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Research paper

Smaller but sweeter: The response of grapevine cultivars to drought determines organ interplay in non-structural carbohydrates allocation

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ABSTRACT

Plant health relies on non-structural carbohydrates (NSC) in plant organs and is jeopardized by different stresses, including drought. Plants may use different hydraulic strategies to cope with drought, often involving modifications in growth and NSC reserves. Our work highlighted the impact of cultivar and drought on the physiological responses at the specific organ levels, utilizing young *Vitis vinifera* cv. Grenache (GR) (near-isohydric) and Cabernet sauvignon (CS) (near-anisohydric) plants grown in pots and subjected to prolonged water deficit. Plants were harvested at cane maturity, and NSC were measured. The cultivar influenced NSC accumulation in cane, favoured in GR rather than CS, which also showed a reduced root biomass. Drought led to a boost of NSC concentration at the expense of biomass, confirming roots as a key organ in plant drought responses. Moreover, our prolonged water deficit enhanced starch accumulation and its degradation products (water-soluble NSC), leaving the other investigated NSC pool unchanged. In conclusion, our work offers direction on managing the accumulation of NSC in specific grapevine organs, minimizing water inputs and considering cultivar-specific traits. Under this light, the resultant plants will have elevated NSC concentrations which might enhance their resilience to future stresses.

1. Introduction

Plants experience severe environmental stresses throughout their lifespan when exposed to extreme temperatures, waterlogging, drought or variable salinity levels (Camisón et al., 2020; De Rosa et al., 2024; Sodini et al., 2023). Between these, drought is widely recognized to jeopardise plant health and survival. Drought compromises some primary physiological functions and growth. In the worst scenario, under severe drought conditions, plant survival can be threatened by hydraulic failure and carbon starvation (Gambetta et al., 2020; McDowell et al., 2008).

Carbon starvation arises when limited non-structural carbohydrates (NSC) cannot sustain vital processes. It is often associated with isohydric behaviour, in which stomata close promptly under water shortage, restricting photosynthesis. Conversely, hydraulic failure results from excessive transpiration relative to water uptake, leading to xylem vessel embolism. The process is believed to be faster than carbon starvation and characteristic in anisohydric species, which tend to maintain stomata open during drought (McDowell et al., 2008; McDowell, 2011; Sevanto et al., 2014).

Independently of the hydraulic strategy, plants rely on NSC to mitigate or restore potential stress-induced injuries (Klein et al., 2018). NSC are produced by photosynthesis and can be divided into soluble NSC (sugars), which are osmotically active and act as an energy source, and starch, an osmotically inactive carbon reserve (Dietze et al., 2014; Omari, 2022). Soluble NSC include ethanol-soluble NSC involved in plant metabolism and osmoregulation, and water-soluble NSC that are mainly composed of glucans (linear or branched), derived from starch degradation. Glucans have low osmotic power but contribute to readily usable sugars for energy supply (Qi and Tester, 2018; Vuerich et al., 2023).

Plants modulate NSC pools depending on demand, which explains temporal fluctuations and organ-specific patterns. For instance, deciduous woody plants typically accumulate reserves after blooming and reach maximum storage before the winter (Charrier et al., 2015; Davidson et al., 2021).

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Drought can strongly impact C reserves, causing either depletion or accumulation depending on species and stress intensity (Kannenberg et al., 2018; Vuerich et al., 2021). NSC depletion has been observed mainly through starch reduction in isohydric species (Santos et al., 2021; Tsamir-Rimon et al., 2021). On the contrary, an increase in soluble NSC often occurs in anisohydric species or under mild and prolonged water stress (Hartmann and Trumbore, 2016). Furthermore, NSC dynamics also reflect the balance among organs and tissues: buds, leaves, and young woody stems require more soluble NSC to guarantee osmotic adjustment under drought (Jupa et al., 2024), bark in young woody stems responds more strongly than to wood (Rosell et al., 2017), whereas in underground organs, NSC dynamics are largely driven by starch accumulated over the year (Petrussa et al., 2018). Soluble NSC may also support hydraulic recovery by refilling embolized vessel through osmotic gradients (Secchi and Zwieniecki (2011).

Drought-driven stomatal regulation not only affects water status but also shapes the balance between growth and carbon storage. As highlighted by Wiley & Helliker (2012), growth and NSC reserves often compete for limited assimilates, especially when photosynthesis is restricted. Isohydric plants, which close stomata early, more rapidly face carbon scarcity and may divert available NSC to osmotic regulation or hydraulic maintenance rather than structural growth. In contrast, anisohydric plants sustain gas exchange longer, supporting growth but potentially limiting reserve accumulation. These contrasting strategies influence how plants prioritize carbon allocation under drought, mediating the trade-off between maintaining growth and building protective reserves, and provide a mechanistic framework for interpreting organ-specific NSC responses.

However, most knowledge on plant drought response derives from experiments applying single and short-term drought stress, which offer only a partial view of real conditions where water deficits are recurrent (Menezes-Silva et al., 2017). Research on NSC dynamics under drought has focused predominantly on forest species (Kannenberg et al., 2018; Signori-Müller et al., 2021; P. Zhang et al., 2020), whereas woody crops remain comparatively understudied. Among these, grapevine (*Vitis vinifera* L.) received more attention due to its high economic relevance and broad distribution across the Mediterranean basin and other countries with similar climates (Schultz and Jones, 2010). Its wide cultivation has generated a diversity of cultivars spanning a continuum from near-anysohydric to near-isohydric behaviours (Gambetta et al., 2020; Schultz, 2003). Finally, an exciting point concerns juvenile grapevine plants raised in nurseries derived from grafting between European and American vines. In this case, drought may shape both the amount and allocation of NSC reserves, with potential consequences for post-transplant performance (Villar-Salvador et al., 2015).

