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# Physiological Traits Combination Shapes Common Strategies of Water and Carbon Use Regulation Across Fruit Tree Species

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**Received:** 30 September 2024 | **Revised:** 29 April 2025 | **Accepted:** 8 May 2025

**Handling Editor:** J. Flexas

**Funding:** This work was supported by the Spanish Ministry of Science, Innovation and Universities (MICINN) through the R&D Program (Grant RTI2018-098961-B-I00).

**Keywords:** carbon traits | *Citrus* | cultivated species | Huber value | hydraulic traits | leaf economics spectrum | *Prunus* | water deficit

## ABSTRACT

Crop plants, including fruit trees, are particularly vulnerable to water scarcity because past selection prioritized productivity over drought resistance, making it challenging to maintain productivity with minimal water use in the context of climate change. This study aims to determine which trait combination of 10 fruit tree species influences their water and carbon use, with the goal of understanding their adaptability to water scarcity. The results showed that water stress traits (turgor loss point, TLP; vulnerability index, VI), a carbon-related trait (specific leaf area; SLA), and a biomass allocation trait (Huber value;  $H_v$ ) define the major axis of variability and present the strongest correlations with other traits. Two distinct strategies emerged: the first, mainly around *Prunus* species, was characterized by high  $H_v$ , low SLA, more negative TLP, and low VI, indicating greater water-stress tolerance due to sapwood redundancy and reduced organ vulnerability. They also exhibited higher maximum photosynthetic rates, indicating greater assimilation rates. The second strategy, mainly including *Citrus* species, exhibited opposite traits and trends. These trait combinations were likely shaped by shared ancestry and environmental factors. Understanding these correlations can guide irrigation practices and the selection of resilient species, contributing to more robust agricultural systems in a changing climate scenario.

**JEL Classification:** Plant ecophysiology and climate

## 1 | Introduction

Defining meaningful plant strategies to respond to restricted resource conditions through approaches based on traits rather than on taxonomic characteristics (Violle et al. 2007) is increasingly used. This is especially the case in studies aiming to capture the vegetation responses to the drought increase projected

by climate change (Soudzilovskaia et al. 2013; Anderegg 2015; Torres-Ruiz et al. 2024; Henn et al. 2024).

One prominent framework is the leaf economics spectrum (LES), which links several correlated leaf traits related to construction costs, nutrient content, and rates of carbon fixation and tissue turnover (Wright et al. 2004). Additionally, a

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broader whole-plant economics spectrum has been proposed, further integrating various resource use strategies for water, carbon, and nutrients (Reich 2014). Indeed, an increasing number of studies are exploring how LES traits interact with more mechanistic traits with a clearer physiological basis, particularly those related to water use (Brodribb 2017). These hydraulic traits help to determine mainly the plant water use regulation, consequently shaping the plants' response to water deficit (Sack et al. 2016).

One hydraulic trait receiving intensive attention in recent years is Huber value ( $H_v$ ) (Gleason et al. 2012; Patiño et al. 2012; Martin-StPaul et al. 2013; Togashi et al. 2015; Mencuccini et al. 2019; Rosas et al. 2019; Hernandez-Santana et al. 2019, 2023), which represents the ratio of sapwood area to leaf area.  $H_v$  is a biomass allocation trait that influences water transport. It reflects the investment in xylem area compared with the potential carbon gains from leaves, providing information about biomass partitioning and photosynthetic area (Mencuccini et al. 2019). Despite its potential importance at the intersection of water transport and biomass allocation, the coordination of  $H_v$  with other key plant traits, both carbon- and water-related, remains poorly understood. Similarly, the relationships between LES and other hydraulic traits are inconclusive (Blonder et al. 2011, 2013; Sack et al. 2013; Li et al. 2015; Rosas et al. 2019), underscoring the need for further research to address these critical gaps, despite the growing interest in trait-based approaches in recent years.

While hydraulic traits have been extensively studied in recent years, most research has focused on wild species (Choat et al. 2012). Consequently, the significance of these traits and their interaction with carbon traits in cultivated species remains underexplored (Garrido and Vergara 2022; Hernandez-Santana et al. 2023). This knowledge gap is critical as we face the challenge of developing crops that can thrive and yield effectively under increasingly warmer and drier conditions, particularly given the growing global population, which exceeds 8 billion and poses significant challenges to agricultural systems. Cultivated species are particularly interesting because they are among the functional groups most vulnerable to water deficit (Bartlett et al., 2012; McCulloh et al. 2019), likely due to their selection for reproductive traits at the expense of physiological traits. Fruit trees, in particular, are susceptible to water deficits due to their prolonged life cycles and long productive periods compared with annual crops. Studying cultivated species can also offer novel insights into the drivers of trait correlations. Unlike natural stands, which are subject to similar selection pressures, some cultivated species can co-occur without naturally coexisting, meaning they may not share an evolutionary history. As a result, the relative importance of drivers such as functional coordination, non-coordinated evolution of traits driven by drought stress, and shared ancestry (Bartlett et al. 2016) may differ from those observed in natural ecosystems.

Within this context, our study aims to identify the key trait combinations that shape water and carbon use strategies in cultivated tree species, offering insights into their potential to respond to water scarcity scenarios. We hypothesize that: (i) by analyzing key trait correlations across fruit tree species, we would be able to identify shared strategies and their underlying drivers, which are likely to be more similar among species within the same genera; and (ii)  $H_v$  would play a central role in these strategies,

linking carbon and water use traits by indicating how biomass is partitioned between leaf area and sapwood area, ultimately influencing water loss and movement through the plant.

To explore these hypotheses, we studied 10 artificially co-occurring species, which provided a valuable opportunity to investigate trait correlations and offer an integrative view of carbon and water plant traits at the leaf and stem levels. The species were selected within two genera, each with multiple species, allowing us to evaluate the role of shared ancestry. The studied traits include  $H_v$ , structural carbon economics traits (specific leaf area—SLA, wood density—WD), physiological traits related to leaf gas exchange (maximum photosynthesis rate— $A_{N,max}$ , maximum stomatal conductance— $g_{s,max}$ ), leaf and xylem hydraulic efficiency (maximum leaf hydraulic conductance— $K_{leaf,max}$ , stem hydraulic conductivity— $K_s$ ), and traits indicative of water stress strategies (vulnerability index—VI, turgor loss point—TLP). This approach, extensively used in ecology but not in agronomic studies, will provide novel insights into trait correlations and their drivers, which could be valuable for developing distinct orchard management strategies based on specific plant strategies.

