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HOW WALNUT ROOTS RESPOND TO DROUGHT STRESS: A MORPHOLOGICAL AND ANATOMICAL STUDY

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ABSTRACT. *Drought stress threatens human food security by reducing product yields and by limiting the practice of crop cultivation. Roots are the first to detect water deficiencies and send signals to aerial parts. The current study evaluates several responses of the roots to drought stress by considering measurable features such as the architecture and anatomy of 'Chandler' walnut seedlings. Here, 18 seedlings were divided into two groups: the first group of seedlings was exposed to drought stress by withholding irrigation, and the second group was maintained under normal irrigation conditions. The roots of seedlings in both groups were harvested thirty days after the experiment had begun. Eight of the sampled roots in the two groups were significantly different when considering twenty parameters pertaining to the architectural appearance of roots. Most of these parameters were related to the root thickness and root volume. Also, anatomical studies showed that the suberization of roots increased in seedlings under drought stress, compared to the roots of the control group. Finally, the nutritional analyses of roots showed that* K^+ *and* Ca^{+2} *increased in the roots of seedlings under drought stress. These findings suggest that breeders can focus on the responses of roots to improve drought tolerance when breeding walnut rootstocks.*

KEY WORDS: *water shortage, root architecture, anatomical characteristics, root morphology, suberization.*

INTRODUCTION

Drought stress is a strong limiting factor that can reduce the growth and yield of horticultural crops (Vahdati & Lotfi, 2013). The exposure to drought stress prompts different responses by plants for their survival. These include drought avoidance and drought tolerance (Brunner et al. 2015). Drought avoidance usually involves the closure of stomata and preserving the plant's water balance. This could mean a regulation between water uptake and water loss, besides occasional drawbacks in shoot growth and root growth (Tuberosa 2012, Zokaee-Khosroshahi et al. 2014). However, when avoidance responses are no longer sufficient at times of severe drought, plants try to protect their tissues from cell damage via other mechanisms, including physiological (osmolyte and protein production), anatomical and molecular responses (Farooq et al. 2009; Brunner et al. 2015). On the other hand, the response to drought stress in woody plants can be different from those observed in herbaceous plants (Brunner et al. 2015). Woody plants have evolved more mechanisms for drought tolerance, thereby making more extensive changes, such as in the thickness of the cell wall, the length and the diameter of the xylem conduits (Kozlowski & Pallardy 2002). In general, 20-40% of the biomass in trees are made up of roots (Jackson et al. 1997). Root systems in trees play key roles in storing carbohydrates and nutrients, providing physical stabilization, and being responsible for the uptake of nutrients and water via fine-roots (Brunner & Godbold 2007; Brunner et al. 2015). Furthermore, roots are the first to signal the occurrence of water shortages, and they have the function of alerting the leaves and shoots (Hamanishi & Campbell 2011, Shamshiri & Hasani 2015). Generally, there are two types of roots in trees: roots are classified as being either thicker or thinner than 2 mm (coarse and fine roots, respectively). Coarse roots absorb water from the depths of the soil, whereas fine roots absorb nutrients and cause carbon sequestration, besides absorbing water. These two types of roots are characterized by their different lifespan, biomass, lignin content and specific root length (Brunner & Godbold 2007). Clearly, there are many indications that drought stress affects the growth and structure of both fine and coarse roots in trees (Kozlowski & Pallardy 2002). At times of drought stress, the identification, observation and analysis of the responses staged by roots are more difficult than when dealing with shoots. Among trees, few studies have been conducted on root responses to drought stress. Several of such studies have been on olives (Sofo et al. 2004); *Vitis vinifers* L. (Król et al. 2014), citrus species (Ollas et al. 2013) and peach (Arndt et al. 2000). Considering the walnut species, trees require a lot of irrigation to produce high amounts of yield with good quality. Drought stress can strongly hamper the growth, yield and quality of walnuts (Jerszurki et al. 2017). In this context, Vahdati et al. (2009) reported that drought stress reduces the germination rate of seeds belonging to 16 genotypes of walnut. In other studies, researchers reported that water deficiency can substantially slow down the growth rate of walnuts (Tyree et al. 1993; Cochard et al. 2002; Shi et al. 2003; Lotfi et al. 2010; Sun et al. 2011; Vahdati & Lotfi, 2013). Nevertheless, there has been an undeserved amount of focus on root response to drought stress, as compared to the abundance of studies on the shoot response. Recently, Jerszurki et al. (2017) reported that drought stress significantly reduces the plant's hydraulic conductance, along with the decrease in stem and soil water potential. It is precisely unclear to what extent drought stress can affect the anatomy and morphology of walnut roots under drought stress. The main purpose of this study is to develop an understanding of these responses by analyzing the architecture, anatomical features and nutritional status of walnut roots during drought stress.

