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Nutrient resorption of two evergreen shrubs in response to long-term fertilization in a bog

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Abstract Plant resorption of multiple nutrients during leaf senescence has been established but stoichiometric changes among N, P and K during resorption and after fertilization are poorly understood. We anticipated that increased N supply would lead to further P limitation or co-limitation with N or K [i.e. P-(co)limitation], decrease N resorption and increase P and K resorption, while P and K addition would decrease P and K resorption and increase N resorption. Furthermore, Ca would accumulate while Mg would be resorbed during leaf senescence, irrespective of fertilization. We investigated the effect of N, P and K addition on resorption in two evergreen shrubs (*Chamaedaphne calyculata* and *Rhododendron groenlandicum*) in a long-term fertilization experiment at Mer Bleue bog, Ontario, Canada. In general, N addition caused further P-(co)limitation, increased P and K resorption efficiency but did not affect N resorption. P and K addition did not shift the system to N limitation and affect K resorption, but reduced P resorption proficiency. *C. calyculata* resorbed both Ca and Mg while *R. groenlandicum* resorbed neither. *C. calyculata* showed a higher resorption than *R. groenlandicum*, suggesting it is better adapted to nutrient deficiency than *R. groenlandicum*. Resorption during leaf senescence decreased N:P, N:K and K:P ratios. The limited response of N and K and the response of P resorption to fertilization reflect the stoichiometric coupling of nutrient cycling, which varies among the two shrub species; changes in species composition may affect nutrient cycling in bogs.

Keywords Ombrotrophic · Peatland · Stoichiometry · *Chamaedaphne calyculata* · *Rhododendron groenlandicum*

Introduction

Plants may develop two advantageous strategies to adapt to nutrient deficiency: optimizing nutrient uptake and promoting nutrient conservation (Aerts and Chapin 2000). The withdrawal of nutrients from senescing leaves and the subsequent transportation to storage sites as well as new and growing organs, i.e. resorption (Killingbeck 1986), is an important nutrient conservation strategy, ensuring nutrients are available for future plant growth and reducing the dependence on external nutrient availability (Aerts 1996; Aerts and Chapin 2000). Nutrient resorption efficiency, defined as the proportion of the nutrient that is resorbed during leaf senescence, has global averages of ~65 % for N and P and ~70 % for K (Vergutz et al. 2012). These values for N and P are substantially higher than the widely used global value of ~50 % (Aerts 1996; Killingbeck 1996; Aerts and Chapin 2000).

In general, resorption is in a balance with the acquisition of nutrients from the soil and this balance depends on the relative energy consumption of these two processes: which process is energetically 'cheaper' (Wright and Westoby 2003). One may anticipate that a high resorption plays an essential role in nutrient-poor environments, where the acquisition of nutrients from the soil is usually more energetically costly relative to resorption (Wright and Westoby

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2003). A negative relationship should occur between resorption and nutrient concentration in mature leaves, which is often considered as a good indicator of soil nutrient availability (van den Driessche and Rieche 1974), but this pattern may not occur, for a variety of reasons. First, besides the nutrient concentration in mature leaves (i.e. nutrient availability), other factors can control the resorption process, such as phloem transportation rates and loadings, the extent to which the organic N and P compounds are hydrolysed (Loneragan et al. 1976), the sink strength of different plant organs (Nambiar and Fife 1991) and soil moisture status (Escudero et al. 1992; Pugnaire and Chapin 1993). Second, in addition to employing nutrient resorption from leaves to satisfy nutrient demands, symbiotic relationships with ericoid mycorrhizae can mobilize and/or utilize organic forms of limiting nutrients, especially N [e.g. glycine (Näsholm et al. 1998; Moore et al. unpublished data)] and P, reducing plant dependence on nutrient resorption, even in a nutrient-poor environments (Straker 1996). The unique function of the ericoid mycorrhizae relies on unique enzymology, which can effectively out-compete other nutrient-acquisition mechanisms. Therefore, the relationship between resorption efficiency and nutrient availability is variable, with resorption efficiency being reduced (Kobe et al. 2005; Li et al. 2010; Vergutz et al. 2012), enhanced (Chapin and Kedrowski 1983; Birk and Vitousek 1986; Yuan et al. 2005) or unaffected (Chapin and Moilanen 1991; Aerts 1996; Knops et al. 1997; Vitousek 1998; Aerts and Chapin 2000; Yuan and Chen 2009a) by increasing nutrient availability.

