

Research Paper

Assessment of drought stress sensitivity of kiwifruit rootstocks and grafting combinations through integrated physiological and phenotyping analysis

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ABSTRACT

Kiwifruit has a high-water requirement and is sensitive to reduced water availability. Many kiwifruit growing areas are expected to face increasing water scarcity due to climate change. Although the effects of drought stress on kiwifruit have been widely studied, the sensitivity of different genotypes to drought remains poorly described. The present study evaluated the physiological and phenotypic drought responses of three kiwifruit rootstocks ('Bounty71', *Actinidia macrosperma*; 'D1' and 'Hayward', *Actinidia chinensis* var. *deliciosa*) and scion/rootstock combinations, in which a yellow-fleshed cultivar ('Zesy002', *A. chinensis* var. *chinensis*) was grafted on each rootstock.

A pot experiment was conducted using non-destructive RGB imaging combined with leaf gas exchange measurements. Potted vines were subjected to continuous well-watered conditions or to a mild drought stress cycle, imposed by progressively reducing pot water availability (up to 65% field capacity), followed by five days of full re-watering.

Based on physiological measurements, Hayward and D1 rootstocks were more affected by drought than Bounty71. Drought-induced physiological (reduced stomatal conductance and photosynthetic rate, increased intrinsic water use efficiency, and decreased instantaneous carboxylation efficiency) and phenotypic (changes in projected shoot area and leaf color) responses differed among genotypes, with Hayward identified as the most drought-sensitive. However, the complete recovery of both physiological and phenotypic parameters suggests the ability of all combinations to cope with short-term and mild drought.

The results support the use of phenotypic tools combined with leaf gas exchange measurements for a comprehensive screening of drought sensitivity in kiwifruit genotypes.

1. Introduction

In recent years, kiwifruit has become an important fruit crop with a growing global distribution, attracting the interest of several countries in both hemispheres (Ferguson et al., 2023). In the last decade, the kiwifruit industry has been dominated by China, which produces more than half of the world's kiwifruit, followed by New Zealand and Italy (Costa et al., 2018). The total area of land suitable for kiwifruit cultivation has increased due to the availability of irrigation. Irrigation compensates for deficits in areas where rainfall is insufficient to match the evaporative demand (Salinger and Kenny, 1995), enabling the successful cultivation of kiwifruit in Mediterranean countries (Chartzoulakis et al., 1993). The cultivation of kiwifruit in Italy extends

over the whole length of the country, with the most varied environmental conditions (Costa et al., 2018).

Climate variability and extreme weather events are expected to increase in the coming years, posing a global risk to kiwifruit production (Cradock-Henry, 2017; Chamberlain, 2023). Kiwifruit producing regions are vulnerable to changing environmental conditions (Rajan et al., 2024) and are exposed to increasing water scarcity due to climate change (Calderón-Orellana et al., 2021). In particular, cultivated areas within the Mediterranean basin will experience increased temperature and evaporative demand and decreased precipitation (Lionello and Scarascia, 2018; Prada et al., 2024).

Drought stress is one of the major environmental stresses to plants, negatively affecting their development and performance and causing

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changes at the physiological, morphological, biochemical and molecular levels (Salehi-Lisar and Bakhshayeshan-Agdam, 2016; Seleiman et al., 2021; Sato et al., 2024). Kiwifruit has a high irrigation requirement, especially when grown in Mediterranean environments (Chartzoulakis et al., 1993; Holzapfel et al., 2000; Calderón-Orellana et al., 2021). Here, it can easily experience water deficits due to summer atmospheric conditions combined with an inadequate water supply (Chartzoulakis et al., 1993) and irrigation restrictions at farm level. Water deficit in kiwifruit has been found to reduce fruit expansion and growth (Judd et al., 1989); decrease photosynthetic activity, leaf area development, and photosynthate partitioning, which in turn affects vine growth (Chartzoulakis et al., 1993; Liang et al., 2019); increase leaf and cell membrane damage and oxidation (Wang et al., 2011; Bao et al., 2020); and increase fruit sunburn damage (Calderón-Orellana et al., 2021). Montanaro et al. (2007) reported that kiwifruit is able to cope with the Mediterranean environment through low stomatal conductance and enhanced non-photochemical quenching, sacrificing carbon gain for water conservation, which was also actuated under severe drought stress.

Although the drought stress response of kiwifruit vines has been extensively studied, comparisons between rootstocks and information on rootstock-induced drought tolerance in kiwifruit scion are still lacking. The relatively recent domestication of kiwifruit has involved little breeding research and rootstock selection compared to other temperate tree and vine crops. However, much material is available for the selection of new rootstocks from the rich genetic diversity of *Actinidia* species (Thorp and Barnett, 2023).

Given the impacts of climate change and the expansion of kiwifruit cultivation to semi-arid areas, it is increasingly important to evaluate the drought response of different kiwifruit genotypes to identify more resilient rootstocks and cultivars. A previous study of the drought response of different kiwifruit rootstocks showed that moderate drought impaired photosynthesis, increased cell membrane damage and impacted reactive oxygen species-associated enzyme activity differently among genotypes. However, as drought intensified to severe levels, the effects on kiwifruit growth, photosynthesis, and oxidative damage worsened in all genotypes (Bao et al., 2024). Recent studies have shown that rootstocks belonging to *A. macrosperma* are likely to be more tolerant to drought (Zhong et al., 2018) and intermittent waterlogging (Kataoka et al., 2021; Beppu et al., 2022), proving to be more resilient to unbalanced soil water and environmental conditions.

To evaluate plant growth, physiological, molecular, and biochemical responses to drought, new tools, such as imaging technologies, are needed to enhance the understanding of plant performance in different environments and bridge the phenotype-genotype gap (Chaves et al., 2003). Automated platforms can improve the throughput of plant phenotyping by using integrated sensors, such as visible light, near-infrared, fluorescence, multispectral, and hyperspectral (Fu and Jiang, 2022), and enabling the collection of large amounts of high-quality data in a continuous, non-destructive, and non-invasive manner (Danzi et al., 2019).

Plant phenotyping can effectively detect and monitor changes induced by drought stress, thus contributing to the understanding of how plants cope with water scarcity (Mansoor and Chung, 2024). Though most studies have focused on phenotyping the drought response in vegetables and cereals (Janni et al., 2019; Danzi et al., 2022), a few recent studies have shown the potential of plant phenotyping to detect the stress response of vine crops. Briglia et al. (2019, 2020) evaluated the drought response of grapevines by examining changes in morphological traits, such as leaf greenness, leaf area development, and leaf angle. Meanwhile, morpho-physiological changes in kiwifruit rootstocks and grafting combinations under short-term waterlogging stress revealed that Bounty (*A. macrosperma*) is a more tolerant genotype compared to D1 and Hayward (*A. chinensis* var. *deliciosa*) (Calabritto et al., 2025).

In the present study, an integrated approach based on high-

throughput plant phenotyping (HTPP) and leaf gas exchange measurements is used to i) assess the tolerance/susceptibility of different kiwifruit rootstocks to drought stress, and ii) evaluate the response of the yellow-fleshed cultivar grafted on each rootstock to drought and recovery.

2. Materials and methods

2.1. Plant material and growth conditions

A pot experiment was carried out during the 2023 season at the ALSIA 'Metapontum Agrobios' Research Centre in Metaponto (southern Italy). The plant material consisted of 30 two-year-old rootstocks of 'Hayward' (H) (*A. chinensis* var. *deliciosa*), 'Bounty71' (B) (*A. macrosperma*) and 'D1' (D) (*A. chinensis* var. *deliciosa*) and 42 one-year-old scions of cv. 'Zesy002' (*A. chinensis* var. *chinensis*) grafted on each rootstock (i. e., scion/rootstock: Z/H, Z/B and Z/D), resulting in 10 and 14 replicates per genotype, respectively. All kiwifruit vines were transplanted in March in blue pots of 3 L capacity. The potting medium was a mixture of acid peat and pumice (pH 6, bulk density 0.23 g cm⁻³ and 90% porosity). The vines were grown in an unheated greenhouse under natural light conditions. The pots were randomly distributed in a grid arrangement at least 30 cm apart to reduce vine-to-vine influence and the effects of microclimatic variations. Environmental conditions in the greenhouse during the experiment were: minimum temperature of approximately 20°C and maximum temperature of approximately 40°C, with relative humidity ranging from a minimum of 30% to a maximum of 85%. All vines were trained to a single main shoot and pruned to a similar leaf area (approximately 10 leaves each). Each vine was tied to a wooden support, which was painted blue for image acquisition, segmentation and analysis. Immediately prior to the start and during the experiment, the pots were loaded on the plant phenomics platform and labeled with a barcode for automatic weighing, watering and identification during image acquisition.

2.2. Irrigation treatments and soil water availability

From transplanting to the start of the experiment, all vines were kept at field capacity (FC). Prior to the start of the experiment, each pot was fully watered and the excess water was allowed to drain until no water came out of the bottom of the pots and stable pot weights were achieved. The average weights were used as pot weight at 100% FC, referred to as maximum pot weight.

From 3 July, the vines were assigned to two irrigation treatment groups (control, C and drought stress, DS), following a complete randomization experimental design with five vines for each rootstock and seven vines for each scion/rootstock combination.

Soil water availability (SWA) was calculated as follows (Sapeta et al., 2013):

$$SWA = \left[\frac{(Pot\ Weight - Minimum\ Pot\ Weight)}{(Maximum\ Pot\ Weight - Minimum\ Pot\ Weight)} \right] * 100 \quad (1)$$

Minimum pot weight was considered as the weight of a pot containing a completely dry substrate. For this measurement, the soil was oven-dried at 105°C until a constant weight was reached.

In the C treatment, vines were grown continuously under well-watered conditions by maintaining the soil water content of the pots close to FC.

Drought stress was imposed by gradually reducing pot SWA (by 20% the first day and then up to 35% based on pot weight) and was followed by five days of full re-watering (R). A three-step SWA reduction was done to simulate the progressive drought that typically occurs at the field level.

The platform automatically replenished the amount of water lost from each pot by weighing and watering the pots two or three times per

day. This restored the maximum pot weight defined at FC in the C treatment and maintained the level of SWA imposed in the DS treatment.

