

DIVERSE STRATEGIES OF RHODODENDRON (*Rhododendron* sp.) GENOTYPES IN THE WATER SHORTAGE MANAGEMENT

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ABSTRACT

Rhododendrons in numerous gardens in Central Europe are frequently endangered by adverse summer drought periods associated with the climate change. Therefore, in this work drought-resistance strategies in recent genotypes of these highly aesthetic shrubs were investigated. Dehydrated *Rhododendron groenlandicum* ‘Helma’, *R. obtusum* ‘Michiko’ and *R. hybridum* ‘Polarnacht’ showed high initial stomatal conductances (g_s), after few days steeply falling to the stable minimum at ca. 20, 85 and 70% leaf relative water content (RWC), respectively. Except of ‘Polarnacht’, they had relatively large specific leaf area and ‘Michiko’ also free proline accumulation. On the other hand, *R. repens* ‘Scarlet Wonder’ and *R. hybridum* ‘Red Jack’ started with half g_s values, continuously declining 1.5–2 fold longer compared to the first group of genotypes (RWC of ca. 60 and 75%, respectively). Both produced relatively thick leaves but did not show any osmotic adjustment. Among observed drought-resistance strategies, lower and longer period active transpiration with stomata sensitive to the water loss, as found in *R. repens* ‘Scarlet Wonder’ and *R. × hybridum* ‘Red Jack’, were accepted as the most effective for drought-affected rhododendron plantations.

Key words: rhododendron, cultivars, stomatal conductivity, specific leaf area, osmotic adjustment

INTRODUCTION

Rhododendrons (*Rhododendron* sp., Ericaceae), shrubs with a large scale of habitus, leaf characteristics as well as inflorescence frequency, colour and richness, are jewels of parks, botanical gardens and arboretums. Compared to late sixties of the past century, when the classical work of Krüssmann [1968], listing 131 most important species and 306 cultivars of rhododendron, was published, nowadays, web site Hirsutum.info contains 1,279 species records and almost 14,600 cultivar records.

As specified in a recent guide for rhododendron breeders [Böhm 2004], these beautiful shrubs, coming from woodland (tall species) or alpine environments (dwarf species), avoid sites with dry winds and

strong sunlight. In opposite, they prefer half-shadow of deep-rooting trees, forming a pleasant microclimate for their growth. Concerning soil conditions, rhododendrons require humous soils of low pH (4.5–5.5) with adequate moisture content. Because of very fine and relatively shallow root system, they rely on rain/regular watering particularly in the period of flowering and annual shoot growth.

However, more frequent and extreme summer droughts nowadays affecting ornamental plantations in Central Europe are in accordance with the Fifth assessment report of the International Panel on Climate Change [IPCC 2014] more precisely stating negative follows of the climate change on the global level,

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among them further surface temperature growth, alterations in precipitation distribution and increase of the extreme event frequency.

Drought has detrimental effect on the aesthetic value of ornamental woody plants. It is manifested by leaf wilting, colour defects and precocious fall-off, lower vegetative growth, phenological anomalies, and in extreme cases by branch/plant die-back [Cameron et al. 2008, Augé et al. 2003]. However, in the case of soil water deficit after inflorescence initiation, rhododendrons flower sooner with richer inflorescence [Sharp et al. 2009]. In general, before these marked visual changes become obvious, protective mechanisms turn on consecutively to avoid the water deficit. As the water supply decreases, elongation growth slows down, stomata close, assimilates start to allocate more into root and provide deep-growth for water and finally osmolyte accumulation switches on. Better water conductive system, represented by thicker leaves with massive cuticle and dense venation can be an important advantage [Larcher 2003].

Sensitivity of the leaf stomatal system to leaf water potential (ψ) loss strongly varies among forest tree species in different biomes. Species-specific curves formed a continuum rather than dichotomy between isohydric and anisohydric behaviours with a strong relation to xylem characteristics. Ring-porous species had higher absolute stomatal conductivity (g_s) at $\psi < -2$ MPa than diffuse porous and coniferous species [Klein 2014].

Drought resulted in an increase of specific leaf area (SLA) and decrease of total leaf area per plant in four silver birch (*Betula pendula* Roth) genotypes. Leaf area reduction was more pronounced in the genotypes from high than those from low rainfall origin [Aspelmeier and Leuschner 2006]. Olive tree (*Olea europea* L.) cultivars ‘Negrinha’ and ‘Manzanilla’ enhanced their sclerophylly by building parenchyma tissue and increasing protective structures like upper cuticle and both the upper and lower epidermis when grown under field conditions with low water availability [Bacelar et al. 2004].

