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Structural and hydraulic changes in grape shoot xylem under different root zone volumes

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ABSTRACT

Root zone restriction, an efficient cultivation technique in grape production, alters the morphology and function of both the root system and the above-ground parts. The xylem serves as a crucial conduit connecting the root system to the above-ground structures, facilitating the transport of water and nutrients. However, there is currently limited research on how root zone restriction affects the structure and function of the xylem. In this study, two-year-old 'Shine Muscat' grapevines were planted in six containers of varying volumes to investigate the growth and anatomical structure of their shoots, particularly focusing on vessel structure and hydraulic conductivity in the shoots' xylem. The results indicate that a decrease in container volume leads to a decrease in shoot growth and xylem vessel size. Changes in root zone volume significantly affected the water conduction in the upper shoots. The isolation of xylem vessel elements revealed that a reduction in root volume decreased the proportion of wider vessel elements (d > 150 µm) and those with single perforation plates, but increased the inclination angle of the end walls of the vessel elements. Consequently, the restriction of root zone volume resulted in longer and narrower vessels in the shoots, a decrease in ratio of the single perforation plates, and an increase in the end wall tilt angle. These structural changes heightened transport resistance and consequently inhibited shoot growth. This study elucidated how root zone volume influences the growth of grape shoots in terms of changes to the structure of xylem vessels, thereby opening up new avenues for the management of grape cultivation.

KEYWORDS: grape, root zone volume, shoot, xylem, vessel structure, hydraulic conductivity

INTRODUCTION

Grapes are cultivated all over the world and are used for raw food, raisin production and wine making (Torregrosa *et al.*, 2015). In agriculture, pruning and spraying are commonly carried out to regulate plant vigour, which is time-consuming, requires labour, increases management costs, and can pollute the environment. Root zone restriction technology can be used for improving efficiency in cultivation and has been widely used in nectarines (Thomas *et al.*, 1991), apples (Wang *et al.*, 2019a), and grapes (Wang *et al.*, 2008; Wang *et al.*, 1997; Wang *et al.*, 2001). It has been found to suppress the vegetative growth of the aboveground parts by limiting the growth and distribution area of the root system, resulting in a dwarfed plant (Wang *et al.*, 2001). This reduces management costs and avoids the environmental pollution issues associated with the chemical regulation of plant vigour. Moreover, compared with conventional cultivation, vines cultivated using root zone restriction have been found to bear fruit earlier, and to produce better yield and grape quality (Wang *et al.*, 2001; Xie *et al.*, 2009), thus meeting grapevine production quality and efficiency goals.

The aboveground and underground parts of a plant are interdependent, thus forming a unified entity. When the length of the plant's main root is restricted, aboveground growth is significantly inhibited, which manifests itself with the plant being dwarfed, the stem becoming thinner, the leaf area reducing, and the root-to-shoot ratio decreasing or increasing (Rieger *et al.*, 1994; Guo *et al.*, 2014; Zakaria *et al.*, 2020). In research on young poplar trees, the dry weight of their root system decreased by 70 % compared to the control group after root zone restriction treatment. At the same time, because the growth of the root system was restricted, the growth of shoots and yield also decreased (Carmi *et al.*, 1983; Blake *et al.*, 1983), which is consistent with Meon (2001) findings on the root system of starfruit. Previous studies have also found that a reduction in cultivation volume causes the root system to become shorter and thicker (Ronchi *et al.*, 2006). Additionally, the smaller volume also reduced the vitality of the root system, leading to insufficient absorption of water and nutrients by the roots, which in turn further decreased the plant's photosynthetic rate and inhibited the growth of the plant (Xie *et al.*, 2009; Alan *et al.*, 1991; Wang *et al.*, 2001).

Being the primary channel for water and mineral transport in plants, xylem vessels play an important role in the exchange of substances between the underground and aboveground parts of plants, their main function being to transport water and mineral elements. The water transport capacity of xylem is significantly influenced by the morphological structure of the vessels, which, in turn, impacts the vigour of the plant (Wang *et al.*, 2001). Therefore, studying the morphological structure of vessels is essential for understanding the mechanisms underlying stunted plant growth under restricted root conditions. In their research on the xylem vessel structure of three peach tree rootstocks of varying vigour, Tombesi *et al.* (2010) found that the rootstocks exhibiting more vigorous growth had larger vessel diameters and lower vessel densities than in the dwarf varieties. This structural advantage conferred a higher theoretical hydraulic conductivity to the vigorous rootstocks. In their comparative study of the xylem vessel structure of apple dwarfing and non-dwarfing rootstocks, Bauerle *et al.* (2011) found a positive correlation between xylem vessel density and the degree of post-graft tree dwarfing: specifically, lower xylem vessel density was associated with weaker tree growth vigour. In the case of pears, Chen *et al.* (2015) dissected one-year-old branches from 15 types of dwarf and standard pear rootstocks and compared the length, diameter, and density of the xylem vessel elements, revealing that the vessels in dwarf pears were significantly smaller than those in standard pears. In their comparison of vines grafted onto five different rootstocks, de Souza *et al.* (2022) found that the high-vigour rootstocks (3309C and Kober 5BB) promoted the most vigorous vegetative growth and the grapevine showed the highest petiole specific hydraulic conductivity ($K_{petiole}$), as well as the highest frequency of large vessels in the stem xylem. Dejong *et al.* (2006) elucidated a relationship between dwarf rootstocks and hydraulic conductivity, noting that the root and stem of the dwarf rootstocks constrained the water supply to the aerial parts of the plant.

To date, comprehensive research on how varying root zone volumes affects the structure and function of xylem is scarce. Consequently, in this study, selected grapevines were subjected to different root zone volumes, and a comparative analysis of shoot growth, vessel morphological characteristics, and hydraulic conductivity was performed. By investigating the interrelationships between these factors and shoot growth from an anatomical perspective, this study established a foundation for further research into the effects of root zone volume on the growth mechanisms of grape shoots.

MATERIALS AND METHODS

1. Plant materials

The experiment was conducted at the vineyard of Wenhui Road Campus of Yangzhou University from March 2023 to November 2023. Two-year-old 'Shine Muscat' grape seedlings with uniform growth were selected and planted in six containers of different volumes (Figure 1). The containers comprised plastic root controllers with a diameter and height of 55 cm × 50 cm (118 L), 50 cm × 45 cm (88 L), 45 cm × 40 cm (63 L), 40 cm × 35 cm (43 L), 35 cm × 30 cm (28 L) and 30 cm × 25 cm (18 L) respectively. There were seven replicates for each of the volume treatments (hereafter referred to as T1, T2, T3, T4, T5 and T6 respectively) with one shoot per pot. All the pots were irrigated once the volumetric soil water content within the root zone 0.15 m below the soil surface had decreased to ~60 % of field capacity. The irrigation water was applied in the following amounts: 7 L, 5 L and 3.5 L and 2.5 L and 1.5 L and 1 L in T1, T2, T3, T4, T5, and T6 respectively.

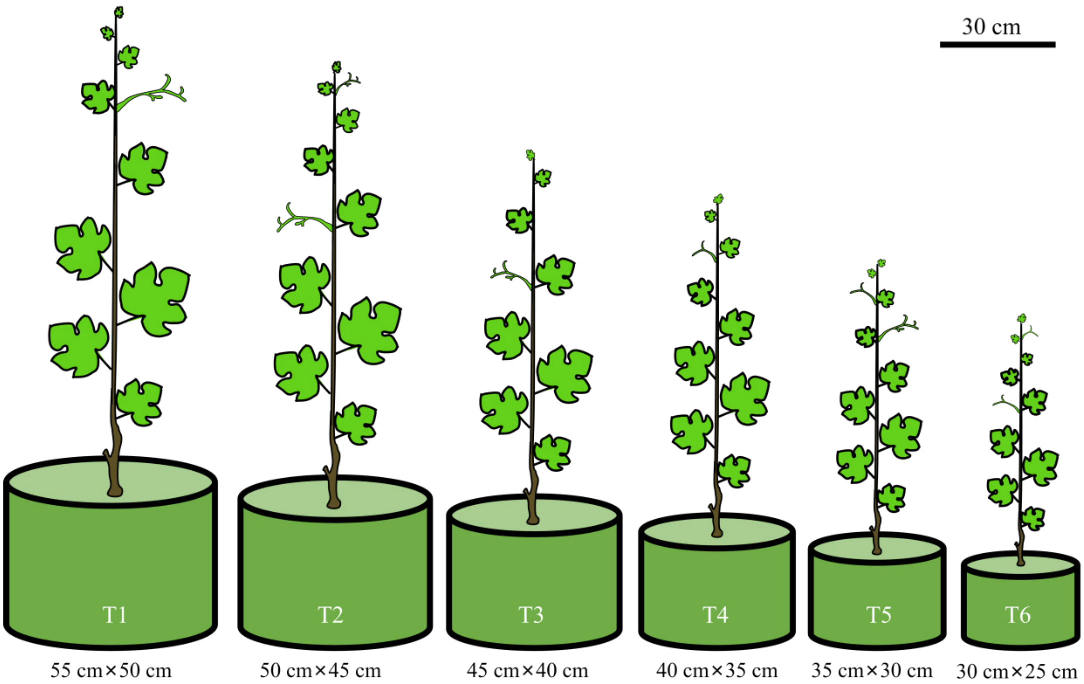


FIGURE 1. Grape plants growing in different root zone volumes.

Grape variety: two-year-old ' Shine Muscat '. Container material: plastic root controller. Grapes were planted in six different containers with the following volumes (diameter × height): 55 cm × 50 cm (118 L, T1), 50 cm × 45 cm (88 L, T2), 45 cm × 40 cm (63 L, T3), 40 cm × 35 cm (43 L, T4), 35 cm × 30 cm (28 L, T5) and 30 cm × 25 cm (18 L, T6) respectively. The scale bar is 30 cm.

2. Shoot growth measurements

The shoot growth of 'Shine Muscat' grape varieties was measured from April to October on seven shoots per treatment. Shoot length was measured every 6 days, and the diameter of the second internode at the basal part of the shoot was recorded with a vernier caliper every 12 days. The average internode length was calculated and the total number of internodes per shoot per treatment were measured at the end of the growing season.

