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Effect of altitude and age of stands on physiological response of three dominant plants in forests of the Western Carpathians

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ABSTRACT

The objective of research was to evaluate physiological reaction of dominant plants (*Fagus sylvatica*, *Dryopteris filix-mas*, *Rubus idaeus*) taking advantage of the altitudinal variations in the area of the Slovenský raj National park (Western Carpathians). Secondary spruce stands are the current edificators of phytocoenoses between the ages of 10–15 and 80–100 years, in undergrowths with a mix of naturally regenerated beech and fir. Nutrient contents in top soils followed the change of conditions, such as climate and soil type. The concentrations of available Ca and Mg were relatively fluctuated (*CV* 44–55%) and decreased with increased altitude. On the other hand, K and P concentrations (*CV* 38–41%) improved with increased altitude. Results of physiological characteristics of plants showed variations between species in rate of photosynthesis (P_n), rate of transpiration (E) and maximum quantum efficiency of photosystem II (F_v/F_m). Effect of altitude appears inconclusive in species monitored and their measured parameters, with the exception of P_n in *R. idaeus* a *D. filix-mas*. Influence of better light conditions in younger stands was proved in the values of F_v/F_m for *F. sylvatica*.

Keywords: secondary spruce forests; elevation; ecological conditions; gas exchange; maximal photochemical efficiency

The current condition of the forest is determined by a complex of primary causes, such as pollution encumbrance, disruption of physiological processes (malfunctions of nutrient and water supplies, pathogens) and conditions within the atmosphere, while the overall decrease of plant vitality is conditional upon their mutual interaction (Jamroz et al. 2014). The environment of a plant may vary daily, seasonally, vertically and horizontally. Chapin et al. (1987) states, that most plants require a similar balance of energy, water and mineral nutrients resources to maintain optimal growth. Natural environment, however, differs by at least two orders of magnitude in the availability of these resources. Gas exchange in natural forest ecosystems is limited by the mutual combination of a wide range of factors, among them are temperature, water, concentrations of CO_2, ontogenic development, mineral nutrients, biotic and anthropogenic factors (Urban et al. 2014, Kuklová et al. 2015).

A significant factor in forest stands composed of a tree and herb layer are light conditions. As light environment varies greatly, plant leaves are considered sensitive to light changes. Irradiation limits photosynthesis rates (Valladares et al. 2002) and is one of the factors regulating the opening of stoma and thus also stomatal conductance and transpiration (Aranda et al. 2012). Along with these factors, the effect of altitude on gas exchange, as well as other physiological parameters were studied (Zhang et al. 2005, Kumar et al. 2006, Körner 2008).

Therefore, physiological response is the keys to understanding the ecological function of diversity

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Table 1. Information on the sampling plots (observation period 2012–2013)

Plot	G1	G2	G3	G4	G5	G6
Geographical coordinates	20°30'43''E, 48°53'18''N	20°30'42''E, 48°53'17''N	20°32'07''E, 48°51'51''N	20°32'12''E, 48°51'49''N	20°28'40''E, 48°52'55''N	20°28'37''E, 48°52'55''N
Altitude (m a.s.l.)	750	760	950	960	1000	1110
Exposure	ENE	ENE	SW	S	NNW	NW
Slope (°)	30	30	10	10	25	25
Stand age (years)	10–15	80–100	10–15	80–100	10–15	80–100
Stocking	0.6–1.0	0.5	0.6–1.0	0.5	0.6–1.0	0.5
Forest vegetation grade	5th fir-beech				6th spruce-beech-fir	
Edaphic-trophic order/interorder	hemioligotrophic				oligotrophic	
Groups of geobiocoene types	*Abieti-Fageta inferiora*				*Fageta abietino-piceosa*	

ENE – East-North-East; SW – South-West; S – South; NNW – North-North-West; NW – North-West

of plants under the influence of environment. Elevation differences often lead to changes in environmental factors such as temperature, precipitation, illumination and soil type, which make the growing environment plants more complex. Three dominant plant species (*Fagus sylvatica* L., *Dryopteris filix-mas* L., Schott, *Rubus idaeus* L.) growing in the secondary spruce forests were selected as objects of this work. The study has focused principally on: (1) evaluation of the content of available macronutrients (Ca, Mg, K, P) in soils; (2) evaluation of differences between the physiological characteristics of plants related to altitudinal gradient and the age of forest stands.