In general, drought causes an imbalance in carbon metabolism (Chaves et al., 2009), often favouring NSC accumulation in plant organs (Muller et al., 2011). Hydraulic strategies (i.e. isohydric and anisohydric), particularly the timing of stomata closure to limit transpiration, can also mediate these patterns (McDowell, 2011). Therefore, we believe that grapevine cultivars with contrasting hydraulic strategies represent a suitable model for studying carbon allocation under water limitation. For this reason, we set up an experiment in controlled watering conditions using a combination of different cultivars. NSC were measured in all the plant organs and related to growth. We raised the following hypotheses: i) the cultivar and plant organ mediate the trade-off between growth and reserves; ii) water shortage treatment would favour an increase in soluble NSC pool; iii) a reduction of growth can allow a significant C accumulation in reserves.

2. Materials and methods

2.1. Plant material and experimental design

We performed an experiment using one-year-old grapevines from March to November 2022 to examine how young woody crops respond to water deficit. All the activities occurred in 2022 under a plastic tunnel with open roll-up sides at the University of Udine research farm (46°03’72.0’’ N, 13°22’64.4’’ E, Udine, Italy).

We induced water stress on two distinct cultivars (Cabernet sauvignon, CS, and Grenache, GR) grafted onto the same rootstock genotype (1103 Paulsen, 1103 P). CS is recognized as a near-anisohydric variety, while GR is reported to be a near-isohydric variety (Vuerich et al., 2023; Williams and Baeza, 2007). We used a full orthogonal design, including the two factors with two levels and their interaction assigning six biological replicates (grapevine plants) to each combination (n = 2x2x6 = 24).

The experiment started on March 14, 2022, planting the grapevines in pots with a substrate of 75 % loam soil and 25 % peat. We used 20 L pots, as suggested by Herrera et al., (2021), to potentially simulate natural growing conditions and reduce the impact of pots on plant metabolism. The pots were arranged in a randomized scheme along five rows.

Irrigation was provided by a drip system and was based on hourly scale measurements triggered by the CR1000 datalogger (Campbell Scientific, USA). We kept our pots at the maximum water-holding capacity before the phenological stage of budburst (BBCH 10, 01/05/2022; following the phenological development scale of grapes - Lorenz et al., 1994), when we started imposing two water regimes: the supply of 100 % and 33 % evapotranspiration (ET). Only one shoot per vine was retained during the experiment, and all the bunches were removed at bloom (BBCH 65, 31/05/2022) to standardize all experimental measurements (the schedule of sampling is shown in Fig. S1)

All the plants were weekly fertigated from 01/05/2022–14/09/2022, (BBCH 89, berry ripe for harvesting) administering Nitrogen, 70 kg/ha of P_2O_5, and 80 kg/ha of K_2O.

2.2. Stem water potential and gas exchange

Stem water potential (Ψ_{STEM}) and gas exchange assessments, including net photosynthesis (P_N) and stomatal conductance (g_s), were measured on mature leaves between 11:00 and 14:00. Five measurements were conducted between from 10/06/2022–30808/2022 June and August 2022, specifically measuring leaves taken from randomly chosen plants. We utilized three replicates for each treatment combination (n = 2 water regimes per 2 cultivars per 3 replicates = 12 mature leaves for each sampling day).

The Ψ_{STEM} was performed using a Scholander chamber (Soil Moisture Corp, CA, USA), following the guidelines proposed by (Scholander et al., 1964); while the gas exchange measurements were conducted using the Licor 6400XT equipment (LICOR, Inc., NE, USA), at ambient conditions, delivering constant CO_2 and light intensity levels, set at 400 μmol mol^{-1} and 1000 μmol m^{-2} s^{-1}, respectively.

2.3. Biomass measurement and sample collection for NSC analysis

All the plants were harvested before dawn at senescence (BBCH 97, 08/11/2022) and prepared for the analyses of NSC and biomass. Pieces of secondary roots, cane (second basal internode) and rootstock trunk were collected and microwaved (700 W for 3 min) for the subsequent NSC measurements. Each organ’s dry weight was determined by weighting all the organ parts (including the NSC samples) after 72 h at 55°C. Since leaves were mostly fallen at this stage, they were not considered. The ‘structural biomass’, was calculated as biomass minus weighed NSC (Canham et al., 1999; Reyes-Bahamonde et al., 2021).