Osmotic adjustment (OA), a slow process comprising net accumulation of inorganic cations and anions, organic acids, carbohydrates and amino acids, causes osmotic potential decrease, which in turn can improve the degree of cell hydration and maintaining turgor.

Moreover, compatible solutes rich in (-OH) groups can help to protect cellular proteins, enzymes and membranes against drought. In other words, plant can survive longer and maintain metabolic processes in drying soil if OA is active [Sanders and Arndt 2012].

In this work, analysis of drought resistance in recent rhododendron cultivars combined with the identification of the most effective strategies was carried out and recommendations for horticultural practice under continuous climate change formulated.

MATERIAL AND METHODS

Plant material and cultivation conditions. Reactions of five rhododendron genotypes – *R. groenlandicum* ‘Helma’, *R. obtusum* ‘Michiko’ and *R. repens* ‘Scarlet Wonder’, then *R. hybridum* ‘Polarnacht’ and *R. hybridum* ‘Red Jack’ were studied in two separate lab experiments. Since drought periods in Slovakia usually occur in summer, when the annual shoot growth is resumed, they were positioned to the late summer–autumn 2016. Two years old cutting regenerants, growing in 3 and 5.5 litre plastic pots, respectively, with peat-perlite (1 : 1) substrate in the half shaded stand of the Mlyňany Arboretum IFE SAS plant nurseries, were transferred into air-conditioned growth room with photoperiod 16/8 h, artificial illumination (Osram L36W/840 Lumilux® Cool White) intensity $100 \mu\text{mol m}^{-2} \text{s}^{-1}$, air temperature 27/20°C and air humidity 50/60%, and ensured regular watering, for three weeks lasting acclimation.

Experimental treatment and physiological measurements. After three weeks of acclimation, one half of the plants was submitted to the dehydration process triggered by water shortage (16–34 days). The second half of individuals was regularly watered. Every two-three days of the dehydration cycle, stomatal conductivity (porometer SC-1, Decagon Devices Inc., USA) was measured in top 2–4 mature leaves on highly positioned sprouts, three hours after light was switched on (4 values from each plant). At the beginning of the dehydration cycle and two days after stomata was closed, these leaves were analyzed for relative water content (RWC) [Verslues et al. 2006] or frozen for later free proline determination [Bates et al. 1973]. Simultaneously, specific leaf area (SLA; scanner and Image J software), total leaf area (A) and total shoot

dry matter (W_{sh}) [Blum 2011] were ascertained. Since low growth, these three parameters have not been defined separately for hydrated and dehydrated plants.

Free proline determination. Near 0.5 g leaf material was homogenized in 10 ml of 3% sulfosalicylic acid. After 15 min centrifugation at 6000 rpm, 2 ml ninhydrin solution (1.25 g ninhydrin in 30 ml cold acetic acid and 20 ml 6 M phosphoric acid) and 2 ml cold acetic acid were added to 2 ml supernatant and the reaction mixture was incubated at 95°C for one hour. The reaction was stopped by submerging into the ice bath, and chromophore extraction was realised thorough shaking with 4 ml toluene. Subsequently, absorbance of the upper layer at 520 nm was measured against toluene. Concentrations were then converted on the 100% RWC basis (^{100}PRO).

Statistical analysis. Results represent means \pm SE of four replicates, each from an individual plant. To evaluate cultivar effect (cv), drought stress effect (s) and their interaction (cv \times s), data on g_s , RWC, ^{100}PRO , SLA, A and W_{sh} were submitted to the two-way ANOVA in the Statgraphics Plus v. 4.0 environment. Comparison between means was performed using Duncan's multiple range test. The symbols *, ** and *** indicate significant differences at the confidence levels of $P \leq 0.05$, 0.01 and 0.001, respectively.