MATERIAL AND METHODS

Study plots. The research was performed in the first half of July in 2012–2013 in segments of forest type group *Abieti-Fageta inferiora* and *Fageta abietino-piceosa* localised close to Spišská Nová Ves city in the buffer zone of the Slovenský raj National Park (Western Carpathians, Slovakia).

Vertical transect (750–1110 m a.s.l.) consisted of 3 localities with 6 geobiocoenological plots. Three plots represented stands at the age of 10–15 years and others three parallel ones represented stands at age of 80–100 years. At present, secondary spruce stands with small amounts of naturally regenerated beech and fir in undergrowth are grown in the mentioned segments. Geobiocoenological characteristics of the research plots are shown in Table 1. Determination and classification of the studied geobiocoenoses was made in terms of Zlatník (1976). Description of the climatic characteristics of the studied plots is presented in Table 2 (Miklós 2002).

Soil analysis. The soils of the studied transect were derived from different rocks, however with very similar (very poor) mineral strength. For this reason the soil reaction is also very similar (very acid) and plant communities were classified into similar edaphic-trophic order of geobiocoens (oligotrophic, hemioligotrophic). Soil samples were taken from organic-mineral Ao horizons in triplicate. The thickness of Ao horizons varied as follows: plot G1 – 8 cm; G2 – 8 cm; G3 – 7 cm; G4 – 9 cm; G5 – 12 cm; G6 – 12 cm. Values of soil reaction were determined potentiometrically by a digital pH meter Inolab pH 720 (Weilheim, Germany). N_{tot} and C_{tot} content was determined by the NCS analyser, type FLASH 1112 (Hanau, Germany). Available forms of macronutrients (Ca, Mg, K, P) were extracted according to the Mehlich-2 (AES-ICP, Australia; LECO ICP-3000,

Table 2. Climatic characteristics of the studied plots (observation period 1961–1990)

Climatic region	Cold (C)
Climatic subregion	moderately cold (C1) July ≥ 12°C to < 16°C
Mean annual precipitation totals	700–800 mm
Mean annual air temperature	4–5°C

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USA). Amount of humus in the soil was calculated by multiplying C content by factor 1.724.

Analysis of plant species. The forest ecosystems were classified according to Zlatník (1976). On the study plots (area about the size of 400 m^2) *Fagus sylvatica* L., *Rubus idaeus* L. and *Dryopteris filix-mas* (L.) Schott were monitored. The gas exchange – rate of photosynthesis (P_n) and rate of transpiration (E) were measured on the upper surface of leaves (the middle part of the leaf blade) *in situ* using the portable gas exchange system LCpro+ (ADC BioScientific Ltd., Hoddesdon, UK). These characteristics were measured under adjusted light and temperature conditions, the irradiance was 650 μmol/m^2/s of photosynthetically active radiation (PAR), the temperature in the chamber was 25°C, the CO_2 concentration was 420 ± 35 vpm (μmol/mol) and the duration of the measurement of each sample was 20 min after the establishment of steady-state conditions inside the chamber. The minimum chl *a* fluorescence (F_0) and the maximum chl *a* fluorescence (F_m) were also measured *in situ* with the portable fluorometer ADC:OSI 1 FL (ADC BioScientific Ltd., Hoddesdon, UK) with 1 s excitation pulse (660 nm) and saturation intensity 3000 μmol/m^2/s after 20 min dark adaptation of the leaves. The maximum quantum efficiency of photosystem II (F_v/F_m) was calculated as F_v/F_m ($F_v = F_m - F_0$). Gas exchange and chlorophyll fluorescence were always measured from 9:00 to 12:30 h central European time. Average ± standard error for the physiological characteristics was measured within 20–30 individuals.

Data analysis. Analyses were made with the use of a statistics program Statistica 9 software (Tulsa, USA) and the variability of the measured characteristics in relation to altitude and age of forest stands was tested by ANOVA model and the Tukey's-*HSD* (honest significant difference) test.