2.3. Leaf gas exchanges

Stomatal conductance (g_s , $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), transpiration (E , $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$), photosynthetic rate (A , $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), leaf temperature (T_{leaf} , $^{\circ}\text{C}$), photosystem II operating efficiency (ΦPSII) in the light-adapted state and electron transport rate (ETR, $\mu\text{mol e}^{-} \text{m}^{-2} \text{s}^{-1}$) were measured using a portable gas exchange system (Li-Cor 6800, Li-Cor Inc., Lincoln, NE, USA). Measurements were taken at different levels of SWA reduction (-17% FC, -22% FC, and -35% FC in rootstocks and -19% FC, -23% FC and -37% FC in scion/rootstock combinations) at the time of maximum efficiency (10:00–12:00 h, solar time). In addition, a diurnal trend of leaf gas exchanges was monitored at approximately three-hour intervals when SWA reached the maximum reduction. Measurements were also taken during the five-day recovery period at the time of maximum efficiency (10:00–12:00 h, solar time). Intrinsic leaf water use efficiency (A/g_s , $\mu\text{mol CO}_2 \text{mol}^{-1} \text{H}_2\text{O}$) and instantaneous carboxylation efficiency (A/C_i , $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1} \text{ppm}^{-1}$) were also calculated. Leaf gas exchange measurements were performed at a CO_2 concentration fixed at ambient values of $400 \mu\text{mol mol}^{-1}$, with temperature and irradiance maintained at the prevailing external environmental conditions according to Medrano et al. (2010), and an operating flow rate of $500 \mu\text{mol s}^{-1}$.

To reduce the effects of leaf position and developmental age, a fully expanded and sun-exposed leaf with no visual symptoms of stress was chosen from the mid-shoot region of four randomly selected vines for each irrigation treatment, rootstock and scion/rootstock combination.

2.4. High-throughput plant phenotyping

For HTPP measurements, all vines were phenotyped non-destructively and non-invasively using a Scanalyzer 3D plant phenotyping platform (LemnaTec GmbH, Aachen, Germany). The platform is part of the 'PhenoLab project' which encompasses multiple platforms dedicated to plant phenotyping. It is located at the ALSIA 'Metapontum Agrobios' Research Centre, which is part of the Phen-Italy and European Plant Phenotyping Network and infrastructures. Five vines per each irrigation treatment, rootstock and scion/rootstock combination were imaged before the application of drought stress (referred to as 'Time 0'), during the drought and recovery phases.

The vines were automatically transported on a conveyor belt into the RGB imaging chamber and identified using the barcode and RFID tracking system. The imaging chamber was equipped with a fluorescent white lighting and 2 Megapixel RGB camera (Basler sca1600–28gc).

Three images per vine were acquired, one from the top of the vine (Top View, TV) and two from the lateral sides at an orthogonal angle (0° and 90° Side View, SV).

2.5. RGB-imaging

Image segmentation, which was conducted to separate the plant from the background by creating sufficient contrast, and image analysis were performed using Python v3.9 and PlantCV v3.11 open source software (Fahlgren et al., 2015).

Traits collected from the RGB images included plant projected shoot area (psa) and solidity (sol), which indicate morphometric changes, and plant color (hue), which indicates colorimetric changes associated with green, healthy tissue and/or yellow, chlorotic tissue.

The total number of pixels corresponding to the plant area, derived from the RGB images of the two orthogonal SVs and the TV, was used to calculate the psa, following the procedure reported by Calabritto et al. (2025). The plant sol was calculated as the ratio between the plant area and the convex hull area analyzed from the orthogonal SVs. Plant color was analyzed using hue channels, which quantify color in terms of

an angle around a color hexagon with values ranging from 0° to 360° . Leaf color is usually included in the hue range from 120° (green healthy tissue) to 60° (yellow chlorotic tissue). Hue was derived from the TV image of the plant to easily extract the color of the adaxial leaf surface and to reduce the influence of the stem in the hue.

2.6. Data analysis

All data analyses were performed in R 4.3.3 (R Studio: Integrated Development for R., Boston, MA, USA. R Core Team, 2024), with Sigmaplot 15.0 (Systat Software, Inc., San Jose, CA, USA) also used for data plotting. Physiological and phenotyping measurements were reported as means and standard errors of the means ($\pm$ SE). A two-way ANOVA was performed to determine the effects of irrigation treatment and cultivar, as well as their interaction, on physiological parameters separately for each level of drought stress or recovery. Normality (Shapiro-Wilk's test) and equal variance (Levene's test) hypotheses were tested. A one-way ANOVA was used to examine the differences between irrigation treatments within each cultivar at each level of drought stress or recovery. For phenotyping parameters, irrigation treatments were compared using Student's *t*-test after checking the normality of the data distribution. A Principal Component Analysis (PCA) was performed including physiological (g_s , A and T_{leaf}) and phenotypic (psa, sol and hue) variables, with the superimposition of confidence ellipses ($\alpha = 0.05$), to investigate the responses of rootstocks and scion/rootstock combinations to the least water availability achieved using a multivariate approach.

3. Results

3.1. Soil water availability

Three successive reductions in SWA were imposed, reaching 83%, 78%, and 65% FC in rootstocks (Fig. 1a) and 81%, 77%, and 63% FC in grafting combinations (Fig. 1b). SWA was progressively reduced by approximately 35% compared to FC at the maximum level of drought stress.

3.2. Leaf gas exchange response

The leaf gas exchange responses of the rootstocks were not significantly affected by irrigation treatment throughout the experiment. Values of g_s and E were significantly reduced in H at the maximum SWA reduction (Fig. 2a, b). At maximum stress (i.e., SWA = 65% FC), g_s was reduced by 42% (in H) and 35% (in D) compared to C vines, dropping to values of $\sim 0.05 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$. Values of A under drought followed the trend of g_s , with significant reductions in H at maximum stress, where values were reduced by 46% compared to C vines (Fig. 2c). B was unaffected by the imposed drought in terms of leaf gas exchange response, as the values of g_s , E , and A remained within the range of the C vines (Fig. 2a–c).

Variations in g_s in C vines were in the range of 0.08 – $0.14 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$ in H and D and of 0.11 – $0.16 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$ in B (Fig. 2a). Variations in E in C vines were in the range of 2.0 – $3.5 \text{ mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ in H and D and of 3.2 – $3.6 \text{ mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ in B (Fig. 2b). Variations in A in C vines were in the range of 7.0 – $10.8 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ in H and D and of 9.7 – $11.7 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ in B (Fig. 2c).

One day after re-watering, H recovered g_s and A (Fig. 3a, c). D vines previously exposed to drought showed significantly lower values at this time, but fully recovered their physiological activity three days after re-watering (Fig. 3a, b).

Leaf gas exchange activity decreased under progressive drought in grafting combinations, with a significant treatment effect at the maximum level of stress (Fig. 4). Significantly lower drought-induced g_s , E , and A values were observed in Z/H at the maximum SWA reduction. At maximum stress (i.e., SWA = 63% FC), g_s was reduced by 66% in Z/H, 45% in Z/D, and 32% in Z/B compared to C vines, dropping to values

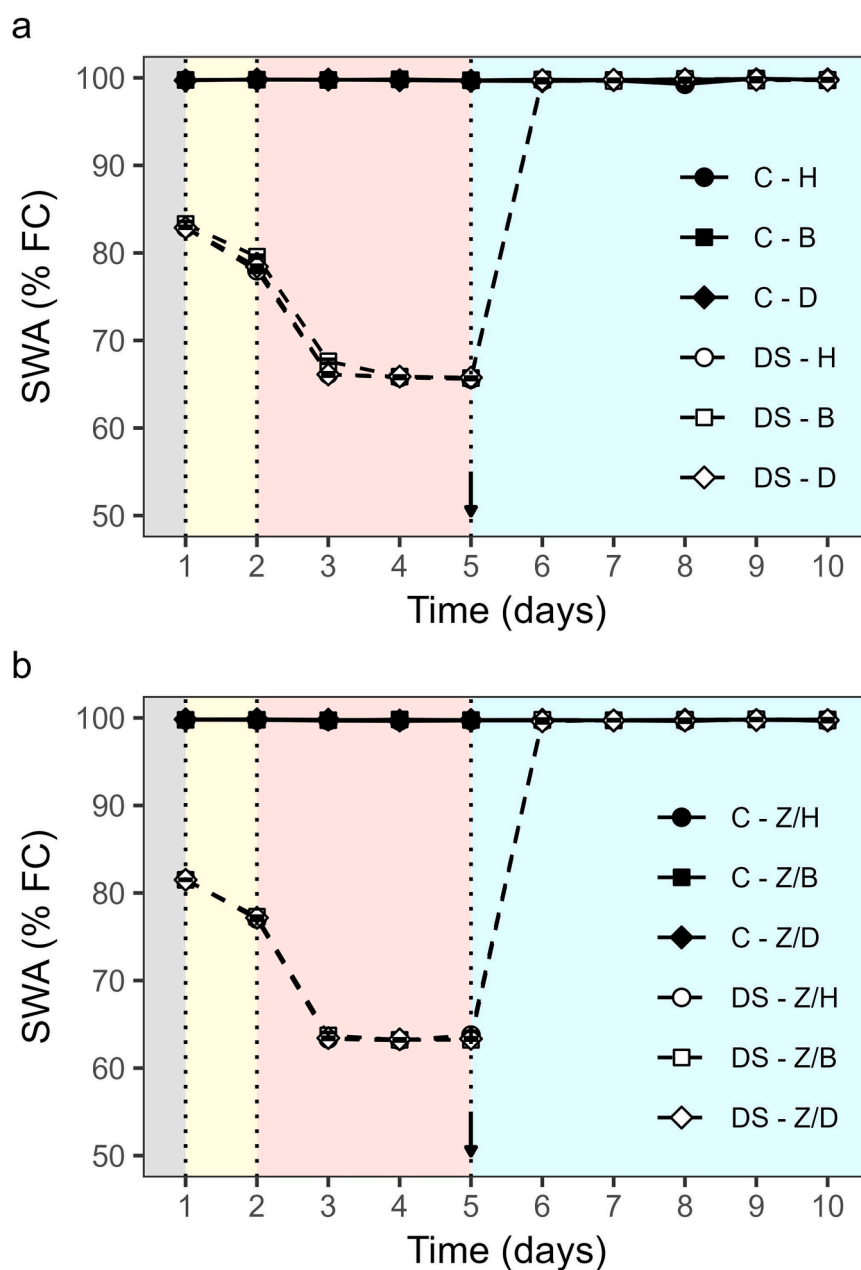


Fig. 1. Soil water availability (SWA) during the experiment for three kiwifruit (a) rootstocks: 'Hayward' (H), 'Bounty' (B), and 'D1' (D) and (b) grafting combinations: 'Zesy002/Hayward' (Z/H), 'Zesy002/Bounty' (Z/B), and 'Zesy002/D1' (Z/D), under well-watered (C) or progressively dry (DS) conditions followed by five days of re-watering. Background colors indicate different SWA reductions and stress levels, approximately: 83–81% FC (light grey); 78–77% FC (light yellow); 65–63% FC (light pink); 100% FC re-watering (light blue). The arrow indicates the start of re-watering. Data shown are means $\pm$ standard error of the mean ($n = 5$).