3. Paraffin section

2-3 cm-long fresh stem segment of the middle of the internode were cut off from the upper parts (the fifth internode from the shoot tip downward), middle parts (mid-shoot internode) and lower parts (the fifth internode from the base of shoot upward) of the shoots, and this was was carried out in triplicate for each treatment. The cut-off sections were fixed in FAA (5 mL 38 % formaldehyde, 5 mL glacial acetic acid, and 90 mL 70 % alcohol) fixing solution (Zhang *et al.*, 2021). A conventional paraffin section method was carried out, as well as staining with saffron-solid green, sealing with neutral gum, and observation and photo taking with a microscope (Cai *et al.,* 2024). In the xylem, five square regions with an area of 0.1 cm × 0.1 cm were randomly selected using Image J. The wand (tracing) tool in Image J was used to select the vessel in a region, and the threshold was adjusted until the entire vessel was selected to obtain the area of a single vessel. Vessel density and the ratio of vessel area to xylem area were calculated as follows:

$$\text{Vessel density} = \text{number of vessels/xylem area.} \qquad \text{(Eq. 1)}$$

$$\text{Ratio of the vessel area to xylem} = \text{vessel area} \times \text{vessel density} \times 100\ \% \qquad \text{(Eq. 2)}$$

Pith diameter, xylem thickness, and phloem thickness were calculated by first determining the semi-major (a_1, µm) and semi-minor (b_1, µm) axes of pith, pith and xylem sum, and pith, xylem and phloem sum using the ellipse tool in Image J (Schneider *et al.*, 2012). The diameter of pulp (dp), the diameter of the sum of pulp and xylem (dpx), and the sum of pulp, xylem and phloem (dpxp) were calculated respectively (Equation 5; see Section 5 of Methods). Xylem thickness and phloem thickness were each calculated as follows:

$$\text{Xylem thickness} = \text{dpx-dp} \qquad \text{(Eq. 3)}$$

$$\text{Phloem thickness} = \text{dpxp-dpx} \qquad \text{(Eq. 4)}$$

4. Xylem separation

Xylem segregation tests were modified and prepared according to Patil *et al.* (2019). 2-3 cm-long stem segments were cut from the the upper parts (the fifth internode from the shoot tip downward), middle parts (mid-shoot internode) and lower parts (the fifth internode from the base of shoot upward) of the shoots respectively, and only the xylem was cut into small segments measuring 1.0 cm × 0.3 cm × 0.3 cm (length × width × height respectively). The xylem samples were put into a glass vial in a segregation solution comprising 10 % chromic acid and 10 % nitric acid, and the vial was isolated in an incubator at 54 °C for 7 hours. The segregation solution was changed several times. Once the sample had softened, it was rinsed repeatedly with water to remove the acid. Finally, the separated xylem samples were stored in 50 % ethanol for later use. The samples were observed, dyed with 1 % safranin O, and temporary loading was carried out. The stems were observed under a microscope (Axio Imager, Zeiss, Germany), and the length and width of the xylem vessels were measured using the straight line tool of Image J. Three stems were selected per treatment, the length and width of 100 vessel were randomly measured in each stem, and the average value was calculated. The distribution of the vessel elements with tail, end wall inclination and perforated plate was calculated.

5. Xylem hydraulic conductivity

In order to estimate the hydraulic characteristics of the xylem, Image J was used to select xylem regions from the stem cross-sectional images, and the number of corresponding vessels (*n*) was measured. Semi-major (a_1, μm) and semi-minor (b_1, μm) axes of xylem vessels were determined using the ellipse tool in Image J (Schneider *et al.*, 2012). The idealised vessel diameter (d_1, μm), as the equivalent circle diameter of the vessels, was obtained using Equation 5 (White & Majdalani, 2006).

$$d_1 = \left(32\text{x}\frac{(a_1 \text{x} b_1)^3}{(a_1{}^2+b_1{}^2)}\right)^{\frac{1}{4}} \qquad \text{(Eq. 5)}$$

Stem hydraulic conductivity K_{hp} (kg/m/s per MPa) was calculated using the Hagen-Poiseuille equation (Tyree *et al.*, 1991):

$$K_{hp} = \sum_1^n \frac{\pi\rho}{n\eta} d_1{}^4 \qquad \text{(Eq. 6)}$$

where ρ is the density of water at 20 °C (998.205 kg·m^{-3}); η is the viscosity coefficient of water at 20 °C (1.002 × 10^{-9} MPa·s), d_1 is the xylem vessel radius and *n* is the number of vessels.

6. Data analysis

All data were statistically analysed using SPSS software. The results were subjected to one-way ANOVA, and the significance level was set to α = 0.05.

RESULTS

1. Effects of different root zone volume on shoot growth

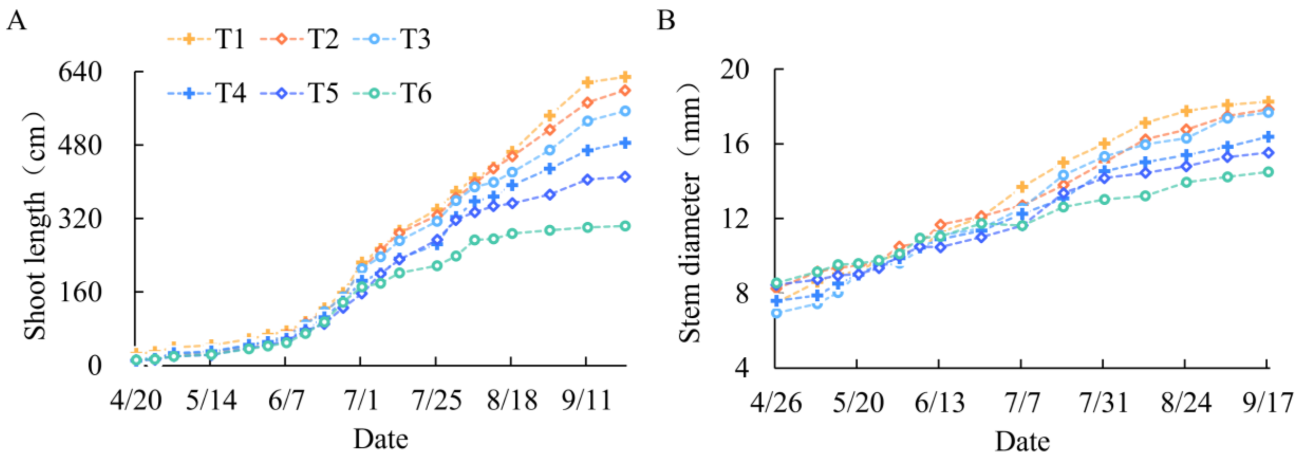
The growth trends of the shoots in the different treatments were consistent, following an S-shaped growth curve over time (Figure 2A). In the later stages of the experiment, the growth of the shoots was vigorous, with significant differences observed between the treatments. As the root volume decreased, the length of the shoots decreased. T1 had the longest shoot length, reaching a maximum of 628.7 cm, while T6 had the shortest shoot length (304.0 cm). The stem diameters followed the same trend as the length (Figure 2B). On 17 September, the stem diameters in T1, T2 and T3 were significantly greater than in T4, T5 and T6. The stem diameters were 18.3 mm, 17.9 mm, 17.7 mm, 16.4 mm, 15.5 mm, and 14.5 mm for T1, T2, T3, T4, T5 and T6 respectively. Thus, the larger root volume treatments showed significantly longer shoot lengths and smaller diameters than the smaller volumes. These results show that the root restriction treatment regulated the vegetative growth of the vine to produce a short shoot. A very small root volume seriously inhibited the growth of shoots, even causing the shoots to stop growing prematurely.

The number of internodes decreased with the reduction in root volume (Figure 2C). T4, T5 and T6 had significantly fewer internodes compared to T1, T2 and T3. The average internode lengths for T1 to T6 were 8.7 cm, 9.7 cm, 8.7 cm, 8.0 cm, 8.1 cm, and 7.9 cm respectively, T2 having the longest average length and T6 the shortest, with no clear pattern observed among the treatments (Figure 2D). Root volume was found to affect the number of internodes, but its impact on internode length was not evident. The reduction in root volume led to a decrease in number of internodes.

2. Anatomical structure of the xylem

The pith diameter, xylem thickness and phloem thickness in the lower part of the shoots decreased with the decrease in root zone volume (Table 1). Specifically, the pith diameter and phloem thickness of T1 were significantly greater than those of T5 and T6. In addition, The T1 xylem was 278.3 μm, 378.8 μm, 591.9 μm, 760.6 μm and 893.6 μm thicker than the T2, T3, T4, T5 and T6 xylems respectively. The ratio of xylem to phloem thickness also decreased gradually with the increase in root zone restriction, and the T1, T2 and T3 ratios were significantly higher than those of the other treatments. The ratios of all the treatments were higher than 3.0. The trend associated with the growth of the middle part of the shoots was similar to that of the lower part: pith diameter, xylem thickness, phloem thickness and xylem to phloem thickness ratio all decreased with the increase in root zone volume restriction. It is worth noting that phloem development was also significantly affected by root zone volume: T6 phloem in particular was 426.0 μm, 430.2 μm, 364.8 μm, 277.1 μm, and 100.1 μm narrower than that of T1, T2, T3, T4 and T5 respectively. In addition, the ratio of xylem thickness to phloem thickness in the middle of the shoots was lower than that in the lower part, with ratios of between 2.0 and 3.0. Further analysis of the upper part of the shoots showed that pith diameter, xylem thickness, phloem thickness and xylem to phloem ratio were similar to those in the middle and lower parts of the shoot, and they all decreased with the intensification of root zone volume restriction. It is worth noting that the T6 xylem thickness to phloem thickness ratio was lower than 2.0, which is significantly lower than that of the other treatments. In conclusion, the increase in root zone restriction inhibited the growth and development of shoot pith, xylem and phloem, with xylem development being the most sensitive to root zone volume. This sensitivity eventually led to a mismatch in the growth rates of xylem and phloem, resulting in a decrease in the ratio of xylem thickness to phloem thickness.