MATERIAL AND METHODS

Plant material, growth conditions and drought stress

The current study was carried out during summer 2018 (June-July), using 18 'Chandler' walnut seedlings which were two years old. The seedlings were grown in 15 L pots containing perlite and peat (1/1, v/v). The surface layer of pots was covered by plastic sheets to prevent evaporation from the soil. For the treatments, 18 seedlings were divided into two groups, each consisting of nine seedlings. The first group of seedlings was exposed to drought stress (DS) by withholding irrigation, and the second group was maintained under normal irrigation conditions (control treatment).

Root imaging and root architecture study

The roots of seedlings in the control group and in the drought stress treatment were harvested and photographed thirty days after the start of the drought stress. Then, the images were processed and transferred to the relevant software [Gia Roots, (Galkovskyi et al. 2012)]. Finally, twenty parameters pertaining to the root were measured. These were the maximum number of roots (MXNR), minor ellipse axes (MIEA), ellipse aspect ratio (ELAX), median number of roots (MDNR), average root width (AVRW), number of connecting components (NOCC), major ellipse axes (MAEA), specific root length (SPRL), network solidity (NWSD), network bushiness (NWBS), network depth (NWDP), network area (NWAR), network length (NWLN), network length distribution (NWLD), network convex area (NWCA), network width (NWWI), network volume (NWVL) network perimeter (NWPM), network width depth ratio (NWWD), lifespan and network surface area (NWSA). The software Gia Roots was used for the calculations. The control group and the drought stress treatment yielded comparable results in terms of the mentioned parameters.

Anatomical study

After harvesting the roots from the seedlings of both groups, hand cross sections were taken by allowing 50 mm from the root tip. A total of five roots were sampled from three different plants. These were stained via the double-coloring technique (Methyl green and Carmen Zaji). The samples were subsequently observed using a fluorescent microscope.

Ion concentration in roots

At the end of the experiment, the concentrations of several ions were evaluated in the roots. Briefly, the roots were separated from the seedlings. They were washed with water and then rinsed with distilled water. The roots were subsequently dried in an oven (at 140 °C for 24 h) before being eventually powdered. The calcium concentration was measured by a complex meter method with EDTA (Loeppert & Suarez 1996). The potassium concentration in the extract was calculated by a flame photometer JENWAY (version 7 PFP) (Hemke & Sparks 1996). Finally, the concentrations of manganese and copper were measured by atomic absorption via a spectrophotometer (GBC model AVANTA).

Statistical analysis

Student's t-test was used to compare each mean parameter difference between the control and drought stress treatments. We considered two significance levels; $P < 0.05$ and $P < 0.01$.

RESULT AND DISSCUSSION

Growth of roots, measurements and root architecture

Imaging the ‘Chandler’ roots 30 days after the start of the experiment showed significant differences in the root architecture when comparing the

