

Postprint of Analysis of Embolism Vulnerability in Petals and Leaves of Three Rhododendron Shrub Species

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Abstract

The frequency and intensity of drought induced by climate change severely affect plant growth and development. Against the backdrop of global climate change, quantifying the capacity of plant xylem to resist embolism is particularly crucial for evaluating plant drought tolerance. To assess drought tolerance among Rhododendron cultivars and screen for varieties with strong drought resistance, this study employed three shrub Rhododendron species as experimental materials: *Rhododendron × pulchrum* ‘zihe’, *Rhododendron × hybridum* ‘yangmeihong’, and *Rhododendron simsii*. Optical techniques were utilized to construct vulnerability curves to embolism for both petals and leaves, anatomical structural traits of petals and leaves were measured, and the correlation between xylem hydraulic function and anatomical structural traits was analyzed. The results demonstrated: (1) The P12, P50, and P88 values (water potential values corresponding to 12%, 50%, and 88% embolism, respectively) of petals for the three Rhododendron species were greater than those of leaves. (2) Variation existed in embolism vulnerability between petals and leaves among the three Rhododendron species, with inconsistent rates of embolism development in petals and leaves; this variation may represent an important characteristic of hybrid horticultural floral plants. (3) Correlation analysis between P50 values and morphological characteristics revealed that leaf P50 values were negatively correlated with leaf palisade tissue thickness, whereas petal P50 values were positively correlated with petal thickness. The study concluded that petal embolism vulnerability was higher than leaf embolism vulnerability in the three Rhododendron species, and that plants preferentially sacrifice petals to protect leaves under drought stress. Embolism vulnerability may be associated with leaf palisade tissue thickness and petal thickness. This research provides a scientific basis for the selection and configuration of Rhododendron plants in gardens in arid regions and establishes a foundation for screening and breeding drought-resistant Rhododendron cultivars.

Full Text

Analysis of Embolism Vulnerability in Petals and Leaves of Three Shrub Rhododendron Species

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Abstract: Climate change has increased the frequency and intensity of drought, severely impacting plant growth and development. Quantifying xylem resistance to embolism is crucial for assessing plant drought tolerance under global climate change. To evaluate drought tolerance among Rhododendron cultivars and identify drought-resistant varieties, we examined three shrub rhododendrons: *Rhododendron × pulchrum* ‘Zihe’, *Rhododendron × hybridum* ‘Yangmeihong’, and *Rhododendron simsii*. Using optical techniques, we constructed embolism vulnerability curves for petals and leaves, measured anatomical structural traits, and analyzed correlations between xylem hydraulic function and anatomical structure. Results showed: (1) P_{12} , P_{50} , and P_{88} values (water potential at 12%, 50%, and 88% embolism, respectively) were higher in petals than in leaves for all three species. (2) Embolism vulnerability varied between petals and leaves, with inconsistent rates of embolism development between organs, which may represent an important characteristic of hybrid horticultural plants. (3) Correlation analysis revealed that leaf P_{50} values were negatively correlated with palisade tissue thickness, while petal P_{50} values were positively correlated with petal thickness. We conclude that petals exhibited higher embolism vulnerability than leaves in all three Rhododendron species, suggesting that plants sacrifice petals to protect leaves during drought. Embolism vulnerability appears related to leaf palisade tissue thickness and petal thickness. These findings provide a scientific basis for selecting and configuring Rhododendron species in arid regions and lay the foundation for screening and breeding drought-resistant cultivars.

Keywords: embolism vulnerability, drought tolerance, xylem vessel structure, morphological structure, optical method

Introduction

The World Meteorological Organization's *State of the Global Climate 2021* report indicates that global CO₂ concentrations reached 413.2 mg·kg⁻¹ in 2020, representing 149% of pre-industrial levels and setting a new historical record. Global mean temperature has risen approximately (1.11±0.13)°C above pre-industrial levels, with continued warming projected for the future (Luo, 2022). Global climate warming, particularly the increased frequency of extreme drought events, has caused large-scale tree mortality and forest degradation, severely affecting global forest ecosystem structure and function (Bennett et al., 2015; Duke et al., 2017; Blackman et al., 2019). Drought accounts for 5% of all natural disasters globally but contributes to approximately 30% of associated economic losses (He et al., 2011). More critically, anthropogenic climate change is expected to intensify the global hydrological cycle, leading to more frequent and severe drought events in many regions.