The cross-sectional microstructures of the upper, middle, and lower parts of grapevine shoots subject to six different



	4/20	5/2	5/14	5/26	6/7	6/19	7/1	7/13	7/25	8/6	8/18	8/30	9/11	9/23
T1	a	a	a	a	a	a	a	a	a	a	a	a	a	a
T2	b	b	b	b	ab	ab	ab	ab	ab	ab	a	ab	ab	ab
T3	b	b	b	b	ab	ab	ab	ab	ab	ab	ab	bc	bc	b
T4	b	b	b	ab	bc	ab	bc	b	bc	bc	bc	cd	cd	c
T5	b	b	b	b	bc	b	c	c	c	c	c	d	d	d
T6	b	b	b	b	c	b	c	c	d	d	d	e	e	e

	4/26	5/8	5/20	6/1	6/13	6/25	7/7	7/19	7/31	8/12	8/24	9/5	9/17
T1	a	a	a	a	a	a	a	a	a	a	a	a	a
T2	a	a	a	a	a	a	a	a	ab	ab	ab	a	a
T3	a	a	a	a	a	ab	a	a	ab	ab	abc	ab	a
T4	a	a	a	a	a	a	a	a	ab	ab	bcd	bc	b
T5	a	a	a	a	a	a	a	a	ab	b	cd	c	bc
T6	a	a	a	a	a	a	a	a	b	b	d	c	c

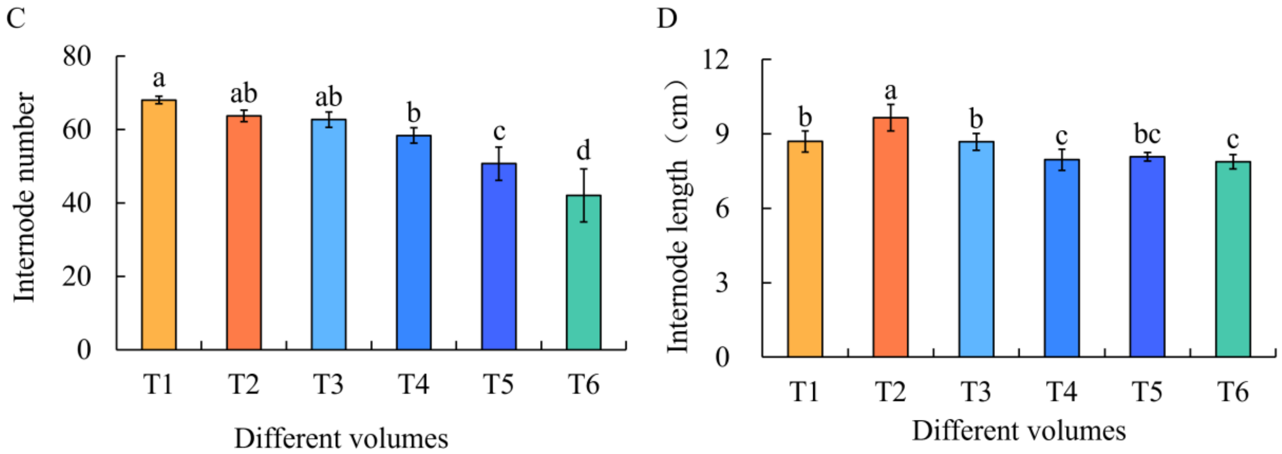


FIGURE 2. Growth pattern of shoots under different root zone volume treatments.

A: length of the shoot; B: diameter of the stem. C: number of internodes; D length of internodes. The table below panels A and B gives the significance labelling of shoot length and stem thickness between different root zone volume treatments. Different lowercase letters represent significant differences at $p < 0.05$ between different treatments.

treatments were observed. The vessels were found to be circular, elliptical and polygonal in shape, and they were all dispersed within the rays (Figures 3–4). There were significant differences in the structure of the vessels between the root volume treatments. T2 exhibited the largest vessel diameter, area, and total vessel area to xylem area ratio (116.5 μm, 10219.6 μm^2, and 31 % respectively; Table 2), while T6 showed the smallest vessel diameter, area, and total vessel area to xylem area ratio, as well as the highest vessel density. The diameter of the vessels in the middle of the shoots gradually decreased as root restriction increased. T1 had the largest vessel diameter (146.1 μm), and no significant differences were observed between T1 and T2, or between T3, T4, T5 and T6. The differences in vessel area between the treatments followed a similar pattern to those in vessel diameter, with T1 showing the largest vessel area (15081.8 μm^2) and T6 the smallest (8002.7 μm^2). Vessel density showed an opposite trend to vessel diameter and area, T6 having the highest density. T1 achieved the highest total vessel area to xylem area ratio (35 %). The results obtained for vessel diameter and upper stem area were consistent with those in the lower part, T2 exhibiting the largest vessel diameter and area in both parts (92.7 μm and 7389.8 μm^2 respectively). Regarding vessel density, T6 had the highest value with 82.5 pieces/mm^2, and T2 the lowest with 29.7 pieces/mm^2. Regarding the ratio total vessel area to xylem area, T1 had the highest ratio with 25 %, and T6 the lowest with 10 %. Thus in conclusion, high root volume restriction reduced the vessel size and total vessel area to xylem area ratio; it increased vessel density and significantly affected vessel size in the xylem, especially in the upper stem.

TABLE 1. Pith thickness, and xylem and phloem thickness and their ratio in different root zone volume treatments.

		T1	T2	T3	T4	T5	T6
pith diameter (μm)	Lower	1678.6±43.2 a	1675.5±131.9 a	1526.8±74.7 b	1518.9±30.1 b	1343.3±57.2 c	1259.1±52.3 c
	Middle	2254.2±73.4 a	2214.7±87.1 ab	2099.7±30.0 bc	2061.5±81.8 bc	1997.5±70.0 c	1980.0±69.1 c
	Upper	3145.3±109.7 a	3044.1±87.8 a	2439.5±164.5 b	2243.0±79.0 c	2230.7±84.7 c	1565.8±104.8 d
xylem thickness (μm)	Lower	3514.5±204.2 a	3236.2±137.6 b	3138.7±144.5 bc	2922.6±67.6 cd	2753.9±92.0 de	2620.9±136.0 e
	Middle	2692.3±29.7 a	2629.6±135.3 a	2356.5±5.0 b	2047.3±35.6 c	1493.9±27.8 d	1245.3±49.9 e
	Upper	2175.0±185.7 a	1743.1±92.0 b	1126.8±130.9 c	1060.1±45.8 c	782.4±106.3 d	467.9±75.2 e
phloem thickness z(μm)	Lower	913.9±38.9 a	873.2±41.3 ab	856.8±38.5 ab	856.0±12.2 ab	848.8±18.1 b	835.2±24.8 b
	Middle	958.7±52.2 a	935.8±28.1 ab	897.5±26.8 b	809.7±36.8 c	632.7±23.7 d	532.7±13.3 e
	Upper	759.9±118.7 a	661.6±92.0 a	466.2±130.9 b	465.1±45.8 b	377.9±106.3 bc	338.7±75.2 c
xylem thickness/ phloem thickness	Lower	3.9±0.2 a	3.7±0.04 a	3.7±0.1 a	3.4±0.03 b	3.2±0.1 bc	3.1±0.1 c
	Middle	2.8±0.1 a	2.8±0.1 a	2.6±0.1 b	2.5±0.1 b	2.4±0.1 c	2.3±0.04 c
	Upper	2.9±0.2 a	2.6±0.1 ab	2.4±0.1 bc	2.3±0.1 c	2.1±0.1c	1.4±0.2 d

Different letters indicate the significant difference of pith thickness, xylem, phloem thickness and ratio of xylem thickness to phloem thickness in the same part of different treatments ($p < 0.05$).

TABLE 2. Shoot vessel element diameter, area, density and ratio in each root zone volume treatments.

		T1	T2	T3	T4	T5	T6
Vessel diameter (μm)	Lower	87.8±2.9 c	116.5±6.1 a	104.1±1.5 b	103.8±2.3 b	99.6±2.6 b	87.6±5.3 c
	Middle	146.1±4.9 a	140.1±8.1 a	116.9±2.7 b	119.9±3.7 b	105.6±8.2 bc	99.3±7.9 wc
	Upper	82.0±2.3 a	92.7±9.3 a	68.9±1.8 b	58.3±6.1 c	49.6±2.5 c	35.7±3.5 d
Vessel area (μm²)	Lower	7144.8±1604.4 ab	10219.6±1370.2 a	9431.2±706.8 a	8392.3±2183.3 ab	7936.3±442.8 ab	6041.0±278.9 b
	Middle	15081.819±1920.1 a	14171.1±1539.0 ab	10980.3±461.3 bc	11322.1±2015.4 bc	8099.7±110.9 c	8002.7±224.1 c
	Upper	6479.4±695.5 a	7389.8±808.1 a	3816.9±61.7 b	2964.2±137.8 bc	2024.7±307.8 cd	1244.2±36.3 d
Vessel density (pieces/ mm²)	Lower	41.4±3.3 a	30.0±2.1 b	29.1±1.0 b	32.4±2.8 b	31.6±2.6 b	42.2±3.1 a
	Middle	23.0±0.8 d	22.5± 1.3 d	29.4±1.4 b	23.7±1.5 cd	28.5±2.7 bc	37.7±3.5 a
	Upper	38.0±5.6 cd	29.7±0.1 d	44.5±2.9 c	40.0±0.4 cd	67.8±5.0 b	82.5±7.6
Ratio of vessel area (%)	Lower	30±1.0 ab	31±1.9 a	27±1.7 ab	27±1.5 ab	25±1.9 b	26±2.6 b
	Middle	35±6.3 a	32± 1.7 ab	32±2.9 ab	27±0.4 bc	23±2.0 c	31±0.8 abc
	Upper	25± 2.3 a	22±2.8 a	17±0.9 b	12±1.9 c	13±0.8 bc	10±1.6 c

Different letters indicate the significant differences in vessel element structure in the same part of different treatments ($p < 0.05$).

