, ROS defense [34] and increased biochemical activity [35] were observed in scion leaves in response to grafting.

Considering all the described effects of grafting over scion development, it is reasonable to expect an effect of grafting on the photosynthetic performance, and specifically the leaf gas-exchange governing carbon and water balance. Even very similar rootstocks, with comparable commercial traits (enhanced scion yield, vigor…), may have different effect over photosynthesis (positive or negative) depending on

---

[*] Corresponding author.
E-mail address: jeroni.galmes@uib.cat (J. Galmés).

https://doi.org/10.1016/j.plantsci.2019.110250
Received 5 June 2019; Received in revised form 22 August 2019; Accepted 30 August 2019

many factors. Leaf gas-exchange is regulated by stomata, epidermal pores composed by two specialized guard cells, modulating their aperture in response to environmental conditions [36]. When stomata open, atmospheric CO_2 enters the leaf at a rate depending on photosynthetic CO_2 fixation and diffusive resistances to CO_2, which are imposed by the stomata itself and the leaf mesophyll. Concomitantly, water vapor is lost at a rate depending on the leaf-to-air vapor pressure deficit and on the stomatal conductance (g_s). Under saturating irradiance, the CO_2 fixation into sugar phosphates in the chloroplasts mostly depends on the activity of Rubisco (V_{cmax}) [37]. Increasing the photosynthetic capacity is widely accepted as critical to enhance crop yield [38–40], and both diffusive and biochemical traits have been identified as targets to improve the net CO_2 assimilation rate [41–43]. However, crop water status and the link to stomatal conductance are also important considerations determining leaf photosynthesis and field crop performance [44,45]. In this sense, the ratio between leaf CO_2 assimilation and water loss determines the intrinsic water-use efficiency (WUE_i), a key measure of the efficiency of the use of water resources and a target for crop selection and breeding [46,47]. Nevertheless, plants with increased WUE_i are often endowed with reduced biomass and yield, with an ongoing debate about the tradeoff between water use and actual yield [48–50]. In this sense, grafting may become an achievable way to disrupt this tradeoff by selecting superior rootstock × scion combinations with improved both WUE and yield. In a scenario of climate change, with higher variability of rainfall [51,52] and higher temperatures [53], finding new strategies or mechanisms to maximize WUE become unavoidable.

To our knowledge, this is the first time that a review study aims at compiling recent literature (since late 20th century) on rootstock-mediated effects on photosynthesis in grafted species with agronomic interest. Data on $A_{N,}$ g_s and $WUE_{i,}$ among other photosynthetic parameters, have been integrated with the following objectives: (i) to determine if grafting has an effect over crops' photosynthetic performance, (ii) to analyze if the used rootstock influences any of the compiled parameters under non-stress conditions, and (iii) to examine the role of grafting and rootstocks maintaining the photosynthetic capacity under abiotic stress conditions. Moreover, in spite of the scarce information available, an attempt has been done to correlate the rootstock effect on photosynthesis and crop yield.

2. Methods

Peer-reviewed literature containing data of the net CO_2 assimilation rate (A_N) of grafted plants from different species with agronomic interest published over the last 20 years was compiled (Table 1). Literature was identified by Thompson-ISI Web of Science (Philadelphia, USA) and Google-Google Scholar (Mountain View, USA). Aside of A_N, when available, data of other photosynthetic parameters were also extracted from the original reports and included in the database: stomatal conductance (g_s), intrinsic water-use efficiency (WUE_i), sub-stomatal CO_2 concentration (C_i), transpiration rate (E), mesophyll conductance (g_m), CO_2 concentration in the chloroplast (C_C), actual photoshemical efficiency of photosystem II (ΦPSII), maximum quantum efficiency of photosystem II (F_v/F_m), maximum rate of electron transport (J_{max}), photochemical (qP) and non-photochemical quenching (NPQ), chlorophyll content, maximum rate of Rubisco carboxylation (V_{cmax}), Rubisco activity, Rubisco content, yield, use of triose-P (TPU), leaf water potential (Ψ_W), mesophyll thickness, leaf nitrogen content (leaf N), carbon to nitrogen ratio (C/N), leaf mass per area (LMA), carbon isotope composition ($\delta^{13}C$) and plant hydraulic conductivity (K_L). All measurements included in the present analysis were performed in a prudential time after grafting, in order to ensure a complete re-establishment of vascular and tissue connections and avoid any kind of post-grafting stress.

When not provided, WUE_i was calculated from A_N and g_s values reported in the original papers as:

$$WUE_i = \frac{A_N}{g_s}$$

Finally, the database also included information on the scion and rootstock species and variety name, primary target environment for the rootstock selection, growth conditions and bibliographic data.

Compiled articles followed different criteria when defining the used rootstock, depending on the aim of the study. Hence, according to the literature available information, we classified the rootstocks in 5 main categories, using the following criteria: rootstocks commonly used to increase vigor or frequently used in commercial fields were labeled as commercial (C); rootstocks defined as drought tolerant or with enhanced performance under drought stress were labeled as drought tolerant (D); rootstocks defined as salt tolerant or with enhanced performance under salt stress were labeled as salt tolerant (S), rootstocks defined as tolerant to low temperatures or with enhanced performance under low temperatures were labeled as cold tolerant (T); wild species used as rootstocks were labeled as wild relative rootstocks (W); and rootstocks without particular tolerances to biotic or abiotic stresses, not being wild species, and not used in commercial fields were labeled as experimental rootstocks (E). Supplementary Table 1 compiles all the included rootstocks in our analysis, indicating their genus, species, cultivar, common name and the rootstock group where it belongs.

Compiled data was classified according to the type and intensity of abiotic stress applied to the plants. Although there were data belonging to plants subjected to different aerial CO_2 concentration, soil flooding, low and high nutrient conditions, salt, drought, heavy metal toxicity and high and low temperatures stresses, only drought and salt stress provided enough data for a quantitative analysis. For drought stress, two intensities were defined: moderate stress when the plant water potential (Ψ_w) was -1.1 MPa $< \Psi_w <$ -1.99 MPa or when the leaf relative water content (RWC) was 80% < RWC < 90%; and severe stress at $\Psi_w < -2$ MPa, RWC < 79% or irrigation lower than 30% as compared to non-stressed plants. For salt stress, three intensities were defined depending on the concentration of NaCl in the solution used to irrigate the plants: mild stress at 30–50 mM, moderate stress at 51–100 mM and severe stress above 100 mM.

One-way ANOVA was performed to compare among non-grafted, self-grafted and rootstock combinations, and also among rootstock combinations ($P <$ 0.05 after Duncan *post-hoc* test). Dunnett's multiple comparison test was performed to assess differences of rootstock combinations with non- and self-grafted plants. Pearson's correlations (r) were calculated to determine the relationships among the studied parameters. All statistical analyses were performed using R software (ver. 3.5.0.; R Core Team, Vienna, Austria).

3. Results

3.1. Increasing interest in improving photosynthetic performance via grafting

Over the last 20 years, 57 original research papers including data on the net CO_2 assimilation rate (A_N) of grafted plants with agronomic interest have been published in peer-reviewed journals. The number of published articles has been kept more or less constant between one and 5 papers per year, with the exception of 2017 when 12 papers were published (Fig. 1a). The number of citations for these articles has been increasing up to approximately 250 in the last 3 years (Fig. 1b), denoting an increasing interest on the effect of grafting on photosynthesis and its interaction with agronomic performance.

In these articles, 19 species have been tested as scions and 23 as rootstocks (Table 1). The main target of the compiled articles was to test new rootstocks (41%), and rootstocks with an improved tolerance to salt (22%) and drought stress (19%). Also, other topics as to assess the effect of the grafting method on plant growth or to test the effects of rootstock on biotic stresses were studied. Different growth conditions

Table 1

Summary of the grafted species included in this study. From left to right: common name, species and family of the scion, rootstock species, primary target environment, growth conditions (greenhouse or open field, pot or soil), measurements included in the articles (divided in four categories: gas-exchange, fluorescence, Rubisco and other parameters) and references.

Common name and species of the scion (Family)	Rootstock species	Primary target environment	Growth conditions	Measurements				References
				Gas-exchange	Fluorescence	Rubisco	Other	
Pepper *Capsicum annuum* L. (Solanaceae)	*C. annuum*, *C. chinense*, *C. baccatum*	Drought tolerance, salinity tolerance, temperature tolerance	Greenhouse, open field, pot, soil	A_N, g_s, WUE, C_i	ΦPSII, F_v/F_m, J_{max},	V_{cmax}	Yield, TPU	[24,35,54,55,56,57]
Watermelon *Citrullus lanatus* (Thunb.) Matsum and Nakai (Cucurbitaceae)	*C. lanatus*, *C. maxima* x *C. moschata*, *L. siceraria*, *C. maxima*, *C. pepo*, *C. moschata*	Low nitrogen tolerance, salinity tolerance, cadmium toxicity, low Mg	Greenhouse, open field, pot, soil	A_N, g_s, E, WUE, C_i	qP, NPQ, ΦPSII, ETR, F_v/F_m,, J_{max}, chlorophyll content	V_{cmax}, Rubisco activity	Ψ_w, mesophyll thickness, leaf N	[34,58,59,60,61,62,63,64]
Muskmelon *Cucumis melo* L. (Cucurbitaceae)	*C. maxima* x *C. moschata*, *C. melo*	Salinity tolerance, photosynthetic performance improvement	Greenhouse, pot	A_N, g_s, E, WUE, C_i	Chlorophyll content		Leaf N	[65,66]
Cucumber *Cucumis sativus* L. (Cucurbitaceae)	*C. sativus*, *L. cylindrical*, *C. ficifolia*, *C. pepo*, *C. maxima* x *C. moschata*, *C. melo*, *C. moschata*	Temperature tolerance, salinity tolerance, photosynthetic performance improvement, nematode tolerance,	Greenhouse, pot, soil	A_N, g_s, E, WUE, C_i	qP, ΦPSII, ETR, F_v/F_m, NPQ, J_{max}, Chlorophyll content	V_{cmax}, Rubisco content, Rubisco activity	Yield, Ψ_w, LMA, C/N, leaf N	[66,67,68,69,70,71,72,73,74,75]
Tomato *Solanum lycopersicum* L. (Solanaceae)	*S. lycopersicum*, *S. habrochaites*, *S. pennellii*, *S. sessiflorum*, *S. melongena*, *S. pimpinellifolium*, *S. tuberosum*	Temperature tolerance, drought tolerance, graft compatibility, salinity tolerance, photosynthetic performance improvement, resistance to biotic stress, cadmium stress, pesticide tolerance	Greenhouse, open field, pot, soil	A_N, g_s, E, C_i	ΦPSII, F_v/F_m, F_v'/F_m',NPQ, J_{max}, chlorophyll content	V_{cmax}	Yield, meshophyll thickness, LMA, leaf N	[76,77,78,79,80,81,82,83,84,85]
Aubergine *Solanum melongena* (Solanaceae)	*S. melongena*	Cold tolerance	Greenhouse, pot	A_N				[86]
Soybean *Glycine max* L. (Fabaceae)	*G. max*	Photosynthetic performance improvement	Greenhouse, pot	A_N, g_s, E, WUE,	qP, ΦPSII, ETR, Chlorophyll content	Rubisco content, Rubisco activity		[87]
Cotton *Gossypium hirsutum* L. (Malvaceae)	*G. hirsutum*	Plant growth	Greenhouse, pot	A_N	Chlorophyll content			[88]
Sweet potato *Ipomoea batatas* Lam. (Convolvulaceae)	*I. batatas*	Photosynthetic performance improvement	Greenhouse, pot	A_N				[89]
Green bean *Phaseolus vulgaris* L. (Fabaceae)	*P. vulgaris*	Drought tolerance	Greenhouse, pot	A_N, g_s, WUE,				[90]
Radish *Raphanus sativus* L. (Brassicaceae)	*R. sativus*	Photosynthetic performance improvement	Greenhouse, pot	A_N		V_{cmax}, Rubisco content, Rubisco activity	LMA, leaf N	[91,92]
Kiwifruit *Actinidia chinensis* Planch. (Actinidiaceae)	*A. kolomita*, *A. polygama*, *A. macrosperma*, *A. hemsleyana*	Plant hydraulic conductance improvement	Open field, soil	A_N, g_s, C_i			$\delta^{13}C$, K_L	[18]
Atemoya *Annona x atemoya* Mabb. (Annonaceae)	*A. atemoya*	Photosynthetic performance improvement, plant development	Greenhouse, pot	A_N, g_s, E, WUE,			Leaf N	[93]
Orange tree *Citrus* x *sinensis* L. Osbeck (Rutaceae)	*C. limonia*, *C. paradisi* x *P. trifoliata*, *C. sunki*, *C. aurantium*, *C. jambhiri*, *C. reticultata*, *P. trifoliata*	Photosynthetic performance improvement, tolerance to boron toxicity, flooding and salt stress	Greenhouse, open field, pot, soil	A_N, g_s, g_m, C_i, C_C,	F_v/F_m, NPQ, J_{max}, chlorophyll content	V_{cmax}	Ψ_w, K_L	[94,95,96,97,98,99]
Apple tree *Malus domestica* Borkh (Rosaceae)	*M. domestica*	Plant growth	Greenhouse, pot	A_N				[100]
Sweet cherry *Prunus avium* L. (Rosaceae)	*P. avium*, *P. cerasus*	High CO_2 response	Greenhouse, open field, pot, soil	A_N, g_s, E, WUE, C_i	F_v/F_m, chlorophyll content		Ψ_w, LMA	[101,102]