## 2 | Materials and Methods

### 2.1 | Field Site

The study was conducted in the Research Farm La Hampa-CSIC located in Seville (Spain, 37°17'N, −6°3'W) from May to October of 2020 and 2021. The study was conducted in 5/6-year-old trees of 10 species (almond, *Prunus dulcis*; apricot, *Prunus armeniaca*; peach, *Prunus persica*; plum, *Prunus domestica*; grapefruit, *Citrus × paradisi*; lemon, *Citrus limon*; orange, *Citrus sinensis*; olive, *Olea europaea*; grapevine, *Vitis vinifera*; pomegranate, *Punica granatum*), planted in 2018, in a 6 m × 4 m formation. Thus, there were two main genera: *Prunus* and *Citrus*, so we can evaluate the role of shared ancestry. The trees were distributed in two plots of 480 m<sup>2</sup> per species, with 20 trees per plot. Four central trees were used for most of the measurements. The soil in the Research Farm is a sandy loam Xerochrept (USDA 2010), with a depth of 0.9–2 m. The climate of the area is Mediterranean, with mild, rainy winters and hot, dry summers, with hardly any rain during the months of the study. Average annual potential evapotranspiration (ET<sub>o</sub>) and precipitation are 1176 and 470 mm, respectively. Trees were irrigated to replace their irrigation needs (IN) fully since spring 2018, when they were planted. IN was calculated as  $IN = ET_c - P_e$ , with  $ET_c$  being the maximum potential crop evapotranspiration calculated with the crop coefficient approach (Allen et al. 1998) and  $P_e$  the effective precipitation recorded in the orchard (Orgaz and Fereres 2001).  $ET_c$  for each species is reported in Table 1. The drip irrigation system installed consisted of a pipe along each row of trees with two drippers (4 L h<sup>−1</sup> each) 30 cm away from the tree's base. Fertilization was applied following a carefully designed irrigation schedule.

### 2.2 | Huber Value

To obtain the  $H_v$ , defined as the ratio between sapwood allocation relative to leaf area (cm<sup>2</sup> cm<sup>−2</sup>), we used 6–8 branches

**TABLE 1** | Crop evapotranspiration (ETc; mm) calculated for each species.

	Almond	Apricot	Peach	Plum	Olive	Pomegranate	Orange	Lemon	Grapefruit	Vine
2020										
April	3.99	0.18	1.35	1.66	1.02	1.54	0.54	0.52	0.33	5.10
May	57.02	2.78	20.65	25.33	11.60	22.44	5.92	6.49	3.69	84.25
June	78.08	3.14	23.30	28.59	13.10	27.75	7.50	8.13	4.68	110.93
July	92.73	3.61	26.79	32.87	15.06	31.91	9.57	10.29	5.97	127.55
August	53.32	1.68	12.45	15.27	9.69	20.53	6.66	4.81	4.15	76.20
September	53.32	1.68	12.45	15.27	9.69	20.53	6.66	4.81	4.15	76.20
October	15.74	0.69	5.14	6.31	4.37	7.42	3.13	1.99	1.95	24.22
2021										
May	106.85	8.73	37.01	32.57	24.35	24.50	6.63	13.00	9.18	85.48
June	139.77	9.41	39.90	35.11	26.25	28.95	8.02	15.58	11.11	107.51
July	170.65	11.13	47.16	41.50	31.03	34.22	10.51	20.25	14.56	127.08
August	95.57	5.04	21.34	18.78	19.45	21.44	7.13	9.23	9.87	73.95
September	95.57	5.04	21.34	18.78	19.45	21.44	7.13	9.23	9.87	73.95
October	32.86	2.42	10.28	9.04	10.21	9.03	3.90	4.44	5.40	27.39

Note: The irrigation period started in 2020 earlier (April 27) than in 2021 (May 3), but both years ended the same day (October 17).

for each species sampled in June and July 2020 and 2021, with diameters from 6.2 to 20 mm. No significant differences in the  $H_v$  were observed among the branches of the same species, collected on different dates. The branches were sampled from border trees, and the total leaf area and basal sapwood area were measured. The diameters were measured with a caliper, and the corresponding leaf area was measured with a portable leaf area meter (LI-3000C, Li-Cor).

### 2.3 | Maximum Stomatal Conductance and Net Photosynthesis Rate

Measurements of stomatal conductance and net photosynthesis rate were measured on different clear days from April to June of 2021 in the 4th and 5th leaf from the apex of current-year shoots from the outer part of the canopy facing south, at about 1.5 m above ground. We measured healthy, young, fully expanded leaves with similar age (two leaves per plant, in two plants in each of the two plots of each species) using three open gas-exchange systems Li-6400 (Li-Cor) equipped with a  $2 \times 3$  cm standard chamber under ambient light ( $740\text{--}1240 \mu\text{mol photon m}^{-2}\text{s}^{-1}$ ) and  $\text{CO}_2$  conditions ( $420\text{--}430 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$ ). Measurements were taken every 30–60 min from 8.30 to 15.00 to capture the maximum rates of net photosynthesis ( $A_{N,\text{max}}$ ;  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) and stomatal conductance ( $g_{\text{smax}}$ ;  $\text{mol m}^{-2}\text{s}^{-1}$ ).

### 2.4 | Specific Leaf Area

To determine specific leaf area (SLA), defined as the ratio of leaf area to leaf dry mass ( $\text{m}^2 \text{g}^{-1}$ ), one fully developed, current-year, and sun-exposed leaf from six border individuals per species

was sampled during July 2020. Leaf area was measured with a portable leaf area meter (LI-3000C, Li-Cor) and weighed with a precision balance (Metler Toledo) after being dried for at least 48 h in an oven at  $70^\circ\text{C}$ .

### 2.5 | Osmotic Potential

The leaves used to measure osmotic potential ( $\pi$ ; MPa) were sampled in the morning of different days of May and June 2021 from central trees. The petioles of these samples were immediately submerged in distilled water for 2 h to rehydrate them. Following rehydration, the samples were frozen and stored at  $-80^\circ\text{C}$ . A 7-mm-diameter disk was obtained from each sample (two leaves from four central trees per species) using a cork borer to measure osmotic potential. The disk was punctured 15–20 times with forceps to promote equilibration. Osmotic potential was then determined with a thermocouple psychrometer with six standard C-52 sample chambers (Wescor Inc.) connected to a datalogger (PSYPRO, Wescor Inc.). The measurements were carried out under constant temperature conditions. A waiting time of 2 h was determined for sample equilibrium.

