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Drought and aluminium as stress factors in Norway spruce (*Picea abies* [L.]Karst) seedlings

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ABSTRACT: Effects of drought, Al and their possible interaction on physiological characteristics were studied in four-years-old Norway spruce seedlings in a pot experiment. Drought stress was imposed by withholding irrigation. Al was applied to the soil as an $AlCl_3$ solution at a concentration of 1,500 $\mu mol \cdot l^{-1}$. Water deficit caused a decrease in needle water potential, net photosynthetic rate (P_n) and an increase in proline accumulation. On the other hand, water potential, P_n and proline concentration in seedlings subjected to Al remained unchanged. During the experiment, no significant variation was registered in the chlorophyll *a* fluorescence parameters. Chlorophyll content was significantly reduced in the Al presence. Drought led to a lower Al accumulation in needles in comparison with well-watered seedlings. Progressive dehydration influenced the physiological state of spruce seedlings. The presence of Al in soil did not cause any negative changes in the physiological parameters under an optimal water regime. By contrast, the synergic effect of drought and Al induced the most marked changes in measured characteristics, which may indicate a possible enhanced impact of drought and Al interaction in comparison with the single effect of these stress factors.

Keywords: drought; aluminium; proline; water potential; photosynthesis; chlorophyll fluorescence

Plants growing in the natural environment are constantly subjected to various environmental stresses. Among abiotic stress factors, drought and toxic elements receive great attention. Drought is one of the most important environmental factors limiting plant growth, development and productivity (Zhang et al. 2005). Drought stress affects many metabolic and physiological processes in plants. Among others, it causes growth inhibition, reduction in photosynthesis and changes in fluorescence parameters (Zlatev, Yordanov 2004; Nayyar, Gupta 2006).

Elevated concentrations of aluminium are apparent in surface waters and in soil solutions from forest soils impacted by acid deposition (Oulehle, Hruška 2005). In spite of a sharp decrease in SO_2 and NO_x emissions, soil acidification continues to be a serious environmental and forestry related issue, and the degradation of soil-forming processes in forest soils is still in progress (Hruška et al. 2001; Pichler et al. 2006). Dissolved Al in soils, mobilized by acid deposition, is considered a threat to the forest health through hampering root growth and nutrient uptake. The presence of Al leads to decreasing concentrations of K, Ca and Mg and a decrease of the base cations to Al molar ratio in the soil solution (De Witt et al. 2010). The Ca:Al ratio in roots and soils has been used as a useful indicator of the health status in plants and a diagnostic tool for the prediction of potential stress in forest ecosystems (Konôpka, Lukáč 2010; Richter et al. 2011).

Forest environments are characterized by strongly fluctuating conditions for tree growth and development. Tree species are exposed to single and combined stresses throughout their lifetime, and

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many of the simultaneous and successive stress factors strongly interact. The knowledge of how plants respond to multiple successive or multiple combined stresses is of key significance in understanding the effects of future climate on vegetation (Niinemets 2010).

A decrease in soil water content during droughts can increase Al to toxic levels for the tree growth (Schier, McQuattie 2000). Tamás et al. (2006) observed the correlation between Al uptake, Al-induced drought stress, oxidative stress, cell death and root growth inhibition. Aluminium impairs root systems by constraining their water and mineral element uptake (Slaski 1994). It has been found that both drought and Al stress can be accompanied by decreasing chlorophyll concentrations and photosynthetic rates (Schlegel, Godbold 1991; Elsheery, Cao 2008).

Norway spruce (*Picea abies* [L.] Karst.) is an important tree species in the Carpathian Mountains. Recently, the vitality of spruce ecosystems in this region and in Central Europe has been affected by a complex of stress factors, among which water deficit and soil degradation associated with Al^{3+} mobilization are considered to be significant.

In the present study we focus on a simulated stress load in Norway spruce seedlings. The objectives of this work were to assess the physiological responses of spruce seedlings to drought stress under optimal soil conditions and in the presence of elevated concentration of Al and to characterize the effect of drought, Al and their possible interactions in slightly acid soil conditions.