(*continued on next page*)

Table 1 (*continued*)

Common name and species of the scion (Family)	Rootstock species	Primary target environment	Growth conditions	Measurements				References
				Gas-exchange	Fluorescence	Rubisco	Other	
Peach *Prunus persica* L. Batsch (Rosaceae)	*Prunus sp.*	Salinity tolerance	Greenhouse, pot	A_N, g_s			Ψ_w	[103]
Common pear *Pyrus communis* L. (Rosaceae)	*C. oblonga*	Drought tolerance	Open field, soil	A_N, g_s	ΦPSII, NPQ			[104]
Grape vine *Vitis vinifera* L. (Vitaceae)	*V. berlandieri, V. champanii, V. longii,V. olonis V. riparia, V. rupestris, V. vinifera*	Photosynthetic performance improvement, nutrient uptake	Greenhouse, open field, pot, soil	A_N, g_s, E, WUE, C_i	qP, ETR, chlorophyll content	Rubisco activity	Ψ_w. δ^{13}C, SLA	[31,105,106,107,108,109]

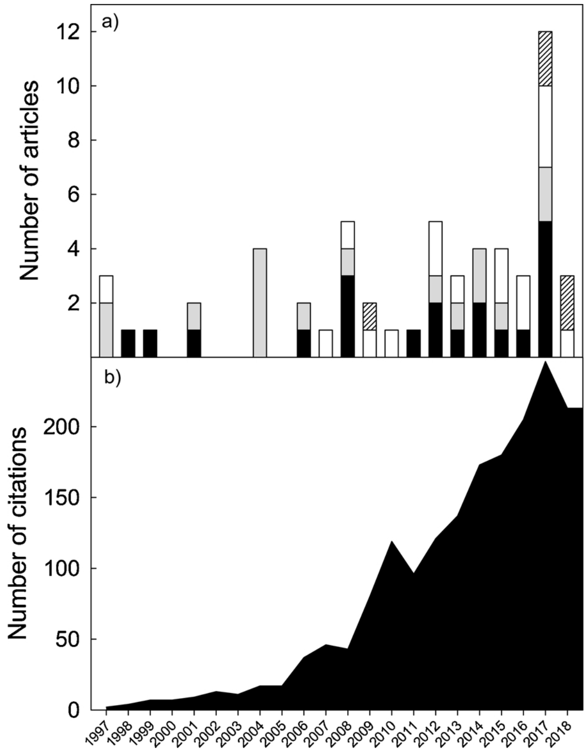


Fig. 1. a) Number of articles published per year in peer-reviewed journals since late 20th century containing values of A_N of grafted combinations from species with agronomic interest. Different colors of stacked bars indicate the number of articles containing as controls of rootstock combinations both non-grafted and self-grafted plants ▨, only non-grafted ■, only self-grafted □ or neither ▩; b) number of citations per year of the articles showed in Fig. 1a.

were observed across the compiled articles, with 21% of the studies performed in open field and 79% in greenhouse conditions. Plants were grown in pots in 74% of the studies (7% hydroponically) and 21% directly in soil (Table 1). No differences were observed in A_N or other photosynthetic parameters between pot and soil grown plants for any of the species (data not shown), and therefore no distinction between growth conditions was considered in the analyses performed in this study.

From the 57 compiled studies, 9% included both non-grafted and self-grafted plants as controls of the rootstocks' combinations, 28% only self-grafted, 35% only non-grafted and 28% did not use neither as controls (Fig. 1a).

3.2. *Effect of grafting on photosynthesis under non-stress conditions*

When combining data for the same species, no differences were observed between non-grafted and self-grafted plants for any of the included scion species in A_N, stomatal conductance (g_s) or intrinsic water-use efficiency (WUE_i) under non-stress conditions (Table 2). In consequence, from now on, we considered both non-grafted and self-grafted as control plants. Similarly, there were non-significant differences when comparing control plants with graft combinations where the rootstock genotype is different to the scion genotype (here defined as rootstock combinations) (Table 2).

Although no differences were observed within each scion species for any photosynthetic parameter under optimal growth conditions, some differential trends were observed when considering the type of rootstock (Fig. 2). Plants grafted onto salt tolerant rootstocks significantly increased A_N in 23% as compared to control plants (Fig. 2a). When comparing among rootstocks, scions grafted onto salt tolerant rootstocks had significantly higher A_N than scions grafted onto low temperature tolerant,

Table 2
Net CO_2 assimilation rate (A_N), stomatal conductance (g_s) and intrinsic water-use efficiency (WUE_i) for the different scion species and graft combinations under non-stress conditions. 'Non' refers to non-grafted plants, 'Self' to self-grafted plants and 'Root' to rootstock combinations. 'NA' for non-available data. Data are means ± SE. Number of replicates indicated in brackets near each value. Letters denote significant differences among graft combinations within each scion species by one-way ANOVA after Duncan *post-hoc* test ($P < 0.05$).

Scion species	A_N µmol CO_2 $m^{-2}s^{-1}$	g_s mol H_2O $m^{-2}s^{-1}$	WUE_i µmol CO_2 mol^{-1} H_2O
Capsicum annuum			
Non	19.29 ± 2.59 ^{a} (*n* = 6)	0.45 ± 0.09 ^{a} (*n* = 6)	49.32 ± 6.96 ^{a} (*n* = 6)
Self	NA	NA	NA
Root	20.63 ± 1.04 ^{a} (*n* = 18)	0.46 ± 0.05 ^{a} (*n* = 18)	52.01 ± 5.29 ^{a} (*n* = 18)
Citrullus lanatus			
Non	13.76 ± 5.54 ^{a} (*n* = 3)	0.24 ± 0.02 ^{a} (*n* = 2)	77.68 ± 12.13 ^{a} (*n* = 2)
Self	16.01 ± 2.78 ^{a} (*n* = 5)	0.65 ± 0.14 ^{a} (*n* = 2)	28.94 ± 6.19 ^{a} (*n* = 2)
Root	15.17 ± 2.89 ^{a} (*n* = 7)	0.49 ± 0.10 ^{a} (*n* = 5)	48.04 ± 12.18 ^{a} (*n* = 4)
Cucumis melo			
Non	18.18 ± 4.22 ^{a} (*n* = 2)	0.26 ± 0.05 ^{a} (*n* = 2)	76.29 ± 29.87 ^{a} (*n* = 2)
Self	NA	NA	NA
Root	19.57 ± 2.15 ^{a} (*n* = 3)	0.31 ± 0.04 ^{a} (*n* = 3)	67.32 ± 18.36 ^{a} (*n* = 3)
Cucumis sativus			
Non	19.73 ± 1.94 ^{a} (*n* = 6)	0.46 ± 0.2 ^{a} (*n* = 4)	93.07 ± 23.45 ^{a} (*n* = 3)
Self	13.94 ± 1.11 ^{a} (*n* = 4)	0.27 ± 0.06 ^{a} (*n* = 4)	62.45 ± 16.84 ^{a} (*n* = 4)
Root	16.40 ± 1.95 ^{a} (*n* = 11)	0.51 ± 0.13 ^{a} (*n* = 9)	60.91 ± 14.96 ^{a} (*n* = 8)
Ipomoea batatas			
Non	NA	NA	NA
Self	11.17 ± 2.44 ^{a} (*n* = 2)	NA	NA
Root	9.08 ± 1.33 ^{a} (*n* = 4)	NA	NA
Solanum lycopersicum			
Non	19.95 ± 3.69 ^{a} (*n* = 5)	0.37 ± 0.09 ^{a} (*n* = 5)	62.65 ± 8.64 ^{a} (*n* = 5)
Self	19.55 ± 1.91 ^{a} (*n* = 7)	0.39 ± 0.07 ^{a} (*n* = 5)	58.86 ± 9.37 ^{a} (*n* = 5)
Root	19.85 ± 1.04 ^{a} (*n* = 29)	0.45 ± 0.09 ^{a} (*n* = 15)	62.46 ± 6.45 ^{a} (*n* = 15)
Solanum melongena			
Non	18.79 ^{a} (*n* = 1)	NA	NA
Self	NA	NA	NA
Root	19.61 ± 0.30 ^{a} (*n* = 2)	NA	NA
Raphanus sativus			
Non	NA	NA	NA
Self	18.03 ± 2.97 ^{a} (*n* = 4)	NA	NA
Root	20.26 ± 4.01 ^{a} (*n* = 4)	NA	NA
Phaseolus vulgraris			
Non	NA	NA	NA
Self	19.15 ± 1.89 ^{a} (*n* = 2)	0.6 ± 0.18 ^{a} (*n* = 2)	37.76 ± 4.09 ^{a} (*n* = 2)
Root	19.06 ± 0.65 ^{a} (*n* = 2)	0.57 ± 0.24 ^{a} (*n* = 2)	39.29 ± 15.31 ^{a} (*n* = 2)
Gossypium hirsutum			
Non	NA	NA	NA
Self	16.34 ± 2.77 ^{a} (*n* = 2)	NA	NA
Root	16.44 ± 1.61 ^{a} (*n* = 2)	NA	NA
Glycine max			
Non	13.69 ^{a} (*n* = 1)	0.19 ^{a} (*n* = 1)	72.05 ^{a} (*n* = 1)
Self	13.79 ^{a} (*n* = 1)	0.19 ^{a} (*n* = 1)	72.58 ^{a} (*n* = 1)
Root	15.91 ± 0.29 ^{a} (*n* = 2)	0.26 ± 0.05 ^{a} (*n* = 2)	63.30 ± 11.08 ^{a} (*n* = 2)
Annona x atemoya			
Non	5.7 ^{a} (*n* = 1)	0.12 ^{a} (*n* = 1)	47.5 ^{a} (*n* = 1)
Self	6.1 ^{a} (*n* = 1)	0.11 ^{a} (*n* = 1)	55.45 ^{a} (*n* = 1)
Root	6.4 ± 1.0 ^{a} (*n* = 3)	0.13 ± 0.01 ^{a} (*n* = 3)	47.51 ± 4.36 ^{a} (*n* = 3)
Vitis vinifera			
Non	10.75 ± 1.65 ^{a} (*n* = 4)	0.27 ± 0.07 ^{a} (*n* = 4)	49.47 ± 8.73 ^{a} (*n* = 4)
Self	NA	NA	NA
Root	11.12 ± 0.43 ^{a} (*n* = 22)	0.26 ± 0.01 ^{a} (*n* = 22)	42.34 ± 2.61 ^{a} (*n* = 22)

drought tolerant and wild relatives' rootstocks. Regarding g_s, only scions grafted onto commercial rootstocks differed significantly (24% increase) from control plants (Fig. 2b). No significant differences were observed in g_s among the used rootstocks due to the large variability, although scions grafted onto wild relatives and drought tolerant rootstocks tend to decrease, respectively, 40% and 20% their g_s as compared to control plants. As for WUE_i, scions grafted onto wild relative rootstocks significantly increased 61% their WUE_i as compared to control plants, due to the low g_s (Fig. 2c), presenting also higher WUE_i than any other rootstock combination except scions grafted onto drought tolerant rootstocks. Scions grafted onto low temperature tolerant rootstocks significantly decreased their WUE_i (Fig. 2c).

Regarding other photosynthetic parameters under optimal conditions, non-significant differences were observed when comparing between control plants and rootstock combinations or among rootstock combinations for the sub-stomatal CO_2 concentration (C_i), the actual photochemical efficiency of photosystem II (ΦPSII), the photochemical and non-photochemical quenching (qP and NPQ) and the maximum quantum efficiency of photosystem II (F_v/F_m) (Table 3 and data not shown). On the contrary, scions grafted onto salt tolerant rootstocks had significantly higher values for the maximum velocity of Rubisco carboxylation (V_{cmax}) than control plants, although no differences were found among rootstock combinations for this parameter (Table 3).

