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Variation in Anatomical Properties and Hydraulic Conductivity of Persian Oak (*Quercus brantii* Lindl.) Trees Affected by Dieback

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ABSTRACT

Aims The present study aimed to investigate the anatomical properties of wood and xylem functioning of Persian oak affected by crown dieback.
Materials & Methods Affected Persian oak trees were categorized into four different classes based on the severity of crown dieback (healthy, slight, moderate, and severe trees) with three replicates. The target trees were randomly selected from three forest stands. Branch samples at the age of 4-6 years were randomly taken from the trees' crowns and the anatomical traits such as tree ring width (TRW), vessel density (VD), average vessel size (AVS), and relative specific conductivity (RSC) were determined. One-way ANOVA and LSD comparison of means were used to analyze the data and their mean comparison.
Findings The results showed that oak trees are using different hydraulic strategies in different habitat conditions. The effect of severity of canopy dieback on xylem anatomical traits was significant. The narrowest ring width as 257.67, 365.56, and 159.17μm was observed in trees with a severe degree of dieback (with more than 66% canopy dieback). The RSC was decreased in response to reduction in the vessel size (2905.7μm^2) and density (26.09mm^{-2}) for declining oak trees from the last site. The AVS was increased in moderate and severe degree of canopy dieback from two sites, resulting in enhanced conducting efficiency. Whoever, their resistance decreases because of the risk of cavitation.
Conclusion: Healthy oak trees showed the highest values of RSC and VD. However, the AVS was not increased. The results suggest that larger and more abundant vessels would allow for more efficient water transport. However, these larger vessels may also promote a greater risk of cavitation during a drought that illustrates the tree's incompatibility with water deficit stress.

Keywords Oak Forest; Crown Dieback; Ring Width; Xylem; Ilam

CITATION LINKS

[1] An analysis of climate and competition as ... [2] Drought and Phytophthora are associated ... [3] The role of environmental factors in oak ... [4] Effect of drought stress on some growth, ... [5] Forests and rangelands role in absorbing ... [6] Main stress factors in Coppice Oak ... [7] Anatomical and morphological changes in scion of ... [8] Olives (crop production science in ... [9] Consequences of environmental stress on ... [10] Abiotic and biotic factors and their interactions as causes ... [11] How do trees die? A test of the hydraulic failure and carbon starvation ... [12] Studying global change through investigation of the plastic responses ... [13] Nonstructural leaf carbohydrate dynamics of Pinus edulis during drought-induced ... [14] The hydraulic architecture of trees and other ... [15] Histological differences in moisture- ... [16] Impacts of water stress on gas exchange ... [17] The anatomical traits of trunk ... [18] A multi-proxy assessment of dieback ... [19] Decline modelling of oak trees ... [20] Investigating the oak decline in ... [21] Growth reactions of Pinus ... [22] Temporal and spatial variations of ... [23] Duration and extension of anatomical ... [24] Physicochemical and ... [25] Effects of a severe drought on growth and ... [26] Effects of a severe drought on Quercus ... [27] Wood anatomy and hydraulic ... [28] Change in hydraulic traits of ... [29] Ecology and growth of European ... [30] Associations between growth, wood ... [31] Leaf anatomical characteristics ... [32] Phenotypic and developmental ... [33] Water relations, growth, and foliar ... [34] Xylem structure and the ascent ... [35] Developmental control of ... [36] Xylem embolism in ring-porous ... [37] Einfluß der Jahreswitterung 1959 auf ... [38] Climatic signal of earlywood... [39] Climate sensitivity of wood-anatomical ... [40] Persisting soil drought reduces leaf ... [41] Hydraulic efficiency and coordination ... [42] Dynamics of leaf hydraulic conductance... [43] Environmental factors influence ... [44] Changes in radial growth of earlywood ...

Introduction

Forest dieback is a complex phenomenon characterized by decreasing in tree growth, defoliation, change in leaf size, shape, and color leading to the immediate or gradual death of trees [1]. It is usually triggered by extreme climate events such as droughts and biotic factors like pathogens and pests [2]. For more than a century, most oak forests in the world have encountered this great challenge becoming an acute problem [3].