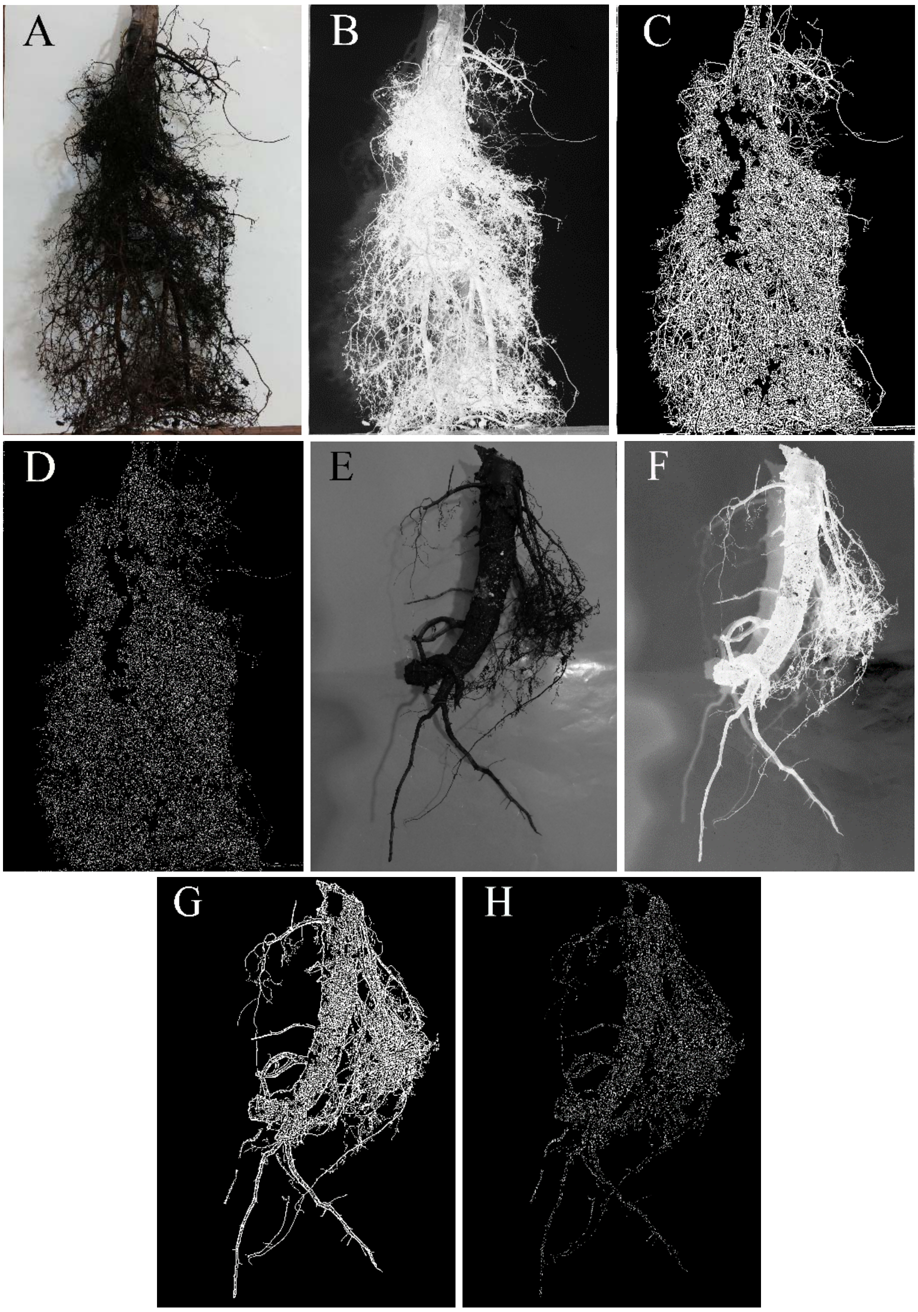

Figure 1. Roots of walnut under control [A (cleaned image), B (gray image), C (threshold image) and D (thinned image)] and drought stress conditions [E (cleaned image), F (gray image), G (threshold image) and H (thinned image)] 30 day after starting of experiment. Except for the A and E photos, other photos are Gia Roots software output.

control group and the drought stress treatment (Fig.1). Generally, the growth of roots decreased significantly under drought stress. Specifically, however, the lifespan of fine roots (> 2mm) in ‘Chandler’ seedlings increased under drought stress (Fig.1). The control group and drought stress treatment caused significantly different results in terms of eight of the observed architectural parameters of the root, i.e. the NWBS, MDNR, NWAR, NWPM, NWSD, NWSA, NWLN and NWVL (Fig. 2 and 3). Among these parameters, the NWBS, NWAR, NWPM and NWVL described the thickness of roots. Apart from NWBS, three of the other parameters showed higher values in the control samples, compared to the drought-stressed samples. In this regard, the average values of NWAR, NWPM and NWVL were 5485.25 cm^2, 48596.48 cm, and 1895.80 cm^3, respectively, in the control group. Meanwhile, the average values of these parameters in