RESULTS AND DISCUSSION

Soil analysis. The results showed that active soil reaction on the study plots situated at the altitude of 750 to 960 m a.s.l. varied from 4.0–4.8, at the altitude of 1100–1110 m it was 3.4 (Table 3). The carbon content (C_{tot}) in the organic-mineral soil (0–10 cm) ranged from 63–114 mg/g. The absolutely lowest value was found in Dystric Cambisol (760 m a.s.l.), while the absolutely highest one occurred in skeli-humic podzol (1110 m a.s.l.). The C improved with increased altitude. It is probably because there is relatively lower soil temperature in higher altitude, which causes slower decomposition rate of soil C (Zhong et al. 2014). The results showed that nitrogen (N) accumulation at study sites was relatively stable (3.9–6.5 mg/g). In general, mineralization occurs intensively if the organic material is rich in N. A common disturbance in the N cycle involves the loss of nitrate by leaching (Han et al. 2015).

The content of available macronutrients (Ca, Mg, K, P) in soils was relatively fluctuated. Coefficients of variation varied in the interval 38–55%. Ca content in the investigated soils with increased altitude decreased (fitted by liner equation) (Figure 1). Most of Ca in Ao horizons was accumulated in Cambisol at 960 m (1340 mg/kg) and approximately 4.7 times less in podzol at 1100 m a.s.l. Also Mg content in soils on higher situated plots

Table 3. Chemical properties of Ao soil horizons of secondary spruce forests

Plot	G1	G2	G3	G4	G5	G6
Parent rock	grey schist		quartz conglomerates		violet-grey schist	polymict conglomerates
Soil subtype	Dystric Cambisol				Skeli-Humic Podzol	
pH_{H_2O}	4.8	4.5	4.8	4.0	3.4	3.4
pH_{KCl}	3.6	3.3	3.6	3.1	2.5	2.4
C_{tot} (mg/g)	99	63	75	65	96	114
N_{tot} (mg/g)	5.1	4.7	4.8	3.9	5.1	6.5
Humus (%)	17.1	10.9	12.9	11.2	16.6	19.7
C/N	19.4	13.4	15.6	16.7	18.8	17.5

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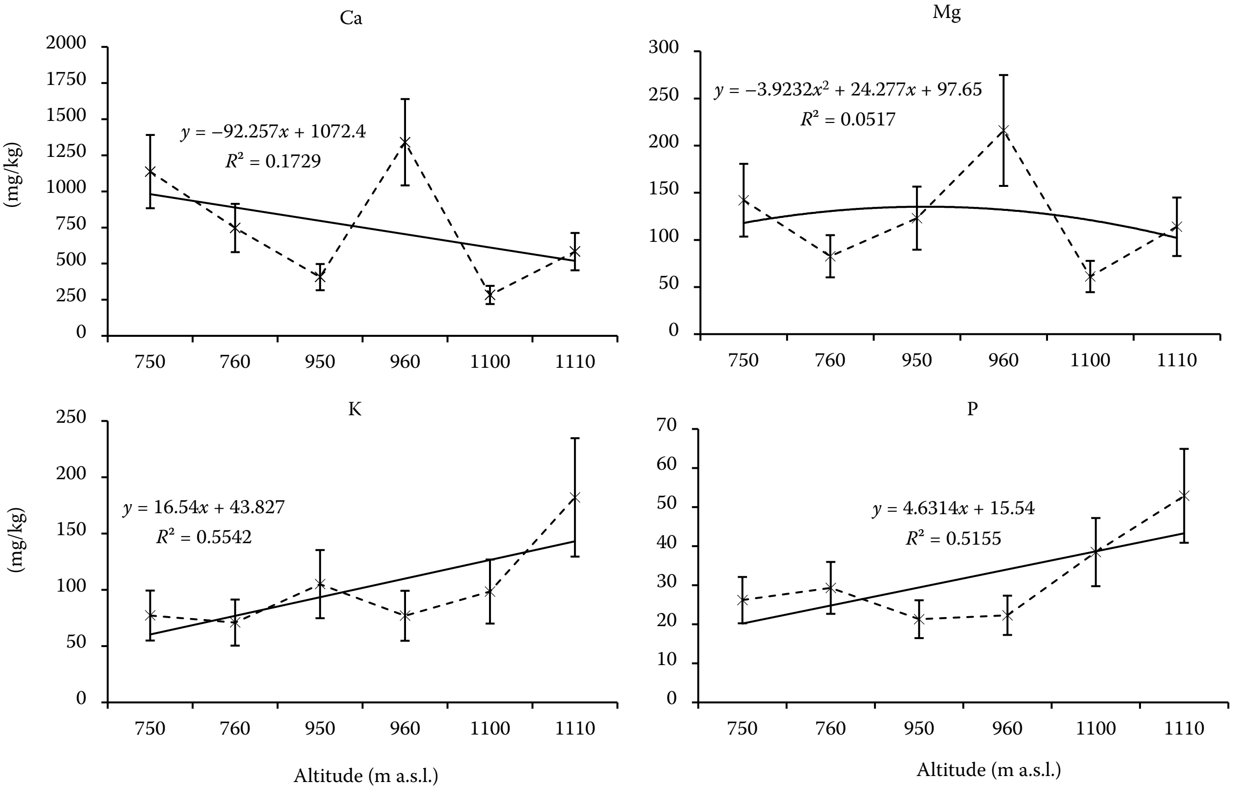

