

BRIEF COMMUNICATION

The combined effect of branch position, temperature, and VPD on gas exchange and water-use efficiency of Norway spruce

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Abstract

The impact of climate change on the physiological processes of Norway spruce in Central Europe is a significant concern. The increased temperature and evaporative demand associated with climate change may negatively affect its photosynthesis and carbon-water balance. This study tests the combined effect of branch position, temperature (T) and water vapour pressure deficit (VPD) on net photosynthetic rate (P_N), water vapour stomatal conductance (g_s), and intrinsic water-use efficiency (WUE_i) of Norway spruce. More than 11 000 gas-exchange measurements during the summer of 2018 revealed that branch position significantly affects gas exchange and WUE_i of juvenile Norway spruce trees. Northern branches showed on average 21% increased P_N , 35% higher g_s , and 8% lower WUE_i compared to the southern branches (across T and VPD conditions). The P_N and g_s differences between the branches were temperature- and VPD-dependent. We observed the negative impact of raising temperature on gas exchange and WUE_i for both treatments, with a 40°C threshold causing a rapid decline in WUE_i . Variability of the southern branches' WUE_i at 42°C was abruptly increased due to the decoupling of P_N and g_s (low P_N , high g_s). Surprisingly, raising VPD showed no significant impact on WUE_i of Norway spruce. The results of this study provide necessary information for upscaling and process-based modelling of whole-crown gas exchange. Moreover, experimental studies of gas exchange should take into consideration the branch position effect to prevent possible bias errors.

Keywords: intrinsic water-use efficiency, photosynthesis, *Picea abies*, stomatal conductance.

Norway spruce (*Picea abies* (L.) Karst.) is essential species for the maintenance of the vital forest ecosystems in Europe, but its decline due to climate change poses a threat (Zanchi and Brady 2019). The decline of Norway spruce forest has been exacerbated by the combined effects of biotic, abiotic, and anthropogenic stresses (Zavadilová

et al. 2023). While higher-altitude trees may benefit from a moderately warmer and drier climate, lower-altitude trees may be more stressed and impaired (Jamnická et al. 2020, Salomón et al. 2022). Understanding the capacity of Norway spruce forests to sequester carbon is important for the recognition of their overall ecological function and

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Abbreviations: E - transpiration rate; g_s - stomatal conductance; P_N - net photosynthetic rate; VPD - water vapour pressure deficit; WUE_i - intrinsic water-use efficiency.

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potential response to climate change (Martínez-Sancho *et al.* 2022). Proper modelling of carbon sequestration in forest ecosystems requires a deep awareness of net photosynthetic rate variability within the crown, as the rate of CO₂ uptake can vary greatly across different parts of the tree crown (Liu *et al.* 2018).

Branch position significantly affects the net photosynthetic rate (P_N) and stomatal conductance (g_s) of trees as it influences their exposure to irradiance and air flow, causing variations not only in P_N but also in transpiration rate (E) (Özçelik *et al.* 2022). Within-crown variability of P_N can be influenced by a number of factors, including the age and size of needles, the position of needles within the crown, and the overall health of the tree (Kerhoulas *et al.* 2020). Studies have shown that the upper and outer parts of the crown tend to have a higher rate of gas exchange than the crown's lower and inner parts (Ngao *et al.* 2017). Moreover, east-oriented branches of Norway spruce showed lower leaf temperatures and had lower carbon efflux compared to the west-oriented branches (Acosta *et al.* 2011). The water-use efficiency ($WUE = P_N/E$) of needles can also vary depending on their crown position, but the results are so far inconclusive regarding the question if the inner or outer position has greater WUE (Christina *et al.* 2016). Branch position acclimation affects WUE by regulating the balance between water loss through transpiration and carbon gain through photosynthesis (Stojnić *et al.* 2019).

Temperature, VPD, and crown position can significantly affect coniferous trees' gas-exchange rate, with varying effects influencing the tree's CO₂ uptake and water vapor loss (Durand *et al.* 2020). Temperature affects P_N in trees, with higher temperatures increasing photosynthesis within certain limits, while extremely high temperatures can damage the photosynthetic machinery and decrease P_N (Konôpková *et al.* 2020). Temperature and VPD play a crucial role in regulating stomatal conductance, as high temperatures and high vapour pressure deficit lead to increased E in trees (Urban *et al.* 2017). Moreover, temperature and VPD can have a significant impact on the WUE of trees, with increased evaporative demand leading to increased water loss through E , which can lower the tree's WUE (Klein *et al.* 2013, Petrik *et al.* 2023). Understanding of combined effects of temperature, VPD, and branch position on gas exchange and WUE is a key milestone for upscaling the processes from leaf to whole canopy (Hatfield and Dold 2019).