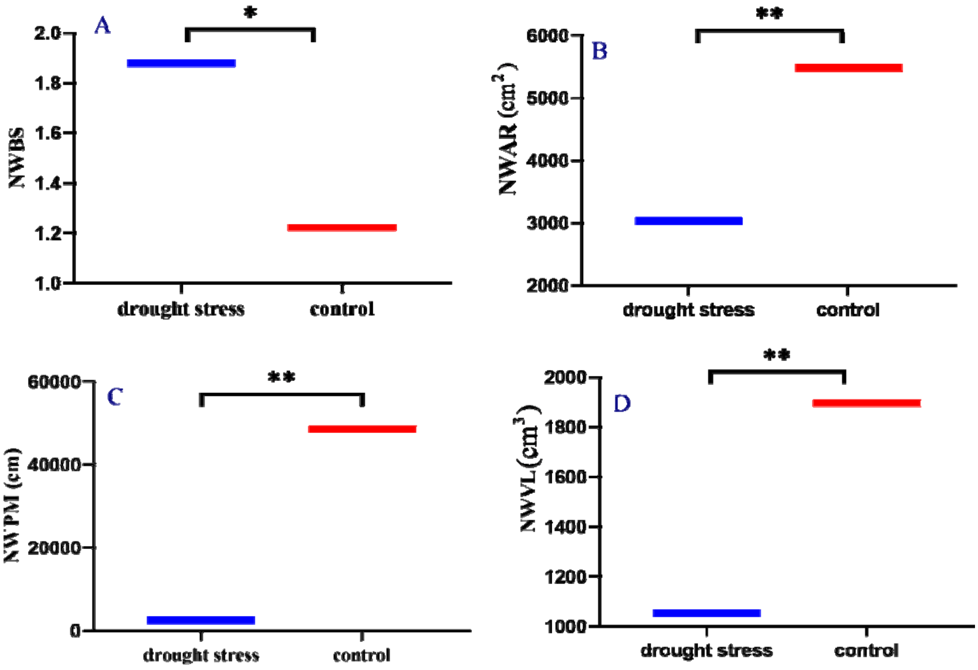

Figure 2. Root architectural variables related to thickness of walnut seedlings under control and drought stress conditions. Roots of walnut seedlings were imaged and analysis by Gia Roots software, 30 d after starting the experiment. NWBS-Network bushiness (A); NWAR- network area (B); NWPM- network perimeter (C) and NWVL-network volume (D). Statistical significance is indicated by **P<0.01; *P<0.05.

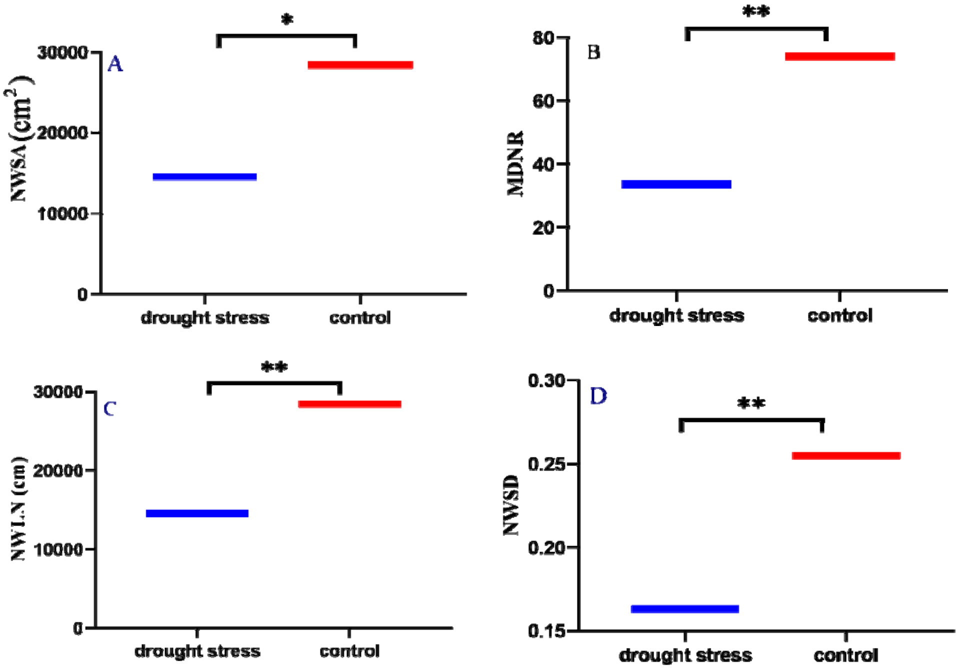

Figure 3. Root architectural variables related to root volume of walnut seedlings 30 d after starting the experiment. NWSA- network surface area (A); MDNR- median number of roots (B); NWLN- network length (C); NWSD- network solidity (D). Statistical significance is indicated by **P<0.01; *P<0.05.