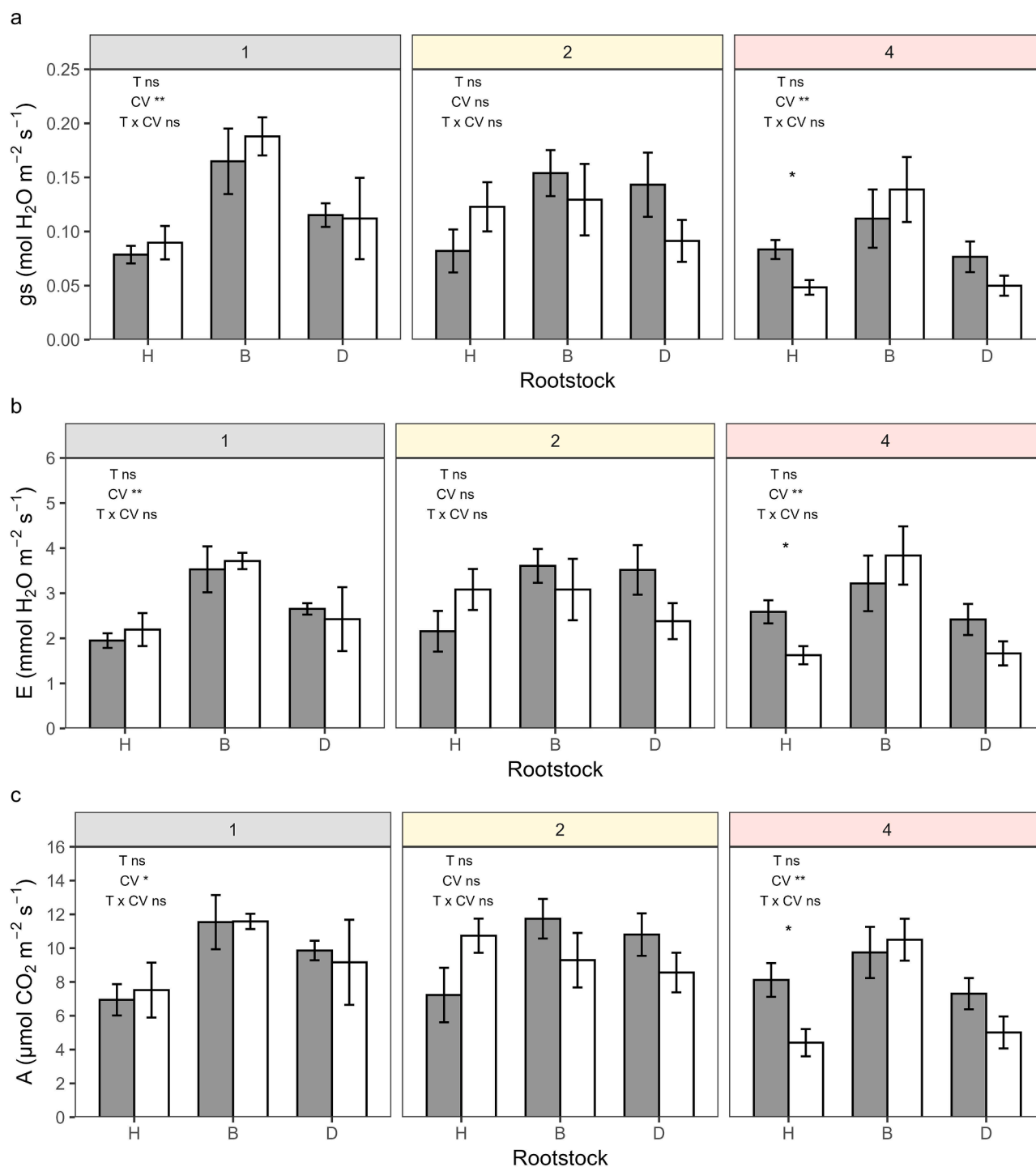


Fig. 2. Effect of drought stress on (a) stomatal conductance (gs), (b) transpiration (E), and (c) photosynthetic rate (A) measured for the three kiwifruit rootstocks 'Hayward' (H), 'Bounty' (B), and 'D1' (D). Vines were subjected to two irrigation treatments: well-watered (grey bars, C) or progressive drought (white bars, DS). Data shown are means ± standard error of the mean ($n = 4$). Two-way ANOVA results are shown for each parameter and level of stress. Asterisks indicate significant differences between C and DS vines within each rootstock according to one-way ANOVA. Note that each panel corresponds to a different day of experiment and level of SWA achieved in drought-stressed vines: light grey (83%), light yellow (78%), and light pink (65%). Significance codes: "*" $p < 0.05$, "***" $p < 0.01$, "ns" not significant. T = treatment, CV = cultivar.

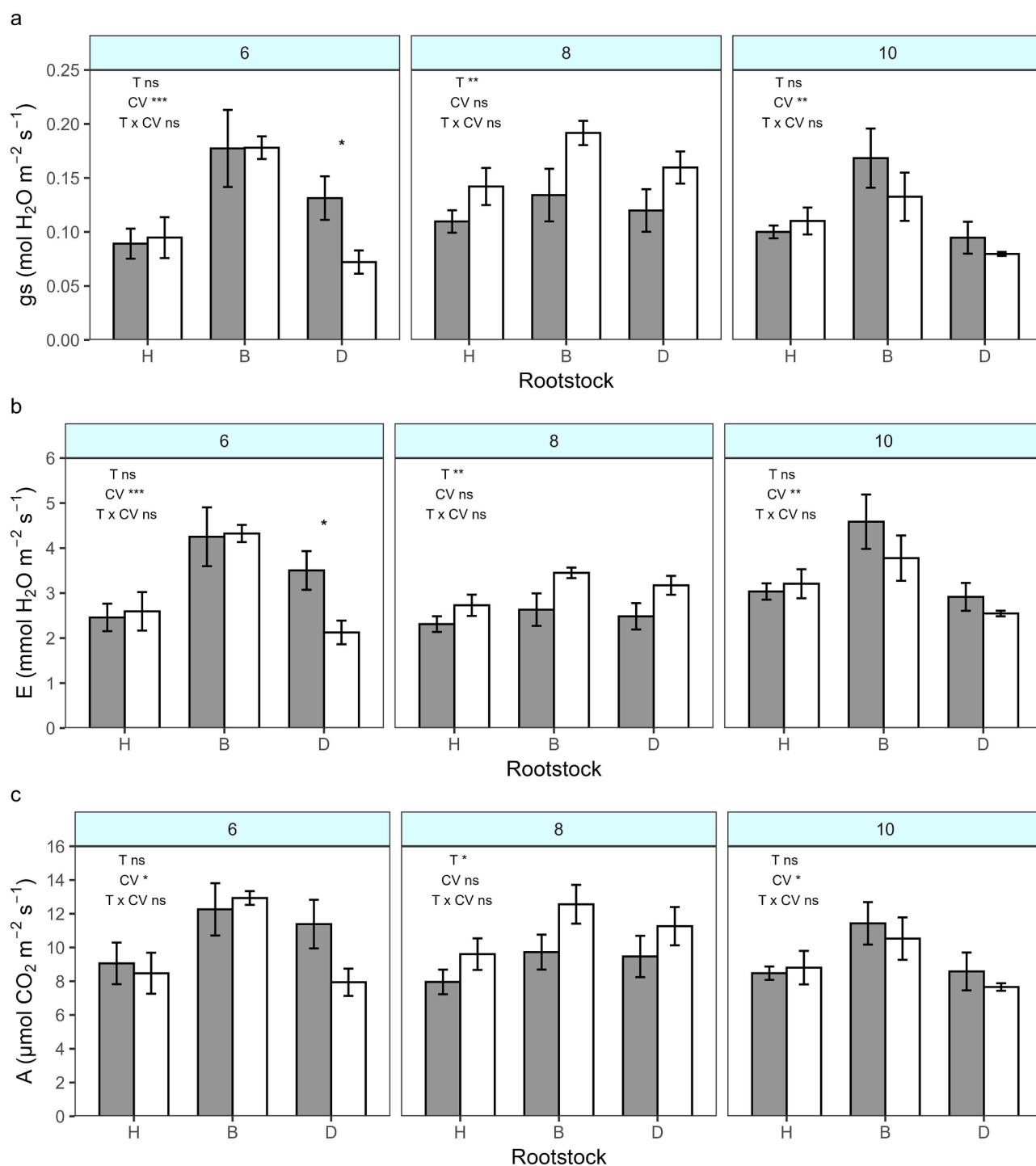


Fig. 3. Effect of re-watering on (a) stomatal conductance (gs), (b) transpiration (E), and (c) photosynthetic rate (A) measured for the three kiwifruit rootstocks 'Hayward' (H), 'Bounty' (B), and 'D1' (D). Vines were subjected to two irrigation treatments: well-watered (grey bars, C) or progressive drought (white bars, DS), followed by five days of re-watering. Data shown are means $\pm$ standard error of the mean ($n=4$). Two-way ANOVA results are shown for each parameter and recovery day. Asterisks indicate significant differences between C and DS vines within each rootstock according to one-way ANOVA. Note that each panel corresponds to a different day of experiment during re-watering. Significance codes: "*" $p < 0.05$, "***" $p < 0.01$, "****" $p < 0.001$, "ns" not significant. T = treatment, CV = cultivar.