### 2.6 | Turgor Loss Point

Between five and eight branches from central trees were collected from different almond, olive, grapevine, peach, lemon, and orange trees in May and June 2021 to determine pressure-volume (PV) curves. One leaf from each branch was left to rehydrate in complete darkness at  $2^\circ\text{C}\text{--}4^\circ\text{C}$  for about 20 h. PV curves were obtained by weighing the leaves immediately before

measuring their water potential ( $\Psi_{\text{leaf}}$ ) using a Scholander-type pressure chamber (PMS Instrument Company). After measuring the entire PV curve, the dry weight of the leaf was determined by placing the samples in a drying oven maintained at 65°C for 48 h. The PV curves for each leaf were generated by plotting relative water content (RWC) against the corresponding  $\Psi_{\text{leaf}}$ , where values were plotted for (100-RWC) against  $(-1/\Psi_{\text{leaf}})$ . Based on these plots, the turgor loss point (TLP; MPa) was determined by the inflection point of the relationship  $1/\Psi_{\text{leaf}}$  versus 100-relative water content.

For the remaining species, TLP was calculated using the method proposed by Bartlett, Scoffoni, Ardy, et al. (2012). In this method, TLP can be predicted using the  $\pi$  measured as described previously. They proposed using an empirical equation that is mechanistically based, calculated with several species with a wide range of leaf structures and drought tolerances. After validating this equation (Figure S1) with the species for which both TLP and osmotic potential were measured in water-stressed and well-watered plants, we calculated TLP for the remaining species (pomegranate, plum, apricot, and grapefruit).

## 2.7 | Maximum Leaf Hydraulic Conductance

To determine maximum leaf conductance ( $K_{\text{leafmax}}$ ) using the Dynamic Rehydration Method (Brodribb and Holbrook 2003; Blackman and Brodribb 2011), eight small branches were sampled between June and July 2021 from border individuals. The branches were recut under distilled water and allowed to rehydrate in a dark, cool environment for ~24 h.

One leaf from each branch was then connected to a flowmeter as described in Hernandez-Santana et al. (2016), and the flow rate was monitored as the leaves rehydrated. Initial flow rate ( $I$ ) was determined by fitting an exponential curve through the first 20 s of the rehydration flow data and extrapolating back to the initial point of leaf excision, considering the time (seconds) required to connect the leaf to the flowmeter (Blackman and Brodribb 2011). After connecting the leaves to the flowmeter, they were covered with moist paper and kept in darkness to prevent transpiration. Leaf area ( $A_{\text{leaf}}$ ) was measured using a portable leaf area meter (LI-3000C, Li-Cor).

Before determining flow rate, initial leaf water potential ( $\Psi_0$ ) was measured in a neighboring leaf. To account for temperature-dependent changes in water viscosity and their impact on  $K_{\text{leaf}}$ , standardized  $K_{\text{leaf}}$  values at 25°C were calculated (Scoffoni et al. 2012). Thus,  $K_{\text{leafmax}}$  was calculated as:

$$K_{\text{leafmax}} = \frac{-I}{\Psi_0 A_{\text{leaf}}} \quad (1)$$

## 2.8 | Theoretical Specific Hydraulic Conductivity

Six small branches per species of border trees, of ~5 cm diameter, were collected in June–July 2021 for anatomical characterization and fixed in FAA (5% formaldehyde, 2.5% acetic acid, 50% ethanol). Sections 15- $\mu\text{m}$ -thick were cut using a cryostat (Leica CM 1950), stained with a mix of safranin and astra

blue (Gärtner and Schweingruber 2013), and mounted in dibutylphthalate polystyrene xylene (DPX). Images were taken with a light microscope (OLYMPUS BX61), and the area of all the vessels present in a transect of the branch was measured using Fiji (Schindelin et al. 2012). The equivalent diameter of the circle was calculated from these areas, and the theoretical specific hydraulic conductivity ( $K_s$ ;  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ) was determined using the Hagen–Poiseuille equation (Tyree and Ewers 1991):

$$K_s = \left( \frac{\pi \rho}{128 \eta A} \right) \sum_{i=1}^n d_i^4 \quad (2)$$

where  $\rho$  and  $\eta$  are the density and viscosity of water at 20°C (998.2  $\text{kg m}^{-3}$  and  $1.002 \times 10^{-9} \text{MPa s}$ , respectively),  $A$  is the area of the transect, and  $d$  is the equivalent diameter of every vessel within the transect.

## 2.9 | Vulnerability Index

The same images obtained for Theoretical specific hydraulic conductivity were used to calculate the vulnerability index (VI). The vulnerability index ( $\text{mm}^{-2}$ ; Carlquist 1977) is an estimation of the ability of a plant to resist cavitation, and it is calculated as:

$$\text{VI} = \frac{\text{average vessel diameter}}{\text{vessel frequency}} \quad (3)$$

## 2.10 | Wood Density

The wood density (WD,  $\text{kg m}^{-3}$ ), defined as the ratio between the dry weight of a small branch and its volume calculated from the water displacement method, was measured in branches sampled from six border individuals per species in July 2020.

## 2.11 | Generalization of Data to Species Level

To evaluate the generalizability of our results obtained at a single location to the species level, we compared our dataset to global datasets and data from the literature for the same species.

We used the Choat et al. (2012) dataset to compare VI with P50 (water potential at which 50% of hydraulic conductivity is lost due to embolism). VI data from Choat et al. (2012) dataset was available for only 3 of the 10 species studied, and P50 was available for 8 species, and VI can be considered to have an equivalent functional meaning. We also explored the availability of other traits in the Choat et al. (2012) dataset, with the most represented traits (stomatal conductance and SLA) covering only 4 species—less than half of the species in our study.

To expand the comparison, we conducted a search in the TRY Plant Trait Database. Among the traits studied, SLA had the most data, covering 7 species. We complemented this dataset with a literature search in Web of Science (search terms: species name + “specific leaf area” or “SLA”) to increase SLA data coverage



and identify data for TLP and  $H_v$  with similar searches. While the search for  $H_v$  yielded insufficient data, we found at least one study reporting TLP for most species, with the exception of *Prunus domestica*.

Thus, we were able to compare our data on a single location with global datasets on three key traits: VI-P50 with data from Choat et al. (2012), SLA using data from TRY and Web of Science (WOS), and TLP data sourced exclusively from WOS literature searches. References and sample sizes of the different sources searched can be found in Table S1.