The goal of this study was to test the interaction between branch position, temperature, and VPD effects on gas exchange and intrinsic water-use efficiency ($WUE_i = P_N/g_s$) of Norway spruce. We hypothesised that southern branches will be acclimated to higher temperature and VPD, thus maintain greater WUE_i via higher P_N and lower g_s .

The study site of the field experiment was located in the Tatra National Park in Slovakia (49°9'59.67" N; 20°17'6.162" E), at an altitude of 840 m a.s.l. The location lays within the Eastern part of the Carpathian Mountains. The experiment was conducted during the vegetation season of 2018. The meteorological conditions were measured at

the site with EMS33 sensors (EMS, Brno, Czech Republic). The average temperature during the vegetation season (May - August) of 2018 was 16°C and the precipitation sum during the vegetation season was 330 mm (Fig. 1A Suppl.). The long-term (1960 - 1990) vegetation season temperature was 13.2°C and precipitation sum 395 mm. Three soil water potential sensors (EMS) were installed in the near vicinity (<5 m) of studied trees in 5, 10, and 20 cm depth. The soil water potential in 20 cm depth reached a minimum value of -6 kPa during the start of June but recovered shortly to near zero values for the rest of the season (Fig. 1B Suppl.). Analysed trees therefore did not experience soil drought during the observed period.

The gas-exchange measurements were conducted on 15-year-old Norway spruce (*P. abies*) individuals located in the urban park of Tatranska Lomnica town. Measurements were performed weekly from 1st of June to 31st of August 2018 on nine spruce individuals with an average height of 5 m and an average diameter at a breast height of 11 cm. From each individual, three outer branches from the northern and southern sides were measured. The southern branches experienced on average $760 \pm 21 \mu\text{mol m}^{-2} \text{s}^{-1}$ and northern $602 \pm 15 \mu\text{mol m}^{-2} \text{s}^{-1}$ incoming ambient radiation during the measurements. The measured trees were growing in a loose semi-circle, minimally shading each other. The branches from the outer edge of the branch were selected and the height of measured branches varied between 70 and 120 cm.

Gas-exchange measurements were conducted with two open gasometric systems *Li-6400XT*, equipped with a coniferous leaf chamber fitted with a *6400-02B* LED radiation source (*LI-COR Biosciences*, Lincoln, USA). The temperature response curves of P_N ($\mu\text{mol m}^{-2} \text{s}^{-1}$), g_s ($\text{mmol m}^{-2} \text{s}^{-1}$), and intrinsic water-use efficiency ($WUE_i = P_N/g_s$, $\mu\text{mol mmol}^{-1}$) of each branch was measured weekly. The temperature response curve typically consisted of 2°C steps from 22°C to 42°C, the adaptation time for each step lasted from 5-10 min based on the temperature (slower adaptation at a lower temperature). The conditions in the chamber were set to saturating PAR of 1 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and CO₂ concentration was 400 $\mu\text{mol mol}^{-1}$. The airflow ranged from 500 to 700 $\mu\text{mol s}^{-1}$, and RH ranged from 30 to 60% according to measurement cuvette temperature. The gas-exchange measurements were conducted between 8:00 - 17:00 h (mid-day depression does not occur at high altitude). The temperature curves of 16 - 18 branches (approximately three individuals) were measured per day. Measurements were conducted daily, throughout the whole vegetation season and all individuals were measured at least once per week. The leaf area of branches was measured at the end of the experiment from scanned needles using *ImageJ* software (National Institute of Health, Bethesda, Maryland, USA) to normalise values. In total, 11 303 gas-exchange measurements (around 209 measurements per branch) were conducted. Ranging temperature and relative humidity enabled us to evaluate also the VPD response of the gas exchange.