According to the cohesion-tension theory (Dixon, 1938), transpiration pull drives water transport through plant xylem vessels. When this pull exceeds the tensile strength of the water column within xylem, embolism forms (Tyree & Sperry, 1989), resulting in discontinuous water transport. Xylem embolism represents a critical determinant of plant survival or death during drought (Cardoso et al., 2020), making xylem embolism resistance a valuable metric for assessing drought tolerance. Generally, greater embolism vulnerability indicates lower drought tolerance, and vice versa. Consequently, embolism vulnerability has been widely applied to evaluate drought tolerance across many species (Brodrribb et al., 2016; Hochberg et al., 2017; Sorek et al., 2020; Johnson et al., 2021). For example, Zhang et al. (2017) studied embolism vulnerability in leaves of four species—*Polygala myrtifolia*, *Passiflora tarminiana*, *Pisum sativum*, and *Solanum lycopersicum*—to compare their drought resistance. Brodrribb et al. (2016) investigated leaves of species from Myrtaceae, Pittosporaceae, Cunoniaceae, and Asteraceae, demonstrating relationships between leaf hydraulic conductivity and embolism formation. Han et al. (2022) measured embolism resistance and morphological indicators in ten woody species to compare their drought tolerance.

Flowers are essential organs for reproduction, evolution, and diversity in angiosperms (Philip & Regal, 1977; Soltis & Soltis, 2014). Extended flowering periods attract more pollinators and increase reproductive success (Rathcke, 2003). In addition to environmental factors such as temperature and light (Primack, 1985), water availability represents a key abiotic factor affecting flowering. During flowering, insufficient soil moisture or drought stress causes petal wilting and even flower abscission due to water deficit. Consequently, flower development requires substantial water supply (Roddy & Dawson, 2012). According to hydraulic segmentation theory, less costly organs (e.g., leaves) have more vulnerable xylem than more expensive organs (e.g., stems) during drought (Tyree & Ewers, 1991). For instance, under water deficit, grape leaves abscise first to protect stems (Charrier et al., 2016). Compared with stems, leaves and petals show higher vulnerability under drought conditions (Nolf et al., 2015; Zhang &

Brodribb, 2017), and apical shoots experience greater stress than trunks during water deficit (Rood et al., 2000).

Rhododendrons belong to the family Ericaceae and genus *Rhododendron*, representing renowned ornamental plants worldwide (Sharma et al., 2014). Southwest China (Guizhou, Chongqing, Yunnan, Sichuan) hosts abundant Rhododendron resources that play important roles in regional tourism (e.g., the Baili Rhododendron Scenic Area in Guizhou). Recent global warming-induced drought has severely threatened plant survival. As terminal tissues for water exchange, leaves and petals play crucial roles in controlling water loss. Previous studies on plant drought tolerance through embolism resistance have focused primarily on stems (Brodribb et al., 2017; Levionnois et al., 2021; Feng et al., 2021) and leaves (Brodribb et al., 2016; Skelton et al., 2018; Lechthaler et al., 2019), with few reports on petal embolism vulnerability (Li et al., 2015). As ornamental resources, Rhododendron cultivars developed through interspecific hybridization exhibit various flower colors and have been widely marketed, making drought tolerance assessment among cultivars essential. Therefore, this study selected *Rhododendron* × *pulchrum*, *Rhododendron* × *hybridum*, and *R. simsii* as experimental materials. Using optical techniques, we constructed embolism vulnerability curves for petals and leaves, calculated P_{50} values (water potential at 50% embolism), and addressed the following questions: (1) Compare embolism vulnerability differences among the three shrub Rhododendron species to evaluate their drought tolerance; (2) Investigate whether petal tissues undergo embolism under drought conditions; (3) Analyze relationships between morphological traits of petals and leaves and P_{50} values. Our findings provide theoretical support for selecting and configuring Rhododendron species in arid regions and establish a drought resistance index system for evaluating Rhododendron drought tolerance.

Materials and Methods

1.1 Plant Materials *Rhododendron* × *hybridum* ‘Yangmeihong’, *Rhododendron* × *pulchrum* ‘Zihe’, and *Rhododendron simsii* plants (15 pots per species, one plant per pot) were purchased from the Huishui County Flower Base in Qiannan Prefecture, Guizhou Province. Plants with flowers were cultivated in a greenhouse at the Key Laboratory of Plant Physiology and Development Regulation, Guizhou Normal University (12 h photoperiod, 22°C temperature, 350 mol · m⁻² · s⁻¹ light intensity, 60–70% relative humidity) until partial flowering [Figure 1: see original paper], after which experiments were conducted.