## 2.12 | Statistical Analyses

To analyze the relationships between different variables and datasets, we employed simple regression modeling, specifically using simple linear models. For comparing  $H_v$  among various species, we utilized linear models along with Tukey's post hoc comparison, based on average values per species. If normal or homoscedastic residuals were not achieved, we applied appropriate transformations to the variables, such as log transformation or square-root transformation.

Additionally, to analyze further the relationships between traits, two approaches were conducted: principal component analysis (PCA) and trait correlation network analysis. PCA was carried out using the "prcomp" function from the Stats package, and its results were visualized using the "fviz\_pca\_biplot" function from the factoextra package (Kassambara and Mundt 2020). The trait covariation network was utilized to depict how traits are correlated, with statistically significant correlations being visually represented using trait covariation networks via the IGRAPH package (Csárdi and Nepusz 2006; Csárdi et al. 2024). In these networks, traits were depicted as nodes, and their correlations were represented as edges connecting them. For each trait, two measures of network centrality were calculated: the degree ( $D$ ), which is the number of edges connected to a node, and the weighted degree ( $D_w$ ), which is the sum of all significant correlation coefficients associated with a node (refer to Table S2). To test for a significant difference between the two observed groups of species, we performed a multivariate analysis of variance (MANOVA) with all the measured traits as independent variables.

To conduct the phylogenetic analyses, we used cpDNA rbcL sequences downloaded from GenBank. These sequences were aligned using the msa R package (Bodenhofer et al. 2015). Subsequently, we constructed the phylogenetic tree with the phangorn R package (Schliep 2011), applying the maximum parsimony method. We also assessed the strength of the phylogenetic signal for the different traits by calculating Pagel's  $\lambda$  (Freckleton et al. 2002) using the phytools R package (Revell 2024). Finally, we used phylogenetic generalized least squares (pgls) to test whether the phylogenetic relationships had an effect on the correlations observed between traits with the pgls function in the caper R package.

All analyses were conducted using R software (version 4.2.2-4.4.0). Data of the studied species of the different traits obtained in the studied orchard are shown in Table S3.

## 3 | Results

### 3.1 | Traits Correlations

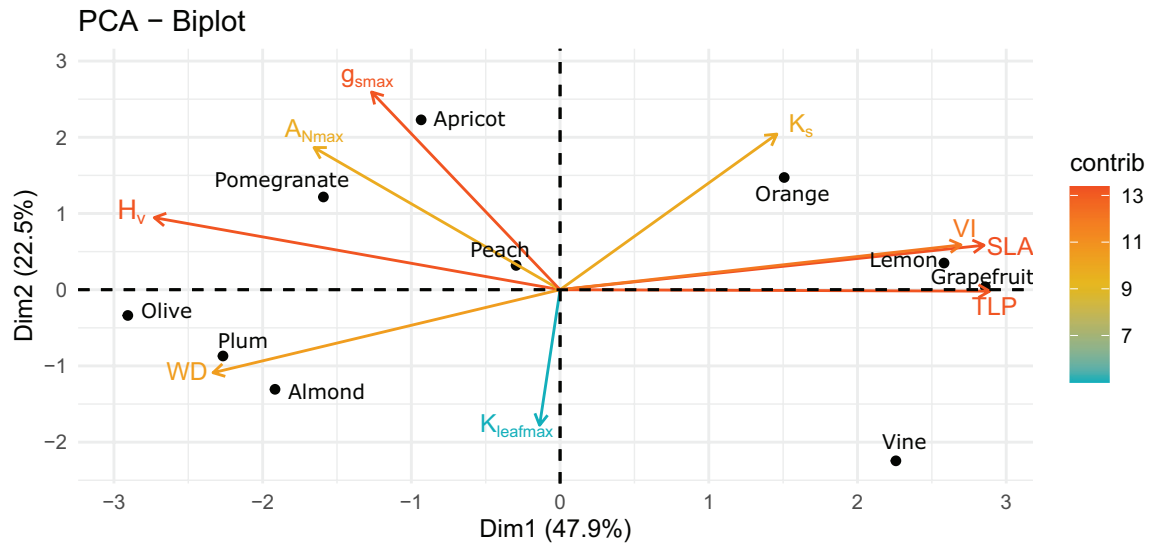
The PCA analysis (Figure 1) revealed two key dimensions explaining the variation among the studied fruit tree species. The first principal component (DIM1) accounted for 48% of the variance and was primarily driven by traits indicative of water stress resistance and carbon use. Notably, TLP, SLA, VI, and  $H_v$  showed the highest contributions to DIM1 (Table S4). The second most important dimension, PC2, explained 22.5% of the variance and focused mainly on maximum water transport capacity ( $K_s$ ,  $K_{leafmax}$ ) and maximum gas exchange ( $g_{smax}$ ,  $A_{N,max}$ ). Interestingly, the  $A_{N,max}$  contribution was also high in DIM1, reflecting its dual nature as a carbon-related trait and a key factor being regulated by stomatal conductance.

The network analysis (Figure 2; Table S2) provided valuable insights into the interconnectedness of traits across the studied fruit tree species. Notably,  $H_v$ , SLA, and TLP emerged as the traits with the strongest correlations with a wide range of other variables. On the contrary,  $g_{smax}$  and  $K_{leafmax}$  were not significantly correlated with any of the traits considered.

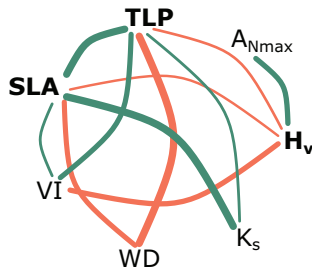
### 3.2 | Species Strategies

The PCA (Figure 1) further revealed distinct species groupings along DIM1. On one end of the axis, we observed *Prunus* species (almond, apricot, peach, and plum), along with pomegranate and olive. These species were characterized by high  $H_v$ , low SLA, more negative TLP, and low VI, indicating greater water-stress tolerance due to sapwood redundancy and reduced organ vulnerability. They also exhibited higher maximum photosynthetic rates, reflecting greater assimilation rates. Conversely, *Citrus* and vine species clustered on the opposite end, displaying traits and strategies associated with lower water-stress tolerance and reduced carbon assimilation rates. Accordingly, the MANOVA test revealed significant differences between these two groups ( $p < 0.0001$ ) visualized in the PCA of Figure 1. ETc calculated for each species varied according to the type of crop and its stage of growth (Table 1). The statistically significant relationships ( $p < 0.05$ , Figure S2) observed in the three comparisons between data obtained in our orchard and global datasets or WOS searches support the robustness and generalizability of our results at the species level, despite being based on data from a single population. Particularly strong was the correlation observed between P50 and VI for these eight species ( $R^2 = 0.88$ ,  $p < 0.001$ , Figure S2). Species with more negative P50 values exhibited lower VI, indicating lower vulnerability and *vice versa*.