Resorption proficiency, defined as the level to which the nutrients are reduced in the senesced leaves, has also been used to quantify resorption, with low nutrient concentration in senesced leaves indicating high resorption proficiency (Killingbeck 1996). Resorption proficiency identifies the nutrients returned to the soil in litter and is generally less proficient (i.e. higher nutrient concentration in senesced leaves and litter) under more fertile conditions (Chapin and Moilanen 1991; Vitousek 1998; Diehl et al. 2003; Wright and Westoby 2003; Li et al. 2010), leaving the litter more rapidly decomposed. The efficiency of resorption reflects plant physiology and metabolic processes, whereas proficiency is directly linked with decomposition processes and hence overall nutrient cycling.

As nutrient-poor ecosystems with slow rates of decomposition, northern peatlands store ~450 Gt of C, which is ~30 % of global total soil C (Gorham 1991), making them important C pools and sinks. Increasing atmospheric N deposition worldwide due to anthropogenic activities has evoked substantial concerns over the functioning of northern peatland ecosystems (Bobbink et al. 1998). The availability of N in boreal ombrotrophic (rain-fed) peatlands (i.e. bogs) is often limited, as it relies on N_2 fixation and atmospheric deposition and the very slow internal decomposition and mineralization processes which lead to a substantial accumulation of N in the peat profile. For example, the N accumulation rate in the Mer Bleue bog over the past 8,000 years averages 0.7 g N m^{-2} $year^{-1}$ (Wang et al., unpublished data) and 1.8 g N m^{-2} $year^{-1}$ in the past 150 years (Moore et al. 2004). Enhanced N input may not only increase the primary production of ecosystems but also change the relative significance of nutrients that limit productivity (Verhoeven et al. 1996; Aerts and Bobbink 1999). In ombrotrophic peatlands, we anticipate that nutrient resorption is important in regulating nutrient cycling, because plants should be obligated to retain nutrients and reuse them as efficiently as possible. However, recent reviews of nutrient resorption mainly covered forests and grasslands, so peatlands have been overlooked (Yuan and Chen 2009a, b; Vergutz et al. 2012).

Plant growth in bogs is often N limited under low atmospheric N deposition (Aerts et al. 1992; Gunnarsson and Rydin 2000), but increasing N deposition may shift to P-(co)limitation (Aerts et al. 1992; Bobbink et al. 1998; Gunnarsson and Rydin 2000; Bragazza et al. 2004). K limitation is rarely studied but can also occur in bogs, especially after N and P enrichments (Hoosbeek et al. 2002). The possible shift in N, P and K interactions highlights that it is the relative balance among multiple nutrients, or ecological stoichiometry (Sterner and Elser 2002), in addition to their absolute amounts, that governs metabolic functioning, plant growth and ecosystem processes. Reed et al. (2012) examined global stoichiometric patterns in foliar N:P resorption ratios in response to plant nutrient limitation and showed a trend of increasing ratios with latitude and decreasing ratios with mean annual temperature, with implications for nutrient cycling and limitation.

While N, P and K are acknowledged to be the predominant limiting nutrients in peatlands, Ca and Mg are important in ecological processes in peatlands but are frequently overlooked. Ca and Mg have an extremely low abundance in ombrotrophic bogs compared to minerotrophic fens or upland mineral soils (Rydin and Jeglum 2006). Bubier et al. (2011) reported a decline in leaf Ca and Mg concentrations in response to fertilization in three dominant bog shrubs, *Chamaedaphne calyculata*, *Rhododendron groenlandicum* and *Vaccinium myrtilloides*, indicating physiological stress under conditions of high N accumulation. The resorption of Ca and Mg differs substantially, with Ca generally accumulating continuously during leaf development, being immobile in the phloem and hence not being resorbed during leaf senescence (Clarkson and Hanson 1980; Negi and Singh 1993; Lambers et al. 1998). In contrast, Mg is tightly bound to polyphosphates, readily mobile (Clarkson and Hanson 1980) and thus more likely to be resorbed than Ca. Most resorption studies have mainly focused on N and P and sometimes K, with little attention paid to Ca and Mg, although the interactions between N, P and K affect resorption in forest ecosystems (Chapin and Moilanen 1991; Knops et al. 1997; Vitousek 1998; Diehl et al. 2003). In bogs where the availability of three potentially limiting macronutrients (i.e. N, P and K) is very small, substantial resorption during senescence is expected to regulate nutrient cycling, and stoichiometric responses to changing nutrient availability from for example nutrient deposition and global warming is important.