The normalized to control plants values of the different rootstock

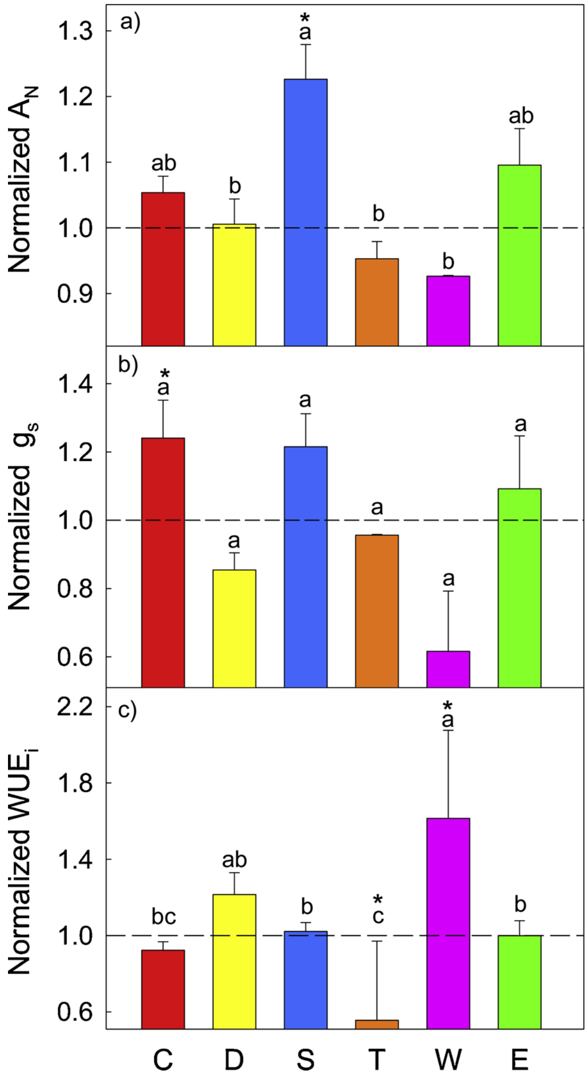


Fig. 2. Variability of a) net CO_2 assimilation rate (A_N), b) stomatal conductance (g_s) and c) intrinsic water-use efficiency of rootstock combinations values normalized to control plants (referring to both non- and self-grafted plants) under control conditions. Data are means ± SE. 'C' refer to commercial, 'D' to drought tolerant, 'S' to salt tolerant, 'T' to cold tolerant, 'W' to wild relative and 'E' to experimental rootstocks. Letters denote differences among rootstock combination normalized values by one-way ANOVA after Duncan *post-hoc* test ($P < 0.05$); and asterisks between each rootstock combination and non- and self-grafted plants after Dunnett's test ($P < 0.05$).

Table 3

Variation of rootstock combinations values normalized to control plants (referring to both non- and self-grafted plants) for the sub-stomatal CO_2 concentration (C_i), the actual photochemical efficiency of photosystem II (ΦPSII) and the maximum velocity of Rubisco carboxylation (V_{cmax}) under non-stress conditions. Data are means ± SE. 'C' refers to commercial, 'D' to drought tolerant, 'S' to salt tolerant, 'T' to cold tolerant and 'E' to experimental rootstocks. 'NA' for non-available data. Letters denote differences among rootstock combination normalized values by one-way ANOVA after Duncan *post-hoc* test ($P < 0.05$); and asterisks between each rootstock combination and non- and self-grafted plants after Dunnett's test ($P < 0.05$).

Rootstock combination	C_i	ΦPSII	V_{cmax}
C	1.03 ± 0.03 ^{a}	1.01 ^{a}	1.05 ± 0.02 ^{a}
D	NA	0.99 ± 0.07 ^{a}	NA
S	1.01 ± 0.04 ^{a}	0.98 ^{a}	1.52 ± 0.39 ^{a*}
T	0.95 ^{a}	0.95 ^{a}	1.04 ^{a}
E	0.99 ^{a}	1.01 ± 0.04 ^{a}	1.23 ± 0.05 ^{a}

combinations for A_N was positively correlated with the analogous normalization for g_s, C_i, ΦPSII and V_{cmax} (Fig. 3). Aside from these general trends, contrasting effects were also visible, particularly in the relationship A_N *vs.* g_s. For instance, it is remarkable that the largest relative increases in g_s without equivalent increase in A_N were observed in plants grafted onto vigorous commercial rootstocks. When these values were not considered, a linear adjustment of the A_N *vs.* g_s relationship was observed (r = 0.69; *P*-value < 0.001), close to the 1:1 ratio. Interestingly, the largest relative decreases in g_s while maintaining or increasing A_N were found in scions grafted onto drought tolerant rootstocks (Fig. 3a).

A positive trend was observed between the normalized values of the different rootstock combinations to control plants for yield and both A_N (r = 0.26; *P*-value = 0.12, Fig. 4a) and WUE_i (r = 0.37; *P*-value = 0.08, Fig. 4b). Despite the lack of significance, this data suggests that grafting onto particular rootstocks, as salt tolerant or wild relatives' rootstocks, could allow increasing WUE_i with no negative impact on yield.

3.3. Effect of grafting on photosynthesis under stress conditions

Grafting is used to mitigate the negative effects on plant growth when plants are subjected to abiotic stress conditions, such as drought, flooding, heavy metal in soil, low nutrient, salt, or extreme temperature environments (Table 1). Unfortunately, with the exception of drought and salt stress, for the rest of abiotic stresses where grafting was used to study the effect of each stress over A_N, not enough data was available to perform a statistically valid analysis. We therefore compiled different morphological and physiological traits identified in literature to the maintenance of net CO_2 assimilation rate in grafted plants for each type of abiotic stress, including anatomical adaptations in scion leaves, changes in shoot:root biomass ratio, different gene expression in scion, different hormone balance, differences in Rubisco activity, enhanced stomata opening control, induced anti-oxidative defense, protection of PSII and reduced heavy metal or ion allocation in scion (Table 4). We found that induction of the anti-oxidative defense and protection of PSII were the most common traits associated to overcome the different stresses through delaying stress-induced leaf senescence, and that the low nutrient supply was the stress involving more changes in the studied traits (Table 4).

For drought and salt stresses, data from different scion species was merged according to the intensity of stress and the graft combination, and the values for A_N, g_s and WUE_i under stress were compared to those under non-stress conditions (Fig. 5). It has to be considered that not all rootstock combinations were found for all the evaluated stress levels. As under non-stress conditions, no differences between non- and self-grafted plants were found for A_N, g_s or WUE_i under any level of drought or salt stress (data not shown). Therefore, data from both non- and self-grafted plants were again combined and considered as control plants to be compared to the different types of rootstock. Under moderate drought stress, no differences were observed between control plants and rootstock combinations or among rootstock combinations in the relative reduction in A_N irrespective of the used rootstock; meanwhile scions grafted onto commercial rootstocks had a lower g_s reduction as compared to control plants (Fig. 5a). Commercial, drought and salt tolerant rootstock combinations had lower WUE_i increase as compared to control plants. Similar to moderate drought stress, no effect of the used rootstock was observed in the reduction of A_N under severe drought stress. Both commercial and drought tolerant rootstock combinations had a lower decrease in g_s as compared to control plants. Nevertheless, no differences were observed in WUE_i between control plants and rootstock combinations or even among rootstock combinations (Fig. 5a).

No differences were observed among control plants, commercial and drought tolerant rootstock combinations under the effect of mild salt stress on A_N, g_s and WUE_i (Fig. 5b). However, both control plants and commercial rootstock combinations had lower decrease in g_s and lower increase in

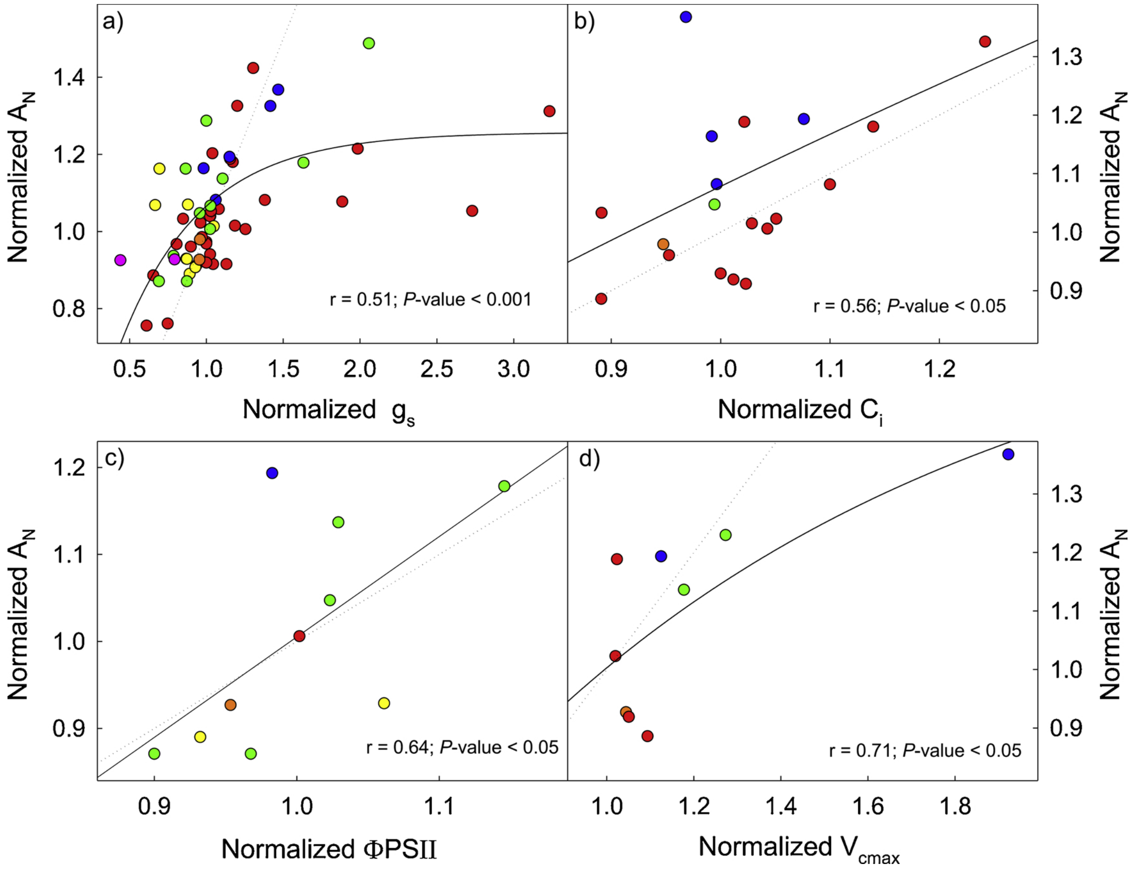


Fig. 3. Relationship between the normalized values of rootstock combinations to control plants (referring to both non- and self-grafted plants) under control conditions for the net CO_2 assimilation rate (A_N) and a) the stomatal conductance (g_s), b) the sub-stomatal CO_2 concentration (C_i), c) the actual photochemical efficiency of photosystem II (ΦPSII) and d) the maximum velocity of Rubisco carboxylation (V_{cmax}). Red dots refer to commercial, yellow to drought tolerant, blue to salt tolerant, orange to cold tolerant, purple to wild relative and green to experimental rootstocks. Data are means. SE is not shown for clarity. Solid lines represent regressions and dotted lines the 1:1 ratio.