Branch values were averaged per individual and the branch position (north vs. south) for further analyses

($n = 9$). The measurements from a single dataset were grouped by temperature (22°C, 24°C, 26°C, *etc.*) and VPD (0.2 kPa, 0.6 kPa, 1 kPa, *etc.*) classes for the further analyses. Assumptions of normal distribution and homoscedasticity were tested for all data by the Shapiro-Wilk test and Bartlett's test. The differences of P_N , g_s , and WUE_i between the branch position treatments for respective temperature and VPD were tested by the Linear Mixed Models with branch and month of measurement as a random factors and branch position and temperature/VPD as fixed factors. The analysis was conducted with the lmer function from “lme4” (Bates *et al.* 2015) R package. The standard deviation of random effects (branch:month) intercepts were 7.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for P_N , 37.15 $\text{mmol m}^{-2} \text{s}^{-1}$ for g_s , and 30.05 $\mu\text{mol mmol}^{-1}$ for WUE_i . The differences between treatments at respective temperature and VPD were tested by Tukey's pairwise tests “multcomp” (Hothorn *et al.* 2008) R package. The relationships between temperature/VPD and P_N , g_s , and WUE_i were analysed with linear and quadratic regressions selected for each measured parameter based on R^2 , P , root-mean-square error (RMSE) and Akaike information criterion (AIC). All statistical analyses were conducted in R 4.2.2 software (R Core Team, Vienna, Austria).

The analysis of variance revealed that branch position had a significant effect on P_N , g_s , and WUE_i (Table 1). The VPD and temperature had a significant effect on the P_N and g_s of Norway spruce, but not WUE_i . Interactions of temperature and branch position had a significant effect on WUE_i . Moreover, VPD and branch position interaction

had a significant impact on the P_N and g_s of Norway spruce. The northern branches had on average 20.76 and 35.01% higher P_N and g_s , respectively, while WUE_i was 8% lower than the southern branches (across temperature/VPD gradients).

The P_N response to temperature was best described by the quadratic regression, with optimum around 24°C for northern branches and optimum at 28°C for southern branches (Fig. 1A). The g_s showed the strongest linear negative trend with raising temperature for the northern branches and the quadratic response for the southern branches (Fig. 1C). The P_N and g_s were decreasing with rising VPD for both branch positions (Fig. 1B,D). Northern branches showed an overall higher P_N and g_s compared to the southern branches. The differences between the branch positions in P_N and g_s were significant across the temperature range. As for VPD, the differences in P_N and stomatal conductance between treatments were significant at lower VPD levels (<3.4 kPa). WUE_i showed a quadratic trend with rising temperature for both treatments, decreasing WUE_i above 28°C for southern branches and above 30°C for northern branches, with rapid reduction of WUE_i above the 40°C threshold (Fig. 1E). Higher variability of the southern branches WUE_i at 42°C was due to the desynchronization of P_N and g_s values (low P_N , high g_s). The quadratic regression also suggests optimal WUE_i of Norway spruce around 28 - 30°C. The differences in WUE_i between treatments were significant only at lower temperatures and above the 40°C threshold, with northern branches showing lower WUE_i values. The regression between VPD and WUE_i for the northern branches was

Table 1. Results of linear mixed models for net photosynthetic rate (P_N), stomatal conductance (g_s), and intrinsic water-use efficiency (WUE_i) with branch and month of measurement as random effects and branch position, temperature (*upper part*) and VPD (*lower part*) as fixed factors.

		Sum Sq	Mean Sq	NumDF	DenDF	F value	P value
P_N	branch position	15 993.91	15 993.91	1	964.62	17.47	<0.001
	temperature	23 134.38	1 927.86	12	893.18	2.11	<0.05
	branch position × temperature	7 016.55	701.66	10	898.87	0.77	0.66
g_s	branch position	15.55	15.55	1	941.86	6.51	<0.05
	temperature	237.99	19.83	12	904.35	8.30	<0.001
	branch position × temperature	10.69	1.07	10	908.15	0.45	0.92
WUE_i	branch position	42 220.63	42 220.63	1	2 053.87	2.12	<0.05
	temperature	226 144.30	18 845.36	11	871.12	0.95	0.49
	branch position × temperature	104 607.30	10 460.73	10	857.48	2.53	<0.05
P_N	branch position	20 971.82	20 971.82	1	1 127.90	26.10	<0.001
	VPD	118 152.80	7 384.55	16	1 177.29	147.07	<0.001
	branch position × VPD	8 090.80	577.91	14	1 166.19	10.07	<0.01
g_s	branch position	34.62	34.62	1	1 133.09	16.91	<0.001
	VPD	575.02	35.94	16	1 163.54	280.93	<0.001
	branch position × VPD	16.07	1.15	14	1 156.61	7.85	<0.01
WUE_i	branch position	6 242.19	6 242.19	1	502.96	3.34	<0.05
	VPD	27 142.01	1 696.38	16	559.66	1.48	0.23
	branch position × VPD	4 921.53	351.54	14	559.66	0.27	0.60

