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Potassium uptake in the epiphytic lichen *Hypogymnia physodes* at concentrations and pH conditions as found in stemflow

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Summary

Samples of the foliose epiphytic lichen *Hypogymnia physodes* were incubated with 0, 100, 500, and 1000 μM KCl solution for up to 120 min. K was absorbed by *H. physodes* only in single replicates of the most highly concentrated solutions. Otherwise a release of K of up to 26 μmol g^{-1} d. wt. was observed. This can be attributed to the low affinity of K for the cation exchange sites in lichen cell walls. The K concentrations applied with the incubation medium correspond to concentrations found in stemflow from dieback-affected *Picea abies* forests in the Harz Mountains, northern Germany. The results suggest that stemflow is not a major source of K for *H. physodes*. The loss of K in the present experiment could be due to changes of the water content in the lichen thalli or due to membrane damage caused by S or heavy metals in the field.

Key words: Extracellular absorption, lichen ecology, nutrient uptake, potassium efflux, precipitation chemistry, spruce forests, forest dieback

Introduction

Epiphytic lichens can satisfy their nutrient requirements from different sources, viz. from precipitation, fog, gases, airborne particles and the substrate (FARMER et al. 1991; HAUCK 2000). FARRAR (1976) showed that PO_4^{3-} uptake in the foliose epiphytic lichen *Hypogymnia physodes* from precipitation is efficient enough to satisfy the requirements of the lichen for PO_4^{3-} from this source. High efficiency in PO_4^{3-} uptake was also found in *Cladonia portentosa* (HYVÄRINEN & CRITTENDEN 1998). Findings that Mn immobilization in polyphosphate granules and extracellular phosphate encrustations in *H. physodes* does apparently not result in intracellular P deficiency support the results of FARRAR (1976) that this lichen species is very efficient in PO_4^{3-} uptake (HAUCK et al. 2002 d, 2003). For most other nutrients, uptake from precipitation is scarcely studied. Findings that high concentrations of S (HAUCK & RUNGE 2002; HAUCK et al. 2002 a), Mn (HAUCK et al. 2002 b; SCHMULL et al. 2002), and maybe NO_3^- (HAUCK & RUNGE 2002; SCHMULL et al. 2002) in stemflow limit the abundance of *H. physodes* and other epiphytic lichens in coniferous forests imply that these substances are taken up from precipitation. Since the Mn/Ca ratio in stemflow was found to be relevant for the abundance of *H. physodes* by HAUCK et al. (2002 b), also Ca must be taken up from precipitation.

Studying the availability of cations from conifer bark by the comparison of the efficacy of different extractants, SCHMULL & HAUCK (2003) found that K was the most readily available metal; further elements included in the investigation were Ca, Mg, Fe, Mn, Zn, and Cu. This result is in line with the significance of leaching for the fluxes of K in forest ecosystems (ELLENBERG et al. 1986; LEVIA & HERWITZ 2000). The contact between stemflow and epiphytic lichens is usually limited to short periods. Metals such as Mn with high affinity for extracellular cation exchange sites are supposed to be absorped in significant amounts on the surfaces of the lichen thallus. The uptake of such elements can still be continued, after the stemflow run down the tree trunk

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(BROWN & BECKETT 1985; HAUCK et al. 2002c). However, this mechanism can be assumed to be rather inefficient for K, because (being a monovalent class A metal; NIEBOER & RICHARDSON 1980) K belongs to the group of metals with the least affinity for extracellular cation exchange sites in lichens (BROWN & BECKETT 1984). Because of this low affinity, on the one hand, and because of the high availability of K from bark, on the other hand, we developed the hypothesis that stemflow is usually not a major source of K in epiphytic lichens. To test this hypothesis, we soaked *H. physodes* thalli with K concentrations (and at pH conditions) as found in stemflow of *Picea abies* forests in the Harz Mountains, northern Germany, and determined the K exchange.

Materials and methods

Lichen incubation and chemical analysis

Hypogymnia physodes (L.) Nyl. was collected one day prior to the experiment in the Harz Mountains (Mt. Brocken, 1000 m) in a stand of *Picea abies* (L.) Karst. affected by pollutant-caused forest dieback (HAUCK et al. 2002a). Lichens were collected on a rainy day and remained moist prior to the incubation with K solution. Immediately after collection, the moist thalli were cut into pieces of about 1 cm^2 (c. 20 mg d. wt.). These pieces were mixed in order to avoid effects due to different vitality of individual thalli; they were stored in Petri dishes for one day at 80% relative humidity, a day temperature (for 13 hours daily) of 13 °C during a photon flux of 30 μmol m^{-2} s^{-1}, and a night temperature of 10 °C. About 30–40 pieces per replicate were incubated in 20 ml either of (1) deionized water, (2) 100 μM KCl, (3) 500 μM KCl, or (4) 1000 μM KCl for 0, 10, 20, 30, 40, 50, 60, 90, or 120 min. The pH was adjusted to 3.1 referring to conditions in the stemflow (and bark) of the Harz Mountains (HAUCK 2000). The experiment was run with five replicates. After incubation, thallus pieces were removed with forceps, dried at 105 °C for 24 h and weighed. The incubation media were filtered with ash-free filters (Blue Ribbon Filters, Schleicher & Schuell, Dassel, Germany) and stored at 0–5 °C until analysis. K concentrations were analyzed with AAS (AAS Vario 6, Analytik Jena, Germany); 0.1% $CsCl_2$ and 0.1% $La(NO_3)_3$ were added prior to analysis to suppress ionization.