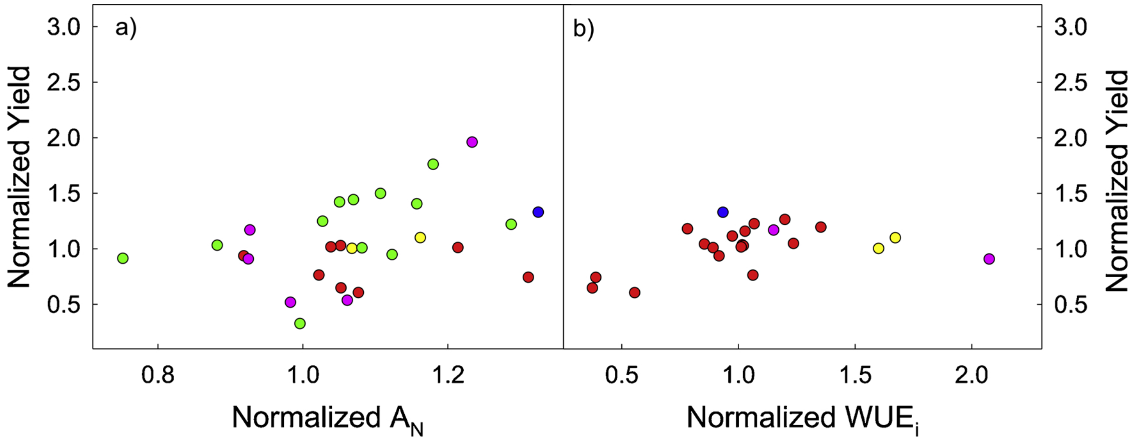


Fig. 4. Relationship between the rootstock combinations values normalized to control plants (referring to both non- and self-grafted plants) under control conditions for yield and a) the net CO_2 assimilation rate (A_N) and b) the intrinsic water-use efficiency (WUE_i). Red dots refer to commercial, yellow to drought tolerant, blue to salt tolerant, orange to cold tolerant, purple to wild relative and green to experimental rootstocks. Data are means. SE is not shown for clarity.

WUE_i than experimental rootstock combinations. Under moderate salt stress conditions, scions grafted onto salt tolerant rootstocks had lower decrease in A_N than control plants with non-significant effect on g_s or WUE_i being observed among rootstock combinations. Under severe salt stress, non-significant differences between control plants and rootstock combinations or among rootstock combinations were observed on any photosynthetic parameter, although there is a trend for lower decrease in A_N and g_s for scions grafted onto salt and drought tolerant rootstocks (Fig. 5b).

Table 4

Morphological and physiological traits associated to the maintenance of net CO_2 assimilation rate in grafted plants under different stress conditions as compared to non-stressed plants. Heavy metals refer to stress caused by accumulation of heavy metals in soil, temperature to stress caused by an extreme (high or low) temperature in the scion or rootstock zone, nutrient to stress caused by a low nutrient supply, and flooding to stress caused by waterlogging.

	Anatomical adaptations in scion leaves	Changes in Shoot:Root biomass ratio	Different gene expression in scion	Different hormone balance	Differences in Rubisco activity	Enhanced stomata opening control	Induced anti-oxidative defense	Protection of PSII	Reduced heavy metal or ion allocation in scion	References
Drought		•		•			•	•	•	[24,31,54,56,95,104,110]
Flooding		•						•		[64,99]
Heavy metals							•	•	•	[62,73,97,98]
Nutrient	•	•	•	•	•		•			[59,60,91,107]
Salt		•			•		•	•	•	[34,35,94,103,56,57,58,63,66,69,72,79]
Temperature					•	•	•	•		[55,67,71,74,75,81,86,96]

4. Discussion

4.1. *There are no differences between non- and self-grafted plants for the main photosynthetic parameters in the studied cases*

Despite all the morphologic and physiologic changes that grafting process implies (Fig. 6), no differences were found between non-grafted and self-grafted plants in any of the included scion species for A_N, g_s, or WUE_i under non-stress conditions (Table 2). Hence, the available data lead to deduce that there is no effect of grafting over photosynthetic parameters when the rootstock is genetically the same than the scion. This result is probably due to the fact that measurements were performed in fully-recovered combinations after grafting. No irregular xylem connections were observed for self-grafted pepper, tomato and aubergine plants 30 days after grafting, denoting no hydraulic restrictions due to grafting [9,56]. Moreover, no differences have been found in plant biomass (fresh or dry), number of flowers or yield (total or marketable) between non-grafted and self-grafted plants for a large range of species [111–113]. According to this study, it seems that either non-grafted or self-grafted plants could be used as controls when comparing with other rootstock combinations under non-stress conditions.

4.2. *The rootstock selection determines the photosynthetic performance of the scion under non-stress conditions*

When comparing control plants (i.e. both non- and self-grafted plants) to rootstock combinations for each scion species, no differences were observed for A_N, g_s or WUE_i (Table 2). The lack of differences in the photosynthetic parameters between control plants and rootstock combinations agreed with the limited influence of the rootstock over the scion growth or yield under non-stress conditions [33,78,114,115]. However, it must be considered that very diverse rootstocks were used in different studies for a single scion species (Table 1). For this reason, we decided to analyse all compiled data from different scion species depending on the used rootstock, and compare to control plants (Fig. 2). The higher A_N observed for scions grafted onto salt tolerant rootstocks and g_s of scions grafted onto commercial rootstocks as compared to control plants can be associated with their larger root system and the higher V_{cmax} of scions grafted onto salt tolerant rootstocks (Table 3, Fig. 2a,b) [56,58,72]. However, this was not translated into higher scion biomass or increased number of leaves for most of the reported data [35,72,78,79], probably because under optimal conditions the shoot development is not limited by the source activity in absence of additional sinks. Indeed, it has to be considered that almost half of the total fixed carbon in the scion is translocated to the root system [116,117]. Hence, even under non-stress conditions, the balance between generative and vegetative vigour when using a vigorous rootstock must be considered in relation to the increased photosynthesis, since extra assimilates can be allocated to roots and fruits, but not to leaves [54]. Unfortunately, not enough data was available to perform a valid analysis of the effect of grafting over scion and rootstock growth, and its interaction with photosynthesis.

When wild relatives, commonly found in non-cultivated areas under harsh conditions [118,119], were used as rootstocks, higher proportional decrease in g_s as compared to other rootstock combinations was observed (Fig. 2b), leading to remarkable WUE_i increase (Fig. 2c). However, no negative effect in yield was found in tomato grafted onto wild relatives despite their higher WUE_i [78,84]. Since graft compatibility is related to the taxonomic distance between scion and rootstock [3,120], the use of closest semi-domesticated species or even landraces usually grown under non-irrigated environments must be considered to obtain new rootstocks with increased WUE_i [4].

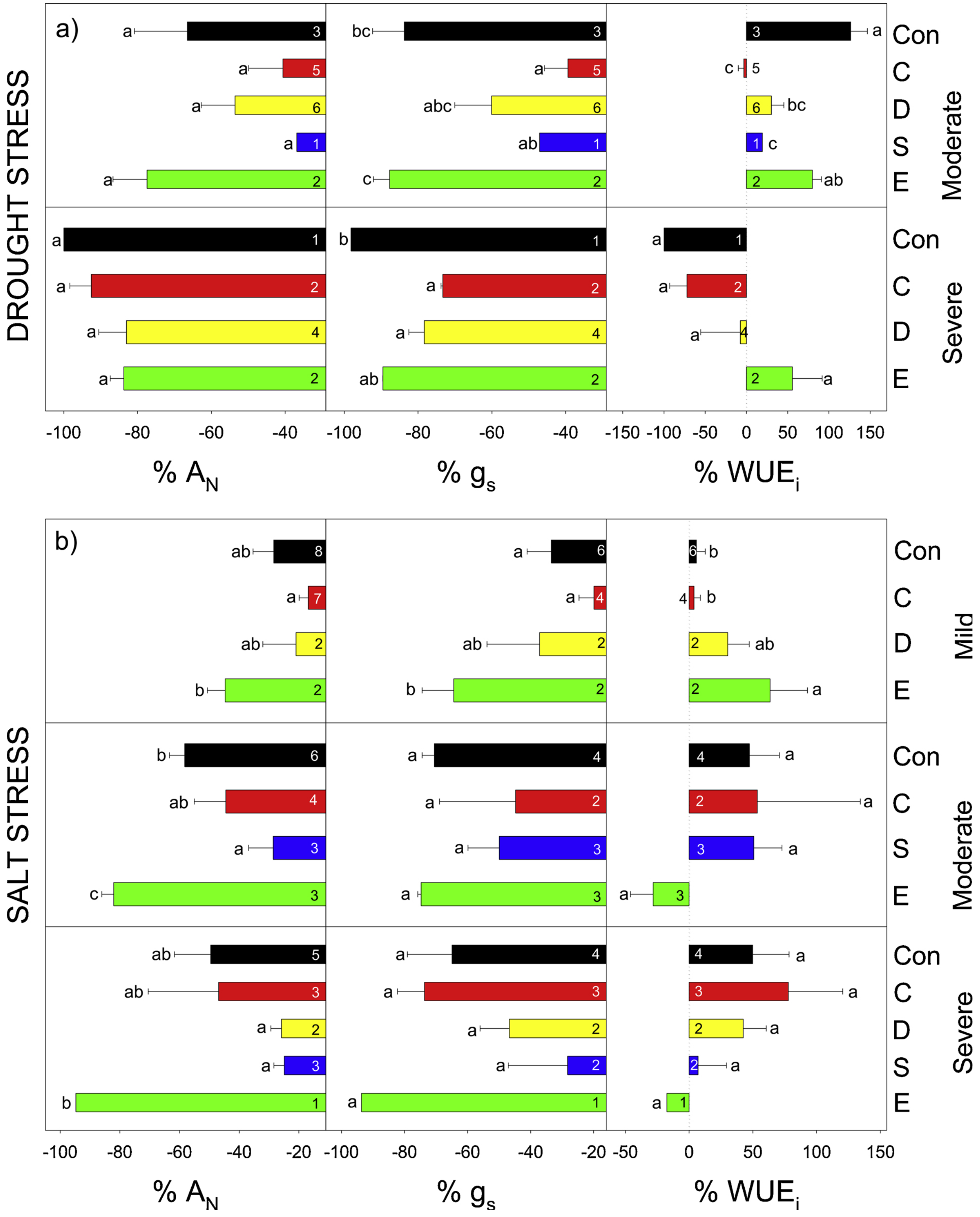


Fig. 5. Percentage of change of net CO_2 assimilation rate (A_N), stomatal conductance (g_s) and intrinsic water-use efficiency (WUE_i) of control plants (referring to both non- and self- grafted plants) and rootstock combinations under different a) drought and b) salt stress conditions as compared to non-stressed plants. Black bars refer to control plants, red bars to commercial, yellow to drought tolerant, blue to salt tolerant and green to experimental rootstocks. Labels as follows: Con refer to control plants, C to commercial, D to drought tolerant, S to salt tolerant and E to experimental rootstocks. Data are means + SE (*n* indicated inside each box). Letters denote differences among control plants and rootstock combination within each stress level by one-way ANOVA after Duncan *post-hoc* test ($P < 0.05$). For drought stress, two intensities were defined: moderate stress -1.1 MPa $< \Psi_w <$ -1.99 MPa or 80% < RWC < 90%; severe stress $\Psi_w < -2$ MPa, RWC < 79% or irrigation lower than 30% as compared to non-stressed plants. For salt stress, three intensities were defined depending on the concentration of NaCl in the solution used to irrigate the treated plants: mild stress 30–50 mM; moderate stress 51–100 mM; severe stress > 100 mM.

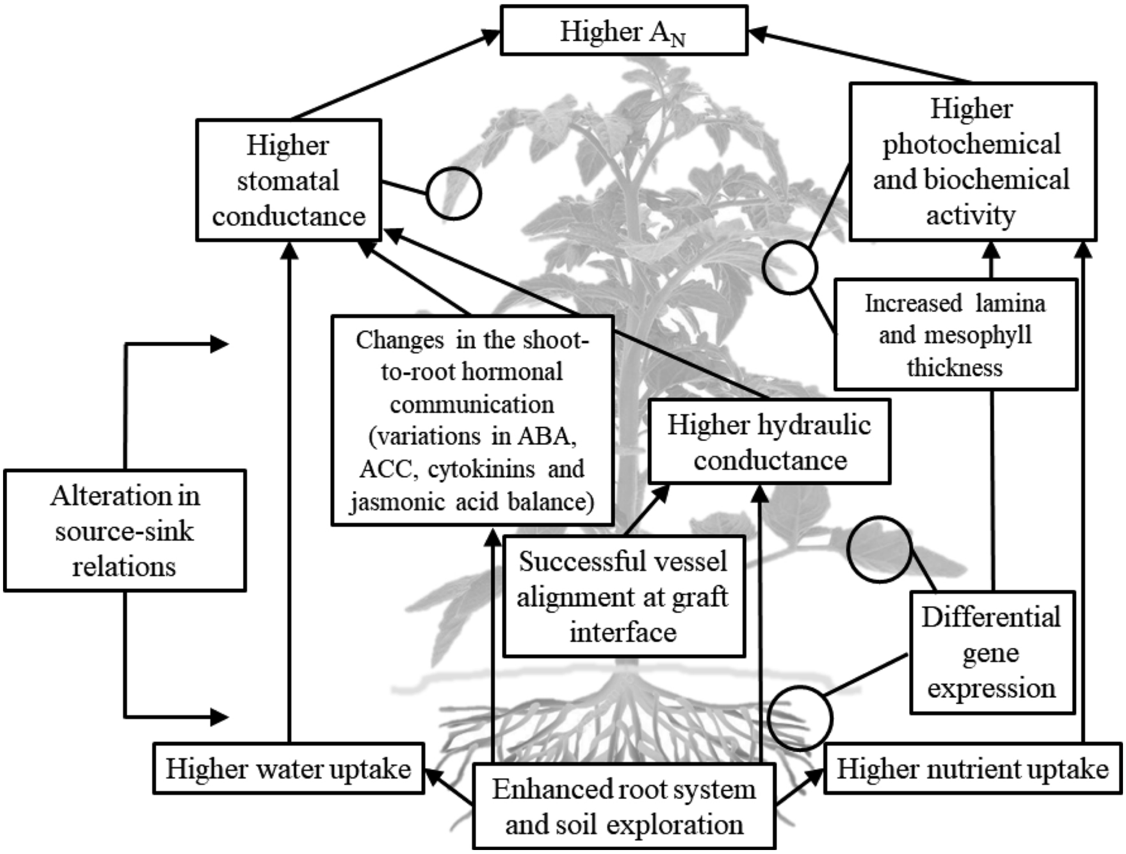


Fig. 6. Main processes involved with increases in the net CO_2 assimilation rate (A_N) regulated by the scion-rootstock interaction under non-stress conditions. Arrows represent positive regulations.