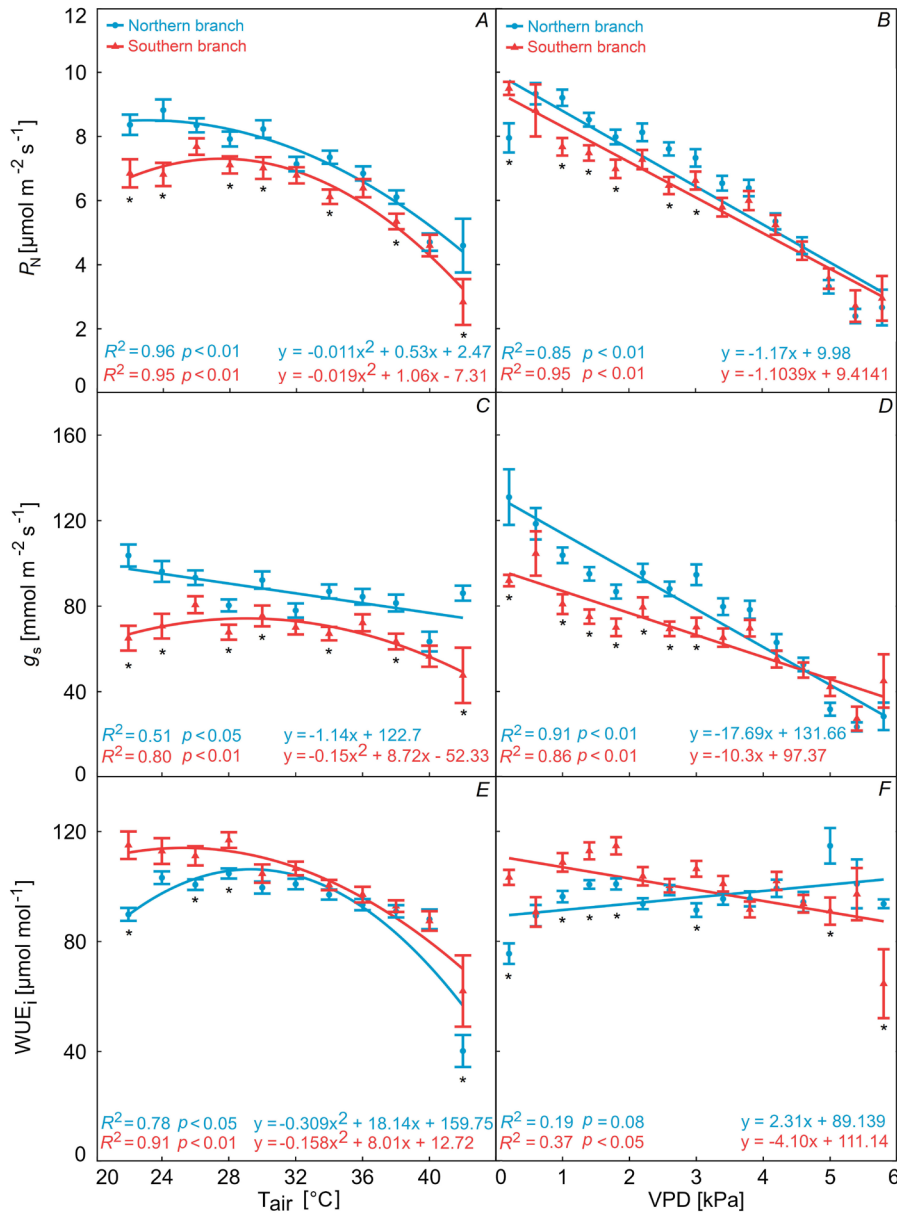


Fig. 1. Temperature and vapour pressure deficit response of net photosynthetic rate (A,B), stomatal conductance (C,D), and intrinsic water-use efficiency (E,F) for the southern (red) and northern (blue) side of the crown (PAR = 1 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The linear or quadratic regression is used based on R^2 , P , RMSE, and AIC values. Variability intervals represent 95% confidence intervals. The asterisk represents a significant difference between treatments for corresponding temperature or VPD, based on Tukey's pairwise test ($P < 0.05$).

not significant, however, the southern branches showed a significant negative regression between raising VPD and WUE_i (Fig. 1F). Northern branches showed significantly lower WUE_i values at lower VPD and higher WUE_i values at higher VPD.