Statistics

Arithmetic means ± standard error (SE) are given throughout the paper. Data was tested for normal distribution with the Shapiro-Wilk test. A two-way analysis of variance (ANOVA) was carried out in order to quantify the effect of the applied KCl concentration and the duration of the treatment on the amounts of K released to or absorbed from the solution. Statistical significance was tested by calculating *F* values. The significance of differences in K concentrations relating to the duration of the incubation as well as to the given KCl supply was tested with Duncan's multiple range test (Table 1). Statistical analysis was computed with SAS 6.04 software (SAS Institute Inc., Cary, North Carolina, U.S.A.).

Results

No net absorption of K took place in any of the solutions with 0, 100, 500 or 1000 μM KCl, in regard to the mean values of the five replicates (Table 1). Instead, *H. physodes* released up to 26 μmol K per g dry weight. The parameters that varied in the experiment had no decisive influence on the amounts of K released from the lichens. Two-way ANOVA revealed that only 25% of the total variation of the change in K concentrations in the solution during the incubation could be attributed

Table 1. K release from *Hypogymnia physodes* during incubation in 0, 100, 500, and 1000 μM KCl solution at pH 3.1.

Time	K release (μmol g^{-1} d. wt.)							
	0 μM		100 μM		500 μM		1000 μM	
10	18.0 ± 2.9	a	16.7 ± 2.4	a	18.5 ± 3.6	a	13.7 ± 4.3	a
20	20.6 ± 2.4	a	21.2 ± 2.0	a	14.6 ± 3.6	a	15.1 ± 7.7	a
30	17.6 ± 2.5	a	21.3 ± 1.4	ab	9.7 ± 1.9	bc	5.7 ± 5.7	c
40	20.8 ± 4.0	a	14.9 ± 3.4	ab	8.4 ± 3.5	ab	4.6 ± 5.1	b
50	14.5 ± 0.7	ab	22.5 ± 6.1	a	16.8 ± 6.9	a	1.6 ± 1.4	b
60	18.9 ± 3.0	a	15.3 ± 2.4	a	14.7 ± 5.0	a	15.9 ± 12.9	a
90	21.0 ± 3.3	a	26.2 ± 5.8	a	22.6 ± 3.8	a	9.3 ± 8.2	a
120	20.1 ± 2.5	a	25.4 ± 3.9	a	16.8 ± 4.2	a	13.1 ± 9.8	a

Notes: Arithmetic means ± SE. Within a row, means sharing a common letter do not differ significantly (Duncan's multiple range test, $P \leq 0.05$, $df = 16$). Differences between different durations of the treatment at given KCl concentration of the incubation medium were statistically insignificant (Duncan's multiple range test, $P \leq 0.05$, $df = 32$).

to a model of the KCl concentration applied with the medium and the duration of the incubation procedure ($F = 1.36$). In contrast to the applied KCl concentration ($F = 7.29$, $P \leq 0.001$), time ($F = 1.22$) and interaction between these two factors had no significant effect ($F = 0.56$). However, there was an insignificant trend towards lower mean K release from *H. physodes* with increasing KCl concentration in the incubation medium. Mean K release tended to be lower in lichens incubated with 1000 μM (and in part also in lichens incubated with 500 μM) compared to lichens incubated with water or with 100 μM KCl. In some replicate samples at 500 μM and especially at 1000 μM KCl, even net absorption of K occurred; the highest absorption rate amounted to 13 μmol g^{-1} d. wt. at 1000 μM KCl and 120 min.

Discussion

At the concentration ranges applied in the experiment, net absorption of K from solution occurred only in single samples at 1000 μM or more rarely at 500 μM KCl. In most samples including all samples incubated with deionized water or with 100 μM KCl, K was released from *H. physodes*. Since stand-related mean concentrations of K found in stemflow of *Picea abies* in the Harz Mountains ranged from 80–200 μM (HAUCK & RUNGE 2002; HAUCK et al. 2002a, b), the results suggest that stemflow is usually not a source of K for *H. physodes* in these forests. Net absorption of K from stemflow is to be expected only during precipitation events with K concentrations above average. On individual trees of the Harz Mountains, mean K concentrations of up to 450 μM were found (HAUCK 2000; HESSE 2002). The results of the experiment parallel results of LANG et al. (1976), who found a release of K from several lichen species sampled from *Abies balsamea* in New Hampshire during incubation with simulated rainwater that contained 0.8 μM K, 4.6 μM Ca, 1.9 μM Mg, 13 μM NH_4^+, and 19 μM NO_3^- at pH 4.2. Lichen species examined in this experiment were *Evernia mesomorpha*, *Hypogymnia* spec. (probably *H. krogiae* and *H. physodes*), *Parmelia saxatilis*, *Pseudevernia cladonia* and *Usnea* spec.