RESULTS

Dehydration cycles started when rhododendron vegetative growth was resumed. In this stage, they had above-ground biomass (W_{sh}) of 8–19.7 g DW (Tab. 1). In the first experiment we found significant differences between cultivars with following order: ‘Scarlet Won-

der’, ‘Helma’ and ‘Michiko’. In the second one, cultivar dry matter was on the same level (ca. 18 g). Similar trends were observed in their total leaf area (A) with average of 3.68 dm² in ‘Scarlet Wonder’, 4.60 dm² in ‘Helma’, 7.60 dm² in ‘Michiko’ and around 10.50 dm² in ‘Polarnacht’ and ‘Red Jack’. However, specific leaf area (SLA) in tested cultivars showed lower variability. In the first experiment, SLA of ‘Helma’ and ‘Scarlet Wonder’ reached approximately 0.8 dm² g⁻¹, and in ‘Michiko’ ca. 1.0 dm² g⁻¹. In the next two cvs. it was about 0.65 dm² g⁻¹.

Dynamics of leaf stomatal conductance (g_s) in ‘Helma’ and ‘Michiko’ showed high values (up to 400–500 mmol m⁻² s⁻¹) on the first few days (4–6 days) of dehydration (Fig. 1A). Then, a steep fall to ca. 100 mmol m⁻² s⁻¹ was observed in the next 4–6 days, followed by a slight decrease to the stable minimum (on 19th and 16th day of the dehydration cycle, respectively). On the other hand, g_s of ‘Scarlet Wonder’ oscillated around 200 mmol m⁻² s⁻¹ for first ten days of dehydration, then fell to the half value and moderately decreased for next 22 days to the minimum values. Very similar stomatal conductance behaviour was recorded in plants of ‘Red Jack’ in the second experiment (Fig. 1B). The opposite reaction was found also in ‘Polarnacht’: a sigmoid curve with insignificantly higher initial g_s level, steep fall and short period of slight decrease to the stomatal closure.

Comparison of leaf relative water content (RWC) between initial and terminal points of the dehydration cycle no. 1 (Fig. 2A) revealed significant decrease in all genotypes. The lowest values at the terminal point were found in ‘Helma’ (approaching 20%), markedly larger in ‘Scarlet Wonder’ (ca. 60%) and only ca.

Table 1. Morphological and production parameters of tested rhododendron genotypes

Experiment	Genotype	W_{sh} (g)*	A (dm ²)*	SLA (dm ² g ⁻¹)*
1	‘Helma’	11.04 \pm 0.30 b	4.60 \pm 0.13 b	0.81 \pm 0.03 a
	‘Michiko’	12.91 \pm 0.42 c	7.60 \pm 0.22 c	1.02 \pm 0.01 b
	‘Scarlet Wonder’	7.99 \pm 0.54 a	3.68 \pm 0.27 a	0.78 \pm 0.02 a
2	‘Polarnacht’	19.73 \pm 1.55 a	10.85 \pm 0.85 a	0.64 \pm 0.03 a
	‘Red Jack’	16.78 \pm 0.78 a	10.47 \pm 0.44 a	0.66 \pm 0.05 a

*Average \pm SE. Letters indicate statistically significant difference between cultivars at the confidence level 95%. W_{sh} – shoot dry matter, A – total leaf area, SLA – specific leaf area

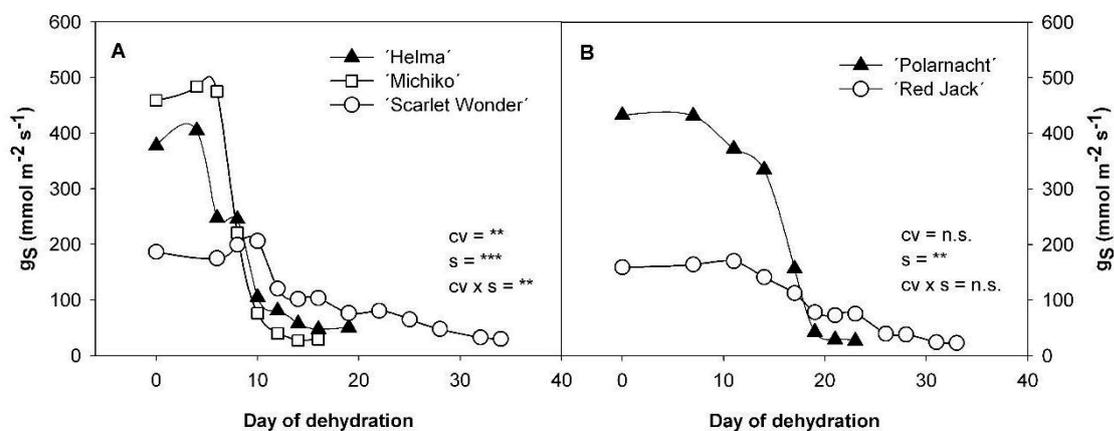


Fig. 1. Average stomatal conductance (g_s) dynamics in leaves of continuously dehydrated rhododendron plants (A – experiment 1, B – experiment 2). Results \pm SE are means of four replicates. A two-way ANOVA was used to evaluate the cv effect (cv), the salt effect (s) and their interaction (cv \times s). The symbols *, ** and *** indicate significant differences at confidence levels of $P \leq 0.05$, 0.01 and 0.001, respectively; n.s. – non significant