Only two traits, SLA and VI, exhibited significant phylogenetic signals (Figure S3). The results for these two traits confirmed that species that are phylogenetically closer within the same genus presented similar values. Furthermore, the relationship between SLA and VI was the only one that differed slightly when comparing results from the general linear model ( $R^2 = 0.49$ ;  $p = 0.01$ ) to those from the phylogenetic generalized least squares (pgls) model ( $R^2 = 0.45$ ;  $p = 0.02$ ). However, this difference remained relatively small.



**FIGURE 1** | Principal component analysis representation with the traits visualized in a gradient of colours depending on their contribution to the main dimensions analysed. Species are also added to visualize their relative positions on the plot.  $H_v$ , Huber value;  $A_{N,max}$ , maximum photosynthesis rate;  $g_{smax}$ , maximum stomatal conductance;  $K_s$ , calculated specific hydraulic conductivity; VI, anatomically derived vulnerability index; SLA, specific leaf area; TLP, turgor loss point;  $K_{leafmax}$ , maximum hydraulic conductance; WD, wood density.



**FIGURE 2** | Trait correlation network across the studied species. Green and orange show positive and negative correlations, respectively. Correlation strength is represented by edge thickness. Only significant correlations are shown ( $p < 0.05$ ). Bold written traits show the highest centrality values in terms of weighted degree (the sum of all the significant coefficients of correlation of a node).  $H_v$  was log-transformed before analysis. TLP, turgor loss point;  $A_{N,max}$ , net photosynthesis;  $H_v$ , Huber value;  $K_s$ , specific conductivity; WD, wood density; VI, vulnerability index; SLA, specific leaf area.

### 3.3 | Huber Value Role

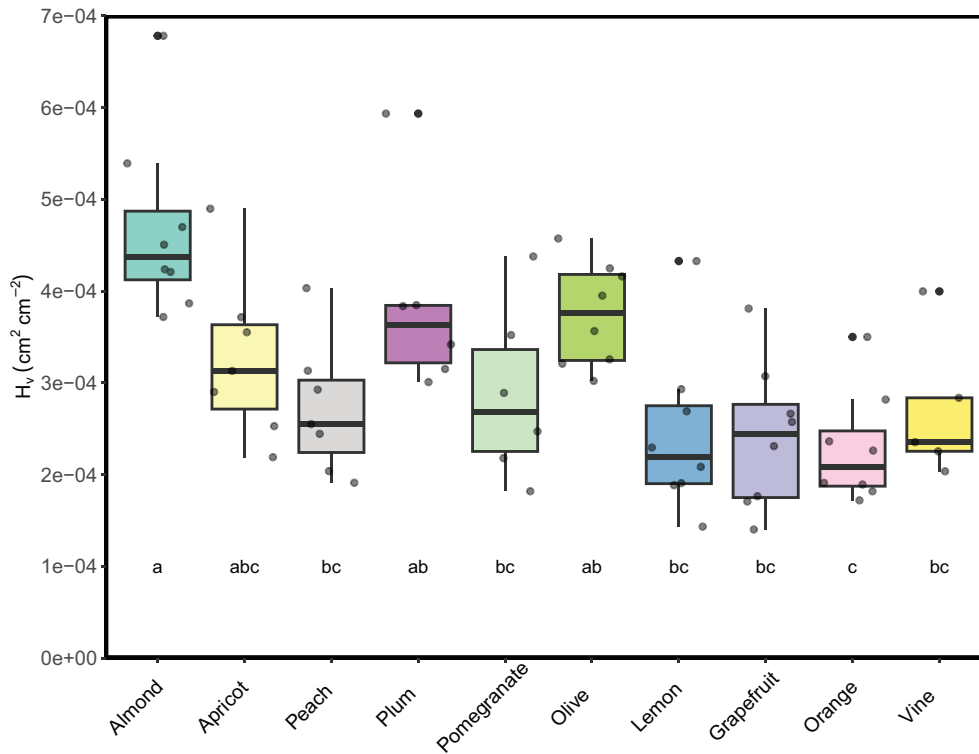
Our results revealed different patterns in  $H_v$  among the studied fruit tree species (Figure 3) following the groups identified in Figure 1. Species belonging to the *Prunus* genus (almond, apricot, peach, and plum), along with olive and pomegranate, displayed the highest  $H_v$  values. Notably, almond had the highest  $H_v$  overall, significantly exceeding most other species ( $p < 0.05$ ). In contrast, *Citrus* species, especially orange, exhibited the lowest  $H_v$  values, significantly lower than almond, olive, and plum ( $p < 0.05$ ).

The bivariate analyses (Figure 4) revealed several key traits significantly correlated with  $H_v$  ( $p < 0.05$ ): TLP, SLA, VI, and  $A_{N,max}$ .  $H_v$  exhibited significant negative correlations with traits

indicating water stress strategies: TLP and VI (Figure 4A,B) and carbon-related traits: SLA and  $A_{N,max}$  (Figure 4C,D), being positive in this last case. Species with the highest  $H_v$  (*Prunus*, olive and pomegranate) also exhibited the highest  $A_{N,max}$ . Conversely, these species had lower SLA, TLP, and VI. In contrast, species with the lowest  $H_v$  (*Citrus* and vine) showed the opposite pattern. The rest of the traits considered in this study presented non-significant correlations with  $H_v$  and are not shown.

