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Resorption of N, P and K from the floating and submerged leaves of the aquatic fern *Salvinia natans*

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ABSTRACT:
Nutrient resorption from senescing leaves and shoots decreases the nutrient losses associated with biomass turnover and represents a significant component of mineral nutrient economy. In submerged aquatic plants, N and P resorption efficiencies (REN, REP) from senescing leaves or shoots are high (usually >40% in dry weight, DW), but K resorption efficiency (REK) is usually very low or zero. The free-floating aquatic fern *Salvinia natans* has a linear, modular shoot structure exhibiting steep growth and a physiological polarity, and consists of oval, floating, natant leaves with photosynthetic functions and thread-like submerged leaves which absorb nutrients. To obtain the basic mineral nutrient characteristics, REN, REP and REK were estimated in the senescent floating and submerged leaves of this species grown in an outdoor culture. The N content in all the leaves was in the range between 1.10–1.42% DW, P 0.33–0.57% DW and K between 4.03–6.20% DW, indicating a partial N growth limitation but a liberal P uptake. Contrary to expectations, the REN values in both types of leaves were relatively low (7–31%), those of REP even negative (-7 to -12%), while the REK values were relatively high (31–44%). These results are in contrast to much higher N and P resorption efficiencies reported in both submerged plants and the similar tropical species *S. molesta*. The REK values found in *S. natans* are in accordance with those reported in *S. molesta,* but are much higher than those in submerged plants. Thus, the submerged leaves (rhizophylls) of the *Salvinia* species do not behave in the same way as the leaves of higher submerged plants in terms of the K economy.

Keywords:
heterosporous fern, foliar nutrient content, N, P and K resorption efficiency

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INTRODUCTION

Aquatic plants accumulate mineral macronutrients in their shoots, both from the bottom sediments and the ambient water, to meet all their metabolic demands and ensure optimal plant growth and development (Dykyjová 1979; Barko *et al.* 1991; McJannet *et al.* 1995; Jampeetong & Brix 2009). Within this ecological group of plants, free-floating non-rooted (e.g. *Lemna, Azolla, Salvinia*) and rootless submerged species (*Ceratophyllum, Utricularia, Aldrovanda*) take up mineral nutrients only from the free water column, and the latter aquatic carnivorous genera also from animal prey (Dykyjová 1979; Room & Thomas 1986; Adamec 2016, 2018). Out of all mineral nutrients, N and P are considered the most important macronutrients in plants and most often represent growth-limiting factors for plants in terrestrial and aquatic habitats (e.g. Marschner 1995; McJannet *et al.* 1995; Güsewell & Koerselman 2002; Vergutz *et al.* 2012). In various higher plant species, however, the tissue content of both N and P in growing or mature leaves (shoots) can be variable, ranging by a factor of 20 between the minimum and maximum (Dykyjová 1979; Marschner 1995; McJannet *et al.* 1995). The availability of N and P in the soil or ambient water is commonly reflected by the N:P content ratio in the shoots or leaves. Generally, optimal N:P ratios range between 10 to 20 when plant growth is co-limited equally by both N and P; moreover, N:P ratios in senescent tissues may serve to evaluate the efficiency of N and P resorption (reutilisation, remobilisation, recycling, retention) from aging tissues (Güsewell & Koerselman 2002; Güsewell *et al.* 2003; Güsewell 2004, 2005).