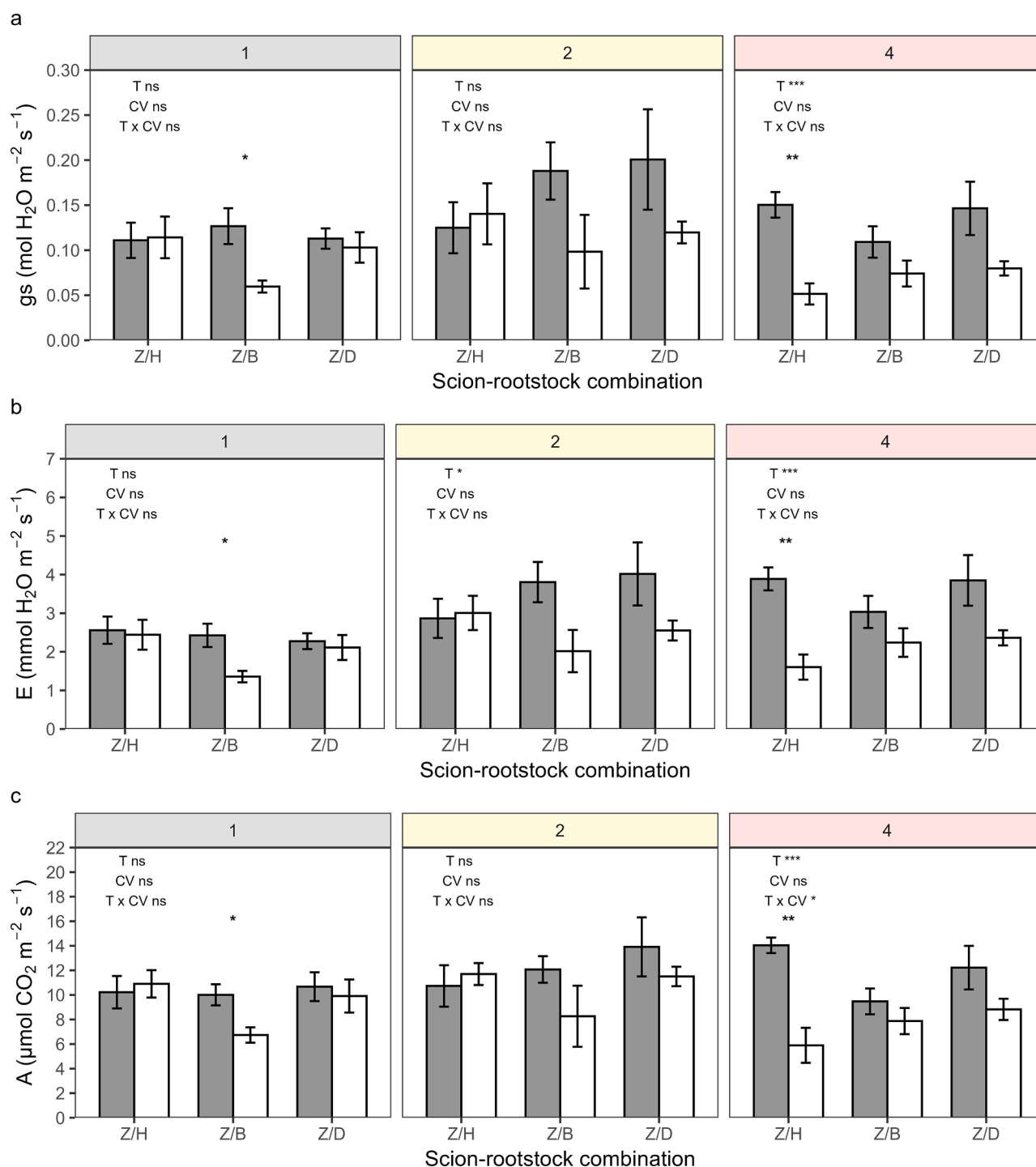


Fig. 4. Effect of drought stress on (a) stomatal conductance (gs), (b) transpiration (E), and (c) photosynthetic rate (A) measured for the three kiwifruit grafting combinations ‘Zesy002/Hayward’ (Z/H), ‘Zesy002/Bounty’ (Z/B), and ‘Zesy002/D1’ (Z/D). Vines were subjected to two irrigation treatments: well-watered (grey bars, C) or progressive drought (white bars, DS). Data shown are means $\pm$ standard error of the mean ($n = 4$). Two-way ANOVA results are shown for each parameter and level of stress. Asterisks indicate significant differences between C and DS vines within each scion-rootstock combination according to one-way ANOVA. Note that each panel corresponds to a different day of experiment and level of SWA achieved in drought-stressed vines: light grey (81%), light yellow (77%), and light pink (63%). Significance codes: “*” $p < 0.05$, “**” $p < 0.01$, “***” $p < 0.001$, “ns” not significant. T = treatment, CV = cultivar.

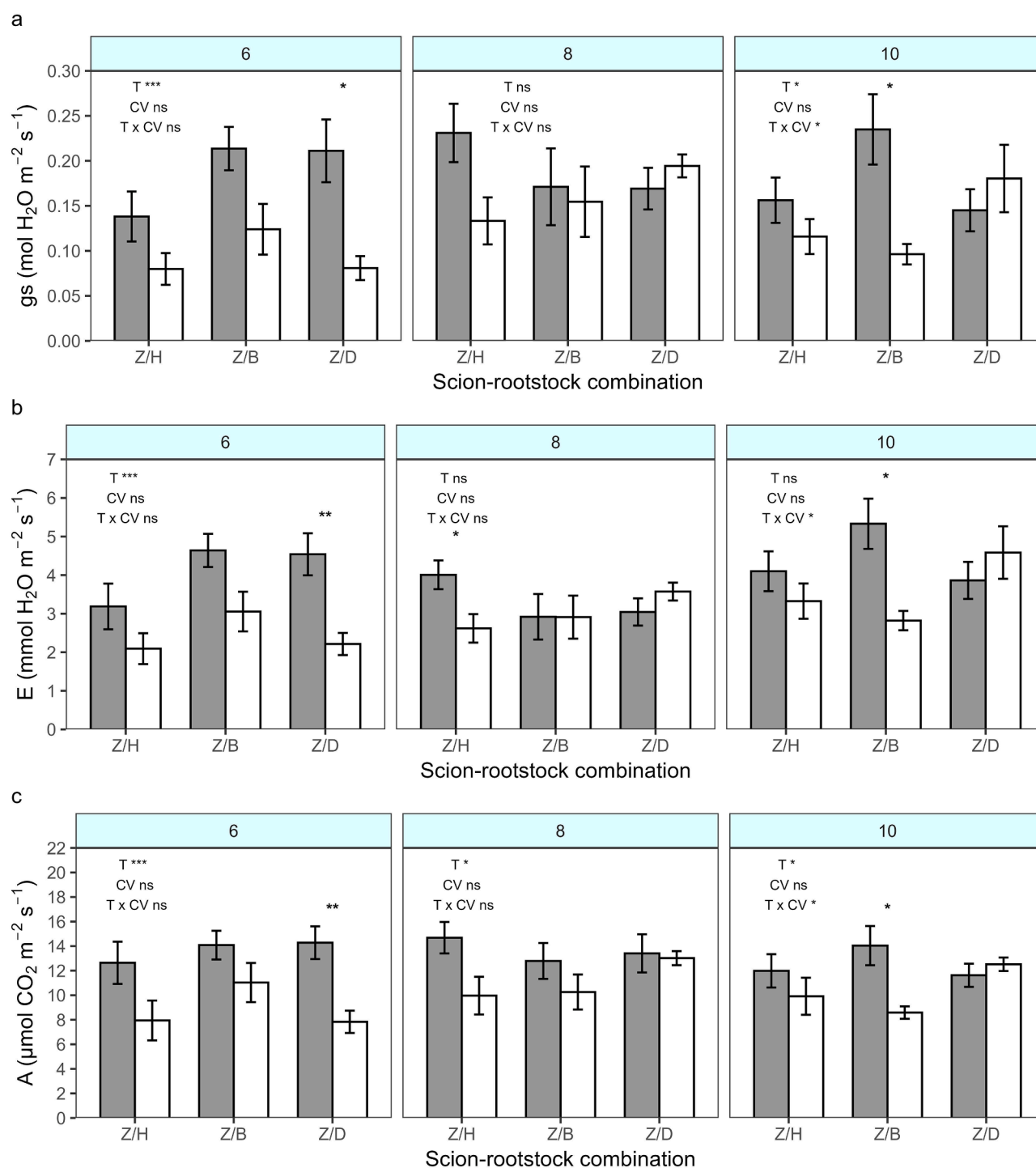


Fig. 5. Effect of re-watering on (a) stomatal conductance (gs), (b) transpiration (E), and (c) photosynthetic rate (A) measured for the three kiwifruit grafting combinations 'Zesy002/Hayward' (Z/H), 'Zesy002/Bounty' (Z/B), and 'Zesy002/D1' (Z/D). Vines were subjected to two irrigation treatments: well-watered (grey bars, C) or progressive drought (white bars, DS), followed by five days of re-watering. Data shown are means $\pm$ standard error of the mean ($n = 4$). Two-way ANOVA results are shown for each parameter and recovery day. Asterisks indicate significant differences between C and DS vines within each scion-rootstock combination according to one-way ANOVA. Note that each panel corresponds to a different day of experiment during re-watering. Significance codes: "*" $p < 0.05$, "***" $p < 0.01$, "****" $p < 0.001$, "ns" not significant. T = treatment, CV = cultivar.