Figure 1. Trend of available macronutrients in Ao soil horizons in relation to altitude

hinted a slight declining trend (Figure 1), just as precipitation increased with increased elevation. The risk of nutrient leaching in regions affected by frequent and intense rainfalls was noted by Maathuis (2009) and Ruidisch et al. (2013).

On the contrary, K content grows with increasing altitude (fitted by liner equation), (Figure 1). Fewer K is contained in soils on lower situated plots (750–960 m a.s.l.) compared to the podzols (more than 1100 m a.s.l.). It is probably because there is relatively more precipitation and slower decomposition rate of soil organic matter in higher altitude. To sum up, soils more than 1100 m a.s.l. were strong skeletal with humus content in A-horizons from 16.6–19.7%. The content of available phosphorus (P) was relatively balanced and with increasing altitude, its content in soils grew (fitted by liner equation). This effect may be explained by weakly bound P in podzols, which reacts readily with water causing higher values of water-soluble P. A similar finding was noted by Pöthiq et al. (2010). Although mean concentrations of nutrients were higher in mature stands (mg/kg) 890 Ca < 137 Mg < 110 K < 35 P, it did not significantly differ from young stands (mg/kg) 609 Ca < 109 Mg < 94 K < 29 P.

Rate of photosynthesis. The rate of photosynthesis in plants along transect ranged from 5.5 to 16.4 μmol $CO_2/m^2/s$ (Table 4). Conclusive differences in P_n were identified between species. The highest average P_n was measured in *F. sylvatica*, while the lowest in *D. filix-mas* on the lowest plot at altitude of 750–760 m a.s.l. (Figure 2). Kuklová et al. (2015) cites P_n in the range of 12.1–10.3 μmol $CO_2/m^2/s$ for beech growing in forest stands of Kremnické and Štiavnické vrchy, Slovakia. Regarding *Dryopteris* sp. for example, Sessa and Givnish (2014) identified P_n values in the range of 2.5–6.7 μmol $CO_2/m^2/s$ and the values measured in this study also correspond to this data.

Differences in P_n between the plots were established (Table 4). In the case of *F. sylvatica*, P_n was conclusively higher at the altitude of 960 m (G4) and 1110 m a.s.l. (G6) in a contiguous stand of older woody plants. The differences between stands of varying ages (G1 a G2) on plots at 750–760 m a.s.l. were inconclusive.

Also, it was not possible to prove the effect of altitudinal gradients between the areas G1–G6 (750–1110 m a.s.l.) on P_n, while, for example, Bresson et al. (2009) identifies higher capacity of

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Table 4. Physiological characteristics of plants in relation to altitude and age of forest stands