4.3. The increase of the photosynthetic capacity is related to the capability of the rootstock to improve scion leaf traits

Under non-stress conditions, the increase in g_s of scions grafted onto different rootstocks as compared to control plants was positively correlated with the increase in A_N (Fig. 3a; r = 0.51; *P*-value < 0.001). For most of the included rootstock combinations, changes in both parameters were proportional (near the 1:1 ratio), indicating a low interaction of the used rootstock in the relationship between A_N and g_s. Nevertheless, specific rootstock combinations did not follow the described general pattern, depending on the used rootstock or even the scion. [78] used a drought tolerant tomato landrace as scion, characterized by low stomatal aperture and maximization of WUE_i [121,122]. When grafted onto commercial rootstocks, the drought tolerant tomato landrace increased g_s up to three times but only increased A_N 20% as compared to control plants, thereby decreasing WUE_i, indicative that increasing g_s may not translate into enhanced A_N when photosynthesis is biochemically-limited [78]. On the contrary, tomato, pepper and bean scions grafted onto wild, commercial, drought tolerant and experimental rootstocks increased WUE_i as compared to control plants by decreasing g_s in most cases, with no negative effect on A_N (Fig. 3a), plant growth or yield [24,56,78,85,90], suggesting that the rootstock can be used to optimize CO_2 fixation per unit of water transpired.

Aside from g_s, the mesophyll anatomical properties are also a key photosynthetic trait determining the pathway of CO_2 from substomatal cavity to carboxylation sites [123,124]. It has been reported that grafting onto commercial rootstocks altered leaf mesophyll thickness and spongy parenchyma thickness as compared to control plants, but its effect on A_N has not been yet studied [60,83]. Not only diffusional parameters, but photochemical and biochemical leaf traits could also limit A_N [125,126]. No major incidence of the used rootstock on ΦPSII was found for the studied scions under non-stress conditions (Table 3), being the changes in both parameters near the 1:1 ratio (Fig. 3c). Apart from the higher stomatal control and increase of water-use efficiency through regulating leaf biomass [33], increases in ABA and cytokinins level of grafted plants has been related with activation of the antioxidant system and increase in mRNA levels of the large and small subunits of Rubisco [14,75]. Hence, higher V_{cmax} and maximum rate of electron transport (J_{max}) were observed in grafted plants, driving to an increase in A_N [35,63]. However, contrasting results were observed when assessing the effect of grafting on Rubisco content [75,87,92].

Overall, different processes and mechanisms are involved in the regulation of photosynthetic parameters in grafted plants (Fig. 6). Scion and rootstock traits, but also their interaction, determine changes in the described diffusive and photo- and biochemical traits. Unravelling how to optimize those processes using particular rootstocks will not only lead to increase A_N, but also to improve agronomic performance and maximize potential yield under control conditions [38,44].

In this sense, Fig. 4a suggests a positive, although non-significant (*P*-value > 0.05), trend between photosynthesis and yield. Several reasons can explain the weakness of this correlation, such the scarcity of studies considering the rootstock effect on both parameters, the additional generative/reproductive effects on assimilate reallocation and the interaction with the environmental conditions. Also, Fig. 4b showed that WUE_i can be increased without negative effect on yield. More studies are required to confirm those rootstock-mediated enhancements, but inclusion of other parameters as rootstock and scion biomass will help to clarify and understand the role of grafting in how carbon is allocated in the plant.

4.4. Grafting promotes different mechanisms to overcome the deleterious effect of abiotic stress over photosynthetic performance

Under abiotic stress, the use of tolerant rootstock to that particular stress leads to the activation of different mechanisms to protect the photosynthetic apparatus and delay the stress-induced leaf senescence (Table 4). Most of those mechanisms are linked among them. For example, the protection of the reaction center of PSII is usually related with the activation of the anti-oxidative defense system [63], which in turn is associated to the capacity to retain ions in roots and avoid their translocation to leaves [94,127,128]. Similarly, rootstock grafting maintains Rubisco activity under stress conditions due to an overexpression of Rubisco related genes, improving the photosynthetic performance [72]. Hence, mitigation of the effect of the stress over A_N when using tolerant rootstocks is mostly related to the alleviation of deleterious effect of stress over scion photochemical and biochemical parameters [35], although an effect through altering diffusive rates or regulating other stomatal related parameters cannot be ruled out [30]. Indeed, elevated A_N, g_s and C_i, and maintaining sink-activity in the aerial organs under stress, explained increased yield in pepper grafted onto a generative rootstock under control and drought conditions [54].

However, the maintenance of elevated transpiration under stress conditions is not always an advantageous trait, particularly when water is scarce. Tolerance to drought and salt stress has been related to a decrease of transpiration, achieved through a reduction of leaf area or biomass accumulation, which in turn increase WUE at the whole plant level [129,130], but decreases crop yield. The tendency of scions grafted onto drought tolerant rootstocks to decrease g_s more than other rootstock combinations under moderate drought stress can be associated to an improved stomatal closure response, regulated by root chemical signals like ABA, cytokinins and jasmonic acid [32] (Fig. 5a). Despite their higher proline concentration and antioxidant activity in leaves [24], the reduction of $\sim 80\%$ in g_s observed for drought tolerant rootstock combinations under severe drought stress unavoidably leads to a reduction in A_N, analogous to the reported in other rootstock combinations. On the other hand, similar A_N reduction was observed under both moderate and severe salt stress conditions when using salt tolerant rootstocks, denoting the capability of these rootstocks to avoid ion translocation to scion and protect the photosynthetic apparatus even under extreme conditions [56,103,131] (Fig. 5b).

Overall, maintenance or optimization of A_N *vs* g_s under stress conditions can be modified by the rootstock through acting on different biophysical and biochemical processes in the aerial part of the plant, existing examples where those advantages can be translated to higher yield. Gaining knowledge about the physiological and genetic determinants of such rootstock-mediated traits is of great interest to increase yield and yield stability through grafting.

4.5. Concluding remarks

The lack of differences in A_N, g_s or WUE_i between non-grafted and self-grafted plants in any of the included species suggests that both non- or self-grafted plants can be selected as controls in future experiments devoted to examine the effect of grafting on photosynthesis. Published data indicate that WUE_i can be improved by grafting onto specific rootstocks under non-stress conditions, with scions grafted onto vigorous rootstocks increasing A_N. There are still gaps to be filled towards a complete understanding of the scion-rootstock communication and the mechanisms through which photosynthesis is affected by grafting. In this sense, we propose that future research should include changes in hormonal balance, and stomatal and leaf anatomy measurements as a complement of the photosynthesis measurements in order to obtain answers to some of those questions. Moreover, more accurate studies considering long-term experiments are required to establish a clear relationship between the affected photosynthetic parameters and crop yield. Overall, the present compilation of data allows to highlight important effects of grafting on photosynthesis and reveals grafting as a viable technique to improve crop photosynthetic performance and to contribute to food security in the context of climate change imposed conditions.

Acknowledgements

This research was supported by the European Union's Horizon 2020 research and innovation program under the Grant Agreement No. 727929 (TOMRES) and the Spanish Ministerio de Ciencia, Innovación y Universidades (project AGL2013-42364-R) awarded to J. Galmés. M. Fullana-Pericàs is recipient of a pre-doctoral fellowship (FPI/1929/2016) granted by the Government of the Balearic Islands. F. Pérez-Alfocea thanks the Government of the Comunidad Autónoma de la Región de Murcia (project Ris3Mur 2I16SA00051) and the Spanish Ministerio de Ciencia, Innovación y Universidades (project RTI2018-099113-B-I00) for funding vegetable grafting research in his lab.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.plantsci.2019.110250.

References

[1] D. Baron, A.C. Esteves Amaro, A. Pina, G. Ferreira, An overview of grafting re-establishment in woody fruit species, Sci. Hortic. (Amsterdam) 243 (2019) 84–91, https://doi.org/10.1016/j.scienta.2018.08.012.

[2] I. Wendling, S.J. Trueman, A. Xavier, Maturation and related aspects in clonal forestry-part II: reinvigoration, rejuvenation and juvenility maintenance, New For. 45 (2014) 473–486, https://doi.org/10.1007/s11056-014-9415-y.

[3] E.E. Goldschmidt, Plant grafting: new mechanisms, evolutionary implications, Front. Plant Sci. 5 (2014) 1–9, https://doi.org/10.3389/fpls.2014.00727.

[4] E.J. Warschefsky, L.L. Klein, M.H. Frank, D.H. Chitwood, J.P. Londo, E.J.B. von Wettberg, A.J. Miller, Rootstocks: diversity, domestication, and impacts on shoot phenotypes, Trends Plant Sci. 21 (2016) 418–437, https://doi.org/10.1016/j.tplants.2015.11.008.

[5] C.W. Melnyk, A. Gabel, T.J. Hardcastle, S. Robinson, S. Miyashima, I. Grosse, E.M. Meyerowitz, Transcriptome dynamics at Arabidopsis graft junctions reveal an intertissue recognition mechanism that activates vascular regeneration, Proc. Natl. Acad. Sci. 115 (2018) E2447–E2456, https://doi.org/10.1073/pnas.1718263115.

[6] H.T. Hartmann, D.E. Kester, F.T. Davies, R.L. Geneve, Plant Propagation: Principles and Practices H, (2011) doi:1624647.

[7] A.R. Davis, P. Perkins-Veazie, Y. Sakata, S. López-Galarza, J.V. Maroto, S.G. Lee, Y.C. Huh, Z. Sun, A. Miguel, S.R. King, R. Cohen, J.M. Lee, Cucurbit grafting, Crit. Rev. Plant Sci. 27 (2008) 50–74, https://doi.org/10.1080/07352680802053940.

[8] H. Yin, B. Yan, J. Sun, P. Jia, Z. Zhang, X. Yan, J. Chai, Z. Ren, G. Zheng, H. Liu, Graft-union development: a delicate process that involves cell–cell communication between scion and stock for local auxin accumulation, J. Exp. Bot. 63 (2012) 4219–4232, https://doi.org/10.1093/jxb/ers109.

[9] M. Kawaguchi, A. Taji, D. Backhouse, M. Oda, Anatomy and physiology of graft incompatibility in solanaceous plants, J. Hortic. Sci. Biotechnol. 83 (2008) 581–588, https://doi.org/10.1080/14620316.2008.11512427.

[10] N. Turquois, M. Malone, Non-destructive assessment of developing hydraulic connections in the graft union of tomato, J. Exp. Bot. 47 (1996) 701–707, https://doi.org/10.1093/jxb/47.5.701.

[11] C.W. Melnyk, C. Schuster, O. Leyser, E.M. Meyerowitz, A developmental framework for graft formation and vascular reconnection in arabidopsis thaliana, Curr. Biol. 25 (2015) 1306–1318, https://doi.org/10.1016/j.cub.2015.03.032.

[12] F.J. Louws, C.L. Rivard, C. Kubota, Grafting fruiting vegetables to manage soil-borne pathogens, foliar pathogens, arthropods and weeds, Sci. Hortic. (Amsterdam) 127 (2010) 127–146, https://doi.org/10.1016/j.scienta.2010.09.023.

[13] G. Colla, Y. Rouphael, C. Leonardi, Z. Bie, Role of grafting in vegetable crops grown under saline conditions, Sci. Hortic. (Amsterdam) 127 (2010) 147–155, https://doi.org/10.1016/j.scienta.2010.08.004.