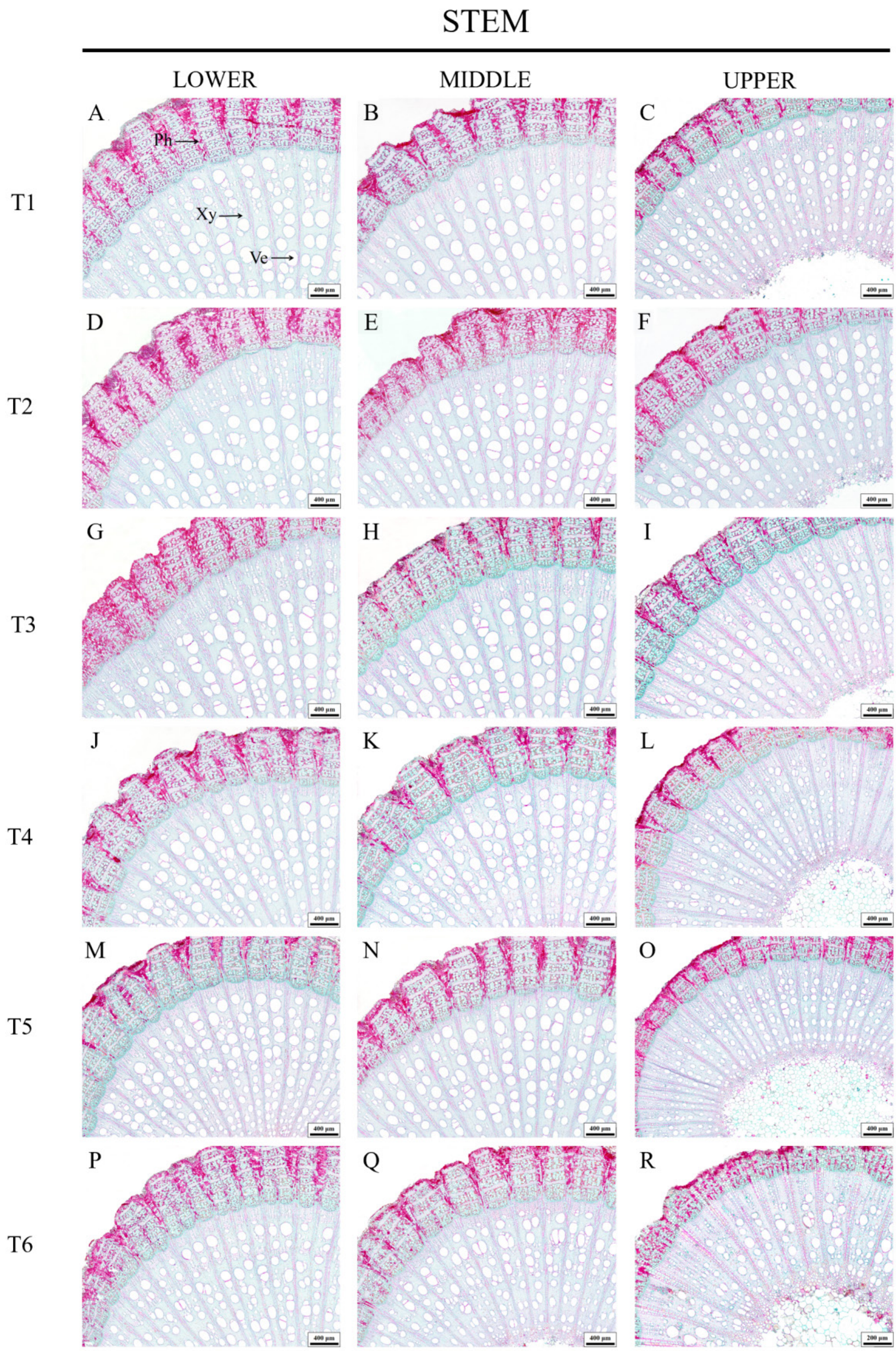


FIGURE 3. Cross sections of grape stems under different root zone volume treatments.

A, D, G, J, M, P: lower part of stem; B, E, H, K, N, Q: middle part of stem; C, F, H, L, O, R: upper part of stem. Xy = xylem; Ph = phloem; Ve = vessel.

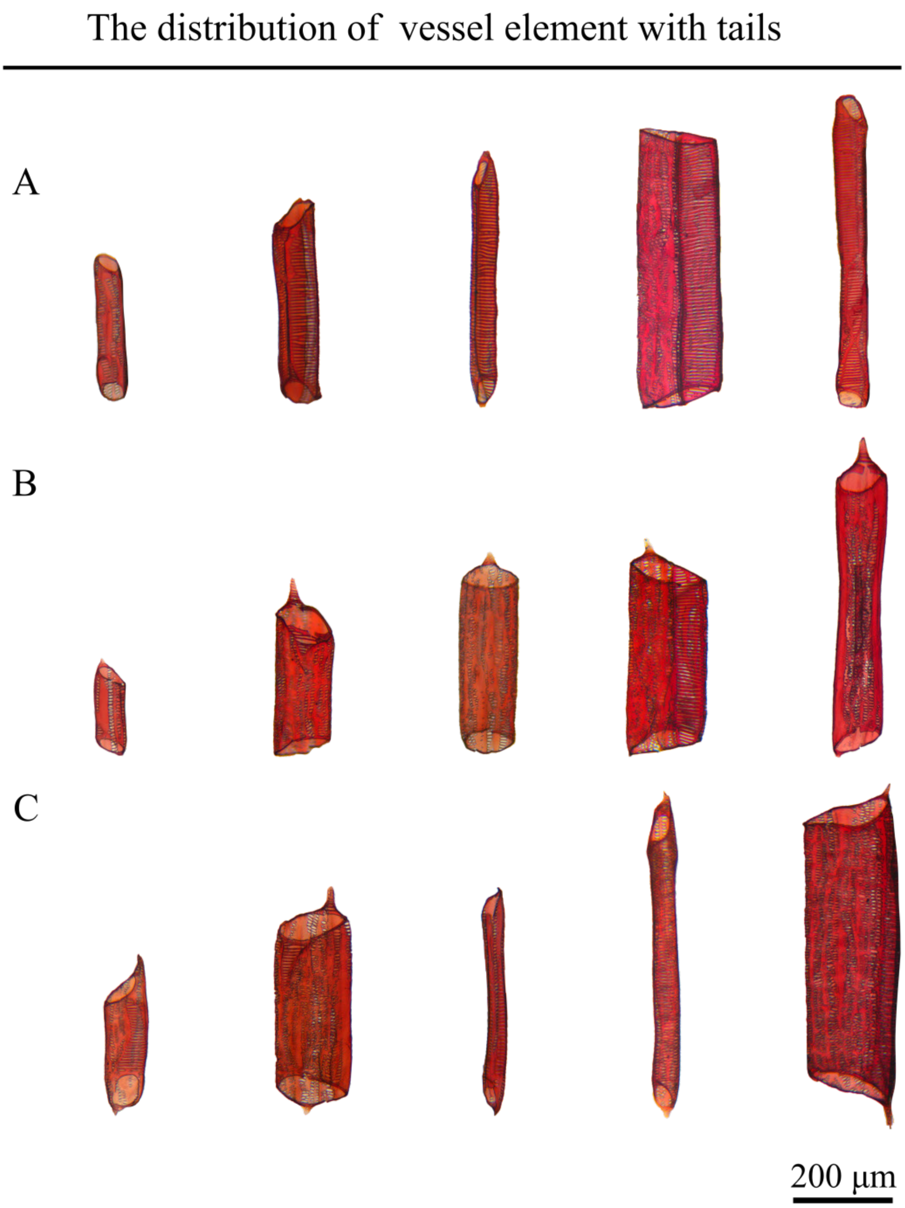


FIGURE 4. The types of vessel elements with tails in the stem under different root zone volume treatments.

A: Vessel elements without tails at both ends, B: Vessel elements with a tail at one end, and C: Vessel elements with tails at both ends. The scale bar is 200 µm.

3. Morphological characteristics of vessel elements

3.1. Vessel type

The vessel elements observed in the different volume treatments comprised predominantly uniform cylindrical cells (Figures 4–6). Based on the presence or not of tails, they were categorised into three types: i) both ends with tails, ii) one end with a tail, and iii) both ends without tails. The tail types of the vessel elements differed depending on volume treatment: the shoots mostly consisted of the type without tails at either end, followed by the type with a tail at one end, and the type with tails at both ends was the least common in the larger volume treatments (Figures 7A–C). The volume treatments were ranked according to the proportion of vessels with tails at both ends in the lower stem: T1 = T2 < T3 < T4 < T6 < T5, increasing gradually from 12 % (T1 and T2) to 25 % T5) (Figure 7A). The vessel elements in the middle and upper stems exhibited a similar pattern to the lower stem (except for those in the T5 middle stem). In the case of the type with a tail at one end, the highest proportions were obtained by T6 in the lower part of the shoot (43 %) and T1in the middle part (42 %), but no significant differences were observed between the treatments in the upper part of the shoot (Figures 7A–C). The proportions of the type without tails at either end in the lower part of the shoot gradually decreased with volume treatment from 54 % to 34 % in the following order: T1 > T3 > T2 > T4 > T5 > T6. The vessel elements in the middle and upper stems followed the same pattern. When examining different parts of the shoot, no significant differences were noted in tail types of the vessel elements between the middle and lower parts; however, a clear difference was observed