2.4. NSC analysis

NSC analysis was performed by separating soluble NSC (including hexoses such as glucose and fructose, dimers such as sucrose and maltose and other short oligomers) and starch. Dried cane, rootstock trunk, and roots samples were ground into 2 mL Eppendorf tubes using a ball mill

(MM500, Retsch, Haan, Germany). Alcoholic extraction of soluble NSC was performed according to (Quentin et al., 2015), with minor modifications recommended by (Casolo et al., 2023). In summary, we performed two ethanol extranctions, with 500 µL + 300 µL of 80 % Ethanol (v/v) respectively. The suspensions were mixed directly into the Eppendorf tubes containing 15 ± 1 mg powder. Samples were incubated for 30 min and centrifugated at 14.000 RPM (with Mikro 120, Hettich, Milan, Italy) to separate the supernatant (Ethanol with soluble NSC) from the pellet (water-soluble NSC + starch). Supernatants collected were dried in an oven till ethanol evaporation to obtain soluble NSC crystalized, and afterwards resuspended into 500 µL of 50 mM Tris-HCl (pH 7.5) to perform the anthrone assay (Yemm and Willis, 1954). Water-soluble NSC were extracted by adding 500 µL of deionized water into the pellet and incubated at 25°C for 24 h. This pool was analysed with the anthrone colorimetric method as alcohol-soluble NSC, converting sample absorbances (recorded with Victor multi-plate reader, Perkin-Elmer, Waltham, USA) into equivalent glucose concentrations.

Starch was hydrolysed and measured with the enzymatic method proposed by Landhäusser et al. (2018) and afterwards adapted for woody tissues by Natale et al. (2023). Briefly, 100 U of α-amylase and 25 U of amyloglucosidase were added to the pellet and incubated overnight for starch digestion. Starch analysis was conducted by inducing glucose (product of starch hydrolysis) conversion in NADH, which is in a stoichiometric ratio 1:1, and measuring NADH absorbance with a spectrophotometer at a wavelength of 340 nm.

2.5. Data analysis

Data analysis was conducted using the R language (version 4.2.2; R CoreTeam, Austria).

We used linear models to test the effect of the experimental factor and their interaction on each response variable. The full model included all the explanatory variables (factors) and their interactions for each response variable (Table 1). We used an Information Theoretic Approach for the selection of significant effect from the full models (Johnson and Omland, 2004; Newland, 2019).

In particular, the full models were compared to nested models in which one element was eliminated, starting with the interaction removal and carrying out an iterative process. The lowest Bayesian Information Criterion (BIC) was used to identify the most reliable models.

The assumptions of the models were evaluated visually using the default functions in R and the diagnostic tools available in the DHARMa package (Hartig, 2022). Outlier screening, also performed using the DHARMa package, was applied only to variables with six biological replicates (maximum one outlier per group); no outliers were removed from datasets based on three replicates (*i.e.* g_s, P_N and Ψ_{STEM}).

The marginal means of the groups in the selected models were contrasted using the pairwise Tukey's test. The presentation of biomass and NSC data was standardized by showing the interactions between the cultivar and organ and between the water regime and the organ.

All the graphical data representation was done using the ggplot2 package (Wickham, 2016).

The relationships between total plant biomass and the NSC pools measured in each of the investigated organs (the roots, rootstock trunk, and cane) were also analyzed using linear models

Table 1
Description of the explanatory variables and their interactions (*)included in the full model response variable.

Response variable	Explanatory variables
Ψ_{STEM}	Cultivar * Water regime * Date
g_s	Cultivar * Water regime * Date
P_N	Cultivar * Water regime * Date
Biomass	Cultivar * Water regime * Organ
Ethanol soluble NSC	Cultivar * Water regime * Organ
Water soluble NSC	Cultivar * Water regime * Organ
Starch	Cultivar * Water regime * Organ
Total NSC	Cultivar * Water regime * Organ

3. Results

3.1. Stem water potential

We measured Ψ_{STEM} to monitor the achievement of water stress conditions across the different treatments. Ψ_{STEM} significantly differed between the water regimes over the experimental duration (i.e. interaction water regime x time) (Fig. 1a, Table S2). The two cultivars also showed different Ψ_{STEM} independently of other experimental factors, where the CS average values were significantly lower than GR (Fig. 1b, Table S2). We found moderate stress in plants subjected to water shortage and values that never dropped below −1,0 MPa since the first measurement dates (June), 45 days from the beginning of the deficit imposition. Moreover, we observed that Ψ_{STEM} values were similar for the two water regimes at the end of August (Fig. 1).

3.2. Photosynthesis and g_s

The photosynthetic rates were significantly different between the cultivars (Table S2). CS was found to have considerably higher photosynthetic rates (estimated marginal means: 11.57 µmol CO_2 m^{-2} s^{-1} ± 0.26 SE for the CS, 9.58 µmol CO_2 m^{-2} s^{-1} ± 0.26 SE for the GR cultivar, Fig. 2). We also found that g_s was affected by all the factors examined, whereas no significant interactions were observed among the experimental factors (Table 1, S2). Similarly to photosynthesis, CS exhibited significantly higher g_s than GR (Fig. 3a). However, a notable difference was observed between the two water regimes and measurement dates. The water deficit negatively impacted the g_s, resulting in values that were 33 % lower than those of well-watered plants (Fig. 3c). Additionally, in all plants we observed an increasing trend of g_s from June (mean value: 0.07 mol H_2O m^{-2} s^{-1}) to August (mean value: 0.11 mol H_2O m^{-2} s^{-1}).

3.3. Biomass

The effects of experimental factors and their interaction on plant organ biomass (cane, rootstock trunk, and roots) were evaluated at the end of the growing season (Table S2).