In recent years, this phenomenon has markedly suffered Zagros oak forest in west of Iran with semi-Mediterranean climate. Different types of Quercus are widely distributed in the Zagros forest, known as oak forest. One of the most common species is Persian oak (*Quercus brantii* Lindl.) that is considered as dominant trees of this forest [4]. These forests have been damaged in recent years by natural and anthropogenic factors. Drought and low rainfall caused by climate change associated with overgrazing, understory cropping, and land-use change have led to the outbreak of some disorders. Oak charcoal disease is one of the most important factors increased mortality and dieback of forest trees [5]. Recent findings suggested that long-term and acute drought stress is among the main triggering factors for oak dieback or weakening the trees against other stress determinants like pathogenic fungi and insects [2, 6].

Drought is one of the most important stress factors leading to plant physiological and structural responses to maintain the water balance [7, 8]. Under drought stress, some physiological changes make severe structural anomalies which could lead to the elimination of the tree species [9, 10]. Attempts to understand mechanisms mortality during the drought have led to investigating the hydraulic failure (anisohydric) and lack of carbon (isohydric) [11]. The structure and hydraulic function of xylem can vary within a single species in response to climate conditions [12].

Drought induces xylem cavitation and reduces the capacity of plants to move water from roots to leaves, altering the tree's hydraulic system and leading trees to shoot and canopy dieback, leaf desiccation and branch mortality [13]. Xylem characteristics (i.e. number, length, and diameter of vessels) determine the capacity for water transport or hydraulic power. Among these features, the number and diameter of vessels are two main characteristics determining hydraulic conductance [14]. Tissues exposed to environments with low water availability have generally shown a reduction in cell size, and an increase in vascular tissue and cell wall thickness [15, 16]. The growth reduction of declining trees is explained by fewer and smaller earlywood vessels, reducing hydraulic conductivity [2, 17].

There are limited researches to understand the drought-related mortality patterns due to why in the same growing site some trees are more susceptible to death than others. Likewise, in the present study, in the field survey in Zagros oak forest, it was distinguished that all individuals in the same habitat were not damaged to the same extent. In spite of widespread oak dieback throughout Zagros forest, there is no specific work on the response of vascular characteristics of Persian oak trees (*Quercus brantii*) to drought stress and crown diebacks.

Some studies were carried out on the causes of oak decline and on the identification of pathogens, oak decline symptoms [2, 18], tree characteristics, forest stands and environmental conditions with oak decline [19, 20], and tree chronology to investigate radial growth pattern and vascular characteristics affected by climate [21]. Thus, understanding the physiological basis of dieback-tree in forest will help us to better manage of forest stand.

Wood anatomy variables, especially the characteristics involved in water transfer in the tree may be related to the oak dieback phenomenon. There is no detailed information about the structure and functioning of xylem of declining oak. Therefore, in the present study, it was hypothesized that the xylem anatomy is altered in declined trees and consequently, this made changes in the hydraulic efficiency of the xylem. Studying the internal structure of the tree can lead to a better understanding of this phenomenon, complementing some of the basic knowledge on the causes of Zagros forests dieback, and ultimately, would help to better predict which will be the most vulnerable forests in response to warmer and drier conditions.

Persian oak covers more than half of the Zagros forest area (west Iran), representing the most important tree species of this region. Due to the widespread mortality of trees, especially oak species in Zagros forests and the ecological value of them in these forests, the necessity of this study is determined. So, the purpose of the present study is to compare the xylem characteristics among four different severities of dieback in Persian oak trees and their relevance to oak vitality. It was hypothesized the changes in the features of the xylem influences oak tree (*Quercus brantii* Lindl.) vitality since; it is responsible for the transfer of water.

Materials and Methods

The study was conducted on Persian oak trees (*Quercus brantii* L.) from three affected stands by dieback as Sheshdar (A), Dalab (B), and Gatchan forest (C) in Ilam, west of Iran (Figure 1).

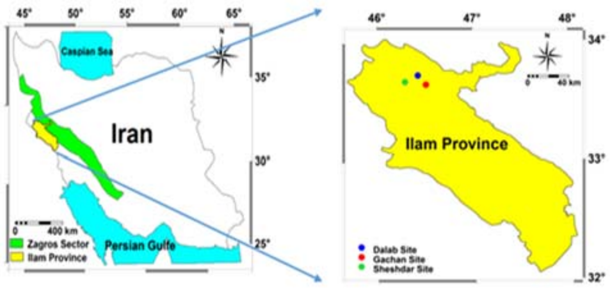

Figure1) The location of Ilam forests in west of Iran

These sites were geographically near to each other and located nearby Ilam City. For all sites, the main vegetation consists of oak trees.