1.2 Optical Embolism Vulnerability Curve Construction Embolism vulnerability curves were constructed following the optical technique of Brodribb et al. (2016) with minor modifications. Branches with leaves and petals (approximately 10 cm long) were excised and immediately placed in water to saturate. The leaf (fifth leaf from the apex) or petal was then positioned on

the stage of a stereomicroscope (XTL-6745TJ4-T1000, Suzhou Beitejia Optoelectronics Technology Co., Ltd.), flattened, and secured with transparent tape. Under greenhouse conditions, images were captured every 60 s until leaf or petal browning was observed. Additionally, other branches were saturated and allowed to dry naturally under the same conditions. Leaf or petal water potential was measured every 20–60 min using a dew point potentiometer (WP4-T, Gene Company Limited, USA), with three biological replicates per species. Embolism was identified and quantified using image subtraction in ImageJ software (National Institute of Health, New York, NY, USA). The Weibull function [$V = (x-100)\log(1-x/100)$] was used to fit water potential against embolism percentage to obtain vulnerability curves (Tomasella et al., 2021).

1.3 Morphological Characteristics of Petals and Leaves Healthy leaves (fifth to eighth from the apex) and petals were sampled. Tissue blocks (~0.5 cm × 0.5 cm) were cut from the midrib region, processed into paraffin sections, photographed under a microscope, and measured using ImageJ software to determine petal and leaf thickness, upper and lower epidermal thickness, palisade tissue thickness, and spongy tissue thickness (Wang et al., 2021). Vein density was determined following Roddy et al. (2013): petals and leaves were decolorized to transparency using 2% NaOH solution, photographed under a microscope, and vein density calculated as total vein length per unit area using ImageJ. Stomatal density was measured following Song et al. (2022): a thin layer of clear nail polish was applied to the abaxial surface, dried for 30 min, peeled off, observed under a microscope, and stomatal density calculated as stomatal number per field area.

1.4 Xylem Vessel Structure Measurement Main veins (~0.5 cm long) were excised 0.2 cm from the leaf base. Permanent slides were prepared following Lu et al. (2021), photographed under a microscope, and anatomical traits measured using ImageJ. Calculations followed these formulas: 1. Vessel density (N) = Total number of vessels in cross-section / Cross-sectional area 2. Vessel diameter (D) = $\sqrt{4A/\pi}$, where A is vessel area 3. Vessel lumen span (b) = $\sqrt{4A_1/\pi} + \sqrt{4A_2/\pi}$, where A_1 and A_2 are adjacent vessel areas 4. $(t/b)^2$, where t is the vertical distance between adjacent vessels and b is vessel lumen span

1.5 Data Analysis All data were analyzed using one-way ANOVA in SPSS 25 ($P < 0.05$). Pearson correlation analysis was performed to examine relationships between variables.

Results

2.1 Optical Embolism Vulnerability of Petals and Leaves in Three *Rhododendron* Species

Optical vulnerability techniques enabled spatiotem-

poral observation of embolism spread in petals and leaves. Embolism appeared earlier in leaves than in petals across all three species [Figure 2: see original paper]. Within species, petal P_{50} values were higher than leaf P_{50} values [FIGURE:3; TABLE:1], indicating greater embolism vulnerability in petals under natural drought. Among species, petal P_{50} was lowest in *R. × pulchrum* ‘Zihe’ and highest in *R. × hybridum* ‘Yangmeihong’, while leaf P_{50} was lowest in *R. simsii* and highest in *R. × hybridum* ‘Yangmeihong’ (TABLE:1). Similar patterns were observed for P_{12} and P_{88} values among species ($P < 0.05$) (TABLE:1).

2.2 Morphological and Structural Characteristics of Petals and Leaves

Significant interspecific differences were observed in petal thickness, upper epidermal thickness, and lower epidermal thickness ($P < 0.05$), while vein density showed no significant differences ($P > 0.05$). No stomata were observed on petals. Leaf morphological structures also varied significantly among the three species ($P < 0.05$) (TABLE:2).

2.3 Xylem Vessel Structural Characteristics

Leaf xylem vessel traits showed significant interspecific differences in vessel density, vessel diameter, vessel lumen span, and vessel wall thickness ($P < 0.05$), while $(t/b)^2$ showed no significant differences ($P > 0.05$) (TABLE:3).