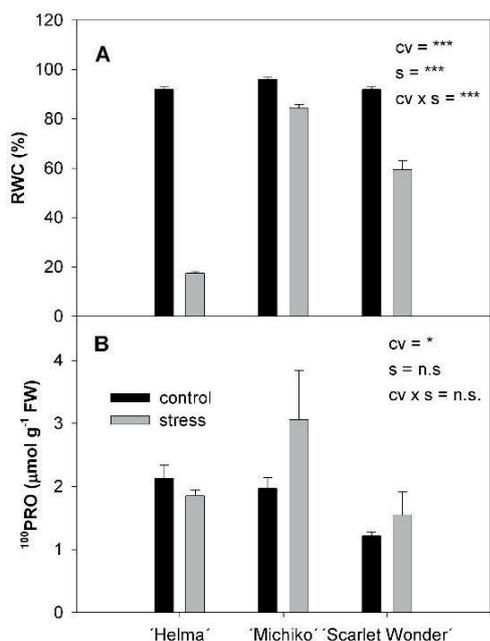


Fig. 2. Leaf relative water content (RWC, A) and free proline concentration at 100% RWC (100 PRO, B) at the initial (control) and the terminal (stress) point of the dehydration cycle (first experiment). Results \pm SE are means of four replicates. A two-way ANOVA was used to evaluate the cv effect (cv), the salt effect (s) and their interaction (cv \times s). The symbols *, ** and *** indicate significant differences at confidence levels of $P \leq 0.05$, 0.01 and 0.001, respectively; n.s. – non significant

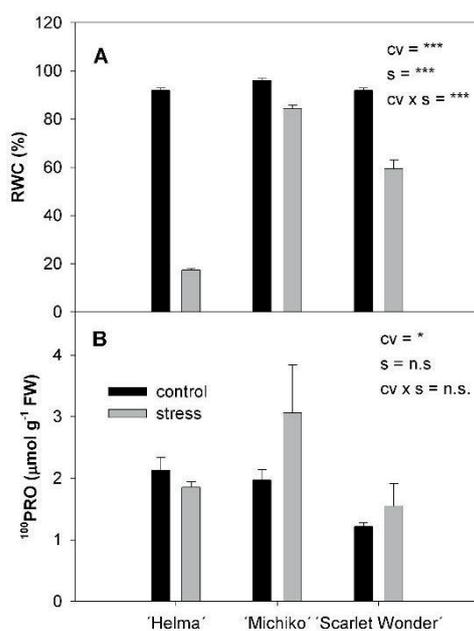


Fig. 3. Leaf relative water content (RWC, A) and free proline concentration at 100% RWC (100 PRO, B) at the initial (control) and the terminal (stress) point of the dehydration cycle (second experiment). Results \pm SE are means of four replicates. A two-way ANOVA was used to evaluate the cv effect (cv), the salt effect (s) and their interaction (cv \times s). The symbols *, ** and *** indicate significant differences at confidence levels of $P \leq 0.05$, 0.01 and 0.001, respectively; n.s. – non significant

10% reduction compared to the control in ‘Michiko’. Free proline concentration at the RWC 100% (^{100}PRO ; Fig. 2B) rose slightly only in dehydrated plants of ‘Michiko’ (from ca. 2 to 3 $\mu\text{mol g}^{-1}$ FW in average). Dehydration cycle caused mild reduction and no change in ‘Helma’ and ‘Scarlet Wonder’, respectively. Experiment no. 2 (Fig. 3A) brought significant RWC reduction at the end of the dehydration cycle with no difference between cultivars (ca. 20%). Changes in ^{100}PRO between initial and terminal points of the dehydration were also mild (Fig. 3B).