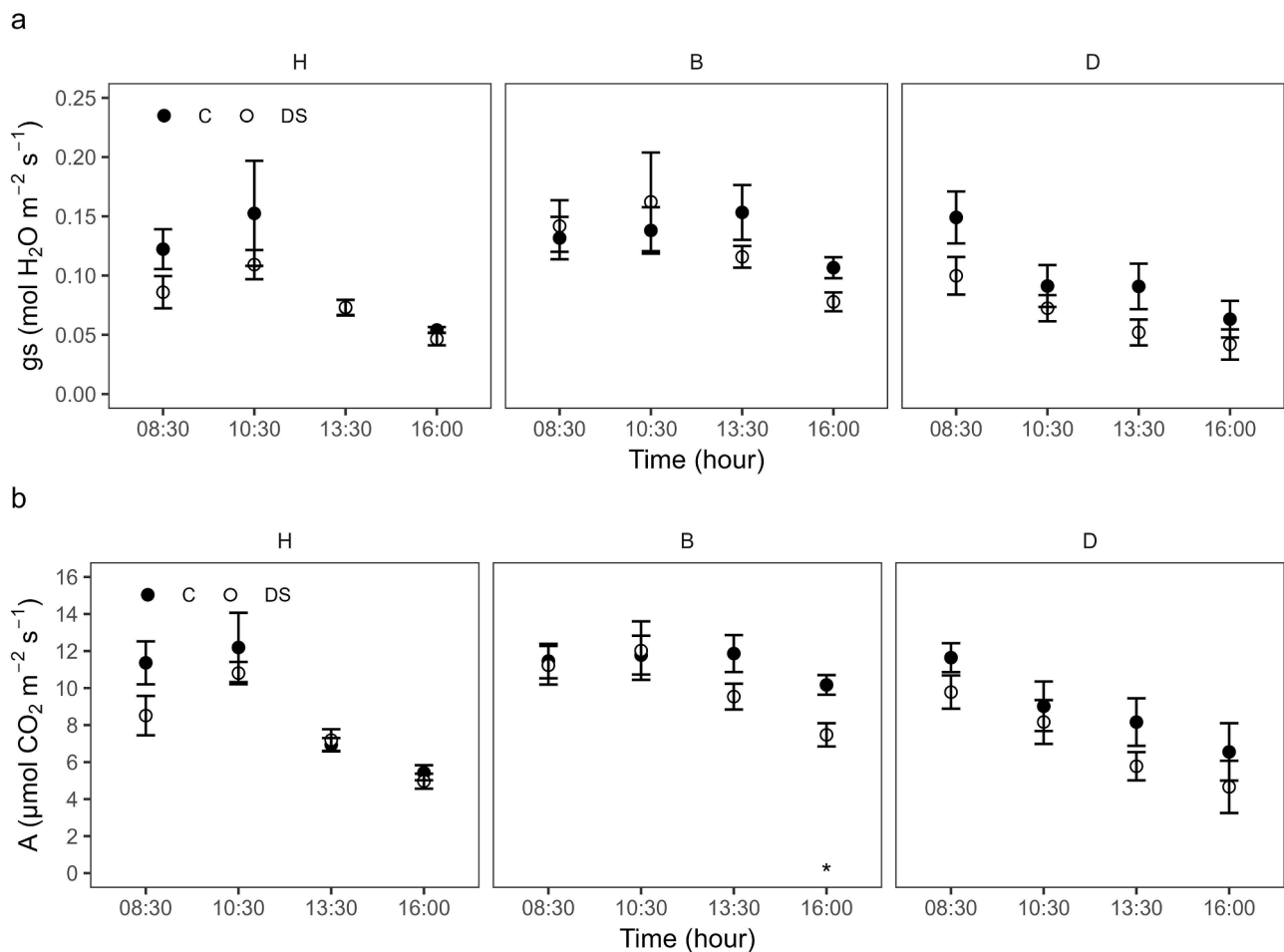


Fig. 6. Diurnal trends of (a) stomatal conductance (gs) and (b) photosynthetic rate (A) in the three kiwifruit rootstocks 'Hayward' (H), 'Bounty' (B), and 'D1' (D) when SWA was reduced by 35% (day three of experiment) (C = well-watered, DS = drought-stressed). Data shown are means $\pm$ standard error of the mean ($n = 4$). Asterisks indicate significant differences according to Student's *t*-test between C and DS within each time of measurement. Significance codes: "***" $p < 0.05$.

of ~ 0.05 – $0.08 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$ (Fig. 4a). At this time, drought-induced E and A were in the range of 1.6 – $2.4 \text{ mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ and 5.9 – $8.8 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, respectively, with reductions of 59% and 58% in Z/H, 39% and 28% in Z/D, and 26% and 17% in Z/B compared to C vines (Fig. 4b, c).

Variations in gs, E and A in C vines were in the range of 0.11 – $0.20 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$ (Fig. 4a), 2.3 – $4.0 \text{ mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ (Fig. 4b) and 10.0 – $14.0 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (Fig. 4c), respectively.

One day after re-watering, all grafting combinations previously exposed to drought stress maintained reduced leaf gas exchange activity compared to C vines, with a significant treatment effect. Z/D drought-stressed vines showed significantly lower values of gs ($\sim 0.08 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$, Fig. 5a) and E ($\sim 2 \text{ mmol H}_2\text{O m}^{-2} \text{s}^{-1}$, Fig. 5b) than C vines. Significantly lower levels of A were also maintained at this time, with a 45% reduction compared to C vines (Fig. 5c). Three days after re-watering, DS vines recovered their leaf gas exchange activity in Z/H and Z/D, whereas a significant difference was found in Z/B.

Diurnal trends of gs and A were measured in DS vines when SWA reached 65% FC and in C vines (Fig. 6). C vines of H and D showed higher values of gs (around $0.15 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$) in the middle and early morning, respectively. Then, the decrease in gs was steep in H until the afternoon (Fig. 6a). B maintained high values of gs even during the most critical hours (i.e., around 13:30 h), with a decrease in the afternoon (Fig. 6a). Variations in A followed those of gs (Fig. 6b). No significant differences were observed between C and DS vines during the day, except for A in DS vines of B in the afternoon, which was reduced by 26% compared to C vines (Fig. 6b).

C vines of Z/H and Z/D showed higher values of gs (from 0.14 to $0.16 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$) in the middle of the morning, then gs gradually decreased until the early afternoon. Z/B showed the highest value of gs in the early morning and maintained constant values until the early afternoon (Fig. 7a).

All vines exposed to drought (SWA = 63% FC) showed reduced gs (below $0.1 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$) from mid-morning and throughout the day compared to C vines. Lower drought-induced gs values were observed in Z/H and Z/D in the middle of the morning and in Z/B in the early afternoon (Fig. 7a). Variations in A followed those of gs, with reductions under drought in the early afternoon in Z/B (reduced by 58% compared to C vines) and Z/D (reduced by 34% compared to C vines) (Fig. 7b).

3.3. Leaf water use and carboxylation efficiency

ΦPSII in the light-adapted state, ETR and A/gs values were unaffected by a 35% reduction in SWA in any rootstock (Fig. 8a–c). Values of A/Ci decreased significantly due to drought in H, but remained unchanged in B and D. However, A/Ci in DS vines of H fully restored C values at the end of the recovery period (Fig. 8d).

The two-way ANOVA analysis revealed a significant influence of the treatment on ΦPSII , ETR, A/gs ($p < 0.001$), and A/Ci ($p < 0.01$) in the grafting combinations (Fig. 9). ΦPSII , ETR and A/Ci decreased significantly in Z/H when SWA was reduced by 37% (Fig. 9a, b, d). A/gs increased in all DS vines, with significant differences in Z/B and Z/D (Fig. 9c). However, all drought-induced responses in the investigated parameters fully recovered to C levels by the end of the recovery.

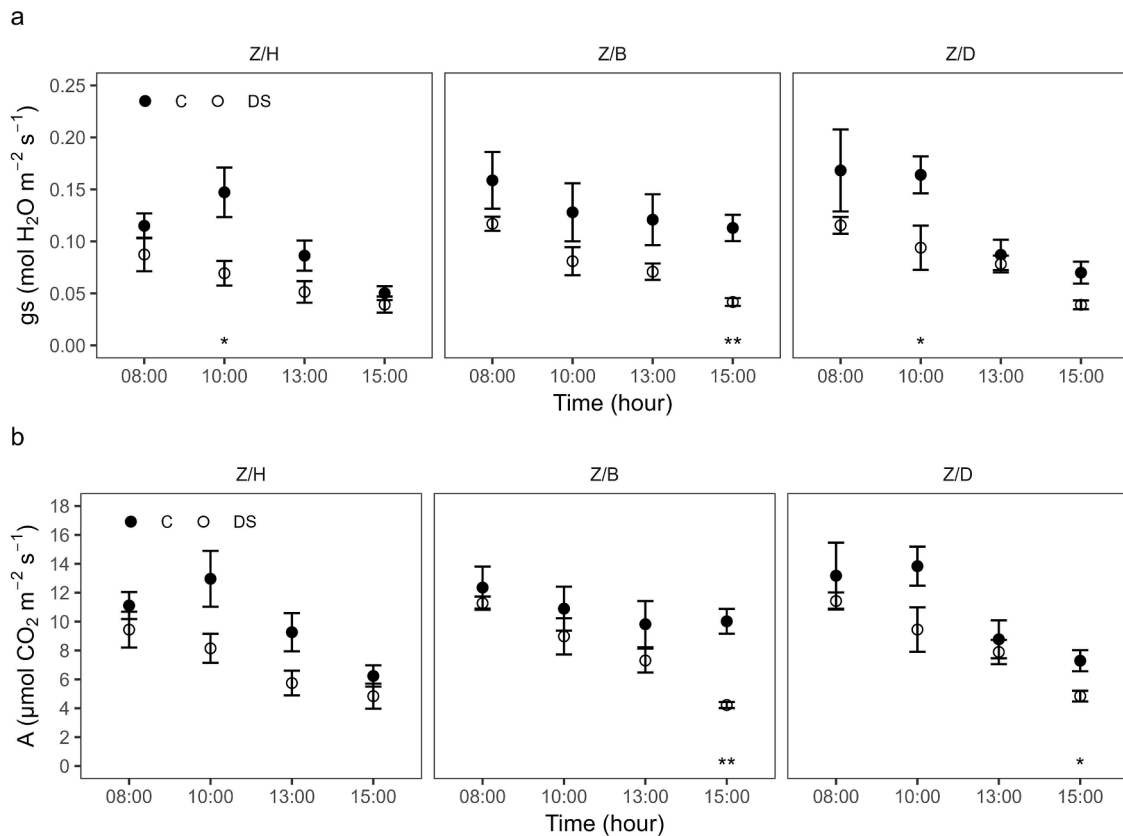


Fig. 7. Diurnal trends of (a) stomatal conductance (g_s) and (b) photosynthetic rate (A) in the three kiwifruit grafting combinations 'Zesy002/Hayward' (Z/H), 'Zesy002/Bounty' (Z/B), and 'Zesy002/D1' (Z/D) when SWA was reduced by 37% (day three of experiment) (C = well-watered, DS = drought-stressed). Data shown are the means $\pm$ standard error of the mean ($n = 4$). Asterisks indicate significant differences according to Student's t -test between C and DS within each time of measurement. Significance codes: "*" $p < 0.05$, "**" $p < 0.01$.

3.4. RGB-imaging

The phenotypic response of different kiwifruit genotypes to drought was investigated through the analysis of morphometric and colorimetric traits (i.e., psa , sol and hue).

During the drought, psa and hue decreased in D until the SWA reached 65% FC. However, these values did not differ significantly from those of C vines (Fig. 10a, c). Values of sol did not change significantly between C and DS vines throughout the experiment in any of the rootstocks (Fig. 10b).

Significant relative decreases in psa were observed in Z/H and Z/D as SWA approached 63% FC. Soon after re-watering, the psa of the drought-exposed Z/H and Z/D vines increased significantly compared to the C vines (Fig. 11a). Values of sol did not change significantly between C and DS vines throughout the experiment in any of the grafting combinations (Fig. 11b). During the drought, the hue decreased in the DS vines, but not significantly compared to the C vines (Fig. 11c).