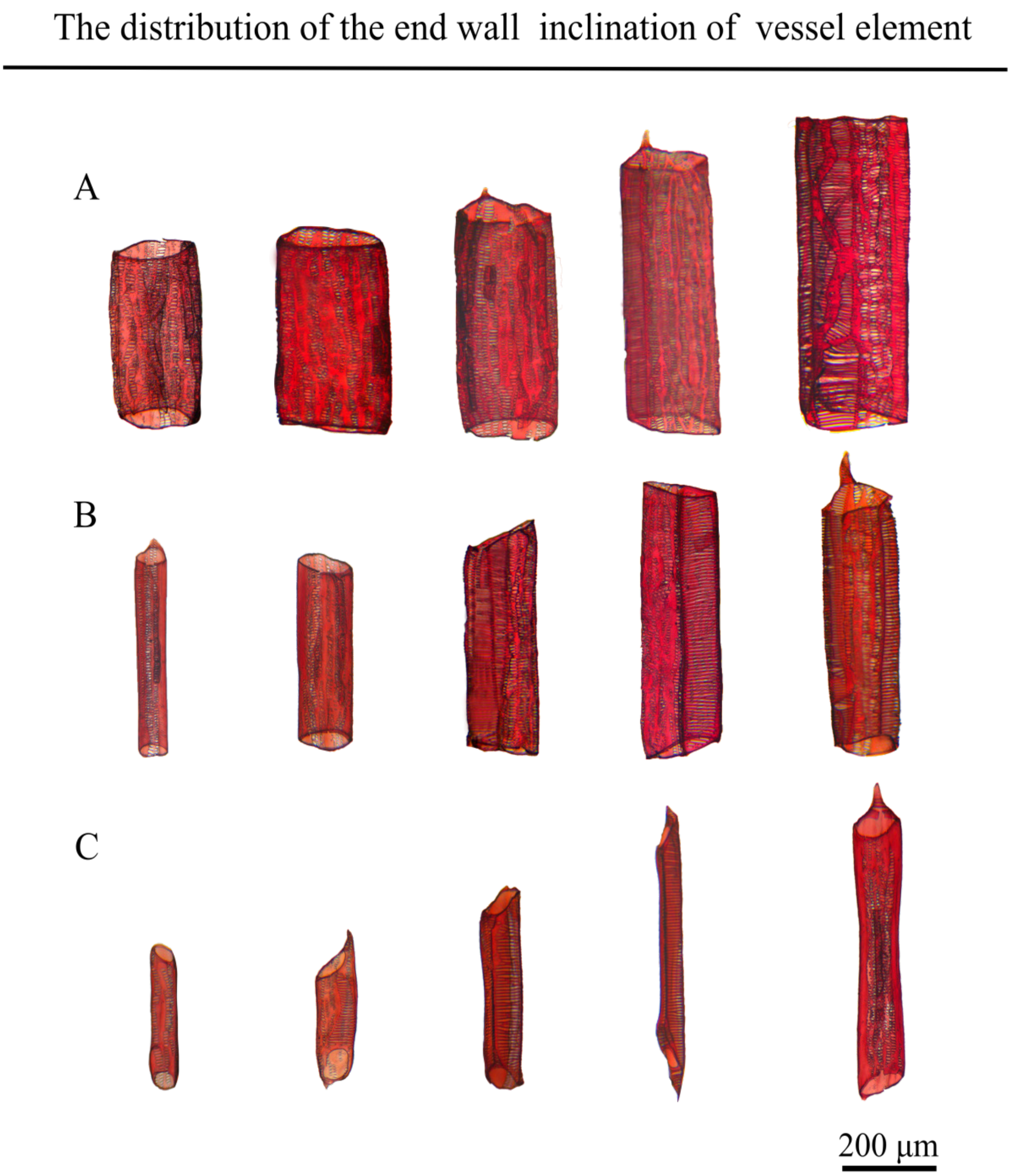


FIGURE 5. The types of end wall inclination in stem vessel elements under different root zone volume treatments.

A: Vessel elements with both ends horizontal, B: Vessel elements with one end inclined and the other end horizontal, C: Vessel elements with both ends inclined. The scale bar is 200 μm.

in the upper part, where the proportion of vessel elements with tails at both ends was higher than that in the middle and lower parts.

The end walls of the vessel elements could be divided into three types according to their inclination: i) both ends inclined, ii) one end inclined, and iii) both ends horizontal (Figure 5). The predominant type observed in all treatments was the one with both ends inclined, followed by the type with one end inclined, while the type with both ends horizontal was the least common (Figure 7D–F). The proportion of both ends inclined in the lower part of the shoots across various volume treatments increased in the following order: T1 < T2 < T3 < T5 < T4 < T6, with T6 showing the highest proportion with 84 % (Figure 7D). The vessel elements in the middle and upper parts followed a similar pattern (Figure 7E–F). Regarding the type with one end inclined, a decrease in volume corresponded to a gradual reduction in its proportion in the upper part of the shoot (Figure 7D). Meanwhile, T2 showed the highest proportion of this type (28 %) in the middle part of the shoot, and T5 the highest proportion (18 %) in the lower part (Figure 7E–F). The proportion of the type with both ends horizontal in the lower part of the shoot decreased from 21 % to 2 % with volume treatment in the order of T1 > T2 > T3 > T4 > T5 > T6 (Figure 7D). The middle and upper parts of the vessel elements followed a similar pattern (Figure 7E–F). Examination of different parts of the shoot revealed variations in the distribution of the vessel elements. Regarding both ends inclined, the lower part had the highest proportion, while the upper part had the lowest. Conversely, the upper part had the highest proportion of the type with one end inclined, and the lower part had the lowest. Meanwhile, the upper part had the highest proportion of the type with both ends horizontal, and the lower part had the lowest (Figure 7D–F).

The vessel elements could be divided into three types based on the pattern of their perforation plates: i) single perforation at both ends, ii) single perforation at one end, and iii) multiple perforations at both ends (Figure 6). All volume treatments were mainly of the type with a single perforation at both ends, followed by the type with single perforation at one end, and the type with multiple perforations at both ends was the least common (Figure 7G–I). The proportion of single perforation at both ends of the vessel elements decreased with the decrease in root zone volume, and T1 was significantly higher than T6 in all three parts of the shoot. Out of all three parts of the shoot, the upper part had the highest proportion of both the type with a single perforation at one end and that with multiple perforations at both ends.

These results indicate that the morphology and proportion of vessel elements are influenced by root volume: in general, as root zone volume decreased, the proportion of vessel elements with both ends without tails and both ends with a single perforation decreased. and the proportion of vessel elements with both ends inclined increased.

3.2. Vessel size

3.2.1. Length and width

In the lower part of the shoot, the length of the vessel elements were found to range from 128.5 µm to 684.5 µm, and the width ranged from 14.11 µm to 204.0 µm (Table 3). The vessel elements in T6 were the longest, reaching up to 447.2 µm in length, but they had the narrowest average width (only 76.2 µm). The length range of the vessel elements in the middle part of the shoot was even wider than that in the lower part (167.8 to 961.6 µm), and the width range also increased (17.6 µm to 217.9 µm). In this part, T1 had the shortest vessel elements, with a length of 489.9 µm, but the widest width, reaching 128.3 µm. Meanwhile, T6 had the longest average length of vessel elements (538.4 µm), and the narrowest average width (86.8 µm). Further observation of the upper part of the shoot revealed that the length range of the vessel elements was between 175.3 µm and 1022.3 µm, and the width range was between 7.8 µm and 237.4 µm. In this part, T6 had the longest average length of vessel elements (516.1 µm) and the narrowest average width (35.8 µm). By contrast, T1's vessel elements were the shortest (482.4 µm), and T2's the widest (92.7 µm). Thus, overall, as root volume decreased, the vessel elements tended to become longer and narrower.

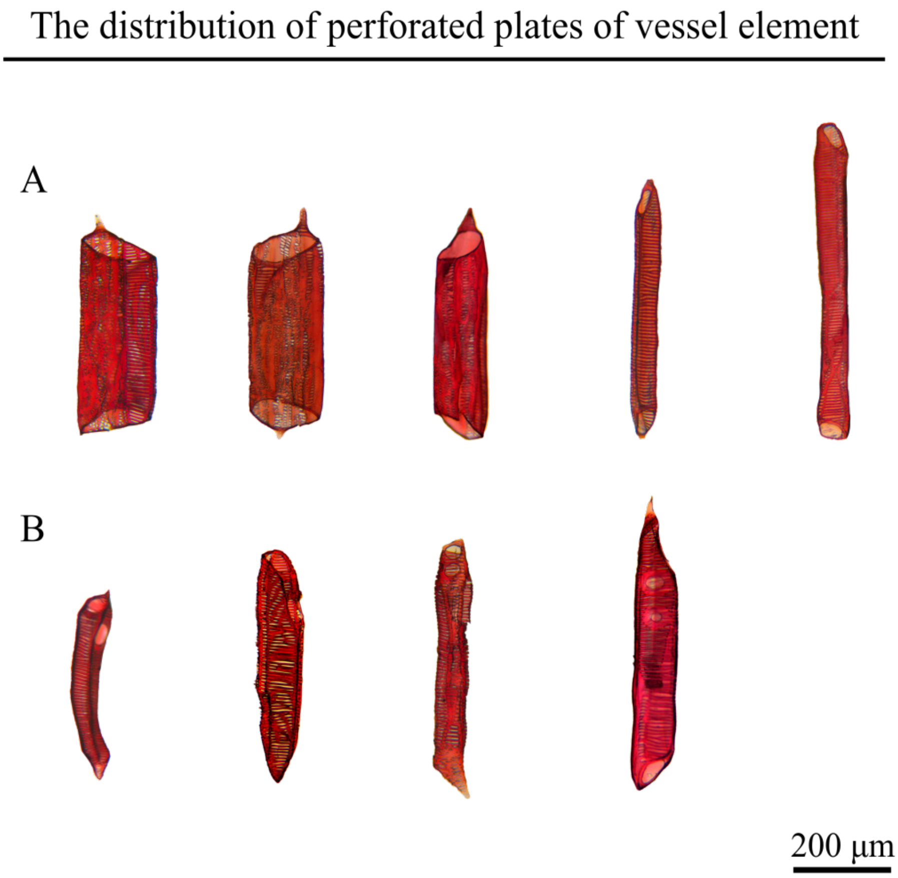


FIGURE 6. The types of perforation plates in stem vessel elements under different root zone volume treatments.

A: Vessel elements with single perforation plates at both ends, B: Vessel elements with a single perforation plate at one end and double perforation plates at the other end. The scale bar is 200 µm.