## 4 | Discussion

Climate change necessitates innovative strategies to address the challenges posed by environmental factors that impact crop growth and productivity. In this context, we examined trait correlations across species, providing a framework to predict plant regulation of water and carbon use by a select subset of key traits. In cultivated species, it is crucial to balance the need for high productivity achieved through irrigation in water-scarce environments with the identification and prioritization of traits that enhance drought tolerance. This requires strategic management of the tradeoff between efficiency and resilience. Thus, our study offers an integrative approach by simultaneously investigating the relationships between traits shaping species' responses to water deficits (VI, TLP), traits defining water use ( $K_s$ ,  $K_{leafmax}$ ,  $g_{smax}$ ,  $H_v$ ), and carbon-related traits (SLA, WD,  $H_v$ ,  $A_{N,max}$ ) at the interspecific level in fruit tree species. We identified common strategies based on a few key traits, primarily TLP, VI, SLA, and  $H_v$ . Notably, these traits appear to be species-specific and conserved, despite the intensive selection crops have undergone to enhance productivity, often at the expense of stress tolerance (Cao et al. 2014). Additionally, we evaluated the drivers of the observed trait combinations, considering both shared ancestry and environmental influences (Bartlett et al. 2016).



**FIGURE 3** | Boxplot comparing Huber values ( $H_v$ ) among the studied species. Each point corresponds to a branch measured. Different letters indicate significant differences ( $p < 0.05$ ).

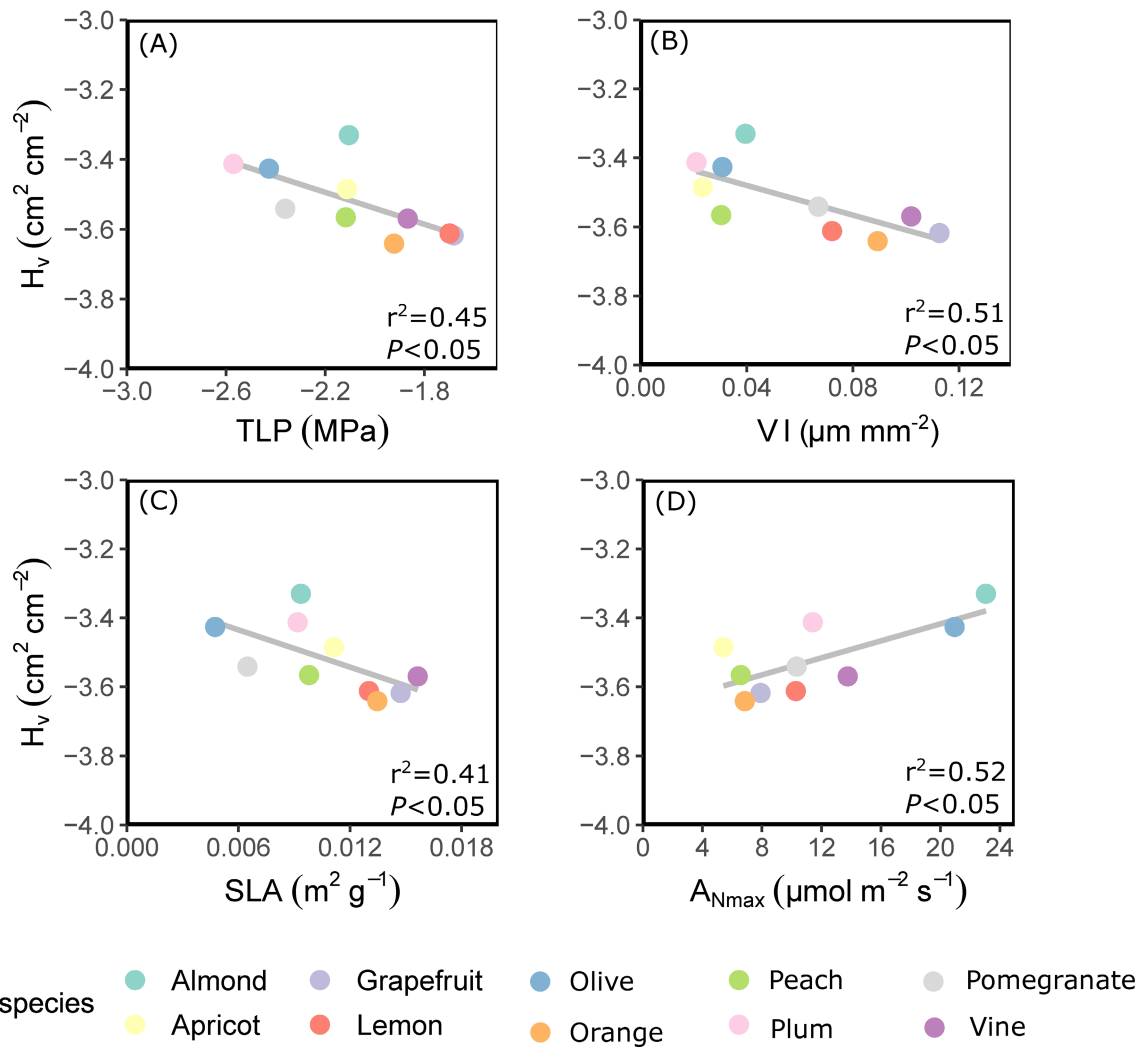
#### 4.1 | Trait Correlations Shape Common Strategies to Regulate Water and Carbon Use

Our results revealed two primary strategies of trait combinations, predominantly grouped within the two genera with multiple species: *Prunus* and *Citrus*. This likely indicates that shared ancestry plays a significant role in driving the observed trait combinations.

The first strategy identified around *Prunus* includes species with limited leaf area relative to their sapwood (high  $H_v$ ), small leaves relative to dry matter (low SLA), and less vulnerable leaves (more negative TLP) and stems (low VI) to water deficit. Moreover, these species with a high  $H_v$  exhibited higher  $A_{N,max}$ , which makes them more efficient at fixing carbon. The reverse is true for the second strategy related to *Citrus*. The first group would be more water-stress tolerant due to the redundancy in sapwood relative to leaf area and the less vulnerability of their organs and more efficient in terms of carbon use due to higher  $A_{N,max}$ .