MATERIAL AND METHODS

Plant material and experimental design

An experiment was conducted during the 2008 growing season, from August to September. Prior to the experiment, in April 2008 four-years-old *P. abies* seedlings of local provenance were planted in pots with 4 kg of peat substrate, and placed in a plastic greenhouse. The physicochemical characteristics of the soil were as follows: pH = 5.75, moisture content 65%, total N, P, K content in dry matter: 1.1%, 0.8%, 0.2%, respectively. The experiment included four treatments: the control – C (well watered and without Al supply), drought – D (water deficit and without Al supply), aluminium – Al (well watered and with Al supply) and combined treatment – D+Al (water deficit and with Al supply). Each treatment consisted of 10 replications.

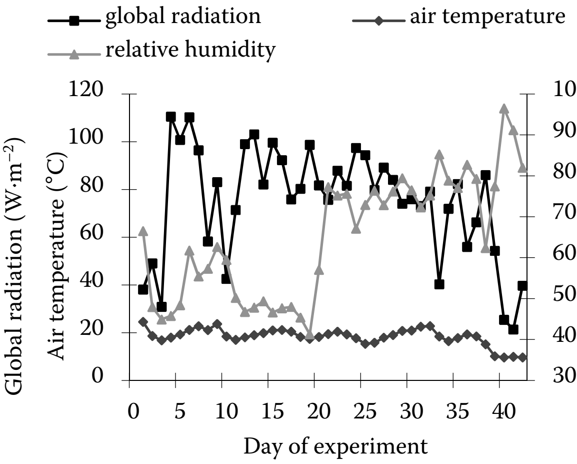

Fig. 1. Mean daily air temperature, global radiation and relative humidity during the experiment

All spruce seedlings were well irrigated until the onset of the experiment and treatments C and Al were then continuously watered to the field capacity every 2–3 days during the experimental period. Drought stress in plants was induced by withholding irrigation. Aluminium was added to the soil at the start of the experiment. It was applied in the form of $AlCl_3$ dissolved in distilled water at a concentration of 1,500 $\mu mol \cdot l^{-1}$.

During the experiment, three microclimate characteristics – air temperature, relative humidity and global radiation were recorded continually at 10-min intervals (Fig. 1). The data were recorded using a data logger supplied by Environmental Measuring Systems, Brno, Czech Republic. The acquired data were processed by the Mini32 software (Environmental Measuring Systems, Brno, Czech Republic).

Throughout the experiment, leaf water potential, gas exchange, chlorophyll *a* fluorescence, pigment and proline content were measured in five new shoots of seedlings randomly selected per treatment. The needle water potential measurements were carried out at approximately 10-day intervals, using a water potential system (Psy Pro, Wescor, Inc., Logan, USA). The measurements of gas exchange and chlorophyll *a* fluorescence were performed on days 0, 22 and 35. For pigment and free proline assessment samples were taken at the beginning and at the end of the experiment, on days 0 and 43.

Gas exchange measurements

Net photosynthetic rate (P_n) measurements were made with a CIRAS-1 portable photosynthesis system (PP Systems, Herts, UK). The CO_2 concentration was kept at 350 ppm, photosynthetically active radiation was set to 1,200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. During the measurements, temperature and ambient vapour pressure were 20°C and 1.8 to 2.3 kPa, respectively.

Chlorophyll fluorescence measurements

Chlorophyll *a* fluorescence characteristics were measured after 30-min dark adaptation, using a fluorimeter (Plant Efficiency Analyser, Hansatech, Ltd., Kings Lynn, UK). The saturating light pulse was delivered at 2,100 $\mu mol \cdot m^{-2} \cdot s^{-1}$. For each sample, we measured initial fluorescence [F_0 – all reaction centres of photosystem II (PSII) open], maximum fluorescence ($F_{m:}$ – all reaction centres of PSII closed) and the photochemical yield of PSII (F_v/F_m).

Determination of pigment content

For the determination of chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*) and carotenoid (Car) concentrations, 50 mg of current-year needles were homogenized in 80% acetone. The photosynthetic pigments were determined by spectrophotometry (Cintra, GBS Australia), and the absorbance was measured at wavelengths of 470, 646 and 663 nm. Pigment concentrations were calculated according to Lichtenthaler (1987). The results are expressed through dry weight of needles (DW).