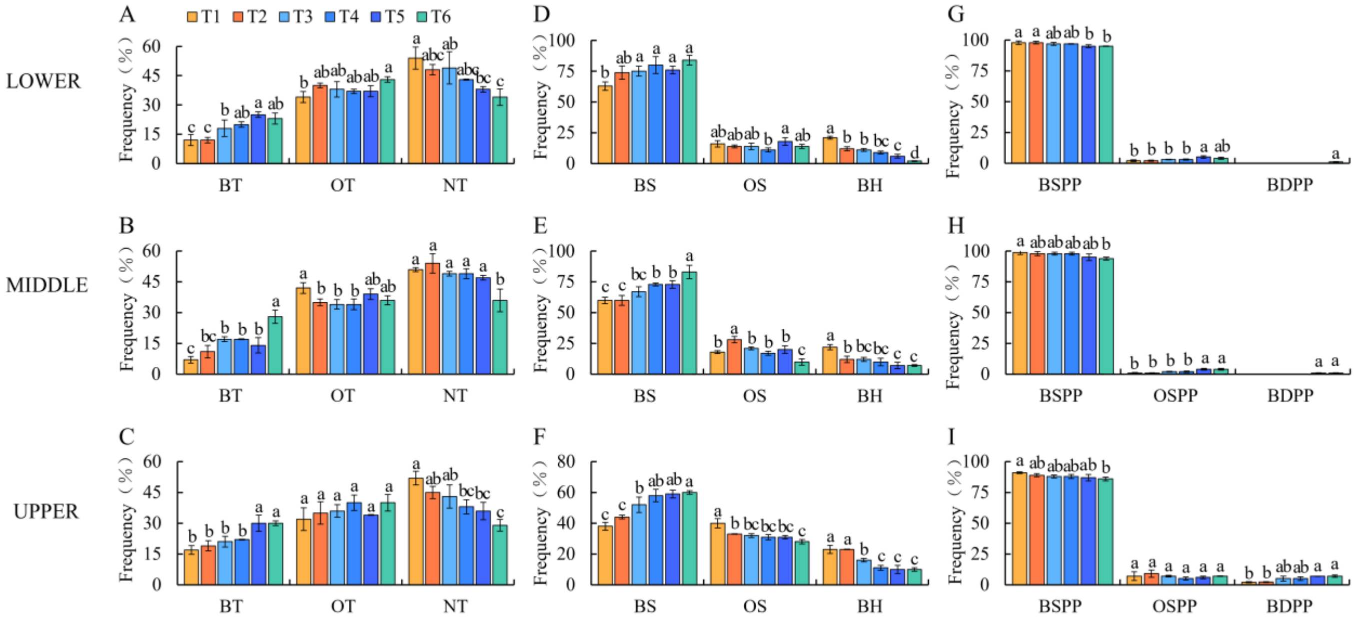


FIGURE 7. Distribution frequency of stem vessel element types under different root zone volume treatments.

A, B and C: distribution of the end wall inclination of stem vessel elements; D, E and F: distribution of stem vessel elements with tails; D, H and I: distribution of perforated plates of stem vessel elements. A, D and F: lower part of the shoots; B, E and H: middle part of the shoots; C, F and I: upper part of the shoots. BT = Both tails, OT = One tail, NT = No tail, BS = Both end walls are sloping, OS = One end wall is sloping, BH = Both end walls are horizontal, BSPP = Both ends have a single perforated plate, OSPP = One end has a single perforated plate, and BDPP = Both ends have a compound perforated plate. Different letters indicate the significant difference of the types of vessel element in the same part of different treatments ($p < 0.05$).

TABLE 3. The length and width of shoot vessel elements ineach root zone volume treatment.

			T1	T2	T3	T4	T5	T6
Length of vessel element	Average length (μm)	Lower	439.2±6.7 a	417.3±10.0 bc	406.6±3.7 c	433.4±13.1 ab	438.7±15.2 a	447.2±9.5 a
		Middle	489.9±25.8 b	514.6±29.3 ab	511.4±15.0 ab	526.0±19.3 ab	528.7±5.8 ab	538.4±28.0 a
		Upper	482.4±1.4 b	491.6±17.0 ab	491.1±17.1ab	496.8±19.9 ab	506.5±3.4 ab	516.1±20.0 a
	Length range	Lower	238.5-597.2	224.1-643.4	128.5-647.1	182.1-684.5	193.0-596.4	236.4-635.2
		Middle	245.4-722.5	246.1-725.2	216.6-860.8	167.8-961.6	259.2-779.1	257.7-762.0
		Upper	175.3-753.1	301.9-891.9	332.0-854.6	460.7-923.4	249.4-1022.2	248.9-920.4
Width of vessel element	Average width (μm)	Lower	79.9±7.2 bc	101.2±2.3 a	93.0±3.0 ab	87.8±4.1 abc	88.2±4.6 abc	76.2±9.3 c
		Middle	128.3±1.3 a	120.4±4.0 a	103.8±2.8 b	105.8±2.2 b	89.9±6.8 c	86.8±4.8 c
		Upper	82.5±2.6 a	92.7±8.2 a	68.9±6.0 b	58.5±5.8 bc	50.1±0.6 c	35.8±0.8 d
	Width range	Lower	16.1-198.6	23.7-204.0	17.3-203.5	14.1-197.8	20.2-185.2	15.3-180.1
		Middle	22.4-200.8	27.8-217.9	18.9-192.8	17.6-207.3	29.0-183.9	19.9-203.1
		Upper	10.3-237.4	13.7-195.6	8.2-146.5	12.3-116.5	10.8-107.7	7.2-87.5

Different letters indicate the significant difference of the length and width of vessel element in the same part of different treatments ($p < 0.05$).

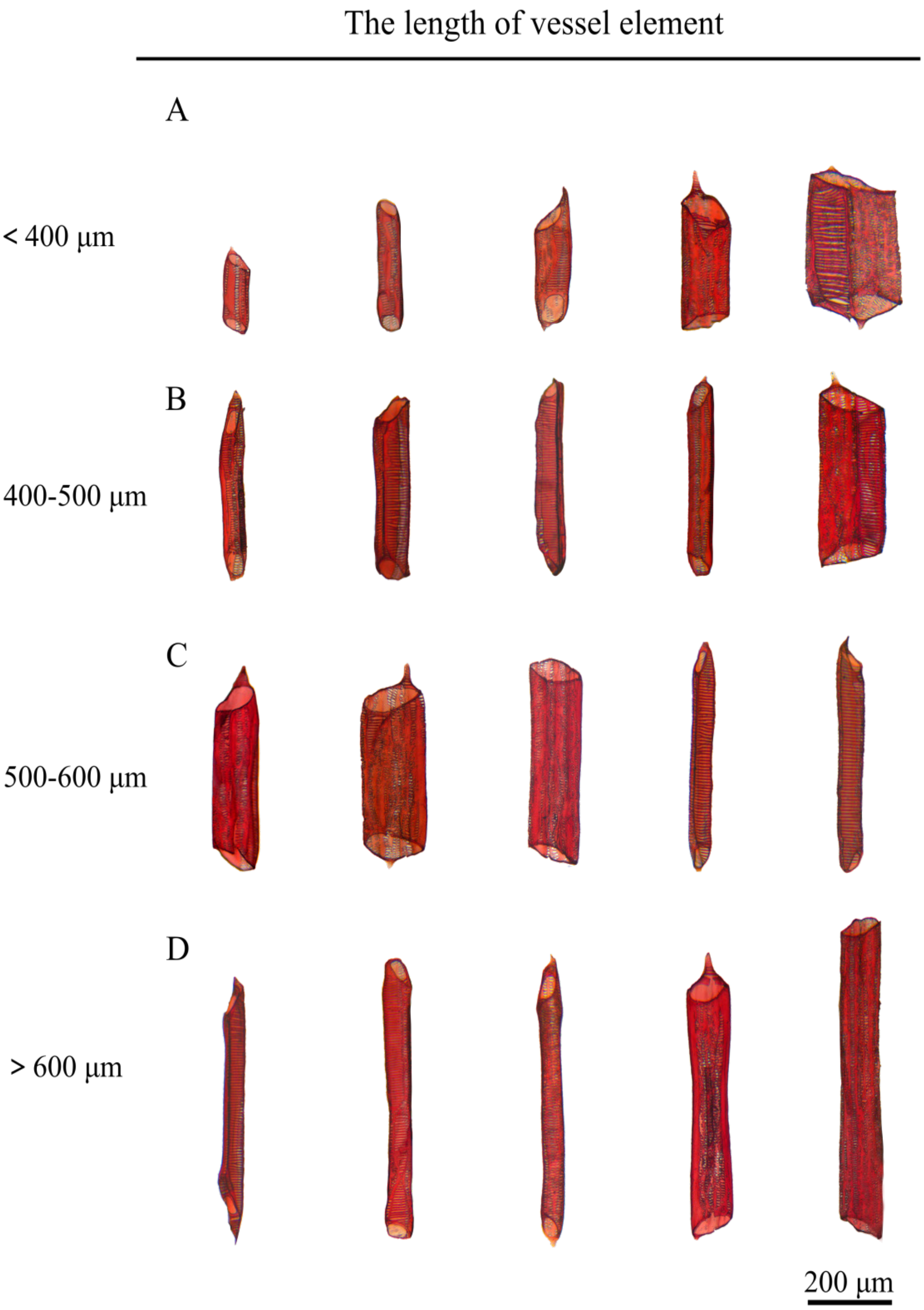


FIGURE 8. Stem vessel element lengths under different root zone volume treatments.

A: vessel elements with a length of less than 400 μm; B: vessel elements with a length of 400-500 μm; C: vessel elements with a length of 500-600 μm; D: vessel elements with a length greater than 600 μm. The scale bar is 200 μm.

3.2.2. Distribution frequency of length and width

The lengths and widths of the vessel elements fell into four groups respectively as follows: i) < 400 μm, ii) 400-500 μm, iii) 500-600 μm, and iv) > 600 μm (length; Figure 8), and i) < 50 μm, ii) 50-100 μm, iii) 100-150 μm, and iv) > 150 μm (width; Figure 9).