the drought-stressed samples were 3030.81 cm^2, 26034.01cm and 1052.90 cm^3, respectively (Fig.2). On the contrary, the average value of the NWBS index in drought-stressed samples (1.879) was higher than the average value in the control samples (1.222) (Fig.2 A). Furthermore, the NWSA, MDNR and NWLN described the root volume. The values of the mentioned parameters were all higher in the control samples (22634.7 cm^2, 74 and 28411.16 cm, respectively), compared to the drought-stressed samples (12091.4 cm^2, 33.75 and 14570.2 cm, respectively) (Fig 3). Finally, the NWSD index showed values that were significantly different between the control samples and the drought-stressed samples (Fig 3.). No other parameter showed significant differences between the drought-stressed samples and the control (Table 1). The severity or malignity of drought stress prompted different responses by the roots. For instance, under mild drought, the production of fine roots was stimulated by the plant to comply with the mild level of drought. Contrariwise, under more severe drought

Table 1. Root architectural variables that showed no significant difference of walnut seedlings under control and drought stress conditions. The roots of walnut seedlings were imaged and analysis by Gia Roots software, 30 d after starting the experiment.

Traits of roots	Treatment	Mean	t-test (*P-value*)
MXNR	Drought stress	63	0.076
	Control	90.25	
MIEA (cm)	Drought stress	98.46	0.50
	Control	88.61	
ELAX	Drought stress	0.53	0.073
	Control	0.44	
AVRW (cm)	Drought stress	0.26	0.66
	Control	0.25	
NOCC	Drought stress	4.75	0.07
	Control	8.5	
MAEA	Drought stress	184.24	0.36
	Control	201.35	
SPRL (cm^2)	Drought stress	14.19	0.69
	Control	14.88	
NWDP (cm)	Drought stress	197.08	0.80
	Control	196.37	
NWLD	Drought stress	0.32	0.88
	Control	0.30	
NWCA (cm^2)	Drought stress	19190.60	0.49
	Control	21579.21	
NWWI (cm)	Drought stress	113.76	0.69
	Control	120.5	
NWWD	Drought stress	0.576	0.65
	Control	0.614	

stress, there was an increase in the mortality rate of fine roots, and new roots were not produced (Gaul et al. 2008). In accordance with the present results, previous studies have demonstrated that severe levels of drought stress can negatively affect several features of tree roots such as their lifespan, rate of production, biomass and length (Brunner et al. 2009; McCormack et al. 2012; Comas et al. 2013; Brunner et al. 2015). In the Paradox rootstock (*J. hindsii* × *J. regia*) of walnut, root growth was reduced because of drought stress (Jerszurki et al. 2017). In the current study, the control and stressed samples did not differ significantly in terms of the descriptors pertaining to the length of roots, i.e. NWDP and SPRL. These results confirm the findings of previous studies, where the root length was affected only slightly by water shortage (Eissenstat et al. 2000; Bardgett et al. 2014; McCormack et al. 2012). Laboratory conditions showed that the biomass of fine roots decreased under drought stress as a consequence of lower respiration and transpiration rates (Eldhuset et al. 2013; Herzog et al. 2014; Zang et al., 2014).

Anatomical study of roots

The root tip (50 mm) showed qualitative changes in terms of suberin in the control and drought-stressed samples. The exodermis of roots were affected by drought. A greater intensity of suberization was observed in the cell walls of drought-stressed roots, compared to the roots of the control samples (Fig. 4 A and B). In addition, the results of the present study showed that the endodermal cells of drought-stressed samples have more suberin lamellae than those of the control samples (Fig.4 C and D). One of the anatomical responses to drought stress in woody plants is the suberization of roots. This mechanism is a defensive countermeasure against the loss of water from roots (Steudle 2000). This study produced results which confirm the findings of many previous works. For example, several instances of increase in the suberization of roots were recorded in sorghum (*Sorghum bicolor*; Cruz et al. 1992) and *A. deserti* (North & Nobel 1991). Furthermore, Vandeleur et al. (2009) reported an increased level of suberin deposition in the roots of grapevine under drought stress.