Grapevines recorded the lowest biomass values in the canes and the highest weight in the roots (Table S1). The difference between the organ's biomasses was also affected by the cultivar interaction. CS produced more roots than GR (root biomass estimated marginal means: 80.33 g ± 2.75 SE, 67.55 g ± 2.75 SE for CS and GR, respectively, Fig. 4a). Moreover, the reduced water regime significantly impacted the growth of canes and roots, reducing biomass by −60 % and −47 %, respectively (Fig. 4b). As opposite, rootstock trunks showed consistent values. The same scenario here evidenced also emerged applying structural biomass (Fig. S2)

3.4. Non-structural carbohydrates

3.4.1. Ethanol-soluble NSC

The ethanol-soluble NSC concentration was driven by the single effect of three factors, i.e. the organ, the cultivar, and the applied water regime (Table S2).

The cane showed the highest concentration of ethanol-soluble NSC among all organs examined (Table S1, Fig. 5a, b). Low and similar values were reported for roots and rootstock trunks (Table S1).

Considering the different organs, the cultivar genotype showed a significant influence on the cane ethanol-soluble NSC concentration, with GR values significantly higher than CS (estimated marginal means: 0.13 mg/mg DW ± 0.01 SE, 0.10 mg/mg DW ± 0.01 SE for GR and CS, respectively, Fig. 5a).

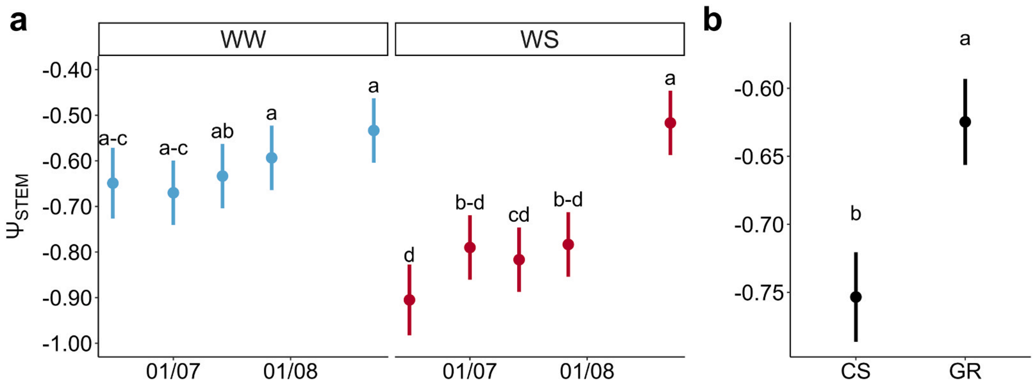

Fig. 1. Effect plots of the stem water potential (Ψ_{STEM}). Interaction between the water regime and the date of measurement (a), and the singular effect of the cultivar (b). The projected values display different cultivars of Cabernet sauvignon (CS) and Grenache (GR) and two water regimes: well-watered (WW), represented by blue dots, and water-stressed (WS), represented by red dots. Each dot corresponds to the marginal mean associated with 95 % confidence intervals. Different letters indicate significant differences as a result of Tukey's test.

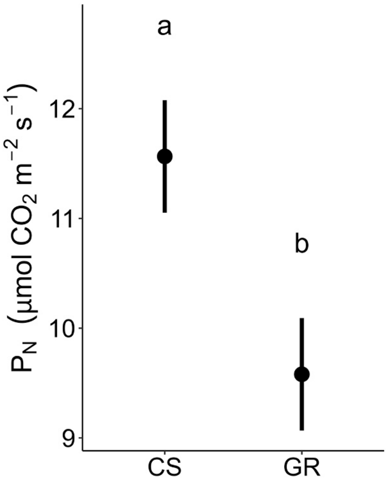

Fig. 2. Effect plots of the photosynthetic rate between the two cultivars of Cabernet sauvignon (CS) and Grenache (GR). Each dot corresponds to the marginal mean associated with 95 % confidence intervals. Different letters indicate significant differences as a result of Tukey's test.

3.4.2. *Water-soluble NSC*

Water-soluble NSC ranged between 0.01 and 0.07 mg/mg DW in all organs (Fig. 5c, d). In general, the data of water-soluble NSC were explained by the interaction between the water regime and the organ and by the single effect of the cultivar (Table S2).

Our findings revealed that the water regime did not affect the water-soluble NSC concentration in canes and rootstock trunks, whereas significant differences were ascertained in the roots. In the latter case, the concentration was significantly higher in the roots of water-deficit-treated plants (Fig. 5d).

Furthermore, significantly higher water-soluble NSC concentrations were observed in the cane of GR (+87 % than CS, Fig. 5c).

3.4.3. *Starch*

The starch concentration varied depending on the plant organ and the water regime applied (Table S2). The roots accumulated more starch (Table S1) than rootstock trunks and canes, which showed similar values (Table S1).

In comparison to well-watered conditions, the accumulation of starch was significantly higher only in the roots of plants subjected to the low water regime (estimated marginal means: 0.29 mg/mg DW ± 0.01 SE for the WS regime, 0.23 mg/mg DW ± 0.01 SE for the WW regime, Fig. 5f).

Although the differences due to the cultivar genotype were observed only in the canes, the interaction between the organ and the cultivar (Fig. 5e) revealed significantly lower starch values in GR canes compared to CS canes (estimated marginal means: 0.18 mg/mg DW ± 0.01 SE for the GR, 0.13 mg/mg DW ± 0.01 SE for the CS).