Through statistical analysis of the distribution frequency of the length and width of the vessel elements, the lengths of the vessel elements were found to be mainly distributed within a range of 400-600 μm (Figure 10 A–C). In the first length group (< 400 μm), the distribution frequencies of the vessel elements first decreased and then increased with the decrease in root zone volume, and T1 showed the highest frequency. In the 400-500 μm group, T4 showed the highest vessel element distribution frequency (41 %) in the lower part of the shoots, and T6 the lowest (24 %). The distribution frequency in the middle and upper part of the shoots increased with the decrease in root zone volume, and the distribution frequency in T6 was significantly higher than in T1. In the 500-600 μm group, the distribution frequency of the vessel elements in the lower part of the shoots increased with the decrease in root

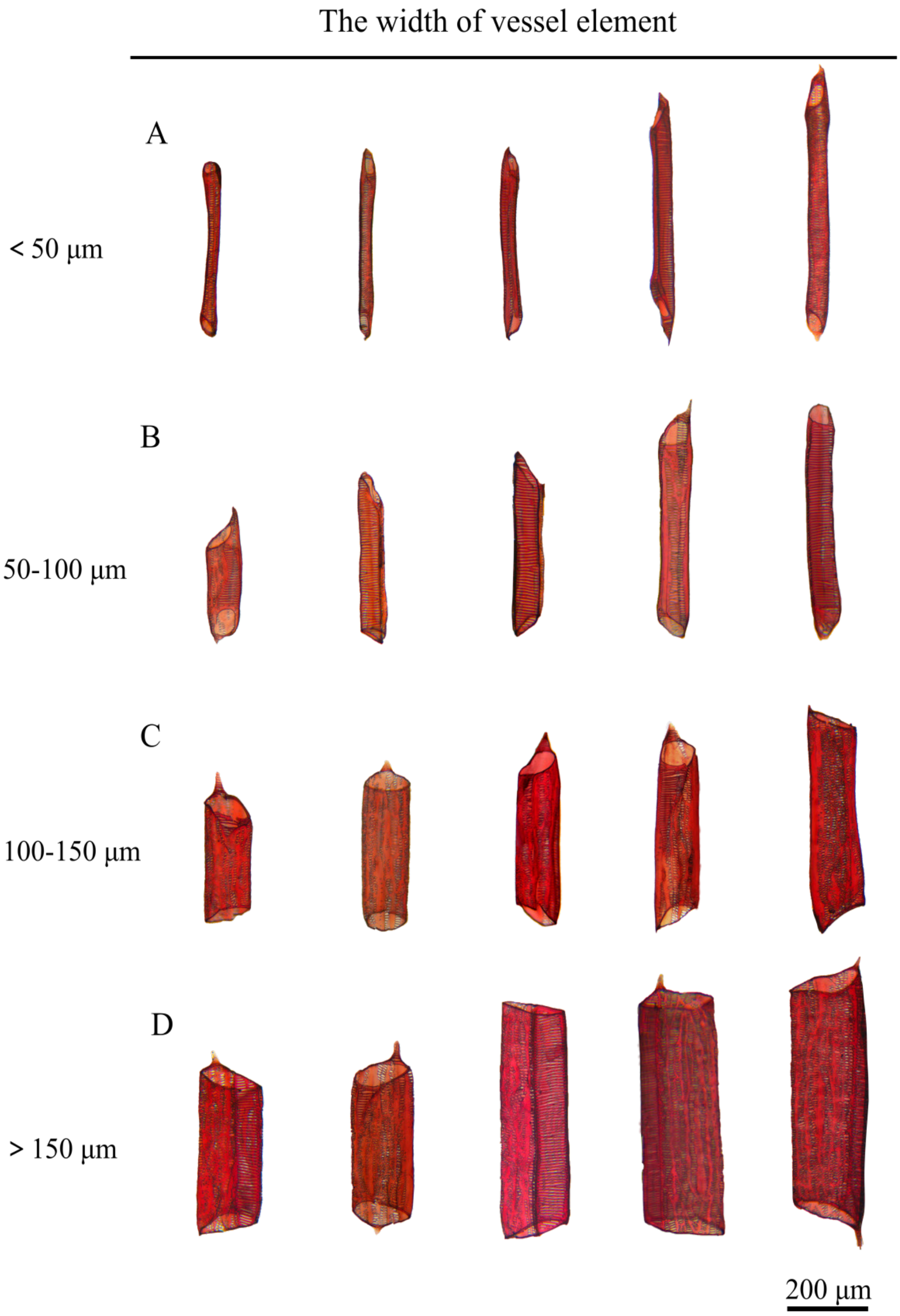


FIGURE 9. Stem vessel element widths under different root zone volume treatments.

A: vessel elements with a width of less than 50 μm; B: vessel elements with a width of 50-100 μm; C: vessel elements with a width of 100-150 μm; D: vessel elements with a width greater than 150 μm. The scale bar is 200 μm.

zone volume: from 27 % in T1 to 42 % in T6. Meanwhile, the distribution frequency in the middle of shoots increased first and then decreased, the highest being 40 % in T2 and the lowest 24 % in T6. The same trend was observed for the upper part of the shoots in this group. Finally, in the > 600 μm group, T2 showed the highest frequency in the lower part of the shoots and T4 the lowest. The distribution frequency in the middle of the shoots increased with the decrease in root zone volume: from 7 % in T1 to 18 % in T6. The distribution frequency of T1 vessel elements in the upper part of the shoots reached 15 %.

Regarding vessel element width, the distribution frequency of the vessel elements with a width of < 50 μm increased with the decrease in root zone volume, with T1 showing a significantly higher freqency than that of other treatments (Figure 10D–F). In the lower part of the shoots, the highest distribution frequency of the vessel elements with a width of 50-100 μm was found in T2 (37 %), and the lowest in T6 (30 %). The distribution frequency in the middle of shoots increased with the decrease in root zone volume: from 21 % in T1 to 30 % in T6. In the 100-150 μm width group, the distribution frequency in the lower and middle parts of the shoots decreased with the increase in root zone volume, and reached 31 % in the upper part of shoots in T2. The vessel elements with a width of > 150 µm showed a distribution frequency that decreased with the decrease in root zone volume, with the highest distribution frequency in the middle part of the shoot, followed by the lower part, and the lowest in the upper part. The results show that both the length and width distribution frequency of the vessel elements were influenced by both root zone volume and their position in the shoot. The decrease in the root zone volume resulted in a decrease in the distribution frequency of wide vessel elements (> 150 µm), and an increase in the distribution frequency of long vessel elements (> 600 µm) in the shoots. In addition, the distribution frequency of the broad vessel elements (> 150 µm) increased first and then decreased the higher their position in the shoot.

4. Hydraulic conductivity of shoots

There were significant differences in the water conduction rates of the shoots under different volume treatments, with an increasing trend with the increase in root volume (Table 4). Specifically, the water conduction rate in the middle part of the shoots exhibited a decreasing trend across the different volume treatments, T1 having the highest water conduction rate, reaching 24.8 × 10^{-3} kg·m·s^{-1}·MPa^{-1}, and T6 the lowest, with 6.4 × 10^{-3} kg·m·s^{-1}·MPa^{-1}. Thus, as the root volume decreased, the water conduction capacity in the middle part of the shoots gradually diminished. The trend observed for the water conduction rate in the upper part of the shoots is consistent with that in the middle part, where T1 had the highest water conduction rate, with 7.3 × 10^{-3} kg·m·s^{-1}·MPa^{-1}. In the lower part of the shoots, T2 treatment had the highest water conduction rate, with 13.5 × 10^{-3} kg·m·s^{-1}·MPa^{-1}. While there were no significant differences between T1, T3, and T4, T6 had the lowest water conduction rate, with 5.2 × 10^{-3} kg·m·s^{-1}·MPa^{-1}. Additionally, the water conduction rates differed depending on the part of the shoots, the middle part having the strongest water conduction capacity and the upper part the weakest. These results show that root volume significantly influenced the water conduction capacity of the shoots; specifically, a smaller root volume led to a greater effect on the water conductance of the upper part.

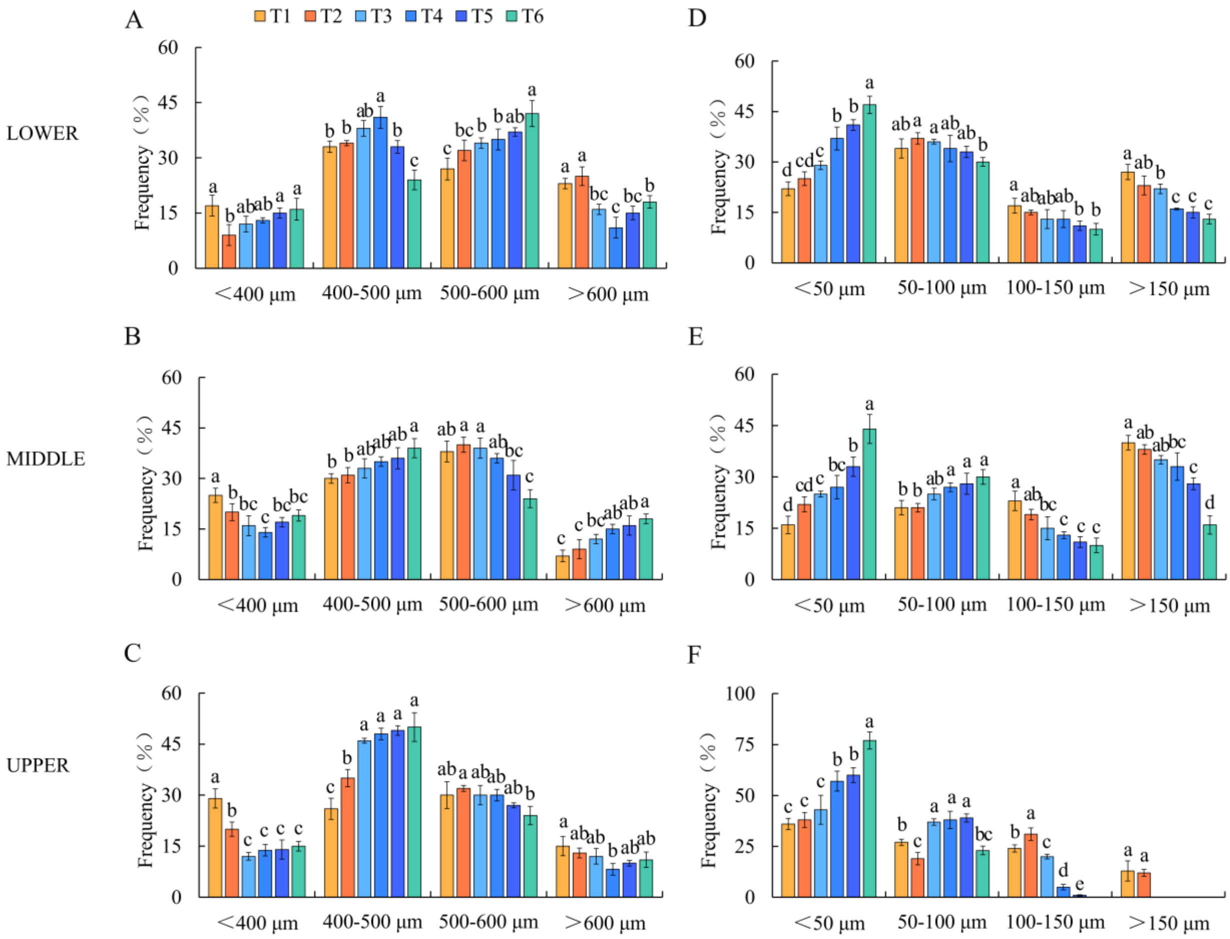


FIGURE 10. Distribution frequency of stem vessel element lengths and widths under different root zone volume treatments.