[14] D. Schwarz, Y. Rouphael, G. Colla, J.H. Venema, Grafting as a tool to improve tolerance of vegetables to abiotic stresses: thermal stress, water stress and organic pollutants, Sci. Hortic. (Amsterdam) 127 (2010) 162–171, https://doi.org/10.1016/j.scienta.2010.09.016.

[15] Y. Rouphael, D. Schwarz, A. Krumbein, G. Colla, Impact of grafting on product quality of fruit vegetables, Sci. Hortic. (Amsterdam) 127 (2010) 172–179, https://doi.org/10.1016/j.scienta.2010.09.001.

[16] D. Schwarz, G.B. Öztekin, Y. Tüzel, B. Brückner, A. Krumbein, Rootstocks can

enhance tomato growth and quality characteristics at low potassium supply, Sci. Hortic. (Amsterdam) 149 (2013) 70–79, https://doi.org/10.1016/j.scienta.2012.06.013.

[17] L.I. Solari, S. Johnson, T.M. Dejong, Hydraulic conductance characteristics of peach (Prunus persica) trees on different rootstocks are related to biomass production and distribution, Tree Physiol. 26 (2006) 1343–1350, https://doi.org/10.1093/treephys/26.10.1343.

[18] M.J. Clearwater, R.G. Lowe, B.J. Hofstee, C. Barclay, A.J. Mandemaker, P. Blattmann, Hydraulic conductance and rootstock effects in grafted vines of kiwifruit, J. Exp. Bot. 55 (2004) 1371–1382, https://doi.org/10.1093/jxb/erh137.

[19] G.A. Gambetta, C.M. Manuck, S.T. Drucker, T. Shaghasi, K. Fort, M.A. Matthews, M.A. Walker, A.J. McElrone, The relationship between root hydraulics and scion vigour across Vitis rootstocks: what role do root aquaporins play? J. Exp. Bot. 63 (2012) 6445–6455, https://doi.org/10.1093/jxb/ers312.

[20] G.B. Oztekin, F. Giuffrida, Y. Tuzel, C. Leonardi, Is the vigour of grafted tomato plants related to root characteristics? J. Food, Agric. Environ. 7 (2009) 364–368.

[21] J.H. Venema, B.E. Dijk, J.M. Bax, P.R. van Hasselt, J.T.M. Elzenga, Grafting tomato (Solanum lycopersicum) onto the rootstock of a high-altitude accession of Solanum habrochaites improves suboptimal-temperature tolerance, Environ. Exp. Bot. 63 (2008) 359–367, https://doi.org/10.1016/j.envexpbot.2007.12.015.

[22] A.E. Richardson, J.M. Barea, A.M. McNeill, C. Prigent-Combaret, Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms, Plant Soil 321 (2009) 305–339, https://doi.org/10.1007/s11104-009-9895-2.

[23] S. Radersma, P.F. Grierson, Phosphorus mobilization in agroforestry: organic anions, phosphatase activity and phosphorus fractions in the rhizosphere, Plant Soil 259 (2004) 209–219, https://doi.org/10.1023/B:PLSO.0000020970.40167.40.

[24] C. Penella, S.G. Nebauer, A.S. Bautista, S. López-Galarza, Á. Calatayud, Rootstock alleviates PEG-induced water stress in grafted pepper seedlings: physiological responses, J. Plant Physiol. 171 (2014) 842–851, https://doi.org/10.1016/j.jplph.2014.01.013.

[25] C. Martínez-Andújar, J.M. Ruiz-Lozano, I.C. Dodd, A. Albacete, F. Pérez-Alfocea, Hormonal and nutritional features in contrasting rootstock-mediated tomato growth under low-phosphorus nutrition, Front. Plant Sci. 08 (2017) 533, https://doi.org/10.3389/fpls.2017.00533.

[26] C. Martínez-Andújar, A. Albacete, A. Martínez-Pérez, J.M. Pérez-Pérez, M.J. Asins, F. Pérez-Alfocea, Root-to-shoot hormonal communication in contrasting rootstocks suggests an important role for the ethylene precursor aminocyclopropane-1-carboxylic acid in mediating plant growth under low-potassium nutrition in tomato, Front. Plant Sci. 7 (2016) 1–16, https://doi.org/10.3389/fpls.2016.01782.

[27] A. Albacete, C. Martinez-Andujar, A. Martinez-Perez, A.J. Thompson, I.C. Dodd, F. Perez-Alfocea, Unravelling rootstockxscion interactions to improve food security, J. Exp. Bot. 66 (2015) 2211–2226, https://doi.org/10.1093/jxb/erv027.

[28] J.H. Venema, F. Giuffrida, I. Paponov, A. Albacete, F. Pérez-Alfocea, I.C. Dodd, Rootstock-scion signalling: key factors mediating scion performance, Veg. Grafting Princ. Pract. International, CAB, Wallingford, Oxfordshire, UK, 2017, pp. 94–131.

[29] A. Albacete, C. Martínez-Andújar, M.E. Ghanem, M. Acosta, J. Sánchez-Bravo, M.J. Asins, J. Cuartero, S. Lutts, I.C. Dodd, F. Pérez-Alfocea, Rootstock-mediated changes in xylem ionic and hormonal status are correlated with delayed leaf senescence, and increased leaf area and crop productivity in salinized tomato, Plant Cell Environ. 32 (2009) 928–938, https://doi.org/10.1111/j.1365-3040.2009.01973.x.

[30] F. Pérez-Alfocea, A. Albacete, M.E. Ghanem, I.C. Dodd, Hormonal regulation of source - sink relations to maintain crop productivity under salinity: a case study of root-to-shoot signalling in tomato, Funct. Plant Biol. 37 (2010) 592, https://doi.org/10.1071/FP10012.

[31] F. Iacono, A. Buccella, E. Peterlunger, Water stress and rootstock influence on leaf gas exchange of grafted and ungrafted grapevines, Sci. Hortic. (Amsterdam) 75 (1998) 27–39, https://doi.org/10.1016/S0304-4238(98)00113-7.

[32] N.M. Holbrook, V.R. Shashidhar, R.A. James, R. Munns, Stomatal control in tomato with ABA-deficient roots: response of grafted plants to soil drying, J. Exp. Bot. 53 (2002) 1503–1514, https://doi.org/10.1093/jxb/53.373.1503.

[33] E. Cantero-Navarro, R. Romero-Aranda, R. Fernández-Muñoz, C. Martínez-Andújar, F. Pérez-Alfocea, A. Albacete, Improving agronomic water use efficiency in tomato by rootstock-mediated hormonal regulation of leaf biomass, Plant Sci. 251 (2016) 90–100, https://doi.org/10.1016/j.plantsci.2016.03.001.

[34] Y. Yang, L. Wang, J. Tian, J. Li, J. Sun, L. He, S. Guo, T. Tezuka, Proteomic study participating the enhancement of growth and salt tolerance of bottle gourd rootstock-grafted watermelon seedlings, Plant Physiol. Biochem. 58 (2012) 54–65, https://doi.org/10.1016/j.plaphy.2012.05.026.

[35] C. Penella, M. Landi, L. Guidi, S.G. Nebauer, E. Pellegrini, A.S. Bautista, D. Remorini, C. Nali, S. López-Galarza, A. Calatayud, Salt-tolerant rootstock increases yield of pepper under salinity through maintenance of photosynthetic performance and sinks strength, J. Plant Physiol. 193 (2016) 1–11, https://doi.org/10.1016/j.jplph.2016.02.007.

[36] J. Galdon-Armero, M. Fullana-Pericas, P.A. Mulet, M.A. Conesa, C. Martin, J. Galmes, The ratio of trichomes to stomata is associated with water use efficiency in Solanum lycopersicum (tomato), Plant J. 96 (2018) 607–619, https://doi.org/10.1111/tpj.14055.

[37] C. Hermida-Carrera, M.V. Kapralov, J. Galmés, Rubisco catalytic properties and temperature response in crops, Plant Physiol. 171 (2016) 2549–2561, https://doi.org/10.1104/pp.16.01846 pp.01846.2016.

[38] S.P. Long, A. Marshall-Colon, X.G. Zhu, Meeting the global food demand of the future by engineering crop photosynthesis and yield potential, Cell 161 (2015) 56–66, https://doi.org/10.1016/j.cell.2015.03.019.

[39] M.A.J.J. Parry, M. Reynolds, M.E. Salvucci, C. Raines, P.J. Andralojc, X.G. Zhu, G.D. Price, A.G. Condon, R.T. Furbank, Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency, J. Exp. Bot. 62 (2011) 453–467, https://doi.org/10.1093/jxb/erq304.

[40] R.A. Fischer, G.O. Edmeades, Breeding and cereal yield progress, Crop Sci. 50 (2010) S-85–S-98, https://doi.org/10.2135/cropsci2009.10.0564.

[41] S.M. Whitney, R.L. Houtz, H. Alonso, Advancing our understanding and capacity to engineer nature's CO2-sequestering enzyme, Rubisco, Plant Physiol. 155 (2010) 27–35, https://doi.org/10.1104/pp.110.164814.

[42] M.A.J. Parry, P.J. Andralojc, J.C. Scales, M.E. Salvucci, A.E. Carmo-Silva, H. Alonso, S.M. Whitney, Rubisco activity and regulation as targets for crop improvement, J. Exp. Bot. 64 (2013) 717–730, https://doi.org/10.1093/jxb/ers336.

[43] J. Flexas, Ü. Niinemets, A. Gallé, M.M. Barbour, M. Centritto, A. Diaz-Espejo, C. Douthe, J. Galmés, M. Ribas-Carbo, P.L. Rodriguez, F. Rosselló, R. Soolanayakanahally, M. Tomas, I.J. Wright, G.D. Farquhar, H. Medrano, Diffusional conductances to CO2 as a target for increasing photosynthesis and photosynthetic water-use efficiency, Photosynth. Res. 117 (2013) 45–59, https://doi.org/10.1007/s11120-013-9844-z.

[44] A. Wu, G.L. Hammer, A. Doherty, S. von Caemmerer, G.D. Farquhar, Quantifying impacts of enhancing photosynthesis on crop yield, Nat. Plants 5 (2019) 380–388, https://doi.org/10.1038/s41477-019-0398-8.

[45] S.P. Long, X.-G. Zhu, S.L. Naidu, D.R. Ort, Can improvement in photosynthesis increase crop yields? Plant Cell Environ. 29 (2006) 315–330, https://doi.org/10.1111/j.1365-3040.2005.01493.x.

[46] A.G. Condon, Breeding for high water-use efficiency, J. Exp. Bot. 55 (2004) 2447–2460, https://doi.org/10.1093/jxb/erh277.

[47] A. Condon, R. Richards, G. Rebetzke, G. Farguhar, Improving intrinsic water-use efficiency and crop yield, Crop Sci. (2002) 122–131.

[48] A. Blum, Drought resistance, water-use efficiency, and yield potential – are they compatible, dissonant, or mutually exclusive? Aust. J. Agric. Res. 56 (2005) 1159–1168, https://doi.org/10.1071/AR05069.

[49] A. Blum, Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress, F. Crop. Res. 112 (2009) 119–123, https://doi.org/10.1016/j.fcr.2009.03.009.

[50] F. Tardieu, Any trait or trait-related allele can confer drought tolerance: just design the right drought scenario, J. Exp. Bot. 63 (2011) 25–31, https://doi.org/10.1093/jxb/err269.

[51] F. Giorgi, X. Bi, Updated regional precipitation and temperature changes for the 21st century from ensembles of recenet AOGCM simulations, Geophys. Res. Lett. 32 (2005) 1–4, https://doi.org/10.1029/2005GL024288.

[52] X. Gao, F. Giorgi, Increased aridity in the Mediterranean region under greenhouse gas forcing estimated from high resolution simulations with a regional climate model, Glob. Planet. Change 62 (2008) 195–209, https://doi.org/10.1016/j.gloplacha.2008.02.002.

[53] D.S. Battisti, R.L. Naylor, Historical warnings of future food insecurity with unprecedented seasonal heat, Science (80-.) 323 (2009) 240–244, https://doi.org/10.1126/science.1164363.

[54] J. López-Marín, A. Gálvez, F.M. del Amor, A. Albacete, J.A. Fernández, C. Egea-Gilabert, F. Pérez-Alfocea, Selecting vegetative/generative/dwarfing rootstocks for improving fruit yield and quality in water stressed sweet peppers, Sci. Hortic. (Amsterdam) 214 (2017) 9–17, https://doi.org/10.1016/j.scienta.2016.11.012.