3.4.4. *Total NSC*

Total NSC concentration follows the same starch dynamics (Table S2). The Total NSC showed significantly lower values in rootstock

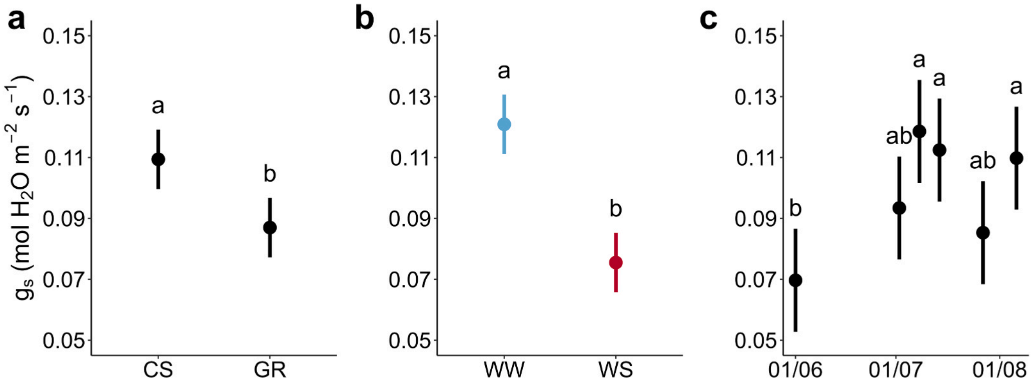

Fig. 3. Effect plots of the stomatal conductance (g_s). The projected values display different cultivars of Cabernet sauvignon (CS) and Grenache (GR) and two water regimes: well-watered (WW), represented by blue dots, and water-stressed (WS), represented by red dots. Each dot corresponds to the marginal mean associated with 95 % confidence intervals. Different letters indicate significant differences as a result of Tukey's test.

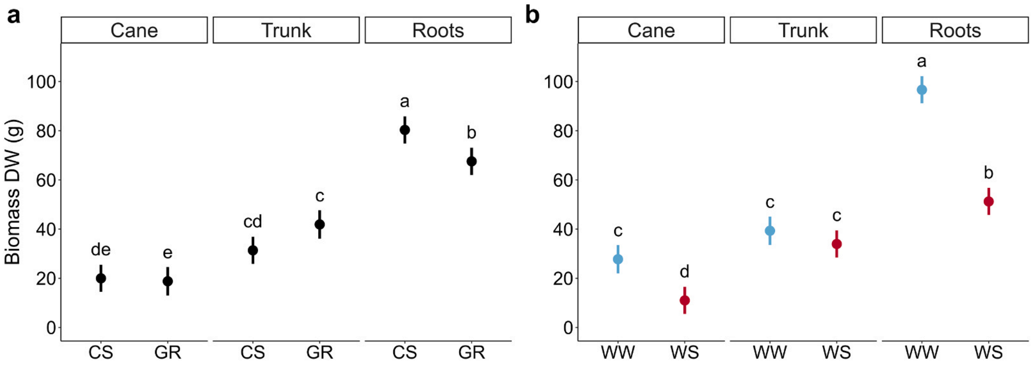

Fig. 4. Effect plots of the total biomass without leaves. Relationships between the organ, the cultivar (a), the organ and the water regime (b). The projected values display different plant organs, cultivars of Cabernet sauvignon (CS) and Grenache (GR) grafted onto 1103 Paulsen, and two water regimes: well-watered (WW) represented by blue dots and water-stressed (WS) represented by red dots. Each dot corresponds to the marginal mean associated with 95 % confidence intervals. Different letters indicate significant differences as a result of Tukey's test.

trunks and higher values in roots (Table S1), with intermediate values reported for the canes (Table S1). However, this scenario is also consistent when analysing the effect of the cultivars (Fig. 5h) and the water regime applied (Fig. 5g).

Between the cultivars, GR is reported to accumulate significantly more total NSC in cane (Fig. 5g). No significant differences due to the cultivar emerged in the other organs.

Regarding the water regime, we observed a significant rise in total NSC in the roots of plants exposed to water deficit (estimated marginal means: 0.41 mg/mg DW ± 0.02 SE for the WS, 0.31 mg/mg DW ± 0.02 SE for the WW, Fig. 5h). On the contrary, the water regime unaffected the total NSC in canes and rootstock trunks (Fig. 5h).

3.5. *Relationships between plant biomass and NSC content*

Significant negative relationships between plant biomass and all considered NSC pools were observed only in the roots (Fig. 6). In contrast, no significant correlations were observed in the other organs (Figure S3, S4).

). The water-soluble NSC and the total NSC were the most reliable predictors among the several NSC measured, providing values of R^2 of 0.41 and 0.50, respectively (Fig. 6).

4. Discussion

This study investigated the physiological responses of different plant organs to prolonged moderate water deficit on two different grapevine cultivars, characterized by employing distinct hydraulic strategies. Our investigation highlighted that the relationships between biomass and NSC concentration differ among the organs. Water shortage caused an increase in the NSC concentration in the roots. Finally, we observed that a reduction of biomass due to drought in the whole plant is reflected in NSC accumulation in the root, suggesting this organ plays a central role in the storage of reserves after a stress event in the grapevine.

i) Cultivar and plant organ mediate the interplay between growth and reserves.