Determination of free proline content

Extraction and estimation of free proline were conducted according to the procedures described by Bates et al. (1973). A sample of approximately 0.5 g of the current-year needles was homogenized with 10 ml of 3% (w/v) aqueous sulphosalicylic acid solution. The homogenate was centrifuged at 3,000 g for 20 min. The supernatant was treated with acid ninhydrin boiled for 1 h, and the reaction was terminated in a water bath at room temperature (25°C) for 10 min. The absorbance at 520 nm was identified using L-proline as a standard. The proline contents are given in $\mu g \cdot g^{-1}$ fresh weight (FW).

Aluminium content in soil and needles

Al concentrations in soil and needles were determined by ICP-AES (Vista PRO, Varian, Mulgrave, Australia) after drying and digestion with aqua regia. Soil samples were collected at the beginning of the experiment, after Al application to the soil. The needles were sampled at the end of the experiment. For substrate and foliar analysis 5 samples from each treatment were used.

STATISTICAL ANALYSES

The data were analyzed by two-way analysis of variance with drought and Al as two fixed factors using STATISTICA 5.5 software. The means were compared by Duncan's multiple range tests at a threshold *P* value of 0.05, for which significant differences between the treatments were found.

RESULTS

Plant water status

Gradual dehydration resulted in a decrease of needle water potential values (Ψ) in treatments subjected to drought. Significantly lower values ($P < 0.001$) of *Y* in water-stressed seedlings were recorded after 22 days in comparison with well-watered seedlings. In well-watered treatments the water potential in needles ranged about –0.36 MPa throughout the experiment, whereas *Y* of water-stressed plants declined to –2.24 MPa and –2.21 MPa in D and D+Al treatments towards the end. Fig. 2 illustrates that the seedlings influenced by drought (D, D+Al) showed similar trends, and that the Al treatment followed the trend of the control. The presence of Al exerted no influence on the water status of seedlings and the decrease in *Y* was caused by drought.

Gas exchange and chlorophyll *a* fluorescence

The water deficit significantly ($P < 0.001$) decreased the values of net photosynthetic rate (P_n) (Fig. 3). After 35 days of progressive drought stress,

Table 1. Dates of measurements and samplings

Physiological parameter	Day of measuring/sampling
Water potential	0, 13, 22, 28, 36, 43
Net photosynthetic rate	0, 22, 35
Chlorophyll fluorescence	0, 22, 35
Photosynthetic pigments	0, 43
Proline	0, 43

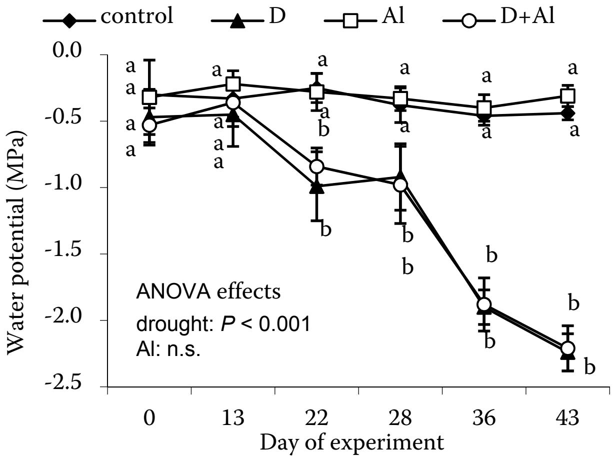

Fig. 2. Changes in water potential during the experiment
The values are the means of five replications ± SD. Different letters in each column indicate significant differences among the treatments at $P < 0.05$ (ANOVA, Duncan's test), n.s. – no significant difference