- Forest District of Sheshdar with an area of 4170 hectares located at six kilometers far from the Ilam City in the southeastern part of it (33°40´26˝ N and 46°17´32˝ E, 1105 to 1680m a.s.l)
- Forest District of Dalab with an area of 3000 hectares located around 25 kilometers far from Ilam City at northwest (33°45´32˝ N and 46°30´45˝ E, 1750m a.s.l.)
- Forest District of Gatchan with an area of 13 hectares located around 7km far from Ilam City at northeast (33°38´55˝ N and 46°30´37˝ E, 2230m a.s.l.)

The climate type is categorized as Mediterranean by dry and warm summers and wet and mild winters, mainly affected by westerly air currents and the Azores High during the cold (November-March) and warm (May-September) seasons, resulting in a clear distinction between a wet winter and a dry summer [22]. According to the synoptic meteorological station of Ilam City for a period of 1988-2019, the mean annual temperature was 16.9°C, and the total annual precipitation was 585.2mm. Precipitation occurs for eight-month from October-May. The average annual relative humidity is 40%. The warmest and coldest months were August and January, respectively, with mean maximum and minimum temperatures of 32.2 and 0.6°C, respectively [22].

Sampling Method

Three sites dominated by Persian oak (*Quercus brantii* Lindl.) were selected for the study. The sites were located in three areas under one meteorological station. Trees in each site were chosen from uniform conditions (habitat, altitude, and topography). In the present study, young twigs at the age of 4-6 years from trees with no sign of damages in the stem were selected. The main reason behind to choose the twigs for analyses was fast tracking changes in any anatomical and hydraulic variations in the trees in spite of destructive sampling method with cutting the conserved trees. The samples collected in the direction of the dominant slope from the middle part of the crown in last days of the growing season in October 2018. Thirty-six seed-originated trees (12 trees from each site) with close DBH ranging from 30 to 40cm were selected. The selected trees were classified based on the severity of the crown dieback as following (i.e. the class of defoliation):

Healthy (I)= up to 5%; Slight (II)= 5-33%; Moderate (III)= 34-66%; Severe (IV)>66% (Figure 2) [3]

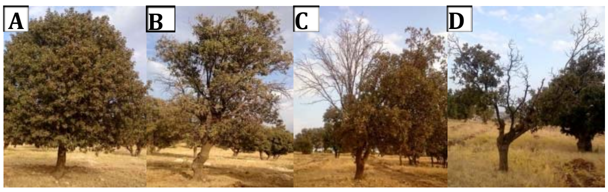

Figure 2) Different classes of crown dieback in Persian oak trees; Healthy (A); Slight (B); Moderate (C); Severe of the crown dieback (D)

Wood sample processing and variables measurement

After selecting the desired trees, the twigs were sampled by gardening scissors and stored in a zipped plastic and tagged based on tree number, severity of crown dieback, and sampling site. To better preserve the samples, they were fixed in FAA solution (For 100ml, 10ml formaldehyde (40%), 50ml ethyl alcohol, 5ml acetic acid, and 35ml distilled water). The conventional method was performed for sectioning. Cross sections with a thickness of 20-25μm were cut using a rotary microtome (POOYAN MK 1110; Iran) and stained with 0.1% (w/v) safranin O, dehydrated with a series of alcohol, xylol, and mounted on the glass slide with Canada balsam. Using a light microscope Olympus microscope cx22LED (Japan) equipped with a Truechrome metrics digital camera (China) to a computer, cross sections images were taken at different magnifications. In ring-porous oak, the bulk water transport takes place in the big earlywood vessels of the youngest outermost tree rings. The last annual ring in the microscopic images was centered for the study aims. Tree ring width (TRW), average vessel size (AVS= total vessel lumen area/ number of vessels in the analyzed range), vessel frequency (VF= number of vessel×%porosity/total vessel lumen area), and porosity (total vessel lumen area/total analyzed area×100) were measured using Image J software (https://imagej.nih.gov/ij/; Bethesda; United States). In Figure 3, different steps taken with Image software are shown. Vessel frequency (number of vessels per mm^2) and average large and small xylem vessels diameter were used to estimate relative specific hydraulic conductivity (RSC, theoretical). This shows the hydraulic capacity of the growth ring in water transfer per unit area. According to the Hagen-Poiseuille formula, it is as follows [23]:

Equation (1)

$$D_{HP}=\sqrt[4]{\frac{1}{n}\sum_{i=1}^{n}\frac{2a_i^3b_i^3}{a_i^2+b_i^2}}$$

Equation (2)

$$R_{HP}=\frac{D_{HP}}{2}$$

Equation (3)

$$RSC=R_{HP}^4\times VF$$

Figure 3 depicts Image editing steps to measure vascular features in an annual ring.