Literature reports that the diverse hydraulic strategies that plants adopt in response to drought affect the NSC concentration in the tissues (McDowell, 2011). However, hydraulic behaviour seems tuned by the phenological stage and kind of stress: long and moderate or short and severe (Gambetta et al., 2020; Hochberg et al., 2018; Serrano et al., 2024). For these reasons, the dichotomy between isohydrics and anisohydric strategy is now considered outdated (Serrano et al., 2024), and further investigations aiming at understanding the role of NSC during drought are needed.

Comparing two cultivars known to have a different hydraulic strategy, we hypothesized a distinct impact on plant growth and the accumulation of NSC reserves in different organs (i.e. cane, rootstock trunks and roots). We also assume that the water-use strategy, directly related to plant physiological processes, might significantly affect this balance.

In our experiment, drought impacted both cultivars, reducing their g_s and Ψ_{STEM}, with a major effect in the first phase after establishing the water deficit regime (Figs. 3, 4). The intensity of the response differed between GR and CS, as expected by the typical iso/anisohydric definitions. In both cultivars, g_s and Ψ_{STEM} reached values indicative of moderate water stress (Gambetta et al., 2020; Romero et al., 2022), which might explain the absence of effect on photosynthesis rates evidencing a constitutive cultivar-driven response (Fig. 2).

According to the literature, anisohydric species should produce more biomass and retain more NSC reserves than isohydric (McDowell, 2011; Sevanto et al., 2014). This scenario has been observed also in grapevine (Vuerich et al., 2021; Williams and Baeza, 2007). Nevertheless, our study showed that the different hydraulic strategies do not depend on the water limitation treatment but appear as a constitutive cultivar trait (Table S2). Consistent with this observation, biomass and NSC were unaffected by the interaction of cultivar and applied water regime (Table S2). We observed two different outcomes when biomass and NSC were considered. CS produced greater root biomass than GR, while other organs showed no differences (Fig. 4a). It is well known that the rootstock genotype influences scion growth (L. Zhang et al., 2016), and we have evidence that scion can also influence root growth (belonging to the rootstock). However, this growth response is not consistent with NSC concentrations. NSC levels were comparable between the two cultivars in all the rootstock trunks and roots but differed in the cane (Fig. 5a, c, e, g). GR has accumulated more reserves in the canes than the CS, suggesting that accumulation of all the NSC pool measured (i.e., ethanol-soluble, water-soluble, and starch) is closely associated with the cultivar.

An additional aspect emerging from our experiment concerns the potential genetic asymmetry between above- and below-ground organs in grafted plants. Although CS and GR differ in hydraulic behaviour, both were grafted onto the same rootstock genotype. It is therefore plausible that scion physiology may have responded to drought under a common root genetic background. This may explain differences in NSC concentration between cultivars in the cane but not in the roots, suggesting that root-driven control of drought responses could attenuate cultivar-specific allocation patterns. Previous works have shown that rootstocks can regulate water uptake, ABA-mediated signalling and hydraulic conductance under water deficit (Flor et al., 2025; Bianchi et al., 2023), sometimes even influencing scion xylem anatomy and carbon allocation. However, the extent to which such below-ground control contributed to the patterns observed here remains to be fully clarified, and warrants targeted investigation.