Despite the absence of net absorption at low concentrations it is plausible to assume that some gross uptake took place, as K is an important macronutrient. However, with regard to the net balance of element transfer, loss of K due to membrane damage counteracted this process. The leakage of K from *H. physodes* in the experiment can be attributed to changes in water content or to toxic substances that were deposited on the lichen prior to collection in the Harz Mountains. Lichens can release significant amounts of K, when they are rewetted after desiccation (BUCK & BROWN 1979; BROWN & BROWN 1991). However, the lichen samples for the experiment were collected in moist, humid conditions and were kept humid prior to incubation. Nevertheless, the increase in thallus water content during the incubation could be sufficient to cause a release of K from the thalli (BROWN & BROWN 1991). Such loss of K during incubation can be supposed to occur in the field as well. Precipitation events after dry periods (e.g., thunderstorms in summer) might result in even higher K leakage than in the experiment. No attempts have been made so far to clarify temporal aspects of the membrane repair and of the recovery of the K status in the field (BROWN & BROWN 1991). Compared to other lichen species, *H. physodes* is a desiccation-resistent species in terms of K leakage (BUCK & BROWN 1979).

Membrane damage induced by chemical agents as a cause for K leakage from lichen thalli has often been demonstrated. As phytotoxic elements are supposed to limit the abundance of *H. physodes* in the Harz Mountains, it cannot be ruled out that such mechanism was involved in the observed K release. While Mn, which is thought to be a major site factor for epiphytic lichens in the spruce forests of the Harz Mountains (HAUCK et al. 2001, 2002b), does not cause K efflux in *H. physodes* (HAUCK et al. 2002c), other factors that are supposed to be a limiting factor for *H. physodes* in the Harz Mountains such as SO_2 and its derivatives formed in aqueous solution as well as Cu (HAUCK et al. 2001, 2002a; HAUCK & RUNGE 2002) are capable of causing significant K efflux from lichens (PUCKETT et al. 1977; BRANQUINHO et al. 1997; TARHANEN et al. 1999). The rates of K release found in *H. physodes* are in the range found for other species incubated with toxic elements. *Umbilicaria muehlenbergii* lost about 20 μmol g^{-1} d. wt. when exposed to 1 mM aqueous SO_2 for 3 h (PUCKETT et al. 1977); total K concentration in untreated *U. muehlenbergii* amounted to about 70 μmol g^{-1} d. wt. (NIEBOER et al. 1979). In *H. physodes* from dieback-affected spruce forests of the Harz Mountains, total K concentrations varied between 50 and 60 μmol g^{-1} d. wt. (HAUCK 2000; HESSE 2002). This infers that lichens releasing about 15 to 20 μmol g^{-1} d. wt. of K in the experiment lost about one third of their total K content. Depending on the species as well as on the physiological status, about 70 to 98% of the total K content of a lichen is located intracellularly (BROWN & BROWN 1991; HAUCK 2000). HAUCK et al. (2002c) found in *H. physodes* 97% intracellular K when separately analyzing K concentrations in the cell interior and at extracellular exchange sites. This indicates that most K lost in the present experiment derived from the cytoplasm. A toxic effect of Cl^- in the concentrations applied is not very probable. In a growth experiment with soredia of *H. physodes*, 7 mM KCl applied in combination with 7 mM $MnCl_2$ had no effect compared to treatments with

7 mM $MnCl_2$ alone (HAUCK et al. 2003), whereas addition of $CaCl_2$ and $MgCl_2$ to $MnCl_2$ significantly influenced soredia growth (HAUCK et al. 2002d). Exposing thalli of *H. physodes* to 1 mM NaCl for 18 h, did not affect net photosynthesis (PUNZ 1979).

Since stemflow is apparently not the main source of K for *H. physodes* in the Harz Mountains, it is obvious that K could be absorbed from the substrate. The high availability of K from conifer bark (SCHMULL & HAUCK 2003) supports this assumption. Hyphae of *H. physodes* can deeply penetrate the bark (BELTMAN 1978). The present results support conclusions of HAUCK & RUNGE (2002) and HAUCK et al. (2002b) that negative correlations found between the K concentration in stemflow of *Picea abies* and cover of *H. physodes* were due to intercorrelation with other parameters such as the S content of stemflow. Though K concentrations in bark interact with K concentrations in stemflow, as the latter are primarily determined by K concentrations leached from the foliage and from the bark (LEVIA & HERWITZ 2000), bark is also a separate ion source that has to be considered independently of stemflow. This is because ions can be expected to be available from moist bark also under humid conditions in periods without stemflow, e.g., subsequent to precipitation events or during fog periods. Such periods are usually considerably longer than periods with the occurrence of stemflow.

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