Contrary to our hypothesis, the northern branches showed greater P_n than the southern branches. Nevertheless, as per our two other hypotheses, the southern branches showed lower g_s and therefore maintained significantly higher WUE_i than the northern branches.

The gas-exchange differences between the southern and northern branch position correspond to results obtained in coniferous species like *Larix olgensis* (Liu *et al.* 2018) and *Pinus tadea* (Maier *et al.* 2002). As all measurements were conducted at saturating PAR of 1 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, the differences between treatments represent long-term acclimation of the needles to branch position (different irradiance, leaf temperature). Northern branches show greater P_n and g_s as they are probably overcompensating for usually lower irradiance that they experience (Rowland

et al. 2021). Moreover, shaded branches of two *Picea* species showed more effective absorption of diffuse radiation compared to sun shoots (Ishii *et al.* 2012). This can be directly related to different shade needles morphology, including optical differences and differences in needle photosynthetic pigments (Kováč *et al.* 2012). However, needles from the southern position can dispose more effective protection against overreduction of photosystem II (PSII) reaction centres (Špunda *et al.* 1998), whereas the adjustment of photosynthetic capacity and corresponding resistance to photoinhibition depends on PSII excitation pressure under a wide range of growth temperatures and irradiances. The lower WUE_i of northern branches at 1 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, compared to southern branches, is due to a disproportional increase of g_s (35%) with P_N (20%). The desynchronisation of P_N and g_s can lead to a surplus in E (e.g., transition from high to low irradiance), hence reducing WUE_i (Coupel-Ledru 2021). The differences in gas exchange and WUE_i were getting insignificant at higher VPD, suggesting a similar response of stomata to raising evaporative demand for both treatments. This can be caused by the isohydric nature of Norway spruce (Pashkovskiy *et al.* 2019). The reduction of WUE_i at high VPD may be also linked to negative impacts of co-occurring high temperature on primary and secondary photosynthetic processes (Münchinger *et al.* 2023). The heterogeneous nature of gas exchange within the crown should be taken into consideration for whole crown upscaling and modelling of carbon and water fluxes, as well as, for the experimental designs to avoid excessive bias.

Another interesting finding of our study was a rapid decline of WUE_i above the 40°C threshold. This could be caused by thermal damage to photosynthetic apparatus and an overall reduction of photosynthetic efficiency. Húdoková *et al.* (2022) confirmed that temperatures between 38 to 42°C have a significant negative effect on the PSII performance of mature Norway spruce. The PSII thermostability overlaps with the gas-exchange temperature response in Norway spruce (Hrivnák *et al.* 2022). Similarly, several studies have shown that heat stress starts to inhibit the photosynthesis of Norway spruce around the 40°C threshold (Kunert 2020, Münchinger *et al.* 2023). Due to climate change, this temperature threshold can be already reached in Europe during the heat waves, which can negatively impact the carbon sequestration potential and health status of Norway spruce forests (Kunert *et al.* 2022). The variability of WUE_i among the southern branches at 42°C was also higher due to co-occurring low P_N and (relatively) high g_s , suggesting decoupling of photosynthetic apparatus from stomata (McAusland *et al.* 2016, Urban *et al.* 2017). The disturbances of Norway spruce forests will probably increase under the future climate, and heat stress along with drought will play a major role in their decline (Honkaniemi *et al.* 2020).

Proper integration of both temperature and VPD response with crown variability for gas-exchange simulation is necessary to avoid unprecise predictions at a whole tree level. The temperature response observed in

this and other studies pose the question if Norway spruce is a viable species for carbon sequestration in Central Europe. Reduction of assimilation across the crown will lead to even more retarded growth, which is a negative outcome from both economic and ecological perspective.

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