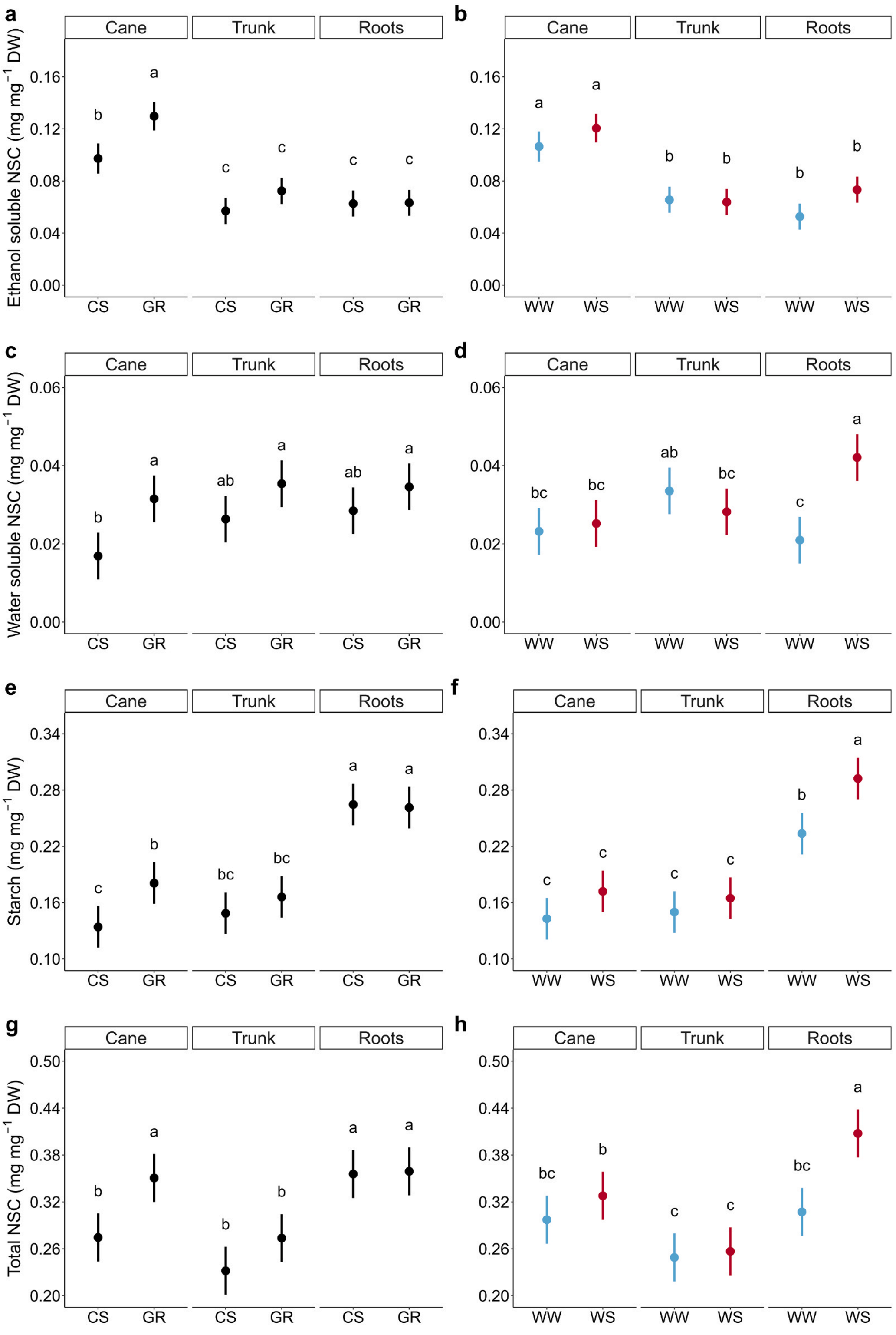

Fig. 5. Effect plots of ethanol-soluble NSC (a, b), water-soluble NSC (c, d), starch (e, f), and total NSC (g, h). Relationships between the organ and the cultivar (a, c, e, g), the organ and the water regime (b, d, f, h). The projected values display different plant organs, cultivars of Cabernet sauvignon (CS) and Grenache (GR) grafted onto 1103 Paulsen, and two water regimes: well-watered (WW) represented by blue dots and water-stressed (WS) represented by red dots. Each dot corresponds to the marginal mean associated with 95 % confidence intervals. Different letters indicate significant differences as a result of Tukey's test.

ii) Effect of water shortage on soluble NSC;

The impact of drought on NSC concentration in plant tissues cannot be generalized. Some researchers observed no changes between well-watered and drought-exposed plants (Anderegg and Anderegg, 2013; Tomasella et al., 2019), whereas other authors reported a rise (Morabito et al., 2022), a reduction in NSC (Tomasella et al., 2021), or both (O'Brien et al., 2015; Regier et al., 2009). Differences in plant NSC accumulation during drought also arise from the different duration and intensity of the drought treatment (He et al., 2020; Li et al., 2018), as well as the different organs investigated (Kannenberg et al., 2018), or

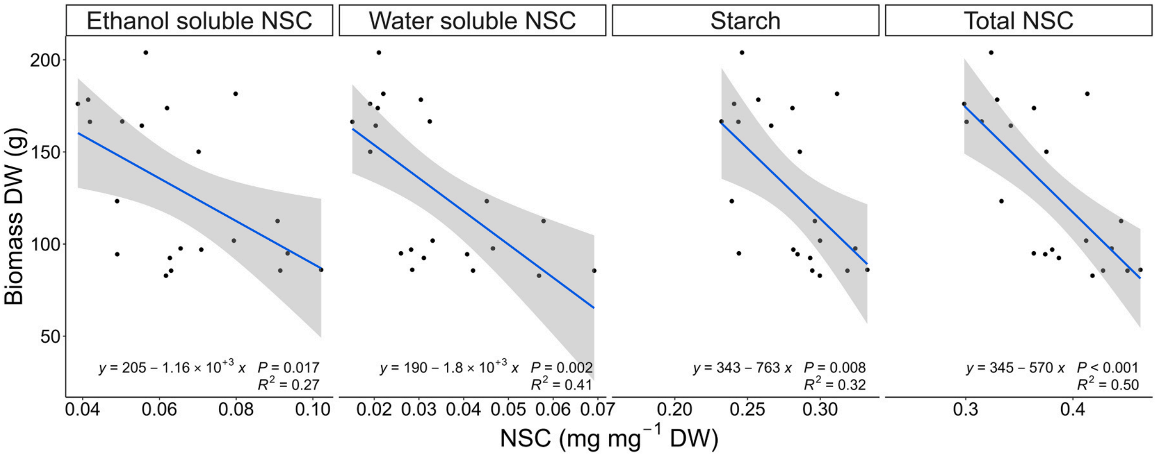

Fig. 6. Relationships between different pools of NSC measured in the roots and the total biomass without leaves. Grey-shaded areas illustrate the confidence intervals (0.95).

the considered NSC pool (Vuerich et al., 2023).

From a broader perspective, drought triggers starch degradation to support the production of sugars because of their important involvement in drought tolerance strategies from osmotic adjustment to plant recovery (Camisón et al., 2020; Secchi and Zwieniecki, 2011; Tomasella et al., 2017; Trifilò et al., 2019).