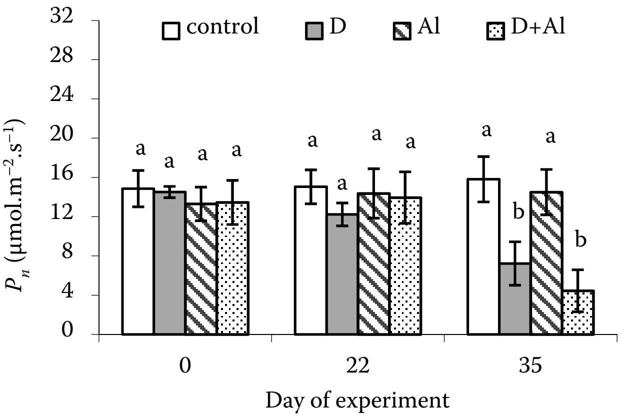

Fig. 3. Changes in net photosynthetic rate (P_n) during the experiment
The values are the means of five replications ± SD. Different letters indicate significant differences among the treatments at $P < 0.05$ (ANOVA, Duncan's test), n.s. – no significant difference

P_n was reduced to 48% in D treatment and to 28 % of the control in D+Al treatment. The presence of Al and interaction of drought and Al did not change P_n values.

During the experiment no significant variation was detected in the F_v/F_m ratio (Fig. 4). In all the treatments, the F_v/F_m values were relatively constant, ranging from 0.785 to 0.806. This parameter was found to have a low sensitivity to the water deficit and to the aluminium presence.

Pigment content

The results for photosynthetic pigments are presented in Table 2. Drought stress did not lead to a significant loss of chlorophylls (Chl *a*, Chl *b*, Chl *a+b*) and carotenoid content. In contrast, Al caused a significant decrease in assimilatory pigments, except carotenoids, in combined treatment D+Al. There was no significant interaction between drought and Al in relation to pigment content.

Table 2. The effects of drought, aluminium and their combination on photosynthetic pigments in spruce seedlings

Day of experiment	Treatment	Pigment concentration (mg·g^{-1} DW)					
		Chl *a*	Chl *b*	Chl *a+b*	Car	Chl *a/b*	Chl/Car
0	C	3.37 ± 1.30^a	1.25 ± 0.51^a	4.62 ± 1.81^a	0.94 ± 0.29^a	2.71 ± 0.12^a	4.80 ± 0.55^a
	D	3.12 ± 1.00^a	1.17 ± 0.34^a	4.29 ± 1.31^a	0.90 ± 0.17^a	2.66 ± 0.17^a	4.74 ± 0.37^a
	Al	2.92 ± 0.19^a	1.10 ± 0.11^a	4.02 ± 0.29^a	0.89 ± 0.05^a	2.66 ± 0.16^a	4.51 ± 0.45^a
	D+Al	2.92 ± 0.14^a	1.08 ± 0.13^a	4.00 ± 0.28^a	0.88 ± 0.03^a	2.73 ± 0.19^a	4.55 ± 0.48^a
44	C	3.40 ± 0.96^a	1.30 ± 0.51^a	4.58 ± 1.47^a	0.96 ± 0.24^a	2.62 ± 0.12^a	4.80 ± 0.53^a
	D	2.85 ± 0.36^{ab}	1.08 ± 0.18^{ab}	3.92 ± 0.52^{ab}	0.77 ± 0.12^a	2.67 ± 0.24^a	5.15 ± 0.67^a
	Al	2.35 ± 0.62^{ab}	0.86 ± 0.24^{ab}	3.21 ± 0.85^{ab}	0.69 ± 0.17^a	2.76 ± 0.23^a	4.65 ± 0.20^a
	D+Al	2.21 ± 0.55^b	0.78 ± 0.17^b	3.00 ± 0.71^b	0.67 ± 0.16^a	2.81 ± 0.24^a	4.45 ± 0.31^a
ANOVA effects	drought	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Al	$P < 0.05$	$P < 0.05$	$P < 0.05$	n.s.	n.s.	n.s.
	drought × Al	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