A B C

Figure 3) Image editing steps to measure vascular features in an annual ring; A) The main image after the application of the black ink and white plaster; B) image after editing; C) The final image that the software uses to provide data.

Where, D_{HP} is Poiseuille average vessel diameter for each tree ring [24], R_{HP} is Hagen-Poiseuille average vessel radius, a_i is the average small diameter of xylem vessels (the tangential lumen diameter), b_i is the average large diameter of xylem vessels (the radial lumen diameter), and VD is vessel density.

Statistical analysis

To examine differences between oak groups in anatomical properties of wood and hydraulic conductivity, Shapiro-Wilk and Leven's tests were used to assess normality and homogeneity of variance, respectively. Given that most of the analyzed data was not normal, during the conversion process, including the logarithmic method normalized the data. All statistical calculations were done with SAS 9.0 software, and means were compared by LSD test at the probability of 5%. Pearson's correlation coefficients were tested among the analyzed characteristics in three forest sites.

Findings

The difference among anatomical features in different classes of crown dieback was statistically significant at probability of the 1% and 5% (Table 1).

Table 1) One-Way ANOVA of wood-anatomical variables in different classes of crown dieback in the three studied sites

Variation Source	Df	TRW (µm)	AVS (µm^2)	VD (n/mm^{-2})	A_V/A_T (%)	RSC
Site	2	1.804**	0.1736**	0.273**	0.5986**	10.583*
Crown dieback	3	0.368**	0.0769*	0.516**	0.2250**	8.126*
Site×crown dieback	6	0.064 ns	0.0962**	0.0484ns	0.1066*	1.645 ns
Error	24	0.030	0.0249	0.028	0.0351	1.879

Variables; VD: Vessel density; AVS: Average vessel size; TRW: Tree ring width; RSC: The relative specific hydraulic conductivity; A_V/A_T (%): Porosity [A_V (total vessel lumen area)/A_T (total analyzed area)]; *Significance at 0.05; **Significance at 0.01

Forest District Sheshdar

The TRW of healthy trees in Sheshdar forest stand was significantly higher than other dieback classes and the value of TRW in classes II, III, and IV of dieback did not show a significant difference. Whereas, AVS in classes III and IV of dieback was significantly higher than the trees in classes I and II. The VD was highest in healthy trees and no significant differences were observed among classes II, III and IV. There were no significant differences among the different classes in terms of A_V/A_T (%) and RSC. However, this change in trees of classes of I and II was higher.

Forest District Dalab

The TRW of trees of classes I and II in Dalab forest stand was significantly higher than other dieback classes. The smallest TRW was found in class IV. The AVS showed reverse responses to crown dieback. The AVS in classes III and IV was higher than trees of classes of I. Also, the VD was the highest in healthy trees and no significant difference was determined in the VD among classes II, III and IV. There were no significant differences among the different classes in terms of A_V/A_T (%) and RSC. However, the highest rate was related to classes I and II.

Forest District Gatchan

The TRW of healthy trees in Gatchan forest stand was higher than the rest classes but did not show significant differences with the classes II, III and IV of dieback. The AVS was the highest in healthy trees and the lowest in severe dieback. The highest VD and A_V/A_T (%) were determined in healthy trees and the lowest in severe dieback. Furthermore, there were no significant differences in the VD and A_V/A_T (%) among trees of class II and class III. The RSC decreased with increasing the severity of dieback. The value of RSC in classes I and II is significantly higher than the fourth class of dieback. There were no significant differences among trees of classes I, II and class III.

Discussion

The present study aimed to determine the relationship between Persian oak xylem characteristics with different severities of crown dieback in three sites followed by recent droughts. Wood anatomical changes due to drought-induced are important concerns as xylem involved in water transportation as strongly associated with trees' survival. Wood anatomical features of oak branches were described in some studies [25-28]. They stated a range of 0.11mm to 0.43mm for TRW, a range of 25.00 to 135.01mm^{-2} for VD, and a range of 6.93 to 51.78% for A_V/A_T. The result of the current study for TRW (ranging from 0.15 to 0.59mm) was at the top range of mentioned values in other researches (Table 2).