3.5. Principal component analysis

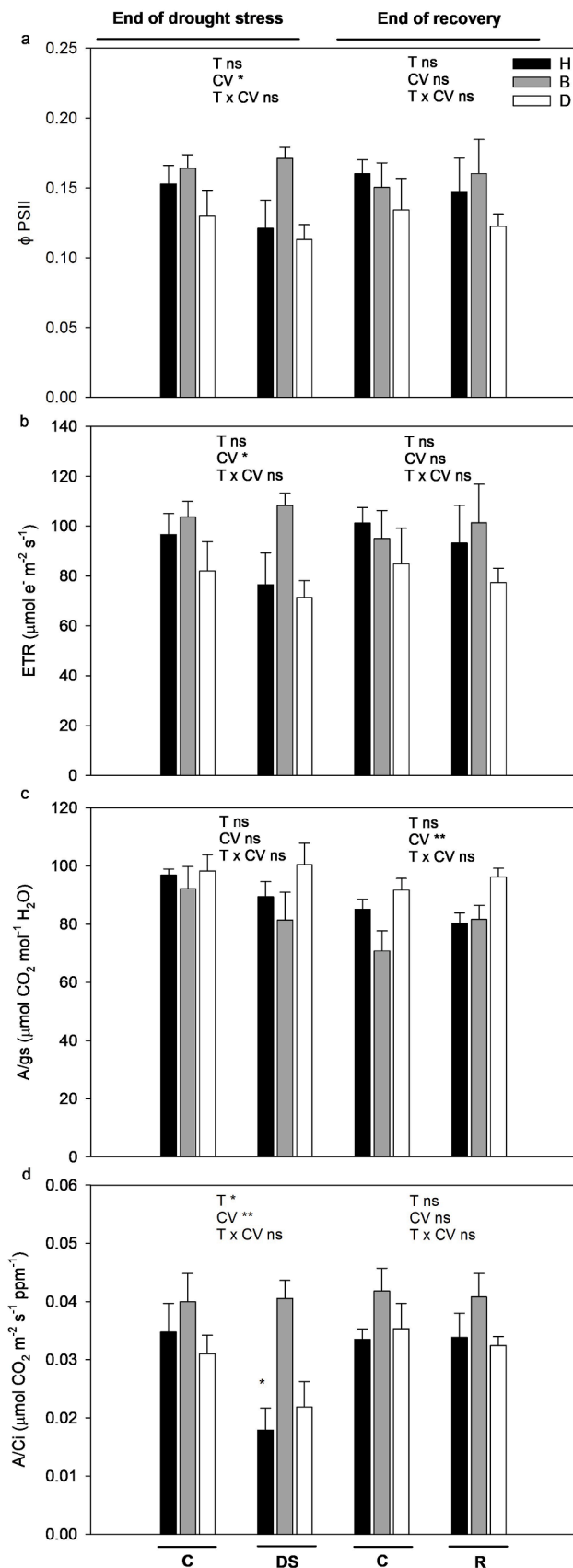
Principal component analysis (PCA) was performed to evaluate the contribution of the physiological and phenotypic variables to the variation between groups at the maximum level of drought stress achieved. The first two principal components (Dim1, Dim2) explained approximately 81.4% and 81.2% of the total variance in rootstocks (Fig. 12a) and grafting combinations (Fig. 12b), respectively. At the maximum stress, the B rootstock did not show a separation by water treatment, whereas H and D showed a separation between C and DS vines along Dim1. In addition, on the x-axis (i.e., Dim1), the rootstocks tended to separate from each other (despite the water treatment applied). Dim1 accounted for 70.7% of the variation and was mainly driven by g_s and A ,

followed by Tleaf and phenotypic variables. Dim2 accounted for 10.7% of the variation and was mainly explained by hue and psa , followed by the physiological parameters (Fig. 12a). B rootstock showed increased A and g_s among the physiological variables, and reduced psa among the phenotypic variables compared to H and D rootstocks.

The water treatments tended to separate on the x-axis of the biplot for all the grafting combinations analyzed at the maximum drought stress. Dim1 accounted for 56.1% of the variation and was driven by g_s and A , followed by Tleaf and phenotypic variables. The left-hand side of the biplot was associated with C vines, with an increase in g_s and A . Dim2 explained 25.1% of the variation and was driven by psa and sol , followed by hue (Fig. 12b).

4. Discussion

Leaf gas exchange measurements on kiwifruit rootstocks and scion/rootstock combinations under progressive drought and re-watering, coupled with phenotypic analysis, revealed differential responses among the studied genotypes: i) drought stress imposed by progressively reducing SWA had no effect on the morpho-physiological responses of the B rootstock, and only minor effects on the H and D rootstocks, with complete recovery after re-watering; ii) all scion/rootstock combinations were affected by drought to different degrees. Reduced values of g_s and A were observed in all combinations under drought (−66% and −58% in Z/H, −45% and −28% in Z/D and −32% and −17% in Z/B) compared to controls. Z/H was the most sensitive to drought, as indicated by significant decreases in A and psa at the end of the drought, followed by Z/D. Z/B showed a reduction in g_s under drought conditions, but no impairments to photosynthetic and phenotypic traits were observed, suggesting lower sensitivity to drought; iii) two way-ANOVA and PCA analysis revealed the great genetic diversity of the rootstocks



(caption on next column)

Fig. 8. Effect of drought stress and re-watering on (a) photosystem II operating efficiency (Φ_{PSII}) in the light-adapted state, (b) electron transport rate (ETR), (c) intrinsic water use efficiency (A/gs), and (d) instantaneous carboxylation efficiency (A/Ci) measured for the three kiwifruit rootstocks 'Hayward' (H), 'Bounty' (B), and 'D1' (D). Vines were subjected to two irrigation treatments: well-watered (C) or progressive drought (DS), followed by five days of re-watering (R). The physiological data correspond to the end of the drought stress (SWA = 65% FC) and the end of the recovery. Data shown are means $\pm$ standard error of the mean ($n = 4$). Two-way ANOVA results are shown for each parameter and stress/recovery phase. Asterisks indicate significant differences between C and DS vines within each rootstock according to one-way ANOVA. Significance codes: "*" $p < 0.05$, "**" $p < 0.01$, "ns" not significant. T = treatment, CV = cultivar.

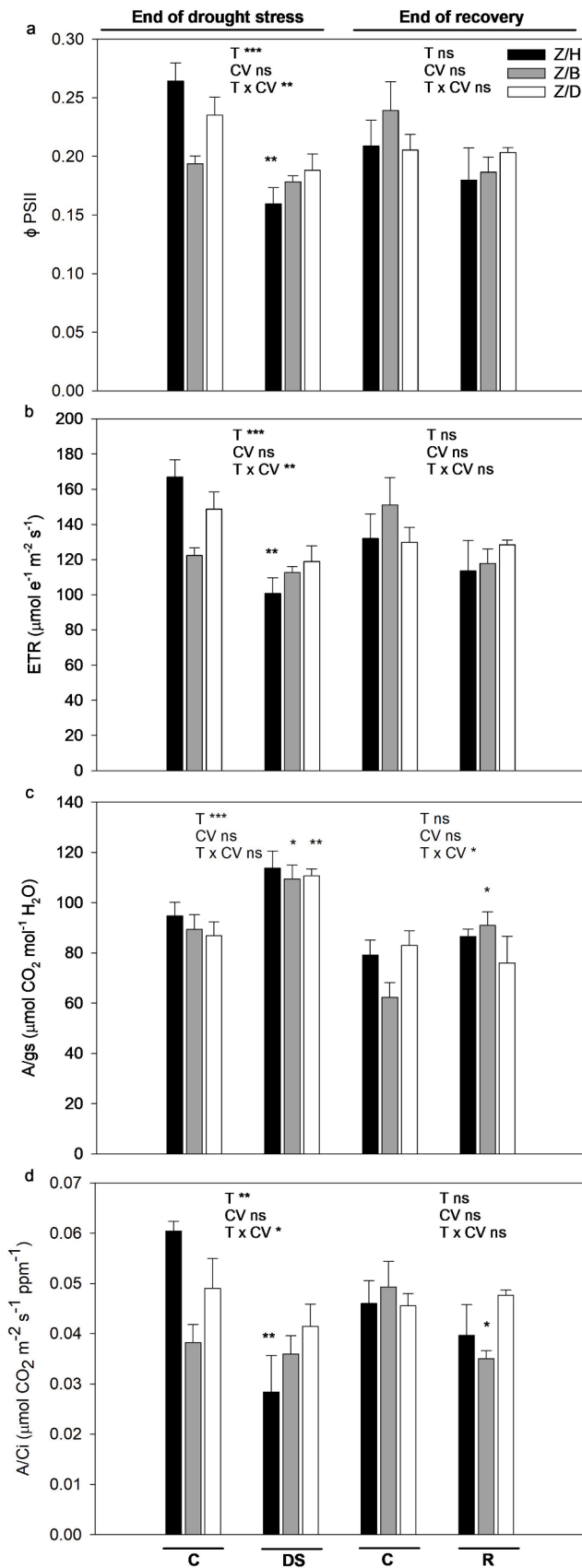
and the poor influence of the imposed drought stress. Instead, scion/rootstock combinations were more influenced by the water treatments, as indicated by changes in physiological and phenotypic variables, but they were able to fully recover after re-watering.

The progressive reduction in pot water availability during the experiment resulted in a mild drought compared to another study which examined the response of different kiwifruit genotypes to moderate (40–45% FC) and severe (25–30% FC) drought conditions (Bao et al., 2024). In line with the aims of this study, the imposed stress was not long-lasting and severe enough to cause detrimental effects on the physiological and phenotypic parameters of the vines. This was done in order to simulate short-term or intermittent drought conditions that can easily occur in kiwifruit orchards due to climate change (e.g., atmospheric conditions during summer combined with water shortage).

According to the two-way ANOVA analysis, the water treatment had no or only minor effects on the investigated parameters of rootstocks, with the cultivar instead having a prevailing effect. On the contrary, a significant and prevailing water treatment effect was found at the end of the drought and at the start of the recovery period in the scion/rootstock combinations. The results showed that gs was sensitive to SWA and decreased under drought in all scion/rootstock combinations. Drought-induced changes in A were consistent with those in gs, in particular for Z/H as SWA was reduced to the minimum level reached (i. e., SWA = 63% FC). Previous studies have reported a significant and immediate decrease in gs after the imposition of drought in kiwifruit (Gucci et al., 1996; Wang et al., 2011; Bao et al., 2024). On a diurnal basis, both A and gs of DS vines were higher in the early morning and decreased during the day, as previously reported for pot-grown kiwifruit (Gucci et al., 1996). In particular, gs responded more rapidly to reduced irrigation than A, which began to be limited in all scion/rootstock combinations when gs dropped below $0.10 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$, as found by Mills et al. (2009).

Concurrent with the consistent decrease in A (at SWA = 63% FC), ETR and Φ_{PSII} were reduced in Z/H followed by Z/D, whereas no differences were observed in Z/B under drought. These results suggest that the photosynthetic metabolism of all scion/rootstock combinations was progressively down-regulated with increasing drought stress, but based on a different stage of inhibition of photosynthesis (Flexas et al., 2004). In particular, Z/B showed a slower decrease in gs and A under drought, without inducing variations in ETR and Φ_{PSII} . Conversely, Z/H reached a successive stage where ETR and Φ_{PSII} were significantly affected by drought imposition at the end of the experiment, suggesting the involvement of metabolic limitations. In addition to stomatal limitation (reduced gs), reduced ETR, Φ_{PSII} and A/Ci are important limiting factors in A, which were observed for Z/H among the combinations studied.