Plot	Age/Altitude (years/m a.s.l.)	Plant species	P_n (µmol $CO_2/m^2/s$)	E (mmol H_2O /m^2/s)	F_v/F_m
G1	10–15/750	*Fagus sylvatica*	$15.9^{ab/A}$	$1.5^{cd/A}$	$0.69^{b/B}$
		Rubus idaeus	$8.9^{e/B}$	$1.2^{de/A}$	$0.79^{a/A}$
		Dryopteris filix-mas	$5.5^{i/C}$	$0.7^{fg/B}$	$0.78^{a/A}$
G2	80–100/760	*F. sylvatica*	$16.4^{a/A}$	$1.5^{cd/B}$	$0.80^{a/A}$
		R. idaeus	$10.2^{d/B}$	$1.9^{ab/A}$	$0.79^{a/A}$
		D. filix-mas	$6.2^{i/C}$	$0.4^{g/C}$	$0.79^{a/A}$
G3	10–15/950	*F. sylvatica*	$13.6^{c/A}$	$1.8^{bc/A}$	$0.69^{b/B}$
		R. idaeus	$8.7^{ef/B}$	$1.9^{ab/A}$	$0.79^{a/A}$
		D. filix-mas	$7.8^{fgh/B}$	$1.7^{abc/A}$	$0.78^{a/A}$
G4	80–100/960	*F. sylvatica*	$15.1^{b/A}$	$1.6^{bc/A}$	$0.80^{a/A}$
		R. idaeus	$8.2^{efg/B}$	$1.8^{abc/A}$	$0.79^{a/A}$
		D. filix-mas	$8.7^{ef/B}$	$1.7^{ab/A}$	$0.79^{a/A}$
G5	10–15/1000	*F. sylvatica*	$13.5^{c/A}$	$1.7^{abc/A}$	$0.75^{ab/A}$
		R. idaeus	$7.4^{gh/B}$	$0.9^{f/B}$	$0.79^{a/A}$
		D. filix-mas	$7.1^{h/B}$	$0.8^{f/B}$	$0.79^{a/A}$
G4	80–100/1110	*F. sylvatica*	$15.8^{ab/A}$	$1.6^{bc/A}$	$0.81^{a/A}$
		R. idaeus	$7.9^{fgh/B}$	$0.9^{ef/B}$	$0.79^{a/A}$
		D. filix-mas	$7.4^{gh/B}$	$0.8^{ef/B}$	$0.78^{a/A}$

Values within a column marked with the same letter are not significantly different ($P \leq 0.01$), altitude^{abc} and age^{ABC}. P_n –rate of photosynthesis; E – rate of transpiration; F_v/F_m – maximum quantum efficiency of photosystem II

P_n in *F. sylvatica* with increasing elevation. The inconclusive effect of the environment obviously shows high physiological plasticity of the *F. sylvatica* species, as also concluded by Valladares et al. (2002). In case of *R. idaeus* the highest conclusive P_n was measured on plot G2 at 760 m a.s.l. (10.2 µmol $CO_2/m^2/s$), while the P_n differences in other areas were insignificant. In general we

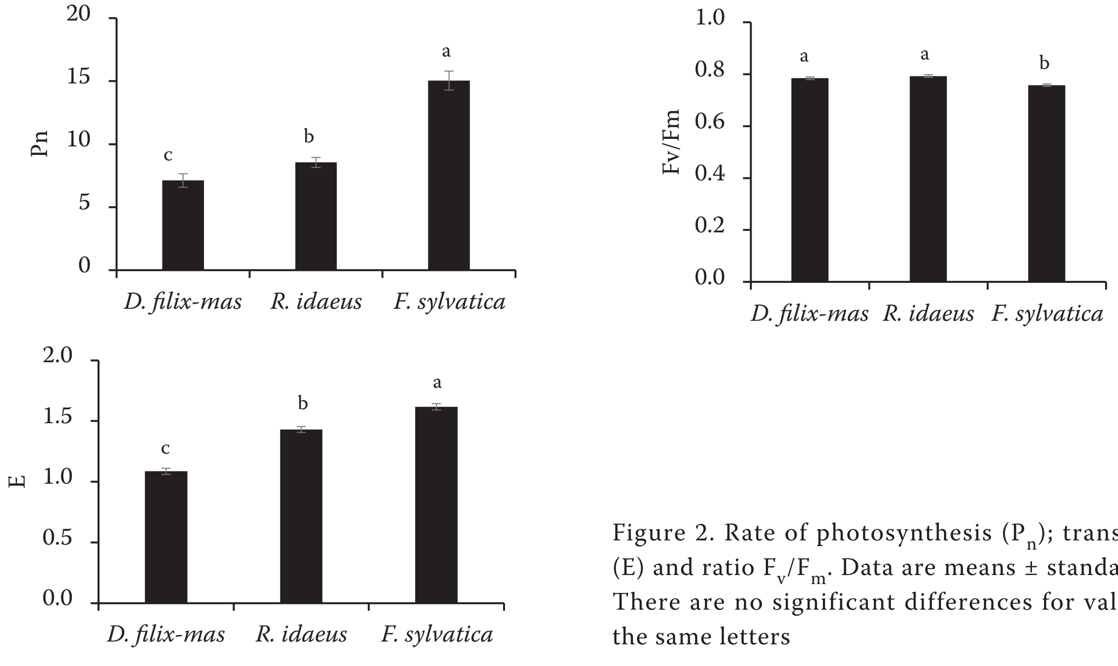

Figure 2. Rate of photosynthesis (P_n); transpiration (E) and ratio F_v/F_m. Data are means ± standard error. There are no significant differences for values with the same letters