Table 2) Comparison of anatomical features (means±SE) obtained for different classes crown dieback in the three studied sites

Anatomical features	(healthy)	Slight Dieback	Moderate Dieback	Severe Dieback
TRW (μm)				
Sheshdar	452.17±38.20^{c}	281.78±21.11^{de}	286±53.17^{de}	257.67±6.73^{e}
Dalab	514.67±55.42^{ab}	597.83±20.88^{a}	372.56±31.85^{cd}	365.56±37.22^{cd}
Gatchan	245.22±20.81^{ef}	242±36.96^{ef}	201.67±2.30^{ef}	159.17±17.42^{f}
AVS (μm^2)				
Sheshdar	3240.4±503.73^{de}	3462.4±34.80^{de}	4663.2±445.31^{abc}	4961.8±207.69^{a}
Dalab	3635.3±322.77^{cde}	4200.7±172.69^{abcd}	5151.2±587.07^{a}	4836.9±401.76^{ab}
Gatchan	3898.4±203.65^{bcde}	3636.6±173.34^{cde}	3565.7±248.16^{de}	2905.7±477.31^{e}
VD (mm^{-2})				
Sheshdar	41.398±2.52^{bc}	27.519±1.59^{de}	26.123±1.84^{e}	26.123±4.28^{e}
Dalab	39.237±0.71^{bc}	33.106±6.24^{cde}	24.196±1.22^{e}	28.823±0.89^{de}
Gatchan	57.932±4.68^{a}	42.162±4.05^{b}	35.96±0.36^{bcd}	26.095±1.93^{e}
AV/AT (%)				
Sheshdar	11.028±0.27^{d}	10.422±1.28^{d}	9.605±2.13^{d}	10.280±0.77^{d}
Dalab	12.279±0.94^{cd}	11.466±1.37^{d}	9.407±1.13^{d}	10.341±0.21^{d}
Gatchan	22.124±1.36^{a}	16.989±1.72^{bb}	15.839±1.57^{bc}	9.459±0.60^{d}
RSC				
Sheshdar	6.372±1.05^{a}	4.420±0.71^{abc}	5.724±0.64^{ab}	4.340±1.11^{abc}
Dalab	5.850±1.65^{ab}	4.802±0.23^{abc}	4.024±0.32^{abc}	4.091±0.69^{bc}
Gatchan	3.500±0.66^{abc}	3.415±0.48^{abc}	3.245±0.33^{cd}	1.401±0.29^{d}

Variables; TRW: Tree ring width (×10-3 mm); AVS: Average vessel size (×10-6 mm^2); AV/AT (%): Porosity [AV (total vessel lumen area)/AT (total analyzed area)]; VD: Vessel density; RSC: The relative specific hydraulic conductivity; Means with the same letters within the same column are not significantly different at p<0.05 using LSD test

However, the values of VD and A_V/A_T (%) for this study were within the range of stated data. The TRW in the trees with crown dieback was less than the healthy trees. This supports the idea that tolerance of individual trees to dieback decreases with weakening their growth vigor [29]. In sites A and B, it was appeared that declining trees with lower TRW and VD were unable to sufficiently reduce AVS and RSC. These results are consistent with Levanic *et al.* [30].

The number and diameter of xylem are considered as the main factors determining the hydraulic conductance affected by water supply [14]. Researches have shown a decreased vessel diameter during drought stress [31, 32], and increased during wet periods [33]. In the site C, the highest AVS and VD were in the healthy oaks and lowest in trees with a severe degree of dieback. The earlywood vessels are the main elements for water conductance in the ring-porous species and the transfer of water to leaves in these species depends on the effective and large wood vessels. Reducing vessel density in class IV had a significant contribution to reduction in potential hydraulic conductivity of affected oak trees. This is indicated by the highly significant correlation of VD in hydraulic conductivity to vessel size. Usually, there is an inverse relationship between the size and the number of the vessel. In this study, simultaneous decrease of both features with increasing the severity of crown dieback suggesting a different strategy adopted by oak trees from site C as stated by Tulik [17] on *Quercus robur* and Eilmann *et al.* [21] on *Q. pubescens.*

In sites A and B, the AVS increased in the trees with severities of III and IV, while decreased in trees with severities of I and II (Figure 4).