2.4 Correlations Between Morphological Structure and P_{50} Values

Correlation analysis revealed that petal P_{50} values were not significantly correlated with upper epidermal thickness, lower epidermal thickness, or vein density ($P > 0.05$) [Figure 4: see original paper], but showed a significant positive correlation with petal thickness ($r^2 = 0.45$, $P = 0.02$) [Figure 4A: see original paper]. Leaf P_{50} values were significantly negatively correlated with palisade tissue thickness ($r^2 = 0.45$, $P = 0.02$) [Figure 4D: see original paper] but not with other morphological structures ($P > 0.05$) [Figure 4: see original paper]. No significant correlations were found between leaf P_{50} values and xylem vessel structural parameters ($P > 0.05$) [Figure 5: see original paper].

Discussion

3.1 Higher Embolism Vulnerability in Petals Than Leaves with Interspecific Variation

Using optical visualization techniques, we successfully observed spatiotemporal changes in xylem embolism in petals and leaves of *Rhododendron* cultivars. This method has been previously applied to evaluate drought tolerance in *Rhododendron* and other species (Xia et al., 2023). Our study revealed interspecific variation in embolism vulnerability between petals and leaves. For example, leaves of *R. simsii* showed the lowest vulnerability, while petals of *R. × pulchrum* ‘Zihe’ were least vulnerable. This contrasts with Rodriguez et al. (2018), who reported that olive individuals with strongest

embolism resistance in roots also showed strong resistance in leaves. We hypothesize that this variation may be attributed to differences in petal color among *Rhododendron* cultivars. Petal coloration is associated with anthocyanin types and content (Heursel, 1981; Tao et al., 2015), and anthocyanins can function as osmotic regulators to enhance drought resistance (Forkmann, 1991). Therefore, variation in anthocyanin content among differently colored petals may influence petal drought resistance, leading to observed differences in embolism vulnerability.

A key objective was to analyze the position of flowers within the hydraulic vulnerability spectrum, particularly regarding hydraulic segmentation theory. In all three *Rhododendron* species, petal P_{12} , P_{50} , and P_{88} values exceeded those of leaves, demonstrating that petals are more vulnerable than leaves. This aligns with hydraulic segmentation theory, suggesting that during water deficit, *Rhododendron* plants may prioritize sacrificing less important, lower-cost petals to protect leaves, which are vital for survival and reproduction (Zimmermann, 1983; Zhang & Brodribb, 2017). This strategy is advantageous for long-term survival and reproductive success in these perennial shrubs.

3.2 Relationships Between Embolism Vulnerability and Morphological Structure in *Rhododendron* Cultivars Vessels are critical water-conducting tissues, and their characteristics (e.g., length, diameter, type, pit membrane ultrastructure) directly influence xylem embolism formation. Embolism vulnerability is also affected by anatomical structures such as stomata and leaf tissue thickness. Our correlation analysis revealed a negative relationship between leaf palisade tissue thickness and P_{50} , indicating that thicker palisade tissue confers greater drought resistance. This may be because dense palisade tissue prevents and mitigates rapid water loss (Pan et al., 2010), thereby enhancing drought tolerance. We observed no correlations between embolism vulnerability and xylem vessel density, diameter, lumen span, wall thickness, or $(t/b)^2$. This may be because drought-induced embolism formation involves multiple structural factors, including xylem sap composition, vessel wall chemistry, pit membrane characteristics, and cell types (Guillermina et al., 2011; Li et al., 2016; Lens et al., 2022). Our study did not examine these parameters, warranting future investigations of additional anatomical features and their relationships with embolism vulnerability.

Unlike leaves, no stomata were observed on either adaxial or abaxial petal surfaces, suggesting that petals may lose water through cuticles. The delayed onset of embolism in petals compared to leaves may be due to slower water loss control through cuticles relative to stomatal regulation, potentially retarding embolism formation in petals. This finding differs from Zhang and Brodribb (2017), who observed stomata on petals of *Polygala myrtifolia*, *Passiflora tarminiana*, pea, and tomato, with embolism appearing slightly earlier in petals than leaves. We therefore propose that the cuticle contributes to petal xylem embolism vulnerability in *Rhododendron*.

In conclusion, both petals and leaves experienced embolism under natural drought, with petals showing greater vulnerability than leaves. Interspecific variation in embolism vulnerability between petals and leaves may be an important characteristic of hybrid horticultural plants. Embolism vulnerability was negatively correlated with leaf palisade tissue thickness and positively correlated with petal thickness. These results are significant for future selection of drought-tolerant *Rhododendron* species and provide theoretical support for species selection and configuration in afforestation projects in arid regions.

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