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can say that P_n of raspberries decreased with the altitudinal gradient. In the case of *D. filix-mas*, measurably lower conclusive values were found in the lowest-situated plots G1 and G2 (750–760 m a.s.l.). The P_n of ferns increased with the altitude, but the differences between plots in individual locations were inconclusive.

Chlorophyll fluorescence. The ratio of F_v/F_m is a very important plant characteristics that indicates how efficiently the light reaction is proceeding property. The measured values of F_v/F_m on the plots ranged from 0.69–0.81 (Table 4). Maxwell and Johnson (2000) indicated the range from 0.79–0.84 as a normal value in a number of species. Differences were measured both between the monitored species and the individual plots (Table 4, Figure 2). Conclusively lower values of F_v/F_m were measured in *F. sylvatica* (0.69) on plots G1 and G3 in comparison to *R. idaeus* (0.79) and *D. filix-mas* (0.78). For instance, Valladares et al. (2002) identify F_v/F_m values in the range of 0.75–0.79 for *F. sylvatica* depending upon irradiation. Irradiation in particular influences the ratio of F_v/F_m where, with increasing intensity of irradiation, the F_v/F_m ratio drops (Sánchez and Quiles 2006). This dependency is apparent in *F. sylvatica* in the non-contiguous stands (G1, G3 and G5), where lower values of F_v/F_m were measured. This relation was not confirmed in herbaceous species *R. idaeus* and *D. filix-mas* adapted to life in the undergrowth and the differences between F_v/F_m values were insignificant in all areas (Table 4). A trend in which high values of F_v/F_m correspond with low levels of P_n was confirmed in studied species.

Rate of transpiration. The transpiration rate of leaves ranged from 0.4–1.9 mmol $H_2O/m^2/s$ in the observed species on plots G1 through G6 (Table 4). Differences in E were established between the individual species. The highest average E was measured in *F. sylvatica* (1.6 mmol $H_2O/m^2/s$) and the lowest in *D. filix-mas* (1.1 mmol $H_2O/m^2/s$) (Figure 2). Among the monitored areas, the highest values of E were measured at altitude of 950–960 m a.s.l. (G3 and G4). No significant differences in E values were established between the non-contiguous (G1, G3 and G5) and contiguous stands on plots (G2, G4 and G6) in all experimental species, with the exception of *R. idaeus* at 950–960 m a.s.l. Granier et al. (2000) identifies significant differences in E between the trees in stand and peripheral zones in *F. sylvatica*, whereas Köstner (2001) stated insignificant differences. The transpiration conditions of *F. sylvatica* in natural forest ecosystems may be further influenced by the age (Misson et al. 2002); tree height and space heterogeny (Emborg et al. 2000). The effect of altitudinal gradient on E was insignificant in all monitored species.

In conclusion, nutrient contents in top soils followed the changes of conditions, such as climate and soil type, caused by the elevation gradient changes. The content of available Ca and Mg in soils along transect was relatively fluctuated and hinted declining trend. Lower contents can be evident caused by different quantity and quality of organic matter in the humid conditions. On the other hand, K and P contents along transect with increasing altitude grew. Higher concentration of potassium in Podzols is apparently connected with higher content of K in feldspars and micas of parent rock, while higher concentration of phosphorus is caused by higher content of humus in A horizons of Podzols.

The results showed significant differences between plant species in the level of P_n, E and F_v/F_m. The influence of altitude in the range of 750–1110 m a.s.l. appears inconclusive in the studied species and measured parameters, with the exception of *R. idaeus*, where P_n decreased with altitude; on the contrary, in the case of *D. filix-mas* P_n increased with altitudinal gradient. A more significant influence of better light conditions on physiological parameters in the younger stands stand proved in the values of maximum quantum yield PSII in *F. sylvatica*. The effect of altitude proves a high adaptation rate to living conditions and plasticity of monitored species.

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