Nutrient resorption from senescing leaves and shoots decreases the nutrient losses associated with biomass turnover and represents a significant component of mineral nutrient economy (Güsewell 2004, 2005; Adamec 2014, 2018; He *et al.* 2020). Plants in nutrient-poor habitats may minimise their relative nutrient losses in senescent leaves/shoots ('resorption efficiency') or the final nutrient content lost in senescent biomass ('resorption proficiency'; Killingbeck 1996) or maintain a longer organ life span. Nutrient resorption traits are an important ecological indicator reflecting both plant taxonomy, plant habit, functional groups and growth rate (Aerts 1996; Aerts *et al.* 1999; Güsewell 2005). Usually, N resorption efficiency (REN) closely correlates with P resorption efficiency (REP). Much less information is available on K resorption efficiency (REK) in terrestrial plants, but REK values usually increase by 50–60% (Marschner 1995; Adamec 2002, 2014). For methodological reasons, information on nutrient resorption efficiencies in aquatic submerged and free-floating species is extremely limited (see Adamec 2000, 2014, 2016). So far, N, P and K resorption efficiencies have been estimated only in *Ceratophyllum submersum* S. F. Gray, *Stuckenia pectinata* (L.) Börner and in two aquatic carnivorous plant genera – *Aldrovanda vesiculosa* L. and some *Utricularia* species (Lytle & Smith 1995; Adamec 2000, 2014, 2016, 2018). As opposed to the high values of REN and REP also found in the senescent shoots/leaves of these submerged species, those of REK were either very low or even negative (i.e. the tissue K content in aging organs was even higher than that in mature tissues). Although the reason why K is not resorbed has not yet been explained, it is possible that maintaining a stable K concentration in cells contributes to the maintenance of cell turgor and an electrophysiological equilibrium as a prerequisite for the effective resorption of growth-limiting N and P from aging shoots (see Adamec 2014).

Salvinia natans (L.) All. is an annual, temperate, freely-floating heterosporous aquatic fern (Babenko *et al.* 2016, 2019) and many similar perennial species (e.g. *S. molesta* D. Mitch., *S. auriculata* Aubl.; both often considered aggregate species) grow in tropical regions (Room & Thomas 1986). *Salvinia natans* has a highly polar, linear and modular shoot structure: trimeric leaf whorls with different leaves are formed in the leaf nodes. Two oval floating, hydrophobic leaves with photosynthetic function stabilise the plant on the water surface, while the third, long, thread-like, submerged leaf bearing many trichomes is root-like in its shape and function ('rhizophyll'). Like some other free-floating plants (e.g. *Azolla*) and many aquatic carnivorous plants, it exhibits distinct growth and physiological polarity (Adamec 2000, 2018; Babenko *et al.* 2016, 2019) as well as rapid apical growth accompanied by permanent senescence of old basal shoot segments. In temperate regions at the end of August, *S. natans* starts forming spherical sporocarps, while the apical shoot growth gradually ceases and the shoots senesce and die, whereas perennial tropical species are evergreen (Room & Thomas 1986). Mineral nutrient relations seem to have never been studied in the true *S. natans* as the study by Jampeetong & Brix (2009) reported to be on *S. natans* was clearly conducted on another species (due to the round-shaped leaves, it was most probably the tropical *S. auriculata*). The authors proved a marked uptake and growth preference of ammonium over nitrate.

In this study, to obtain the basic mineral nutrient characteristics in *S. natans*, this species was grown in an outdoor culture and N, P and K resorption efficiencies were estimated in the senescent floating and submerged leaves. The hypothesis that the REN and REP values are high in both types of leaves but K is resorbed efficiently only in floating leaves has been tested.

MATERIALS AND METHODS

Plant cultivation and sampling. *Salvinia natans* (origin from N Moravia, the Czech Republic) was grown in tap water in an outdoor 80 l laminate container with garden loam and milled limestone as the substrate. In mid-August 2016, the surface water temperature ranged between 16 to 30°C, the pH was 8.65 and the electrical conductivity 36.1 mS/m. The water was considered mildly eutrophic (NH_4^+, 2.6 μM; NO_3^-, 0.21 μM; PO_4, 32.6 μM; K^+, 0.64 mM; Na^+, 0.46 mM; Ca^{2+}, 0.81 mM; Mg^{2+}, 0.42 mM). On 14 August, 9 large plant colonies of *S. natans* ca. 4 cm long were tagged with thread between the first and second mature leaf whorl (as counted from the shoot apex) to estimate the apical shoot growth rate (Adamec 2000, 2016). Five days later, on 19 August, the position of the tag was scored. On this date, the plants started forming small immature sporocarps (ca. 1.5 mm in diameter), but the plants were still growing apically. Mature, green, floating and submerged leaves from the second mature leaf whorls and senescent, brown-green leaves from the 8^{th}–10^{th} leaf whorls were sampled and pooled with 5 plants as mixed samples in 6 parallels. The sampled material was thoroughly washed in tap water and all cohabiting organisms were removed.