However, species from different genera also closely align with the strategies mentioned above. Specifically, *Prunus* species exhibited a common strategy with olive and pomegranate, while *Citrus* species shared a strategy with vine, a liana species. Therefore, in addition to shared ancestry, the trait correlations found may have been influenced by environmental factors. These correlations can be explained mechanistically or more independently through functional coordination or concerted convergence. In functional coordination, several mechanisms potentially link the observed trait coordination to shape the trait correlations to optimize plant function in response to the

same biophysical constraints (Reich 2014; Bartlett et al. 2016). Concerted convergence explains trait correlations when several different characters each undergo convergence in response to similar selective pressure imposed by the same shared environmental conditions (Patterson and Givnish 2002). Indeed, Sanchez-Martinez et al. (2020), who considered many of the hydraulic traits studied here from a global dataset, such as P50 (represented as VI in our study),  $K_s$  and  $H_v$ , found that most of these traits evolved independently and were co-selected by the same environmental pressures. However, the evolutionary correlations between some of these traits, such as the relationship between  $K_s$  and  $H_v$ , showed in their study signs of deeper evolutionary integration due to functional, developmental, or genetic constraints, consistent with evolutionary modules. The trait showing the most numerous correlations and the strongest ones was TLP. Moreover, in this work, TLP is one of the traits considered to define the species' response to water deficit more clearly. Indeed, TLP is a classic measure of drought tolerance (Bartlett, Scoffoni, and Sack 2012), crucial for extending the range of leaf water potential at which the leaf maintains turgor and function (Sack et al. 2003). Lower TLP values allow plants to sustain essential physiological processes under lower soil water potentials, critical for survival during drought (Bartlett, Scoffoni, and Sack 2012), with global syntheses showing that TLP corresponds to water potential at stomatal closure (Martin-StPaul et al. 2013) or occurring just before TLP to maintain leaf turgor (Brodrigg et al. 2003). However, there have also been works questioning the relationships between TLP and stomatal closure or drought strategy (Farrell et al. 2017). In our case, we observed a positive relationship between TLP and SLA, which is increasingly found in different works (Xu et al. 2016; Zhu et al. 2018) and suggests a coordinated function, influenced by leaf density and



**FIGURE 4** | Bivariate plots of Huber value  $H_v$  against other plant traits, that is (A) turgor loss point (TLP), (B) vulnerability index (VI), (C) specific leaf area (SLA) and (D) maximum photosynthesis rate ( $A_{N\text{max}}$ ).  $H_v$  is base-10 log-transformed. Each point corresponds to a different species and it is the average of 4–8 data, depending on the variable. Statistics of the regressions are shown in the figures.

particularly leaf saturated water content. These two variables are components of SLA and, at the same time, they have been demonstrated to affect TLP (Nadal et al. 2023).

Moreover, species with more negative TLP values were also found to have lower VI, the other trait indicative of water stress resistance considered in this study, meaning smaller and more frequent xylem vessels, indicating greater resistance to cavitation (Markesteijn et al. 2011). Moreover, low SLA, or low acquisitive leaves, is inherently linked to smaller canopy areas and conservative leaves, given a specific investment in sapwood area, resulting in higher  $H_v$  (Mencuccini et al. 2019). This association between SLA and  $H_v$ , as well as with TLP and VI, highlights the connection between water transport traits and tradeoffs inherent in LES traits.

#### 4.2 | $H_v$ as a Key Trait in Fruit Tree Water and Carbon Relationships

Although  $H_v$  was not the trait showing the most numerous or strongest relationships, it is key to integrating the mechanisms

explaining the strategies found.  $H_v$  can be considered both a carbon allocation and hydraulic trait, indicative of water deficit tolerance. Notably, it was associated with traits shaping plant response to water deficit, encompassing physiological (TLP) and anatomical (VI) aspects, underscoring the integration of discrete traits in overall tree functioning. Additionally,  $H_v$  exhibited a shared axis of variation with several leaf traits critical for elucidating carbon dynamics, both structurally (SLA) and physiologically ( $A_{N\text{max}}$ ). Indeed, if enhanced photosynthesis is a main goal for most species to achieve good fitness and productivity among other traits (Martin and Isaac 2015), then this equilibrium of resource investment between supply and demand is well represented by  $H_v$ . The maintenance of turgor also plays a key role in keeping productivity through its impact on growth (Hilty et al. 2021). However,  $H_v$  is relevant as it is the only trait showing correlation with  $A_{N\text{max}}$ .

This study builds upon previous research by Hernandez-Santana et al. (2023), emphasizing the pivotal role of  $H_v$  in relating water utilization and carbon dynamics traits. Our findings reinforce existing evidence regarding the relationships between  $H_v$  and various other traits (Gleason et al. 2012; Patiño et al. 2012;



Martin-StPaul et al. 2013; Togashi et al. 2015; Mencuccini et al. 2019; Rosas et al. 2019). However, while prior studies primarily focused on wild species, our investigation focused on fruit tree species, a largely overlooked group in this context. Therefore,  $H_v$  emerges as a central factor integrating carbon dynamics and water-stress-related traits in species with agro-nomical significance, offering valuable insights for predicting a species' position along the whole-plant economics spectrum (Reich 2014).

### 4.3 | Practical Implications for Fruit Tree Management

The trait-based approach used in this study has the potential to be used in the management of cultivated fruit trees. However, applying ecological principles to domesticated fruit trees requires a nuanced interpretation of results, as these species differ fundamentally from natural ecosystems. While natural ecosystems are shaped by selection pressures that drive adaptation, domesticated species are primarily influenced by human intervention for food production.

The strategies described can contribute to assessing not only the optimal conditions under which each species can maximize its potential but also quantifying performance levels under various conditions and management practices. For instance, water stress indexes for deficit irrigation approaches can be more robustly implemented in the context of a broader strategy shaped by additional traits, such as the one proposed here. That can enhance the effectiveness of water stress index application in deficit irrigation approaches. A better understanding of each species' strategy through trait analysis provides a more robust framework for adjusting species-specific irrigation thresholds, which would otherwise rely greatly on experimental determination and thus be overly dependent on the specific experimental conditions, such as cultivar, phenological stage, tree age, or crop load. This could be the case of stem water potential, which is a commonly used threshold for applying deficit irrigation, though its values can vary depending on experimental conditions for each species. However, when comparing these values across the different species considered, they align with the strategies described in this work. For instance, the lowest thresholds reported for species in the first group around *Prunus* range between  $-1.8$  and  $-2.0$  MPa, as seen in peach (Girona et al. 2012), almond (García-Tejero et al. 2018), and olive (Dell'Amico et al. 2012). In contrast, species in the second group have reported thresholds between  $-1$  and  $-1.2$  MPa, as in grapefruit (Nicolás et al. 2018), lemon (García-Orellana et al. 2013), and grapevine (Myburgh and Howell 2022). While these values vary, they highlight the different strategies these two groups would have to cope with water deficit conditions, requiring distinct management approaches.