n.s. = not significant

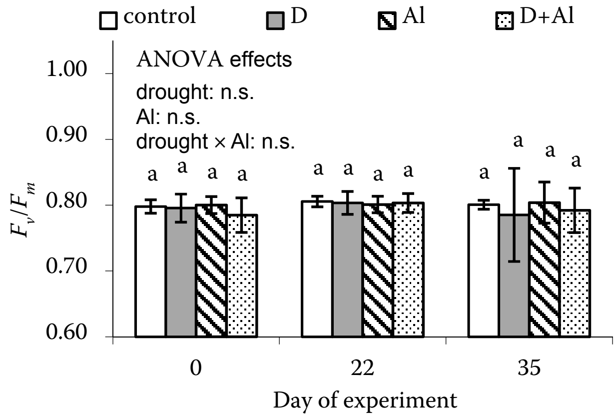

Fig. 4. Changes in F_v/F_m ratio during the experiment. The values represent the means of ten replications ± SD. Different letters indicate significant differences among the treatments at $P < 0.05$ (ANOVA, Duncan's test), n.s. – no significant difference

Proline content

The drought stress induced a significant increase in proline content in the treatments D and D+Al ($P < 0.001$), while the proline level in the seedlings treated with Al remained stable (Fig. 5). Compared with the control, the treatments D and D+Al showed a 5.7-fold and a 4.95-fold increase in proline concentration, respectively. The synergic effect of drought and aluminium presence did not evoke any enhanced proline accumulation.

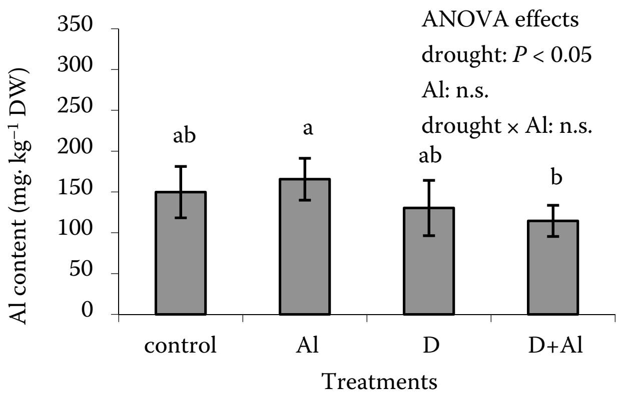

Fig. 6. Aluminium content in spruce needles at the end of the experiment
The values are the means of five replications ± SD. Different letters indicate significant differences among the treatments at $P < 0.05$ (ANOVA, Duncan's test), n.s. – no significant difference

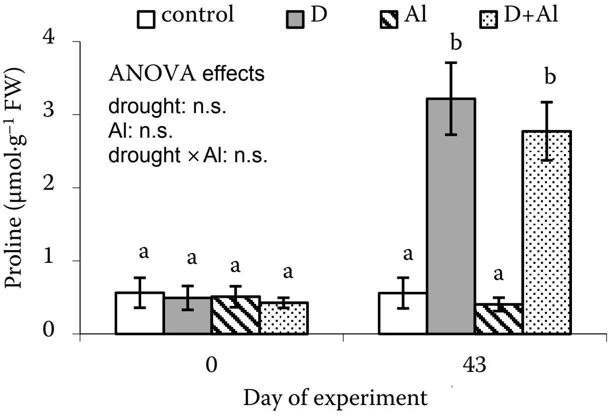

Fig. 5. Proline content in spruce needles at the beginning and at the end of the experiment The values are the means of five replications ± SD. Different letters indicate significant differences among the treatments at $P < 0.05$ (ANOVA, Duncan's test), n.s. – no significant difference

Aluminium content in soil and needles

In the control variant, the Al content in soil was 2,517 mg·kg^{-1}. The addition of $AlCl_3$ resulted in an increase of Al to 3,220 (treatment D+Al) and to 3,271 mg·kg^{-1} DW (treatment Al). The Al content in needles in different treatments is shown in Fig. 6. The control seedlings contained 149.8 mg·kg^{-1} DW of Al. The highest concentration was detected in the well-watered plants with added Al. The drought stress resulted in a lower Al accumulation in needles ($P < 0.05$) compared to well-watered seedlings.