However, the maintenance of A values under mild drought resulted in an increased A/gs ratio in all scion/rootstock combinations, which was significant in Z/B and Z/D compared to C vines, suggesting the adoption of a water-saving strategy and that stomatal closure was the dominant limitation to A (Montanaro et al., 2007; Sapeta et al., 2013). The increase in A/gs is a direct consequence of the reduction in gs before A, which was previously observed and recognized as a typical response



(caption on next column)

Fig. 9. Effect of drought stress and re-watering on (a) photosystem II operating efficiency (Φ_{PSII}) in the light-adapted state, (b) electron transport rate (ETR), (c) intrinsic water use efficiency (A/gs), and (d) instantaneous carboxylation efficiency (A/Ci) measured for the three kiwifruit grafting combinations 'Zesy002/Hayward' (Z/H), 'Zesy002/Bounty' (Z/B), and 'Zesy002/D1' (Z/D). Vines were subjected to two irrigation treatments: well-watered (C) or progressive drought (DS), followed by five days of re-watering (R). Physiological data correspond to the end of the drought stress (SWA = 63% FC) and the end of the recovery. Data shown are means $\pm$ standard error of the mean ($n = 4$). Two-way ANOVA results are shown for each parameter and stress/recovery phase. Asterisks indicate significant differences between C and DS vines within each scion-rootstock combination according to one-way ANOVA. Significance codes: "***" $p < 0.05$, "**" $p < 0.01$, "*" $p < 0.001$, "ns" not significant. T = treatment, CV = cultivar.

of plants to mild drought (Flexas et al., 2010; Sapeta et al., 2013; Talbi et al., 2020).

Under mild to moderate drought stress, the decrease in A is mainly due to a decrease in gs, and the recovery of gas exchange parameters after re-watering is generally quite rapid, with a tendency to return to initial levels after rehydration (Flexas et al., 2004). However, the level of recovery varies with the degree of previous drought stress reached (Gucci et al., 1996; Miyashita et al., 2005). In all scion/rootstock combinations, gs and A recovered after re-watering, restoring C values one and three days after re-watering in Z/H and Z/D, respectively.

Reduced SWA induced physiological changes in kiwifruit even in absence of significant morphological alterations, suggesting that an initial drought response primarily affects physiological traits, with morphometric changes occurring at later stages. Drought decreased psa in both Z/H and Z/D at the end of the experiment. However, psa values returned to control level following re-watering, suggesting that both morphological and physiological responses to mild drought may be reversible. The advantages and potential of HTPP to discriminate between water treatments and its applicability to characterize plant drought responses are usually related to cereal or vegetable crops. Previous studies have reported reduced above-ground biomass, and therefore reduced psa, along with changes in color traits under drought conditions. These findings underscore the ability of HTPP to non-destructively monitor the temporal dynamics of plant responses to varying water availability (Kim et al., 2020; Tolley et al., 2020; Genangeli et al., 2023).

Based on changes in leaf gas exchange activity, morphometric and colorimetric parameters, the *A. macrosperma* genotype was more resilient to drought stress than the other kiwifruit species studied (*A. chinensis* var. *deliciosa*). Root system growth and hydraulic conductivity can be influenced by the rootstock and are important factors in improving water uptake and transport (Clearwater et al., 2004; Gambetta et al., 2012; Serra et al., 2014). It can be hypothesized that the increased tolerance to drought of *A. macrosperma* is likely linked to a higher root-to-shoot ratio, and that increased root development and surface area, together with anatomical features that enhance conductivity, improve overall water uptake and transport to the shoots. However, the root-to-shoot ratio and hydraulic features of this rootstock remain to be investigated in future studies. Alsina et al. (2011) associated increased root growth and root system conductance with drought tolerance in grapevines. A previous study comparing the physiological and growth responses of five *Actinidia* species to drought stress under tissue culture conditions showed that *A. macrosperma* is indeed more resilient than *A. chinensis* var. *deliciosa* and represents promising kiwifruit breeding material (Zhong et al., 2018). However, the drought tolerance of this species should be further investigated under field conditions. This result is not consistent with Bao et al. (2024), who reported that *A. macrosperma*, together with 'Hayward', is among the most sensitive genotypes to drought and could hardly recover after re-watering.

A comprehensive approach, including both phenotypic and

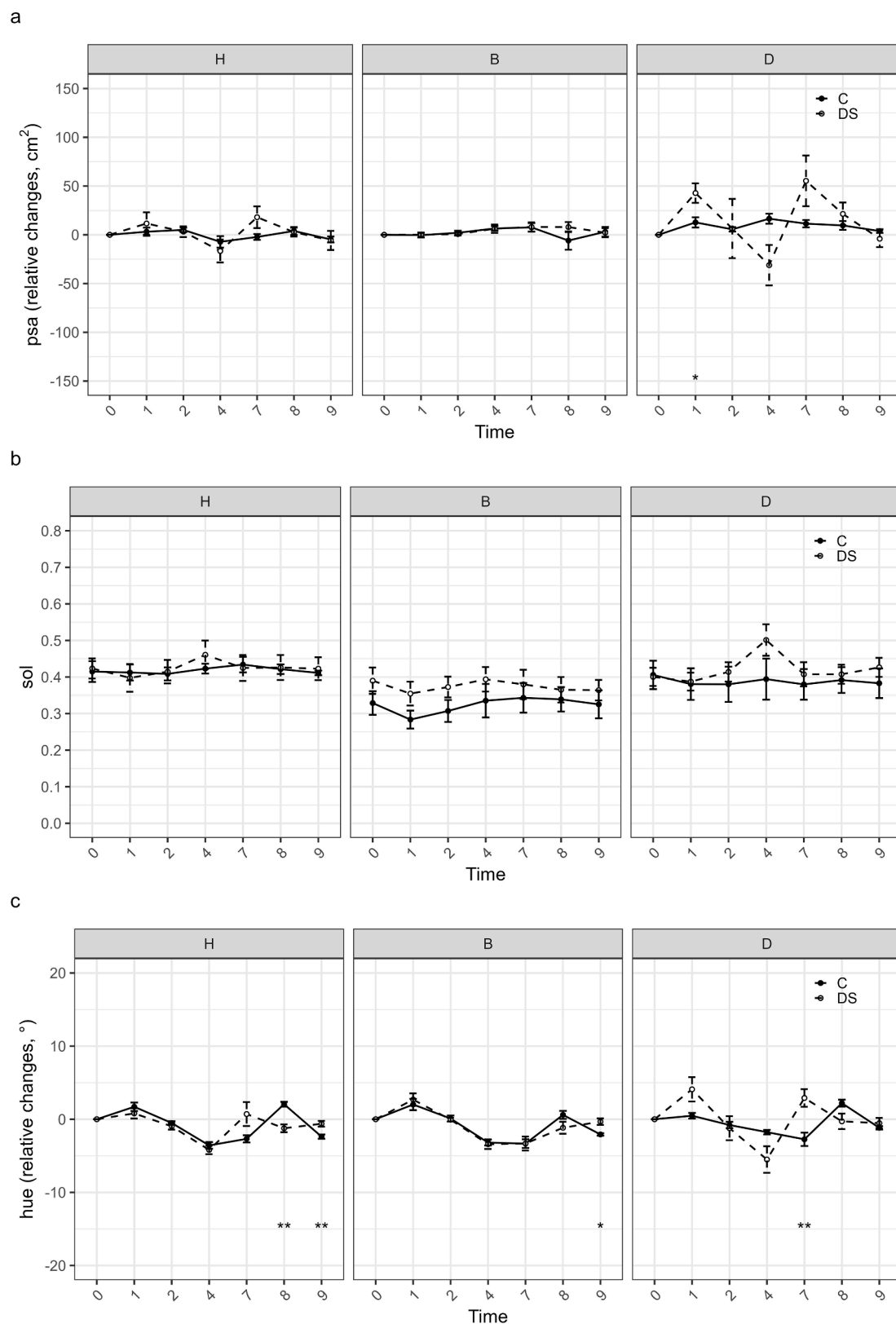


Fig. 10. Effect of drought stress and re-watering on (a) projected shoot area (psa), (b) solidity (sol), and (c) plant color (hue) measured for the three kiwifruit rootstocks 'Hayward' (H), 'Bounty' (B), and 'D1' (D). Vines were subjected to two irrigation treatments: well-watered (C) or progressive drought (DS), followed by five days of re-watering. Re-watering started at day of experiment five. Asterisks indicate significant differences between C and DS vines within each day of measurement according to Student's *t*-test. Data shown are means $\pm$ standard error of the mean ($n=5$). Note that psa and hue are expressed as relative changes with respect to the previous measurement.