In our work, we propose the division of soluble NSC into two pools based on their solubility, resulting in ethanol-soluble NSC and water-soluble NSC, hypothesizing that the accumulation of both soluble NSC would likely have been favoured following water stress at the expense of starch, according to its function of alternative supply of soluble carbohydrates (He et al., 2020; Martínez-Vilalta et al., 2016). Conversely, we found that drought significantly modified the NSC pools only in the roots, increasing the concentration of water-soluble NSC but leaving the ethanol-soluble NSC pool constant (Fig. 5). Interestingly, starch and total NSC also increased, suggesting a prolonged water deficit promotes starch accumulation. Otherwise, a certain quote of starch should be continuously hydrolysed to produce maltodextrin needed to sustain the pool of sugars directed to glycolysis (Smith et al., 2005; Thalmann and Santelia, 2017).

A boost in the soluble NSC pool has been reported in plants as an early response to drought (He et al., 2020). Therefore, it is supposed that soluble NSC might also have increased in our plants at the early stage of stress (around June 2022). However, our NSC analysis was performed at senescence (BBCH 97). Our findings suggest that, during the experiment the concentration of ethanol-soluble NSC increased immediately after the drought stress while reassessing to initial content after during the stress. Instead, the water-soluble pool, starch and total NSC, increased and remained at high levels in plants during the drought.

iii) Drought-induced growth limitation affects the NSC accumulation in reserve organs

Following drought, the level of NSC to sustain physiological activities diminishes as plants prioritise a downregulation of growth and respiration (Palacio et al., 2014). The drop in photosynthesis occurs afterwards, allowing the plant to accumulate higher amounts of soluble NSC in its tissues (He et al., 2020; Kannenberg et al., 2018; Körner, 2015; McDowell, 2011; Oliva et al., 2014). This allowed us to dig into our first hypothesis, which was to understand if a reduction of growth might promote a significant accumulation of reserves in different plant organs as already proposed by other authors (McDowell, 2011; Muller et al., 2011). Although cane and roots are identified to be the main organs negatively affected by drought (Gómez-Del-Campo et al., 2005), several research on drought focused on other organs, such as leaves, petioles or stems (Falchi et al., 2020; Tombesi et al., 2021; Vuerich et al., 2023), resulting in a knowledge gap in unexamined organs and the overall perspective. With our work, we highlighted that the reduction of growth due to drought mainly drives the accumulation of NSC in roots and cane (Fig. 4b, Fig. 5, Table S2).

Considering both cultivars, roots and cane biomass measured in our water-deficient plants decreased by 47 % and 60 %, respectively. The observed drop in growth aligns with the findings of earlier studies on three-year-old productive grapevines subjected to water deficit (Gómez-Del-Campo et al., 2005). However, even if drought stress impacted plant growth and NSC pools (Figs. 4, 5), we believe our results could also be contextualized within the photosynthetic activity monitored throughout the experiment. The photosynthetic activity was not influenced by the water regime applied, probably due to the moderate water stress achieved (Fig. 1). Considering this evidence, we could partially explain the rise in NSC concentrations because plants grow less under drought conditions. Specifically, we identified a strong relationship between the plant's total biomass and all the NSC pools measured only in the roots (Fig. 6). These results allow us to emphasize the significance of the root as a storage organ in deciduous woody crops, particularly under drought conditions (Santos et al., 2021).

5. Conclusions

Our study confirmed that cultivar and drought significantly influence the physiological response of plant organs. We deepened our knowledge of the relationship between growth and reserves, recognizing different exploitations of the pools of soluble NSC and starch breakdown derivatives.

Water deficit has reduced plant biomass at the whole plant level, especially in the roots. Stress leads to an accumulation of NSC inside roots, emphasizing their crucial role in reserve storage during drought.

The two considered soluble NSC pools did not respond to water shortage consistently. Although the ethanol-soluble NSC concentration was not affected by a prolonged moderate drought, being preserved to satisfy metabolic requirements, the water-soluble NSC, represented by maltodextrin derived by starch degradation, and starch increased.

Furthermore, beyond drought, the cultivar adopted hydraulic strategies as constitutive traits, evidencing a decoupled impact on growth and NSC accumulation, particularly in canes and roots.

Our study offers the basis for exploring more complex scenarios to understand the responses of deciduous plants to water stress.

Enhanced NSC levels in plant organs have the potential to respond to future stresses successfully. Our findings should provide new insights into grapevine cultivation, other woody crops, and forest nurseries in light of water saving without limiting reserve accumulation.

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CRediT authorship contribution statement

A. Pichierri: Writing – original draft, Software, Investigation, Data curation, Conceptualization. **S. Gargiulo:** Writing – review & editing, Methodology. **P. Sivilotti:** Writing – review & editing, Supervision, Conceptualization. **F. Boscutti:** Writing – review & editing, Data curation. **G. Masutti:** Writing – review & editing, Investigation. **E. De Luca:** Writing – review & editing, Funding acquisition, Conceptualization. **Y. Zambon:** Writing – review & editing, Funding acquisition. **L. Falginella:** Writing – review & editing. **V. Casolo:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Alessandro Pichierri reports financial support was provided by PON. Alessandro Pichierri reports financial support was provided by Vivai Cooperativi of Rauscedo (VCR, San Giorgio della Richinvelda, Italy). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.envexpbot.2025.106300.

Data availability

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

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