Measurement of nutrients

At the end of the experiment, the concentrations of K^+, Ca^{2+}, Mg^{+2} and Cu^{+2} were measured in the drought-stressed samples and the control samples. The concentrations of K^+ and Ca^{2+} in roots were higher among drought-stressed samples than among control samples (Fig. 5 A and B). Despite this, the control group and the drought stress treatment did not cause significant differences in the concentrations of Mg^{+2} and Cu^{+2} (Fig. 5 C and D). Calcium and potassium ions have certain roles in contributing to the resistance against drought stress. For example, increased levels of K^+ in plants, under conditions of drought, can help moderate the regulation of the energy status, besides assisting in osmoregrulation, protein synthesis, homeostasis and charge balance (Marschner 1995). Furthermore, calcium ions play vital roles in the synthesis of cell walls, cell division, repairing damage caused by biotic and abiotic stress, the translocation of nutrients, the moderation of respiration rates and the regulation of metabolism

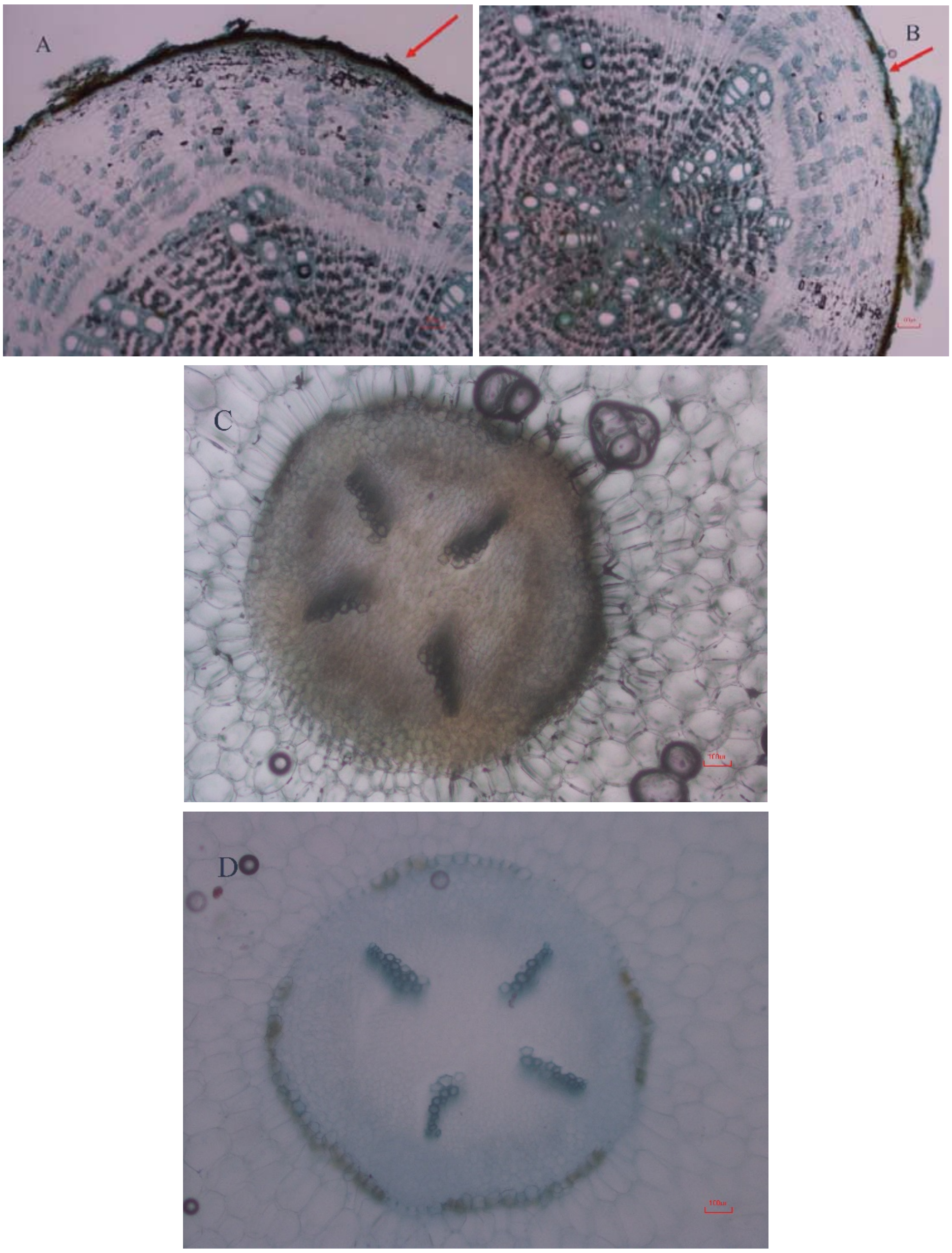

Figure 4. Root suberin lamellae. Cross sections of walnut roots taken 50 mm from the root tip and stained via double-coloring technique (Methyl green and Carmen Zaji) to show suberin lamellae. A and C showed roots from drought stressed walnut and B and D showed roots from control walnut.

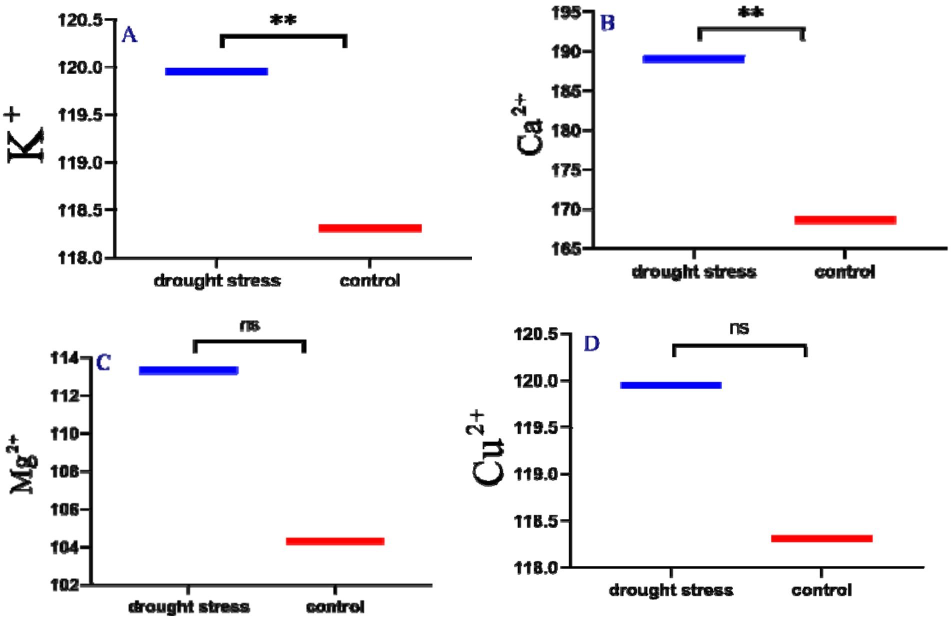

Figure 5. Average K^+ (A), Ca^{2+} (B), Mg^{2+} (C) (mmol kg^{-1} DW) and Cu^{2+} (D) (mg kg^{-1}) concentration in roots of walnut under control and drought stress conditions. Statistical significance is indicated by $^{**}P<0.01$; $^{*}P<0.05$; ns: Non-significant.

(McLaughlin & Wimmer 1999; Hu & Schmidhalter 2005). The findings of the current study are consistent with those reported by Garcia-Sanchez et al. (2007) wherein the concentrations of K^+ and Ca^{2+} increased under drought stress in Carrizo citrange and Cleopatra mandarin.

CONCLUSION

The purpose of the current study was to elaborate on several aspects by which walnut roots respond to drought stress. Under drought stress, several changes occur to the architectural parameters, anatomical features and nutritional indices of roots. The findings of this study support the idea that walnut roots can adapt edaphically by staging different responses to drought stress. Further research is required to examine more closely the links between roots, their responses to drought stress and real-life conditions in orchards. Comparisons can be made between different cultivars and genotypes after experimenting with them similarly. In general, the findings of the current study suggest that breeders can benefit from the descriptions of anatomical specifications in relation to the root response, whereby new rootstocks of walnut can be bred for greater tolerance to drought.

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