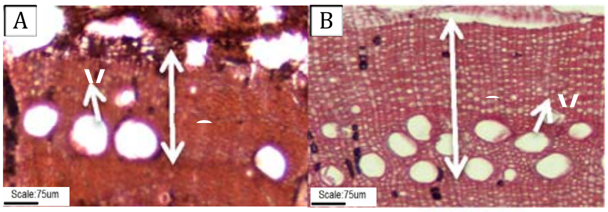

Figure 4) Transverse section through branch of oak sample dieback; Dieback oaks (A) formed narrower rings with bigger vessels comparing with the healthy oaks (B); (CR= Current annual ring, VE= Vessel)

The large earlywood vessels contribute to the greater part of water flow throughout the plant, but due to their large lumen diameter, the vessels are also vulnerable to embolization [34], thus trees that eventually died may have experienced greater risk of hydraulic failure. Embolism is relatively high in genus Quercus [35, 36]. Therefore, the adverse changes in diameter of the vessels as important parameter for hydraulic conductivity may indicate a lack of adaptability to stress factors. Nevertheless, some studies have shown that the average size of earlywood vessels in ring-porous oaks increased with increasing drought for *Quercus spp*. [37], *Q. robur* L. [30], *Q. faginea* Lam. and *Q. ilex* subsp*. ballota* [25, 26], *Q. frainetto* Ten. [18]. Adversely, some studies described decreasing vessel diameters under drought condition [21, 26, 38]. Among the reasons for these discrepancies, it may be related to the dissimilarity among the study sites, the different species examined, and the different climate conditions during growth years [39]. The VD is often increased by drought [40, 41] through improving the hydraulic conductance [42]. However, drought may decrease the density of xylem vessels [43]. Corcuera *et al*. [25] reported a decrease in VD and an increase in AVS under drought stress, which is in line with the results of the present study and suggesting that the response of trees to the drought may be contradictory. It appears that the declined trees in the current study were unable to sufficiently reduce A_V/A_T (%) in sites A and B that is in consistent with Levanic *et al* [30]. Concerning the correlation between measured traits in each site, it could be said that due to the difference in habitat conditions of the three sites, the pattern of connection between vascular characteristics varies. In site C, AVS and VD showed low magnitude of correlation (r= 0.48), however, A_V/A_T was positively affected by both of these variables. A relatively reverse correlation demonstrated between AVS and VD from sites A (r= 0.66) and B (r= 0.69). Studies have shown that by inducing environmental stresses, for example, reduction in tree access to water, the diameter of the vessels and consequently the hydraulic conductivity is reduced [28]. In this case, the tree attempts to compensate for it by increasing the number of vessels [44]. Interestingly, healthy oak trees have a conservative response with reduced vessel size in comparison with classes III and IV. The VD had positive correlation with TRW and RSC in trees of sites A and C. On the other hand, the significant correlation among these variables was not observed in site B. Generally, the lowest VD was observed for the declining oaks and the highest for the healthy individuals, that suggesting abundant vessels under drought stress would allow high water transport efficiency (Table 2) [17]. It seems that VD plays a major role in better water transport. Generally, differences in xylem traits among sites can be partially explained by non-climatic factors, including stand characteristics such as density, competition and soil and individual tree features. At the population level, different behaviors among different canopy dieback classes might be related to a microsite or genotypic differences experienced by different individuals.

Conclusion

According to the results, it could be stated that xylem characteristics are different among different severities of dieback in Persian oak trees. The RSC decreases in response to a reduction in size and density of the vessel which contributes to the loss of viability and ultimately the death of trees. In spite of wide earlywood vessels in the declining trees, they reduced a reduction in TRW and VD. In contrast, healthy oak trees had smaller vessels which in combination with vessel density did not affect the xylem functioning. Production of smaller vessels might be a strategy to decrease vessels vulnerability to cavitation. The results of the present study showed that different patterns of survival and mortality within these stands were contingent on physiological adaptations with microsite conditions or genotypic differences.

Structural characteristics of a tree affect upward water transfer and consequently facilitate the oak dieback phenomenon. Further study is needed to prove this concept. The fully understanding the vulnerability of trees to embolism needs to study branch, stem, and roots whole together. It is suggested that similar study should be carried out on root-to-branch segments with respect to individual tree characteristics with more numbers of sampled trees in different sites of Zagros forests.

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