Our objective was to investigate the effect of N, P and K addition on resorption efficiencies and proficiencies of N, P, K, C, Ca and Mg in two dominant evergreen shrubs (*C. calyculata* and *R. groenlandicum*) in a long-term fertilization experiment established a decade ago in Mer Bleue bog in eastern Ontario, Canada. After decades of elevated atmospheric N deposition in eastern Canada (Turunen et al. 2004), the leaf-level N, P and K stoichiometric relationship derived from the ternary diagram (Olde Venterink et al. 2003) of these two species over the growing season (June–August) indicates that plant growth in this bog is co-limited by P and N, and there is no evidence showing K limitation (Wang and Moore. unpublished). After a decade of fertilization with N, PK, or their combination, we assumed the addition of N has stimulated further P-(co)limitation and reduced N resorption, which has been shown in a sub-arctic bog (van Heerwaarden et al. 2003b). N enrichment should stimulate the resorption of P and K to maintain N:P:K stoichiometric homeostasis. Long-term fertilization with P and K should shift the ecosystem to N limitation with a decline in the resorption of P and K while the resorption of N should be enhanced to maintain the N:P:K stoichiometric homeostasis.

Therefore, we hypothesized:

1. The addition of N would reduce the resorption of N, while the addition of PK would reduce the resorption of P and K (i.e. a direct fertilization effect).
2. The addition of N would stimulate the resorption of P and K, while P and K addition would increase the resorption of N (i.e. stoichiometric interactions).
3. Ca would accumulate while Mg would be resorbed during leaf senescence irrespective of fertilization.

Materials and methods

Study site and species description

The experiment was conducted at the Mer Bleue peatland, which is mainly a bog covering 25 km^2 located 10 km east of Ottawa, Ontario, Canada (45.40°N, 75.50°W). Mean annual temperature is 6.0 °C ranging from −10.8 °C in January to 20.9 °C in July (Bubier et al. 2007). Mean annual precipitation is 944 mm (78 % as rainfall), 342 mm of which falls from May to August (Canadian Climate Normals 1971–2000). The estimated atmospheric inorganic wet N deposition in this site was ~0.8 g N m^{-2} year^{-1} (Turunen et al. 2004).

There are two sets of fertilization experiments each with triplicate 3 × 3-m plots, set up on the hummock microtopography at Mer Bleue bog (see Bubier et al. 2007). Experiment 1 was established in 2000 and 2001, and experiment 2 started in 2005 (Table 1), with 27 plots in total and a spatial extent of ~600 m^2 (20 × 30 m). The fertilization is conducted every 3 weeks from 1 May to 31 August each year, with N added as NH_4NO_3 and P and K as KH_2PO_4. The dominant vascular species are *Chamaedaphne calyculata* (L.) Moench and *Rhododendron groenlandicum* (Oeder) Kron & Judd (formerly *Ledum groenlandicum* Oeder), which are the dominant evergreen shrubs in the boreal bogs of North America (Glaser 1992). *Sphagnum* mosses survive only in some of the plots with low levels of fertilization. *Vaccinium myrtilloides* Michx. and *Kalmia angustifolia* L. were distributed sparsely in some of the plots, but not sampled.

The leaf longevity of both species is two growing seasons (Reader 1980) and to sample leaves that would senesce the coming fall, the previous season's leaves were identified. To guarantee the leaves were sampled from the same cohort with the same age, individual leaves of *C. calyculata* formed in 2010 were marked at the base of the leaf with a dab of latex paint at the end of June 2011, when it was still easy to differentiate the new from the old leaves. This ensured that only leaves that would senesce the coming fall would be sampled. As *R. groenlandicum* produces

Table 1 Design of the fertilization experiment at Mer Bleue bog

Treatment	Start year	N (g m^{-2} year^{-1})	P (g m^{-2} year^{-1})	K (g m^{-2} year^{-1})
Experiment 1				
C1	2000	0	0	0
PK	2000	0	5	6.3
5N	2000	1.6	0	0
5NPK	2000	1.6	5	6.3
10NPK	2001	3.2	5	6.3
20NPK	2001	6.4	5	6.3
Experiment 2				
C2	2005	0	0	0
10N	2005	3.2	0	0
20N	2005	6.4	0	0

N fertilization levels are five, ten and 20 times the estimated summer time atmospheric wet N deposition and treatments are abbreviated accordingly. C1 and C2 are the controls (added distilled water only) for the two sets of experiments, respectively its new leaves and stems by extending from old stem and leaf clusters, it was possible to select old leaves without labelling them.