Chemical analyses. The dried material (80°C) was ground into small pieces and used for N, P and K analyses. The N, P and K contents of the leaves were estimated in diluted samples following acid mineralization of the biomass (0.7–4 mg dry weight, DW; for all details, see Adamec 2002, 2014, 2016). N and P analyses of the mineralizates and NH_4^+, NO_3^- and PO_4 in the filtered cultivation water were determined colorimetrically by an automatic FIAstar 5010 Analyzer (Tecator, Sweden), while K^+ analyses were carried out by flame atomic absorption spectrometry using a Varian AA240FS (Agilent, Santa Clara, CA, USA). The metallic cations in the filtered cultivation water were analysed using ion chromatography (881 Compact IC pro-Cation; Metrohm AG, Herisau, Switzerland; cation column Metrosep C4-150/4.0).

Statistical treatment. The foliar nutrient contents in mature and senescent leaves are always expressed in % DW and presented as such. As no data are available to estimate the relative DW decrease in senescent *S. natans* leaves, data on DW decrease in *Utricularia vulgaris* L. shoots were used as a reference (Adamec 2016). Thus, the arbitrary correction factor of 0.827 was used for both leaf types to multiply the presented estimated values of nutrient content for the senescent shoots in order to calculate the N, P and K resorption efficiencies (in %). The negative values indicate a higher nutrient content in the senescent leaves after the correction. Significant differences in the leaf nutrient content between mature and senescent leaves of the same type and between floating and submerged leaves of the same age were tested using 1-way ANOVA (Tukey HSD test for multiple comparisons, Statistica v. 5). Means ± 1 SE are shown.

RESULTS AND DISCUSSION

Nutrient content and nutrient resorption efficiencies in leaves. At the sampling time, the experimental plants were still growing apically and the measured mean apical shoot growth rate was 0.29 new leaf whorls a day. Thus, the plants were able to allocate the resorbed nutrients (N, P, K) into newly formed shoot segments as well as unripe sporocarps. The N content in the mature floating leaves of *S. natans* was 1.31±0.07% DW (Table 1) and was not significantly different either from that in the senescent leaves (1.10±0.10% DW) or in the submerged mature leaves (1.27±0.06% DW). In line with this, there was no significant difference in the N content between the mature and senescent submerged leaves. Surprisingly, the P content in the mature floating leaves (0.44±0.01% DW) was significantly lower ($p < 0.01$) than that in the senescent floating leaves (0.57±0.01% DW) and the same relationship also applied to the mature and aging submerged leaves. The floating leaves of both ages had significantly higher P content than the submerged ones. The relatively low foliar N but high P contents consequently underlie the very low N:P ratios in all the variants (between 1.93–3.86, Table 1). These ratios were higher in the mature than in the senescent leaves, which indicates greater REN than REP. Indeed, the calculated REN values were 30.8% for the floating leaves and only 7% for the submerged ones, while the REP values were negative for both types of leaves. The very low N:P ratios, together with the relatively low N content in both types of mature leaves in *S. natans,* suggest that the plants were partly N limited but over-fertilised by P (cf. Güsewell & Koerselman 2002; Güsewell *et al.* 2003), which also fits the water chemistry data (see above). The K content in the mature leaves of both types in *S. natans* was around the same (5.99–6.20% DW) and was significantly higher than that in the senescent leaves (4.03–5.18% DW, Table 1). In line with this, the REK was 30.8% and 44.4% for the floating and submerged leaves, respectively. Thus, unexpectedly, K is distinctly resorbed from both types of senescent leaves of *S. natans* and the REK is even somewhat greater in the submerged leaves.