[55] J. López-Marín, A. González, F. Pérez-Alfocea, C. Egea-Gilabert, J.A. Fernández, Grafting is an efficient alternative to shading screens to alleviate thermal stress in greenhouse-grown sweet pepper, Sci. Hortic. (Amsterdam) 149 (2013) 39–46, https://doi.org/10.1016/j.scienta.2012.02.034.

[56] C. Penella, S.G. Nebauer, S. López-Galarza, A. Quiñones, A. San Bautista, Á. Calatayud, Grafting pepper onto tolerant rootstocks: an environmental-friendly technique overcome water and salt stress, Sci. Hortic. (Amsterdam) 226 (2017) 33–41, https://doi.org/10.1016/j.scienta.2017.08.020.

[57] C. Penella, S.G. Nebauer, A. Quiñones, A. San Bautista, S. López-Galarza, A. Calatayud, Some rootstocks improve pepper tolerance to mild salinity through ionic regulation, Plant Sci. 230 (2015) 12–22, https://doi.org/10.1016/j.plantsci.2014.10.007.

[58] V. Bőhm, D. Fekete, G. Balázs, L. Gáspár, N. Kappel, Salinity tolerance of grafted watermelon seedlings, Acta. Biol. Hung. 68 (2017) 412–427, https://doi.org/10.1556/018.68.2017.4.7.

[59] Y. Huang, Y. Jiao, M.A. Nawaz, C. Chen, L. Liu, Z. Lu, Q. Kong, F. Cheng, Z. Bie, Improving magnesium uptake, photosynthesis and antioxidant enzyme activities of watermelon by grafting onto pumpkin rootstock under low magnesium, Plant Soil 409 (2016) 229–246, https://doi.org/10.1007/s11104-016-2965-3.

[60] M.A. Nawaz, L. Wang, Y. Jiao, C. Chen, L. Zhao, M. Mei, Y. Yu, Z. Bie, Y. Huang, Pumpkin rootstock improves nitrogen use efficiency of watermelon scion by enhancing nutrient uptake, cytokinin content, and expression of nitrate reductase genes, Plant Growth Regul. 82 (2017) 233–246, https://doi.org/10.1007/s10725-017-0254-7.

[61] Y. Rouphael, M. Cardarelli, G. Colla, E. Rea, Yield, mineral composition, water relations, and water use efficiency of grafted mini-watermelon plants under deficit irrigation, HortScience 43 (2008) 730–736.

[62] S. Shirani Bidabadi, R. Abolghasemi, S.J. Zheng, Grafting of watermelon (Citrullus lanatus cv. Mahbubi) onto different squash rootstocks as a means to minimize cadmium toxicity, Int. J. Phytoremed. 20 (2018) 730–738, https://doi.org/10.1080/15226514.2017.1413338.

[63] Y. Yang, L. Yu, L. Wang, S. Guo, Bottle gourd rootstock-grafting promotes photosynthesis by regulating the stomata and non-stomata performances in leaves of watermelon seedlings under NaCl stress, J. Plant Physiol. 186–187 (2015) 50–58, https://doi.org/10.1016/j.jplph.2015.07.013.

[64] H. Yetisir, M.E. Çaliskan, S. Soylu, M. Sakar, Some physiological and growth

responses of watermelon [Citrullus lanatus (Thunb.) Matsum. and Nakai] grafted onto Lagenaria siceraria to floodinga, Environ. Exp. Bot. 58 (2006) 1–8, https://doi.org/10.1016/j.envexpbot.2005.06.010.

[65] Y.F. Liu, H.Y. Qi, C.M. Bai, M.F. Qi, C.Q. Xu, J.H. Hao, Y. Li, T.L. Li, Grafting helps improve photosynthesis and carbohydrate metabolism in leaves of muskmelon, Int. J. Biol. Sci. 7 (2011) 1161–1170, https://doi.org/10.7150/ijbs.7.1161.

[66] Y. Rouphael, M. Cardarelli, E. Rea, G. Colla, Improving melon and cucumber photosynthetic activity, mineral composition, and growth performance under salinity stress by grafting onto Cucurbita hybrid rootstocks, Photosynthetica 50 (2012) 180–188, https://doi.org/10.1007/s11099-012-0002-1.

[67] S.J. Ahn, Y.J. Im, G.C. Chung, B.H. Cho, S.R. Suh, Physiological responses of grafted-cucumber leaves and rootstock roots affected by low root temperature, Sci. Hortic. (Amsterdam) 81 (1999) 397–408, https://doi.org/10.1016/S0304-4238(99)00042-4.

[68] A.C.E. Amaro, A.C. Macedo, A.R.P. Ramos, R. Goto, E.O. Ono, J.D. Rodrigues, The use of grafting to improve the net photosynthesis of cucumber, Theor. Exp. Plant Physiol. 26 (2014) 241–249, https://doi.org/10.1007/s40626-014-0023-1.

[69] G. Colla, Y. Rouphael, E. Rea, M. Cardarelli, Grafting cucumber plants enhance tolerance to sodium chloride and sulfate salinization, Sci. Hortic. (Amsterdam) 135 (2012) 177–185, https://doi.org/10.1016/j.scienta.2011.11.023.

[70] A. Giné, C. González, L. Serrano, F.J. Sorribas, Population dynamics of Meloidogyne incognita on cucumber grafted onto the Cucurbita hybrid RS841 or ungrafted and yield losses under protected cultivation, Eur. J. Plant Pathol. 148 (2017) 795–805, https://doi.org/10.1007/s10658-016-1135-z.

[71] H. Li, G.J. Ahammed, G. Zhou, X. Xia, J. Zhou, K. Shi, J. Yu, Y. Zhou, Unraveling main limiting sites of photosynthesis under below- and above-ground heat stress in cucumber and the alleviatory role of Luffa rootstock, Front. Plant Sci. 7 (2016) 1–15, https://doi.org/10.3389/fpls.2016.00746.

[72] Z. Liu, Z. Bie, Y. Huang, A. Zhen, M. Niu, B. Lei, Rootstocks improve cucumber photosynthesis through nitrogen metabolism regulation under salt stress, Acta Physiol. Plant. 35 (2013) 2259–2267, https://doi.org/10.1007/s11738-013-1262-5.

[73] Y. Rouphael, M. Cardarelli, E. Rea, G. Colla, Grafting of cucumber as a means to minimize copper toxicity, Environ. Exp. Bot. 63 (2008) 49–58, https://doi.org/10.1016/j.envexpbot.2007.10.015.

[74] Y. Zhou, J. Zhou, L. Huang, X. Ding, K. Shi, J. Yu, Grafting of Cucumis sativus onto Cucurbita ficifolia leads to improved plant growth, increased light utilization and reduced accumulation of reactive oxygen species in chilled plants, J. Plant Res. 122 (2009) 529–540, https://doi.org/10.1007/s10265-009-0247-3.

[75] Y. Zhou, L. Huang, Y. Zhang, K. Shi, J. Yu, S. Nogués, Chill-induced decrease in capacity of RuBP carboxylation and associated H2O2 accumulation in cucumber leaves are alleviated by grafting onto figleaf gourd, Ann. Bot. 100 (2007) 839–848, https://doi.org/10.1093/aob/mcm181.

[76] S. Chaudhari, K.M. Jennings, D.W. Monks, D.L. Jordan, C.C. Gunter, F.J. Louws, Response of drought-stressed grafted and nongrafted tomato to postemergence metribuzin, Weed Technol. 31 (2017) 447–454, https://doi.org/10.1017/wet.2017.12.

[77] N. Fernandez-Garcia, V. Martinez, A. Cerda, M. Carvajal, Water and nutrient uptake of grafted tomato plants grown under saline conditions, J. Plant Physiol. 159 (2002) 899–905, https://doi.org/10.1078/0176-1617-00652.

[78] M. Fullana-Pericàs, J. Ponce, M.À. Conesa, A. Juan, M. Ribas-Carbó, J. Galmés, Changes in yield, growth and photosynthesis in a drought-adapted Mediterranean tomato landrace (Solanum lycopersicum 'Ramellet') when grafted onto commercial rootstocks and Solanum pimpinellifolium, Sci. Hortic. (Amsterdam) 233 (2018) 70–77, https://doi.org/10.1016/j.scienta.2018.01.045.

[79] Y. He, Z. Zhu, J. Yang, X. Ni, B. Zhu, Grafting increases the salt tolerance of tomato by improvement of photosynthesis and enhancement of antioxidant enzymes activity, Environ. Exp. Bot. 66 (2009) 270–278, https://doi.org/10.1016/j.envexpbot.2009.02.007.

[80] P. Kumar, M. Edelstein, M. Cardarelli, E. Ferri, G. Colla, Grafting affects growth, yield, nutrient uptake, and partitioning under cadmium stress in tomato, HortScience 50 (2015) 1654–1661, https://doi.org/10.1177/1088868310377394.

[81] D. Poudyala, L. Khatria, R. Uptmoora, An introgression of Solanum habrochaites in the rootstock improves stomatal regulation and leaf area development of grafted tomatoes under drought and low root-zone-temperatures, Adv. Crop Sci. Technol. 03 (2015), https://doi.org/10.4172/2329-8863.1000175.

[82] N. Sade, M. Gebretsadik, R. Seligmann, A. Schwartz, R. Wallach, M. Moshelion, The role of tobacco Aquaporin1 in improving water use efficiency, hydraulic conductivity, and yield production under salt stress, Plant Physiol. 152 (2010) 245–254, https://doi.org/10.1104/pp.109.145854.

[83] K. Žanić, G. Dumičić, M. Mandušić, G. Vuletin Selak, I. Bočina, B. Urlić, I. Ljubenkov, V. Bučević Popović, S. Goreta Ban, Bemisia tabaci MED population density as affected by rootstock-modified leaf anatomy and amino acid profiles in hydroponically grown tomato, Front. Plant Sci. 9 (2018) 1–13, https://doi.org/10.3389/fpls.2018.00086.

[84] A.R. Zeist, J.T. Resende, Is.F. Silva, J.R. Oliveira, C.M. Faria, C.L. Giacobbo, Agronomic characteristics of tomato plant cultivar Santa Cruz Kada grafted on species of the genus Solanum, Hortic. Bras. 35 (2017) 419–424, https://doi.org/10.1590/S0102-053620170317.

[85] G. Zhang, H. Guo, Effects of tomato and potato heterografting on photosynthesis, quality and yield of grafted parents, Hortic. Environ. Biotechnol. (2018), https://doi.org/10.1007/s13580-018-0096-x.

[86] Q.H. Gao, K. Xu, X.F. Wang, Y. Wu, Effect of grafting on cold tolerance in eggplant seedlings, Acta Hortic. (2008) 167–174, https://doi.org/10.17660/ActaHortic.2008.771.25.

[87] S.Y. Li, F. Teng, D.M. Rao, H.J. Zhang, H.Y. Wang, X.D. Yao, C.M. Yu, C.H. Li, M.Z. Zhao, S.K.S. Martin, F.T. Xie, Photosynthesis of soybean cultivars released in different decades after grafting onto record-yield cultivars as rootstocks, Photosynthetica 55 (2017) 579–587, https://doi.org/10.1007/s11099-016-0666-z.

[88] H. Dong, Y. Niu, W. Li, D. Zhang, Effects of cotton rootstock on endogenous cytokinins and abscisic acid in xylem sap and leaves in relation to leaf senescence, J. Exp. Bot. 59 (2008) 1295–1304, https://doi.org/10.1093/jxb/ern035.

[89] M. Tsubone, F. Kubota, K. Saitou, Effect of grafting on the activity of adenosine 5′-diphosphate glucose pyrophosphorylase and tuberous root production in sweet Potato(Ipomoea batatas Lam.), Jpn. J. Crop Sci. 66 (1997) 509–510, https://doi.org/10.1626/jcs.66.509.

[90] J. Traub, J.D. Kelly, W. Loescher, Early metabolic and photosynthetic responses to drought stress in common and tepary bean, Crop Sci. 57 (2017) 1670–1686, https://doi.org/10.2135/cropsci2016.09.0746.

[91] D. Sugiura, C.K.A. Watanabe, E. Betsuyaku, I. Terashima, Sink–source balance and down-regulation of photosynthesis in Raphanus sativus: effects of grafting, N and CO2, Plant Cell Physiol. 58 (2017) 2043–2056, https://doi.org/10.1093/pcp/pcx132.

[92] D. Sugiura, E. Betsuyaku, I. Terashima, Manipulation of the hypocotyl sink activity by reciprocal grafting of two Raphanus sativus varieties: its effects on morphological and physiological traits of source leaves and whole-plant growth, Plant Cell Environ. 38 (2015) 2629–2640, https://doi.org/10.1111/pce.12573.