A, B and C: frequency of the length distribution of stem vessel elements; D, E and F: frequency of the width distribution of stem vessel elements. A and D: lower part of the shoot; B and E: middle of the shoot; C and F: upper part of the shoot. Different letters indicate the significant differences between different treatments of the distribution of the length and width of vessel elements in the same shoot part ($p < 0.05$).

DISCUSSION

Through their research on wheat, Wheeldon *et al.* (2021) proposed that plants can sense matrix volume and actively regulate shoot growth. In the present study, when the root zone volume of the grape seedlings "Shine Muscat" was limited, the growth of shoots was effectively inhibited: the length and diameter of the shoots were reduced and the phenomenon of plant dwarfing was observed. This finding is consistent with previous research on other fruit trees, in which root zone restriction caused shoots to become thinner and shorter (Wang *et al.*, 2019b; Webster *et al.*, 2000), and leaf area (Zaharah *et al.*, 2009) and photosynthetic rate to decrease. Similar trends have been observed in studies of other grape varieties (Jupa *et al.*, 2016; Wang *et al.*, 2001). All these results point to the significant effect of root zone volume restriction on the growth of aboveground parts of plants. In our study, the number of internodes on the shoots decreased with the decrease in root zone volume, and T1 had 26 more segments than T6. The longest internode length was observed in T2, and the shortest in T6. These results suggest that plant dwarfing may be mainly caused by a decrease in the number of internode shoots. The rate of cell formation in the cambium is of primary importance in determining stem thickening, and plants regulate their cambium activity according to environmental conditions (such as photoperiod, temperature, and availability of water and nutrients) (Larson, 1994). Therefore, it was necessary to observe and analyse the anatomical structure of the transverse section of the stem in this study, for which paraffin section technology was used. Because the cambium was indistinguishable in the transverse section of the stem vascular bundle, it was considered as a part of the phloem. The decrease in root zone volume resulted in a decrease in pith diameter, xylem thickness and phloem thickness. Xylem growth and development was more sensitive to the change in root zone volume, and xylem thickness in the middle and lower parts of the shoots was greater than pith diameter and phloem thickness. Therefore, the decrease in xylem thickness mainly contributed to the decrease in shoot thickness. The decrease in xylem and phloem thickness associated with the decrease in root zone volume may be due to the influence of cambium activities and a decrease in proliferation rate of the cambium cells, especially those that differentiate into the xylem.

Particular to vascular plants, xylem is a tissue that provides mechanical support and transports water and nutrients in plants, and its transport function is mainly affected by the morphological structure of the vessels (Myburg *et al.*, 2001). Therefore, we analysed the changes in xylem structure and water transport function of shoots under different root zone volume treatments on 'Shine Muscat' grapevine, which are discussed here. We observed that the volume of root zone volume restriction affected the xylem vessel structure of the grapevine. Specifically, the smaller root zone volume caused the shoot vessel elements to become narrower, with the highest relative abundance of the 50-100 µm-diameter vessels in the lower part of the shoot, and the highest relative abundance of the < 50 µm-diameter vessels in the middle and upper parts of the shoot. In addition, the size of the vessels at the top of the shoots was most affected by the volume of the root zone, and there were significant differences in the diameter of the vessel between T1, T2 and other treatments; this indicates that the rate of change in vessel size at the top of the stem was significantly higher than that at the bottom of the stem. This result is similar to the results of previous studies on woody plants (Petit *et al.*, 2014; Petit *et al.*, 2010). According to the Hagen-Poiseuille equation, conductivity is proportional to the fourth power of the vessel radius; therefore, the larger the vessel the stronger the conductivity. In this study, whether at the top, middle or bottom of the shoot, vessel diameter in the small volume treatments was significantly smaller than in large volumes; thus, the theoretical water transport capacity in small volume treatments is also significantly lower than in large volume treatments. Tombesi *et al.* (2010) reported that phenotypic differences in xylem anatomical characteristics between rootstock genotypes directly affect the water transport capacity of this rootstock. In their study on Pinot noir, de Souza *et al.* (2022) found that the specific hydraulic conductivity of the petiole in different genotypes of rootstocks was closely related to the structure of the petiole xylem, which is similar to the results of our study. In addition, Li *et al.* (2024) and Cai *et al.* (2024) also reported that GA-treated grape berries promoted vascular bundle growth and improved water transport capacity. These results indicate that the xylem structure changes induced by root zone volume treatment may affect the water conductivity of shoots. The water environment may play an important role in this phenomenon. Relatively stable soil water conditions, especially deep water conditions, are conducive to the development of large-diameter xylem vessels in roots and shoots (Wang *et al.*, 2022; Hacke *et al.*, 2017). In this study, the soil in the large volume treatments was deeper than that in the small volume treatments; given that summer is the period of rapid shoot growth, higher air temperatures and shallower soil depths led to drastic changes in soil moisture in the small volume treatment. It can be seen that the fluctuation in soil water caused by the smaller root zone volume is a factor limiting the size of the vessel. In addition, studies have shown that although larger vessels can improve water transport efficiency, they are also susceptible to embolism (Mencuccini *et al.*, 2007; Jacobsen *et al.*, 2019; Liu *et al.*, 2019); therefore, in order to to reduce this risk, plants may reduce the diameter and area of the vessels in their shoots at the expense of water transport efficiency. In the present study, we also found that as the volume of the root zone decreased vessel density increased, while the total area of the vessel in the xylem decreased. This suggests that, under root zone constraints, plants may compensate for the decline in the water transport capacity of a single vessel by increasing the number of vessels. This structural adjustment may help sustain shoot growth and development when water supply is limited (Preston *et al.*, 2006).

In addition to the above-mentioned factors, the type of plant vessel element may also affect its water transport efficiency. Some studies have reported that the vessel element length directly determines the extent of water transport resistance and the rate of water transport, and the resistance of long-distance water transport has an extremely significant linear relationship with the reciprocal length of the vessel (Fang, 2003). Koch *et al.* (2004) believe that long vessels can increase the consistency and fluidity of water transport, but water is subject to increased resistance during long-distance transport, which reduces transport efficiency. In the present study, it was found that with the decrease in root zone volume, small-volume vessel elements became longer and narrower, especially the vessel elements with a diameter of > 600 µm. Furthermore, the distribution ratio of small-volume treatment vessel elements in the top, middle and bottom of the shoots was higher than that of large-volume treatment vessel elements. There is mutual restriction between water transport efficiency and resistance to the cavitation of trees; *i.e.*, the stronger the water transport ability, the weaker the resistance to cavitation (Tyree *et al.*, 1994). Therefore, the increase in the length and proportion of the small-volume treatment vessels may be a compensation for the decrease in water transport capacity caused by the smaller diameter of the vessels by increasing the safety of water transport. Liu *et al.* (2016) put forward the view that ductal elements evolved without tails rather than with tails, and that the formation and elongation of end-tails were conducive to improving water transport efficiency. After the root zone volume was reduced, the ratio of inclined vessel element types at both ends in the small-volume treatments was higher than that in the top, middle and bottom parts of the shoots in the large-volume treatments, which indicates that the small-volume treatments improved water transport efficiency by preserving the original vessel characteristics. Studies have shown that the larger the inclination angle of the end wall of the vessel elements and the larger the number of perforated plates, the higher the water transport resistance (Zou *et al.*, 2021; Li & Zheng, 2014). In our study, the proportions of inclined types and multiple perforations at both ends of small-volume treatment vessels are higher than those of large-volume treatment vessels, which may increase the contact area between vessels, and thereby increase water transport resistance and affect water transport efficiency. However, the increase in proportion of multiple perforation vessel element types in the small-volume treatments is not entirely without benefits: the presence of multiple perforations allows water to bypass the blocked pipe and continue to flow along other vessels (Dong *et al.*, 2015), a mechanism that may play a key role in plant adaptation to poor environmental conditions. This study provides an initial understanding of the impact of root volume limitation on the xylem structure and water transport in the stems of grapevines, as well as the potential effects of these changes on plant growth and productivity. Future research should further explore the molecular mechanisms behind the adjustments to xylem structure under root zone restrictions and how these alterations affect plant growth and adaptability.

CONCLUSION

In this study, the reduction in root zone volume inhibited shoot growth. The pith diameter, xylem thickness and phloem thickness of the shoots decreased with the decrease in root zone volume, and the xylem was found to be the most sensitive to changes in root zone volume. In addition, the decrease in root zone volume led to the narrowing of the shoot vessel and had the greatest effect on the upper part of the shoot, where the density of the vessel increased while its total area decreased, and the specific water conductivity of the xylem decreased. The xylem vessel elements were isolated and analyzed for type, size and distribution frequenc. The proportion of inclined end wall type was found to increase and that of the single perforated type to decrease. tVessel length increased while its width decreased, and the relative abundance of long vessels (d > 500 µm) and thin vessels (lower part of shoots: 50-100 µm, middle and upper shoots: d < 50 µm) increased. These vessel changes increased water transport resistance, further reducing water transport capacity. Therefore, by inhibiting xylem growth and development, root zone volume restriction leads to a significant decrease in vessel diameter and an increase in the proportion of long vessels, thereby reducing water transport capacity and the growth rate of shoots. These studies could contribute to a more comprehensive understanding of the application potential of root restriction technology in grape cultivation, and thus provide a scientific basis for optimising cultivation management practices.

AUTHOR CONTRIBUTIONS

WQF, Conceptualisation, Writing original draft, Writing – review & editing, and Funding acquisition; YML, Data curation, Investigation, and Formal analysis; CZ, Investigation, Validation and Formal analysis. ZSX, Project administration, Supervision, and Funding acquisition. All authors have read and approved the manuscript.

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