To our knowledge, mineral nutrient traits in temperate *S. natans* are as yet unknown. On the other hand, a large amount of data on mineral nutrient content are available for certain similar but evergreen (sub)tropical *Salvinia* species, mainly *S. molesta*. In hydroponically grown *S. molesta* and in whole plants, Cary & Weerts (1983) reported the rather variable mineral nutrient content as being dependent on the form and concentration of the added N source (in % DW): N, 1.46–5.52; P, 0.32–0.72; K, 3.21–4.66; the N:P ratios ranged between 4.56–10.8. The highest values of N and P content as well as the growth rate were obtained with an added NH_4^+ salt, which confirms the uptake preference of NH_4^+ over NO_3^-. In an extensive study at 14 sites of *S. molesta* in Papua New Guinea and eastern Australia, Room & Thomas (1986) reported similarly broad mean intervals of nutrient contents for the whole plants from the sites (in % DW): N, 1.08–1.68; P, 0.16–0.27; K, 2.39–4.03; the N and P contents always strongly positively correlated with each other. In hydroponically and greenhouse-grown tropical *Salvinia* (probably *S. auriculata*), Jampeetong & Brix (2009) estimated a significantly higher N content in the mature floating leaves (2.67–3.69%) as compared to the submerged leaves (1.79–2.71%). In the shoots (mainly leaves) of hydroponically grown tropical *Salvinia cucullata* Bory, Jampeetong *et al.* (2012) determined 4.7–5.0% N, 0.97% P and 5.3–5.7% K. Similar high values of N and P contents (N, 3.8–5.0% DW; P, 0.31–0.74%) were also found in the shoots of the ecologically similar and taxonomically related free-floating aquatic fern *Azolla filiculoides* Lam., grown in mineral nutrient solutions (Forchhammer 1999). Therefore, N, P and K contents in the shoots or leaves of tropical *Salvinia* species are highly variable according to the N, P and K availability in the ambient water and also to the growth

Table 1. The comparison of N, P and K content in the tissue of mature and senescent leaves of *Salvinia natans*. Both floating and submerged leaves were evaluated. REN, REP, REK, resorption efficiency of N, P or K in senescent leaves including the correction factor of 0.827 due to biomass decrease. Means ± 1 SE are shown; n = 6. The negative values of resorption efficiency indicate higher nutrient content in the senescent leaves after the correction. Any significant differences in nutrient content within the same type of leaves between different ages (1-way ANOVA, Tukey HSD test) is shown on the right side of the table, while the significant differences in nutrient content within the same age between different types of leaves is shown on the left side of the table. **, $p < 0.01$; *, $p < 0.05$; other cases, non-significant difference.

Leaf type	Leaf age	N content (% DW)	REN (%)	P content (% DW)	REP (%)	K content (% DW)	REK (%)	N:P
Floating	mature	1.31±0.07	–	**0.436±0.013**	–	6.20±0.13*	–	*3.02±0.17**
Floating	senescent	1.10±0.10	30.8	**0.566±0.005	-7.4	**5.18±0.26	30.8	**1.93±0.16
Submerged	mature	1.27±0.06	–	0.330±0.012**	–	5.99±0.15**	–	3.86±0.21
Submerged	senescent	1.42±0.08	7.0	0.448±0.020	-12.1	4.03±0.28	44.4	3.22±0.25

rate – a high growth rate may slightly decrease the tissue nutrient content. Moreover, the ranges of the shoot N, P and K contents found in the tropical *Salvinia* species clearly cover and overlap all the values of the foliar N, P and K contents found in the present study in annual *S. natans* (Table 1).