[93] D. Baron, A.C.E. Amaro, A.C. Macedo, C.S.F. Boaro, G. Ferreira, Physiological changes modulated by rootstocks in atemoya (Annona x atemoya Mabb.): gas exchange, growth and ion concentration, Braz. J. Bot. 41 (2018) 219–225, https://doi.org/10.1007/s40415-017-0421-0.

[94] J. Bañuls, M.D. Serna, F. Legaz, M. Talon, E. Primo-Millo, Growth and gas exchange parameters of Citrus plants stressed with different salts, J. Plant Physiol. 150 (1997) 194–199, https://doi.org/10.1016/S0176-1617(97)80202-7.

[95] N. De Magalhães Erismann, E. Caruso Machado, M.L. Sant Anna Tucci, Photosynthetic limitation by CO2 diffusion in drought stressed orange leaves on three rootstocks, Photosynth. Res. 96 (2008) 163–172, https://doi.org/10.1007/s11120-008-9297-y.

[96] D.F.S.P. Machado, R.V. Ribeiro, J.A.G. da Silveira, J.R.M. Filho, E.C. Machado, Rootstocks induce contrasting photosynthetic responses of orange plants to low night temperature without affecting the antioxidant metabolism, Theor. Exp. Plant Physiol. 25 (2013) 26–35.

[97] I.E. Papadakis, K. Dimassi, A. Bosabalidis, I. Therios, A. Patakas, A. Giannakoula, Effects of B excess on some physiological and anatomical parameters of 'Navelina' orange plants grafted on two rootstocks, Environ. Exp. Bot. 51 (2004) 247–257, https://doi.org/10.1016/j.envexpbot.2003.11.004.

[98] I.E. Papadakis, K.N. Dimassi, A.M. Bosabalidis, I.N. Therios, A. Patakas, A. Giannakoula, Boron toxicity in 'Clementine' mandarin plants grafted on two rootstocks, Plant Sci. 166 (2004) 539–547, https://doi.org/10.1016/j.plantsci.2003.10.027.

[99] J.C.V. Vu, G. Yelenosky, Photosynthetic responses of citrus trees to soil flooding, Physiol. Plant. 81 (1991) 7–14, https://doi.org/10.1111/j.1399-3054.1991.tb01705.x.

[100] H. An, F. Luo, T. Wu, Y. Wang, X. Xu, S. Zhang, Z. Han, Effect of rootstocks or interstems on dry matter allocation in apple, Eur. J. Hortic. Sci. 82 (2017) 225–231, https://doi.org/10.17660/eJHS.2017/82.5.1.

[101] B. Gonçalves, J. Moutinho-Pereira, A. Santos, A.P. Silva, E. Bacelar, C. Correia, E. Rosa, Scion-rootstock interaction affects the physiology and fruit quality of sweet cherry, Tree Physiol. 26 (2006) 93–104, https://doi.org/10.1093/treephys/26.1.93.

[102] M. Pérez-Jiménez, M. Hernández-Munuera, M.C. Piñero Zapata, G. López-Ortega, F.M. del Amor, Two minuses can make a plus: waterlogging and elevated CO2interactions in sweet cherry (Prunus avium) cultivars, Physiol. Plant. 161 (2017) 257–272, https://doi.org/10.1111/ppl.12590.

[103] R. Massai, D. Remorini, M. Tattini, Gas exchange, water relations and osmotic adjustment in two scion/rootstock combinations of Prunus under various salinity concentrations, Plant Soil 259 (2004) 153–162, https://doi.org/10.1023/B:PLSO.0000020954.71828.13.

[104] P. Losciale, L. Manfrini, B. Morandi, B. Novak, E. Pierpaoli, M. Zibordi, L. Corelli Grappadelli, S. Anconelli, F. Galli, Water restriction effect on pear rootstocks: photoprotective processes and the possible role of photorespiration in limiting carbon assimilation, Acta Hortic. 1058 (2014) 237–244, https://doi.org/10.17660/ActaHortic.2014.1058.27.

[105] L. Bascuñán-Godoy, N. Franck, D. Zamorano, C. Sanhueza, D.E. Carvajal, A. Ibacache, Rootstock effect on irrigated grapevine yield under arid climate conditions are explained by changes in traits related to light absorption of the scion, Sci. Hortic. (Amsterdam) 218 (2017) 284–292, https://doi.org/10.1016/j.scienta.2017.02.034.

[106] M.R. Gibberd, R.R. Walker, D.H. Blackmore, A.G. Condon, Transpiration efficiency and carbon-isotope discrimination of grapevines grown under well-watered conditions in either glasshouse or vineyard, Aust. J. Grape Wine Res. 7 (2001) 110–117, https://doi.org/10.1111/j.1755-0238.2001.tb00197.x.

[107] M. Keller, M. Kummer, M.C. Vasconcelos, Soil nitrogen utilisation for growth and gas exchange by grapevines in response to nitrogen supply and rootstock, Aust. J. Grape Wine Res. 7 (2001) 2–11, https://doi.org/10.1111/j.1755-0238.2001.tb00187.x.

[108] C.J. Soar, P.R. Dry, B.R. Loveys, Scion photosynthesis and leaf gas exchange in Vitis vinifera L. Cv. Shiraz: mediation of rootstock effects via xylem sap ABA, Aust. J. Grape Wine Res. 12 (2006) 82–96, https://doi.org/10.1111/j.1755-0238.2006.tb00047.x.

[109] R.G. Somkuwar, P.B. Taware, M.A. Bhange, J. Sharma, I. Khan, Influence of

different rootstocks on growth, photosynthesis, biochemical composition, and nutrient contents in 'fantasy seedless' grapes, Int. J. Fruit Sci. 15 (2015) 251–266, https://doi.org/10.1080/15538362.2015.1031564.

[110] Y. Han, Y. Wang, H. Jiang, M. Wang, H. Korpelainen, C. Li, Reciprocal grafting separates the roles of the root and shoot in sex-related drought responses in Populus cathayana males and females, Plant Cell Environ. 36 (2013) 356–364, https://doi.org/10.1111/j.1365-3040.2012.02578.x.

[111] W. Guan, X. Zhao, D.W. Dickson, M.L. Mendes, J. Thies, Root-knot nematode resistance, yield, and fruit quality of specialty melons grafted onto Cucumis metulifer, HortScience 49 (2014) 1046–1051, https://doi.org/10.21273/HORTSCI.49.8.1046.

[112] M. Edelstein, Z. Plaut, M. Ben-Hur, Sodium and chloride exclusion and retention by non-grafted and grafted melon and Cucurbita plants, J. Exp. Bot. 62 (2011) 177–184, https://doi.org/10.1093/jxb/erq255.

[113] E.M. Khah, E. Kakava, A. Mavromatis, D. Chachalis, C. Goulas, Effect of grafting on growth and yield of tomato (Lycopersicon esculentum Mill.) in greenhouse and open-field, J. Appl. Hortic. 8 (2006) 3–7 http://www.horticultureresearch.net/pdf/journalofappliedhorticulture.pdf#page=5.

[114] M.T. Estañ, M.M. Martinez-Rodriguez, F. Perez-Alfocea, T.J. Flowers, M.C. Bolarin, Grafting raises the salt tolerance of tomato through limiting the transport of sodium and chloride to the shoot, J. Exp. Bot. 56 (2005) 703–712, https://doi.org/10.1093/jxb/eri027.

[115] A. Santa-Cruz, M.M. Martinez-Rodriguez, F. Perez-Alfocea, R. Romero-Aranda, M.C. Bolarin, The rootstock effect on the tomato salinity response depends on the shoot genotype, Plant Sci. 162 (2002) 825–831, https://doi.org/10.1016/S0168-9452(02)00030-4.

[116] J.M. Lynch, J.M. Whipps, Substrate flow in the rhizosphere, Plant Soil 129 (1990) 1–10, https://doi.org/10.1007/BF00011685.

[117] Y. Kuzyakov, G. Domanski, Carbon input by plants into the soil, Rev. J. Plant Nutr. Soil Sci. 163 (2000) 421–431, https://doi.org/10.1002/1522-2624(200008)163:4<421::AID-JPLN421>3.0.CO;2-R.

[118] S. Knapp, I.E. Peralta, The Tomato (Solanum Lycopersicum L., Solanaceae) and Its Botanical Relatives, Springer, Berlin Heidelberg, Berlin, Heidelberg, 2016, https://doi.org/10.1007/978-3-662-53389-5.

[119] I.E. Peralta, D.M. Spooner, S. Knapp, Taxonomy of Wild Tomatoes and Their Relatives, Michigan (2008), https://doi.org/10.1126/science.113.2935.3.

[120] K. Mudge, J. Janick, S. Scofield, E.E. Goldschmidt, A history of grafting, Hortic. Rev. (Am. Soc. Hortic. Sci.) 35 (2009) 437–493, https://doi.org/10.1002/9780470593776.ch9.

[121] J. Galmés, M.A. Conesa, J.M. Ochogavía, J.A. Perdomo, D.M. Francis, M. Ribas-Carbó, R. Savé, J. Flexas, H. Medrano, J. Cifre, Physiological and morphological adaptations in relation to water use efficiency in Mediterranean accessions of Solanum lycopersicum, Plant Cell Environ. 34 (2011) 245–260, https://doi.org/10.1111/j.1365-3040.2010.02239.x.

[122] J. Galmés, J.M. Ochogavía, J. Gago, E.J. Roldán, J. Cifre, M.À. Conesa, Leaf responses to drought stress in Mediterranean accessions of Solanum lycopersicum: anatomical adaptations in relation to gas exchange parameters, Plant Cell Environ. 36 (2013) 920–935, https://doi.org/10.1111/pce.12022.

[123] J. Flexas, M.M. Barbour, O. Brendel, H.M. Cabrera, M. Carriquí, A. Díaz-Espejo, C. Douthe, E. Dreyer, J.P. Ferrio, J. Gago, A. Gallé, J. Galmés, N. Kodama, H. Medrano, Ü. Niinemets, J.J. Peguero-Pina, A. Pou, M. Ribas-Carbó, M. Tomás, T. Tosens, C.R. Warren, Mesophyll diffusion conductance to CO2: an unappreciated central player in photosynthesis, Plant Sci. 193–194 (2012) 70–84, https://doi.org/10.1016/j.plantsci.2012.05.009.

[124] I. Terashima, Y.T. Hanba, D. Tholen, Ü. Niinemets, Leaf functional anatomy in relation to photosynthesis, Plant Physiol. 155 (2011) 108–116, https://doi.org/10.1104/pp.110.165472.

[125] J.R. Evans, Improving photosynthesis, Plant Physiol. 162 (2013) 1780–1793, https://doi.org/10.1104/pp.113.219006.

[126] M. Centritto, F. Loreto, K. Chartzoulakis, The use of low [CO2] to estimate diffusional and non-diffusional limitations of photosynthetic capacity of salt-stressed olive saplings, Plant Cell Environ. 26 (2003) 585–594, https://doi.org/10.1046/j.1365-3040.2003.00993.x.

[127] D.A. Meloni, M.A. Oliva, C.A. Martinez, J. Cambraia, Photosynthesis and activity of superoxide dismutase, peroxidase and glutathione reductase in cotton under salt stress, Environ. Exp. Bot. 49 (2003) 69–76, https://doi.org/10.1016/S0098-8472(02)00058-8.

[128] A. Parida, A.B. Das, P. Das, NaCl stress causes changes in photosynthetic pigments, proteins, and other metabolic components in the leaves of a true mangrove, Bruguiera parviflora, in hydroponic cultures, J. Plant Biol. 45 (2002) 28–36, https://doi.org/10.1007/BF03030429.

[129] F. Tardieu, R. Tuberosa, Dissection and modelling of abiotic stress tolerance in plants, Curr. Opin. Plant Biol. 13 (2010) 206–212, https://doi.org/10.1016/j.pbi.2009.12.012.

[130] A. Blum, Crop responses to drought and the interpretation of adaptation, Drought Toler. High. Plants Genet. Physiol. Mol. Biol. Anal. Springer, Netherlands, Dordrecht, 1996, pp. 57–70, https://doi.org/10.1007/978-94-017-1299-6_8.

[131] M.A. Nawaz, M. Imtiaz, Q. Kong, F. Cheng, W. Ahmed, Y. Huang, Z. Bie, Grafting: a technique to modify ion accumulation in horticultural crops, Front. Plant Sci. 7 (2016) 1–15, https://doi.org/10.3389/fpls.2016.01457.