DISCUSSION

In our former study, drought injury in rhododendron collection of the Mlyňany Arboretum during summer 2015 was investigated [Ferus et al. 2017]. The field research based on evaluation of leaf wilting level as associated with the total leaf area and solar exposition of shrubs, showed *Rhododendron catawbiense*, *R. ponticum* and *R. smirnowii* as well as cultivar ‘Boursault’, ‘Cunningham’s White’ and ‘Purpureum Elegans’ as the most resistant to drought. Similar work of Zhang et al. [2002] revealed that *R. fortunei* and *R. delavayi* were more drought-resistant species than *R. irroratum*, *R. stamineum*, *R. pachypodum* and *R. decorum*. Dang et al. [2005] classified rhododendrons native to Qilian Mountains, China into 2 groups: high drought-resistant *R. thymifolium* and sub-high drought-resistant *R. anthopogonoides*, *R. capitatum* and *R. przewalskii*.

However, only few papers deal with the acclimatory reactions standing behind the resistance. For instance, Tashev et al. [2016] described how the xylem vessel features in *R. ponticum* were changing with the climate change in the natural conditions of Strandja, Bulgaria, with the risk of mortality from drought. They found that the mean vessel area was rising while the mean vessel density was dropping. Then, despite of low soil water potential, *R. arboretum* widely distributed in the central Himalaya, maintains high hydration level, tissue elasticity and stomatal conductance but lower relative water content at the turgor loss [Poudyal et al. 2004, Singh et al. 2006]. Cordero and Nilsen [2002] analysed stem hydraulic conductivity loss (HCL) during summer drought and winter freezing in three native American rhododendron species.

Fifty percent HCL loss obtained from vulnerability curves under dehydration occurred at -1.75 , -2.42 and -2.96 MPa for *Rhododendron catawbiense*, *R. maximum* and *R. macrophyllum*, respectively. Moreover, *R. catawbiense* with small stem diameter suffered high xylem embolism compared to the rest two species. Mayr et al. [2010] studied hydraulic properties of European alpine rhododendron species associated with geological substrate. Highest embolism resistance (water potential at 50% HCL of -3.24 MPa) as well as highest safety margin between water potential at stomatal closure and at 50% HCL (1.57 MPa) were observed in *R. hirsutum* at the limestone site. *R. ferrugineum* growing on silicate and then *R. × intermedium* occupying mixed stands showed lower drought resistance.

Increasing level of soil moisture deprivation (from ca. 80% to 65, 50 and 35% of maximum field water capacity (MFC)) caused significant decreases of stomatal conductance and transpiration rate in *R. fortunei*, by 21 and 33%, 65 and 44%, 67 and 82%, respectively [Ke et al. 2007], showing a steep fall of the stomatal conductance at 50% MFC, similar to that observed in some rhododendron genotypes from our study. In the same research, water use efficiency showed a significant increase in the mildly stressed plants and a decrease in plants treated by moderate and heavy stress [Ke 2007], and free proline content markedly increasing only when moderate and heavy stress were applied [Ke and Yang 2007]. Similarly, fall of the stomatal conductance triggered by the soil water shortage was observed also in hybrid rhododendron cv. ‘Cosmopolitan’ [He et al. 2011]. Further, Li et al. [2015] studying metabolic reactions of *R. simsii* to drought, observed transient free proline increase followed by a decline with prolonged dehydration. Our results indicate no free proline accumulation, thus suggesting no osmotic adjustment employment, in the dehydrated rhododendron plants. However, lower SLA could play a role in the water storage ability of most of the studied genotypes [Bacelar et al., 2004].

This literature overview outlines diverse species-specific strategies concerning drought resistance, spread and survival in the natural environment. Comparing physiological responses of cultivars in our research, three distinct strategies can be seen: 1. lower and longer period active transpiration with stomata

sensitive to the water loss (*R. repens* ‘Scarlet Wonder’ and *R. × hybridum* ‘Red Jack’), 2. higher and short period active transpiration with stomata sensitive to the water loss (*R. obtusum* ‘Michiko’ and *R. × hybridum* ‘Polarnacht’), and 3. higher and short period active transpiration with stomata insensitive to the water loss (*R. groenlandicum* ‘Helma’). The first one is accepted as the most convenient for ornamental plantations endangered by summer drought.

CONCLUSIONS

Tested rhododendron cultivars showed three distinct drought-resistance strategies. Lower and longer period active transpiration with stomata sensitive to the water loss, as found in *R. repens* ‘Scarlet Wonder’ and *R. × hybridum* ‘Red Jack’ are accepted as the most effective one for ornamental plantations endangered by prolonged drought events.

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