In addition to providing a conceptual framework for interpreting more dynamic variables used as water stress indices (e.g., stem water potential), a promising approach to bridging the gap between functional traits and irrigation management is the integration of these traits into mechanistic models. Trait-based mechanistic models are powerful tools for understanding and predicting plant responses to water stress under different climate change scenarios, as they can integrate meteorological

inputs and simulate plant water status variables such as plant water potential. These models could be particularly useful for identifying physiological thresholds beyond which yield, and ultimately plant survival, is compromised, ultimately allowing irrigation scheduling to be optimized to maintain production and ensure orchard continuity while minimizing water use. One such model is the SurEau model (Cochard et al. 2021), which incorporates key hydraulic traits. This model simulates the combined effects of heat and drought on plant function, in particular by estimating the time to stomatal closure, a proxy for growth limitation, and hydraulic failure, the mechanism of drought-induced tree mortality. Although trait-based mechanistic models have not been widely applied to crop species, the SurEau model, for example, has recently been used in grapevine to identify the combinations of traits most suitable for survival, or ideotypes (Dayer et al. 2022). Future research should focus on extending the application of such models to a wider range of fruit tree species, providing a physiologically based framework for irrigation management. Incorporating these findings into agricultural practices could help mitigate the adverse effects of climate change on food production systems and increase crop resilience.

Beyond supporting water deficit irrigation strategies, this knowledge could assist in selecting species that are more efficient in regulating carbon and water use, proving highly valuable for tree breeding, geographical species selection, and overall orchard management. With insights into the limitations and interactions of essential traits, we can contribute to designing and cultivating plants tailored to our specific needs and preferences.

It can also help explain differences in growth, productivity, and survival across resource gradients, similar to findings in ecological studies (Reich 2014). Crop distribution areas might not always represent the best environments for species and will likely shift with climate change. This framework incorporating physiological knowledge is a powerful tool for generating new hypotheses, uncovering physiological regulation mechanisms.

Additionally, the study identifies a key trait,  $H_v$ , linked to water and carbon use, measurable through standard, cost-effective methods. This measurement does not require expensive equipment or advanced knowledge and uses standard measurements of sapwood area and leaf area, making it a practical trait for defining species strategies and informing further management. Growers can use this knowledge to make informed decisions about irrigation practices and pruning based on the different water and carbon use strategies.

These above-mentioned management practices informed by these findings are essential for developing resilient agricultural systems that maintain productivity as climate change intensifies.

### 4.4 | Experimental Design Considerations

The limitation of working within a single site, as in this study, has been addressed by comparing local values with broader

data compilations. Despite the relatively good correspondence between species means derived from global datasets and locally measured values (Figure S2), the sample sizes reported in Table S1 show that some agricultural species (e.g., grapefruit, plum, etc.) are still represented by low sample sizes, which can affect the generalizability of the findings.

One constraint of the study lies in the selection of traits, as some relevant characteristics related to water–carbon use in fruit trees may have been overlooked. In particular, root hydraulic traits, increasingly recognized as playing an important role in plant responses to water stress (Rodríguez-Domínguez et al. 2018; Franzisky et al. 2025), were not included in this work. Indirect correlations of the traits could not be assessed through multivariate analyses due to an insufficient number of replicates, which may explain the lack of relationship with some variables in our study, particularly  $g_{smax}$ . Additionally, our study was conducted under conditions without soil water deficit, which could have limited the expression of certain relationships, as trait variation across species could have been smaller than expected. Despite the exceptionally high atmospheric demand in the region, characterized by vapor pressure deficits exceeding 7 kPa on some days (as evidenced by a study conducted in the same area during similar years; Hernández-Santana et al. 2023), which would typically induce water stress in the plant and its hydraulic system, the absence of soil water deficit may have prevented some traits from showing a relevant role.

This could explain why we did not observe a critical role for calculated xylem transport efficiency ( $K_s$ ) or leaf transport efficiency ( $K_{leafmax}$ ), consistent with findings from other studies (e.g., Rosas et al. 2019). Alternatively, as anatomical traits do not include physiological processes that are not explained by the anatomical traits of the species alone, they may account for the absence of the expected relationship for  $K_s$ . Incorporating factors such as pit membrane resistances could provide a more accurate approximation of actual  $K_s$  (Jansen et al. 2011; Lens et al. 2011), making it more consistent with measured xylem hydraulic conductivity. The lack of a central role for other key plant economic spectrum traits, such as tissue density (i.e., WD), could be due to their involvement in multiple processes, complicating mechanistic interpretations and potentially obscuring significant relationships (Mencuccini et al. 2019).

## 5 | Conclusions

This study underscores the importance of a trait-based approach to understanding the regulation of plant water and carbon use, shaping their responses to water deficits. We conclude that TLP, SLA, VI, and  $H_v$  are crucial in shaping strategies in the species studied. As expected, species of the same genera exhibit similar strategies, with the research revealing distinct groupings, such as *Prunus* species having strategies indicative of more water stress resistance and higher productivity than *Citrus* species. The significant relationships observed between our dataset and data obtained from other locations demonstrate that our results, derived from a single population, can be generalized to the species level.  $H_v$  was shown to be a key integrative trait linking water and carbon fluxes, emphasizing its relevance in assessing plant strategies for water and carbon use.

The synthesis of relationships among the carbon- and water-use traits provides crucial insights into fruit tree species strategies. These trait correlations offer a valuable approach for more precise agronomic management, such as deficit irrigation and pruning, optimizing yield under water deficit conditions with a few sampled traits. This framework can also help to enhance the ability to characterize the response to varying environmental conditions across diverse species, which presents opportunities for informing breeding programs aimed at developing more resilient fruit tree varieties.

Future research should incorporate phylogenetic patterns to explore intraspecific trait variation and investigate the limits of each strategy. Some findings may be constrained due to the conditions of the study, and further investigation under varying soil water deficits is recommended to capture trait variability.

## Author Contributions

V.H.-S. conceived the presented idea, with contributions from J.S.-A., C.M.R.-D., and A.D.-E. All authors performed the experiments and measurements. V.H.-S. and J.S.-A. analyzed the data. V.H.S. wrote the draft, which was reviewed by J.S.-A., C.M.R.-D., and A.D.-E. All authors contributed to the final manuscript.

## Acknowledgments

This work was supported by the Spanish Ministry of Science and Innovation through its R+D program [grant agreement RTI2018-098961-B-I00]. C.M.R.-D. benefited from a postdoctoral scholarship from the Juan de la Cierva Incorporación program (Spanish Ministry of Science and Innovation) and J.S.-A. from the Investigación científica e innovación program (Andalusian department of economy, knowledge and business and university). We also thank two anonymous reviewers whose suggestions improved our manuscript.

## Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section.