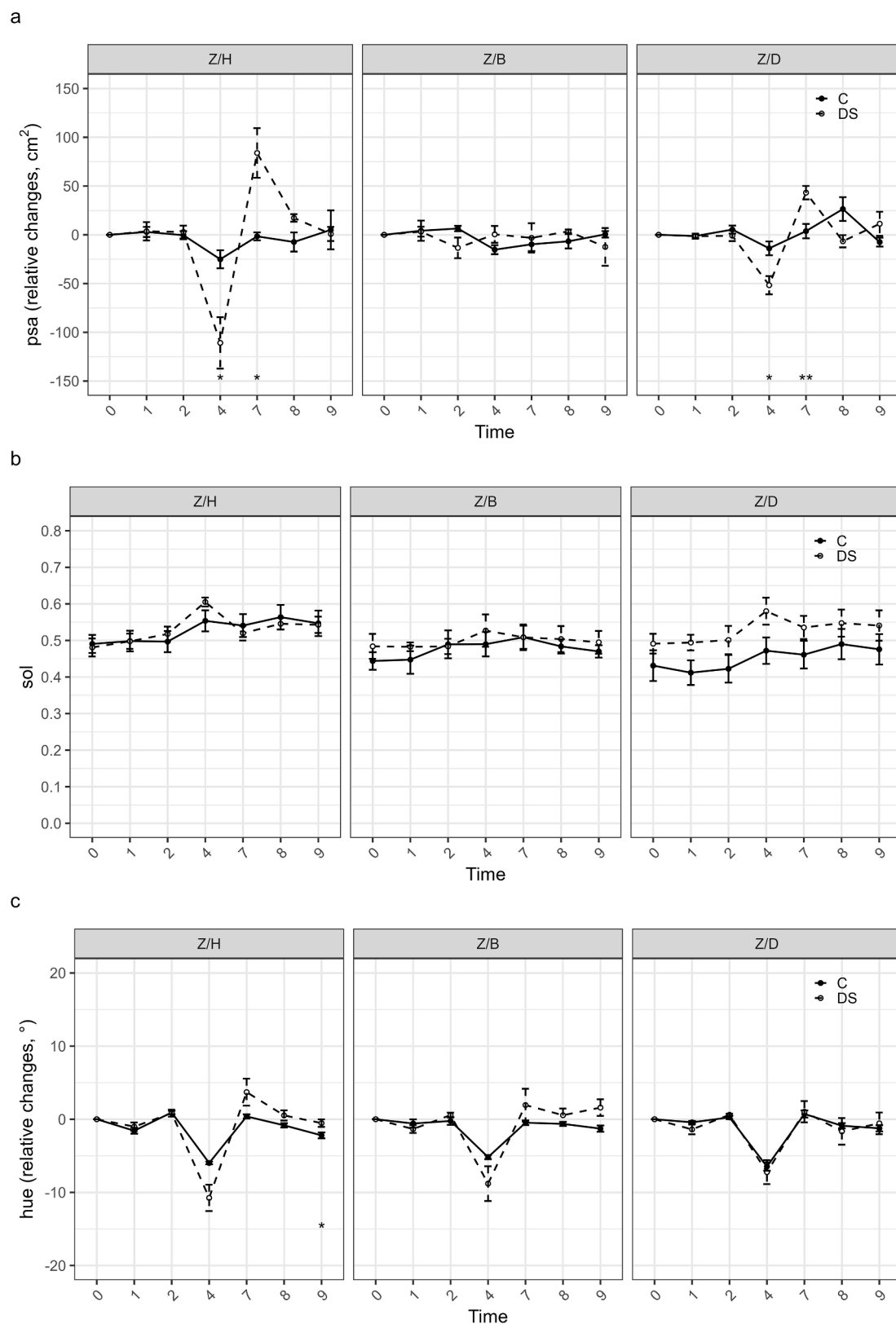


Fig. 11. Effect of drought stress and re-watering on (a) projected shoot area (psa), (b) solidity (sol), and (c) plant color (hue) measured for the three kiwifruit grafting combinations 'Zesy002/Hayward' (Z/H), 'Zesy002/Bounty' (Z/B), and 'Zesy002/D1' (Z/D). Vines were subjected to two irrigation treatments: well-watered (C) or progressive drought (DS), followed by five days of re-watering. Re-watering started at day of experiment five. Asterisks indicate significant differences between C and DS vines within each day of measurement according to Student's *t*-test. Data shown are means $\pm$ standard error of the mean ($n=5$). Note that psa and hue are expressed as relative changes with respect to the previous measurement.

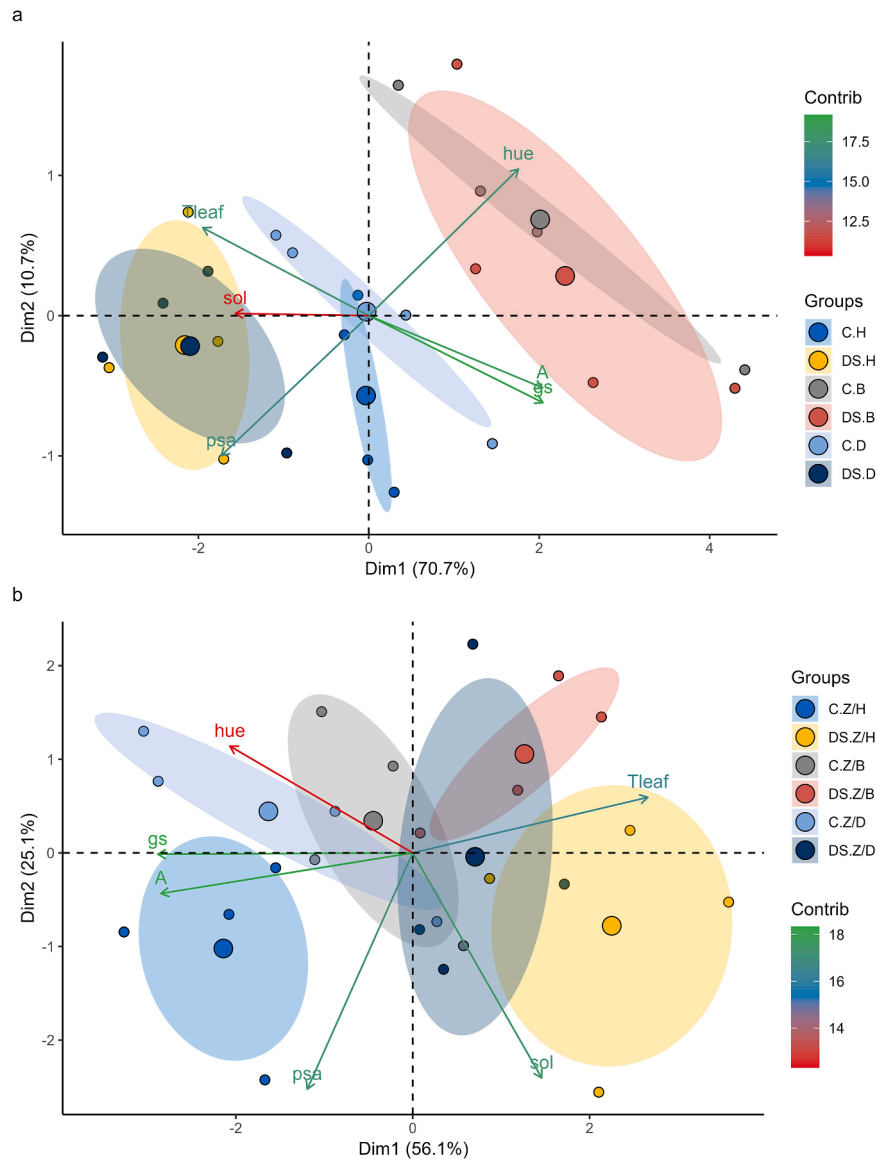


Fig. 12. Principal component analysis (PCA) of individuals based on six main physiological (gs = stomatal conductance, A = photosynthetic rate and Tleaf = leaf temperature) and phenotypic (psa = projected shoot area, sol = solidity and hue = plant color) parameters in three kiwifruit (a) rootstocks 'Hayward' (H), 'Bounty' (B), and 'D1' (D) and (b) grafting combinations 'Zesy002/Hayward' (Z/H), 'Zesy002/Bounty' (Z/B), and 'Zesy002/D1' (Z/D), under well-watered (C) and maximum drought (DS) conditions (SWA = 65% FC in rootstocks and SWA = 63% FC in grafting combinations). The proportion of the variation of the first two PCs (Dim1 and Dim2) is indicated on the axis. The direction of the arrows shows the correlations of the variables with the given PCs, while the color indicates their contribution to the PCs (gradient color). Dim = dimension, Contrib = contribution.

physiological components, was used in the present study and should be established for the accurate assessment of abiotic stress sensitivity in fruit tree crops. On the basis of six physiological (A, gs and Tleaf) and phenotypic (psa, sol and hue) indicators, all scion/rootstock combinations tended to differentiate between C and DS vines. The cultivar grafted on 'Hayward' rootstock showed the highest sensitivity to drought stress. The results of the PCA analysis showed that the most important variables to explain a PC axis included both physiological and phenotypic traits, reinforcing the role of HTPP in understanding the behavior of different genotypes under water deficit.

At the field level, maintaining balanced soil moisture levels through precision irrigation is crucial due to kiwifruit's high sensitivity to water deficit and excess (Dichio et al., 2025). Additionally, promoting the development of a larger root system and a higher root-to-shoot ratio improves vine water uptake and transport to the leaves. The Hayward rootstock, the most widely used in the world, performs optimally in the field when these conditions are met. However, the Hayward root system may suffer in clayey and poorly drained soils. In such conditions, other

rootstocks such as Bounty, which is more tolerant to asphyxiating soil conditions, can maintain high root development and thus improve vine water uptake. These genotype-related traits may also help mitigate the effects of drought, enabling Bounty to develop a more resilient orchard system. For this reason, this rootstock is being used in most of the newly planted Italian kiwifruit orchards.

Although the results of this study suggest that Bounty may be a promising rootstock for areas with less suitable conditions for kiwifruit cultivation and for dealing with temporary water stress, its long-term performance in real field conditions remains to be tested before its wide adoption is justified.

Finally, accurate irrigation and vineyard management should be supported by breeding programs to address the current climate challenges. Further efforts should be made to identify rootstocks with traits that improve water use efficiency and increase vine tolerance to temporary droughts, as well as to other abiotic stresses likely to occur as a result of climate change.

5. Conclusions

Heat waves and droughts are predicted to become more intense and frequent in many regions in the coming years due to climate change, with severe impacts on the Mediterranean basin.

This study revealed the potential of a combined physiological and phenotypic approach to discriminate between the responses of different kiwifruit rootstocks and scion/rootstock combinations to drought stress. The three rootstocks investigated showed no significant morpho-physiological changes during mild drought. However, at the end of the drought, H and D rootstocks showed an initial impairment of physiological parameters, while B remained unaffected, suggesting its lower sensitivity to drought. As pot water availability was progressively reduced, the scion/rootstock combinations were affected by drought to varying degrees. A reduction in A occurred when SWA approached 63% FC due to reduced g_s (below $0.10 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$). All genotypes were able to cope with the imposed drought, as demonstrated by their capacity to recover gas exchange, photosynthetic and phenotypic parameters soon after re-watering. Z/B was identified as the least sensitive combination, while Z/H was recognized as the most sensitive to the imposed drought conditions.

The results revealed that H was the most sensitive to mild drought, influencing the behavior of the grafted vine. B is hypothesized to be a more resilient rootstock that can withstand temporary water stress caused by soil, climate and/or irrigation constraints in less suitable areas for kiwifruit cultivation. However, further investigation into the degree of cultivar-rootstock incompatibility and the different behavior of rootstocks under real field conditions is required before the results of this pot experiment can be scaled up to the orchard level.

Since abiotic stresses threaten crop production, investigating the functional response of currently used kiwifruit rootstocks to drought stress, as well as understanding scion/rootstock interactions in response to mild and intermittent drought, can support breeding and selection programs. In this regard, a combined physiological and phenotypic approach could effectively screen for more drought-tolerant kiwifruit genotypes.

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CRedit authorship contribution statement

Maria Calabritto: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Alba N. Mininni:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Conceptualization. **Angelo Petrozza:** Writing – review & editing, Resources, Methodology. **Stephan Summerer:** Writing – review & editing, Software, Methodology, Formal analysis. **Francesco Cellini:** Writing – review & editing, Resources, Methodology. **Roberto Di Biase:** Writing – review & editing, Methodology, Investigation. **Rocco Sarli:** Writing – review & editing, Methodology, Investigation. **Bartolomeo Dichio:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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