DISCUSSION

Spruce seedlings subjected to drought, to Al excess and to their interactions exhibited physiological changes. The plant water potential (Y) is a frequently used parameter in the assessment of the plant water regime. The drought effect on Y values has been confirmed by several studies (Aliasgharzad et al. 2006; Ditmarová et al. 2010). They are in good accordance with our results showing the decrease of water potential during progressive dehydration. It has been well recognized that the Al presence may inhibit water uptake and initiate drought stress (Barcelo, Poschenrieder 2002; Tamás et al. 2006; Gallé, Feller 2007) – due to the modifications of cell walls and plasma membranes (Rengel 1996). In our case, the elevated Al concentrations had no effect on water potential values.

As it is shown in Fig. 3, the P_n values were markedly altered by drought. They were lower in the drought presence than in the control seedlings. This is consistent with the previous studies (Zlatev, Yordanov 2004; Elsheery, Cao 2008) reporting on water stress inhibiting photosynthesis, usually as a consequence of stomatal closure. With simultaneous Al excess and water deficit, the reduction in P_n was more pronounced, but the differences between D and D+Al treatments were not statistically significant. It has been reported that Al reduced the net CO_2 assimilation rates (Ridolfi, Garrrec 2000; Akaya, Takenaka 2001; Chen et al. 2005). Our results, however, did not confirm the effects of Al on P_n.

The drought and elevated Al contents did not influence the F_v/F_m ratio. The unaffected F_v/F_m values indicate the absence of photo-damage to PSII reaction centres and confirm that the photochemical efficiency of PSII system is resistant to water deficit (Lawlor 2002; Kocheva et al. 2004) and to Al toxicity (Akaya, Takenaka 2001; Chen et al. 2005).

The assimilatory pigments important for photosynthesis are often influenced by environmental stresses. In many cases, drought was confirmed as a factor reducing assimilatory pigments (Haisel et al. 2006; Yang et al. 2007). Similarly, the Al presence can lead to a decrease in chlorophyll content (Ali et al. 2008), either due to inhibited chlorophyll synthesis (Mihailovic et al. 2008) or due to reduced uptake of magnesium (Haug, Vitorello 1996) – an element embedded in chlorophyll molecules. In our study, however, the pigment contents were not found to be influenced significantly. The stress factors induced only a slight decrease in chlorophyll concentrations, without significant differences from the control (except the combined treatment).

Drought stress significantly enhances the proline content in spruce seedlings. The increased proline accumulation as a response to drought has been reported for various tree species (Lei et al. 2007; Ditmarová et al. 2010). Higher levels of proline in the drought presence might contribute to osmotic adjustment allowing the plants to maintain their turgor pressure and to adapt themselves to the limited water availability (Lei et al. 2007). In our case, the proline content was not markedly altered in seedlings exposed to Al excess. This is in contrast to several works which confirmed the Al effect on enhanced proline accumulation (Khan et al. 2000; Giannakoula et al. 2008). It seems that the proline accumulation is associated with Al-induced changes in the plant water regime (Barcelo, Poschenrieder 2002). Ali et al. (2008) related the proline accumulation to water stress generated by Al excess.

The Al content in needles slightly varied between the treatments. The Al concentrations in watered seedlings were higher than those in seedlings without water supply, and the difference between the treatments Al and D+Al was statistically significant. The drought can reduce Al uptake and accumulation, as suggested by the results of Sardans and Peñuelas (2007), who observed a reduction in Al concentration in leaves of *Quercus ilex* due to drought. Considering this, our results might also indicate that Al uptake may be affected by water deficiency. In comparison with the control, higher Al contents in soil did not influence the Al accumulation in needles significantly, probably because Al is predominantly accumulated in roots, while its effect on shoots is only secondary (Chaffai, Marzouk 2009). Richter et al. (2011) observed that the differences in the physiological status of beech roots were connected rather with nutrient availability and drought application than with differences in Al^{3+} concentrations in the soil solution.

In conclusion, the drought caused negative changes in all the measured variables, except chlorophyll fluorescence and induced proline accumulation. The Al presence did not influence the physiological state of spruce seedlings. However, the most marked responses were recorded for the combined treatment. Our results indicate a possible enhanced impact of drought in the Al presence on physiological processes in Norway spruce seedlings.

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