In terrestrial perennial plant species, foliar N, P and K resorption efficiencies are generally highly variable, but the REN is mainly within the range of 40–55%, the REP 50–80% and the REK within 50–80% (Marschner 1995; Aerts 1996; Güsewell 2005; Vergutz *et al.* 2012; He *et al.* 2020). Usually, REN closely correlates with REP. Similar highly efficient N and P resorptions were also found in the shoots of three species of aquatic carnivorous plants and in rootless *C. submersum*: between 28–92% for N and 52–72% for P, but only between -8.5 to 33% for K (Lytle & Smith 1995; Adamec 2000, 2014, 2016). However, in *S. natans* leaves of both types, the REN was only 7.0–30.8% and P resorption did not occur at all (Table 1). Based on the different N and P availability in the ambient cultivation water, the plant growth was likely N limited, while the P uptake was liberal. Thus, the low foliar N content could only be slightly above the physiological threshold for N resorption (N proficiency), while P resorption could be unnecessary. In contrast to several submerged plants, both types of *S. natans* leaves distinctly resorbed K. In the field study conducted by Room & Thomas (1986), the linear shoots of *S. molesta* displayed a marked polarity in N, P and K contents in both types of shoots. When the nutrient contents in the young mature leaf whorls (the second mature ones from the shoot apex) and those in the senescent whorls (9^{th}–10^{th} ones) from the latter study are compared and when the correction factor of 0.827 for a DW loss (Adamec 2016) is applied, the following resorption efficiencies can be calculated: REN for floating/submerged leaves, 68/70%; REP 59/71%; and REK 77/42% (or 84/38% at another site). All these values demonstrate a rather effective N, P and also K resorption from the aging leaves of both types and are reminiscent of the typical values for terrestrial plants (cf. Vergutz *et al.* 2012; He *et al.* 2020). However, the relatively high REK values found in the submerged leaves of temperate *S. natans* (Table 1) and tropical *S. molesta* (Room & Thomas 1986) indicate another strategy of K economy than in other submerged plants.

CONCLUSION

The relatively low or even negative values of N and P resorption efficiencies found in the senescent floating and submerged leaves of the temperate aquatic fern *S. natans* with linear modular shoots are in sharp contrast with the high N and P resorption efficiencies both in tropical *S. molesta* and several rootless submerged plants. However, the relatively high REK in *S. natans* in both the floating and submerged leaves is in accordance with the higher REK values reported in *S. molesta* leaves of both types, but contradicts the very low or zero REK reported in several submerged plants.

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REZIME

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Resorpcija N, P i K iz flotantnih i submerznih listova akvatične paprati *Salvinia natans*

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Resorpcija hranljivih materija iz starih listova i izdanaka smanjuje gubitke hranljivih materija povezane sa prometom biomase i predstavlja značajnu komponentu prometa mineralnih hranljivih materija. U submerznim vodenim biljkama, efikasnost resorpcije N i P (REN, REP) iz listova ili izdanaka koji stare je visoka (obično >40% suve težine, DW), ali efikasnost resorpcije K (REK) je obično veoma niska ili nula. Slobodno plutajuća vodena paprat *Salvinia natans* ima linearnu, modularnu strukturu izdanaka sa strmim rastom i fiziološkim polaritetom, a sastoji se od ovalnih, flotantnih, natantnih listova sa fotosintetičkim funkcijama i od submerznih listova u obliku niti koji uzimaju hranljive materije. Da bi se dobile osnovne karakteristike mineralnih hranljivih materija, REN, REP i REK su procenjeni u starim flotantnim i submerznim listovima ove vrste uzgajane u kulturi na otvorenom. Sadržaj N u svim listovima bio je između 1.10–1.42% DW, P 0.33–0.57% DW i K između 4.03–6.20% DW, što ukazuje na delimično ograničenje rasta N, ali slobodno usvajanje P. Nasuprot očekivanjima, vrednosti REN u oba tipa listova bile su relativno niske (7–31%), REP čak negativne (-7 do -12%), ali su REK vrednosti bile relativno visoke (31–44%). Ovi rezultati su u suprotnosti sa mnogo većom efikasnošću resorpcije N i P koja je prijavljena i kod submerznih biljaka i kod sličnih tropskih vrsta *S. molesta*. Vrednosti REK pronađene u *S. natans* se slažu sa onima koje su zabeležene kod *S. molesta*, ali su mnogo veće od onih u submerznim biljkama. Dakle, submerzni listovi (rizofili) vrste *Salvinia* se ne ponašaju na isti način kao listovi viših submerznih biljaka kada se uzme u obzir promet K.

Ključne reči: heterosporne paprati, sadržaj nutrijenata u listovima, efikasnost resorpcije N, P i K