Sampling and chemical analysis

Two replicates (each ~40 leaves) of sun-exposed and fully expanded mature leaves of both species in each of the 27 plots were collected on 25 and 28 July 2011 and a similar number of recently senesced, but still attached, reddish brown leaves were sampled on 22 October 2011. We scanned the leaves immediately (Epson Expression 10000XL; Epson American, USA) to determine the total projected leaf area per sample using Image J software (version 1.45 s; Wayne Rasband, National Institute of Health, USA). Leaves were then oven-dried at 60 °C to a constant weight and specific leaf area (SLA) was calculated as the leaf area per unit leaf dry mass ($cm^2\ g^{-1}$) (Online resource 1). Samples were ground (Wiley Mini Mill 3383-L10; Thomas Scientific, USA) to fine powder (60-mesh sieve) and total C and N concentrations were determined by dry combustion on an elemental analyser (Leco CNS 2000; Leco, St. Joseph, MI). Subsamples were digested (Technicon BD-40 block digester; Technicon Instruments, Tarrytown, New York) in concentrated H_2SO_4 and H_2O_2 with Se and Li_2SO_4 as catalysts (Parkinson and Allen 1975) and passed through 0.45-μm glass fibre filters (MN 85/90; Macherey–Nagel, Germany). Total P was determined colorimetrically by the ammonium molybdate-ascorbic acid method (Murphy and Riley 1962) on a Lachat Quik-Chem AE flow-injection autoanalyser (Lachat Instruments, Milwaukee, WI). K, Ca and Mg concentrations were measured on an atomic absorption spectrophotometer (PerkinElmer model 2380; PerkinElmer, USA).

Nutrient resorption proficiency and efficiency calculation

Resorption efficiency may be underestimated because the loss of leaf mass or leaf shrinkage during senescence may be up to 10 and 6 %, respectively (van Heerwaarden et al. 2003a). The resorption efficiency can be corrected using leaf mass loss and shrinkage of leaf area, or lignin concentration (van Heerwaarden et al. 2003a) but as the lignin concentration may be affected by our long-term fertilization (Vitousek 1998), we did not measure it to correct for mass loss. Instead, leaf area was used as the metric to calculate resorption efficiency, given that the tough structure of these two sclerophyllous evergreen shrubs was resistant to leaf shrinkage during senescence. Mass-based nutrient concentration was divided by SLA to derive leaf area-based nutrient concentration and the latter was used in the calculation of resorption efficiency (nutrient concentrations in mature leaves are shown in Online Resource 2). Mass-based nutrient concentrations in mature and senesced leaves are presented in Online Resource 3 and 4. Nutrient resorption proficiency was based on the nutrient concentration in senesced leaves: the lower the nutrient concentration, the higher resorption proficiency (Killingbeck 1996). Nutrient resorption efficiency (RE) was calculated as:

$$\mathrm{RE} = \left(1 - \frac{[\mathrm{Nutrient}]_{\mathrm{senesced}}}{[\mathrm{Nutrient}]_{\mathrm{mature}}}\right) \times 100\,\%$$

where $[\mathrm{Nutrient}]_{\mathrm{senesced}}$ and $[\mathrm{Nutrient}]_{\mathrm{mature}}$ are the leaf area-based nutrient concentrations ($mg\ cm^{-2}$) of recently senesced and mature leaves, respectively. N_{RE}, P_{RE}, K_{RE}, C_{RE}, Ca_{RE} and Mg_{RE} were calculated correspondingly.

Statistics

The normality of data was examined by a Shapiro–Wilk test and Levene's test was used to check the homogeneity of variance. Because the data transformations have to be done in different ways to meet the assumptions of homogeneity of variance, a Kruskal–Wallis non-parametric test was performed separately for experiments 1 and 2 with non-transformed data. Differences between individual treatments and the corresponding control were assessed by the Steel method (a non-parametric version of Dunnett's post hoc test) for experiments 1 and 2 separately. We used a *t*-test to examine the interspecific difference between *C. calyculata* and *R. groenlandicum* in mature and senesced leaves' nutrient concentration and nutrient resorption efficiency under the same treatment, and the difference between the resorption efficiency under unfertilized conditions and the global averages of evergreen angiosperms (Vergutz et al. 2012), using raw data from different sites prior to averaging [data from the Oak Ridge National Laboratory Distributed Archive Center (http://daac.ornl.gov)]. The correlation among nutrient concentration in mature and senesced leaves, resorption efficiency and the stoichiometric ratios were conducted by Spearman's rank correlation analysis. Analyses were conducted in JMP 10 software (SAS Institute, Cary, NC).

Results

Resorption proficiency in senesced leaves

Under the same treatment, N, P, K, C and Mg concentrations in senesced leaves were all significantly lower in *C. calyculata* ($P < 0.001$), although the Ca concentration was significantly higher than that in *R. groenlandicum* ($P < 0.001$; Fig. 1). The addition with N, PK or their combinations had little effect on N, K and C concentrations in either species compared to the controls ($P > 0.05$; Fig. 1a, c, d).

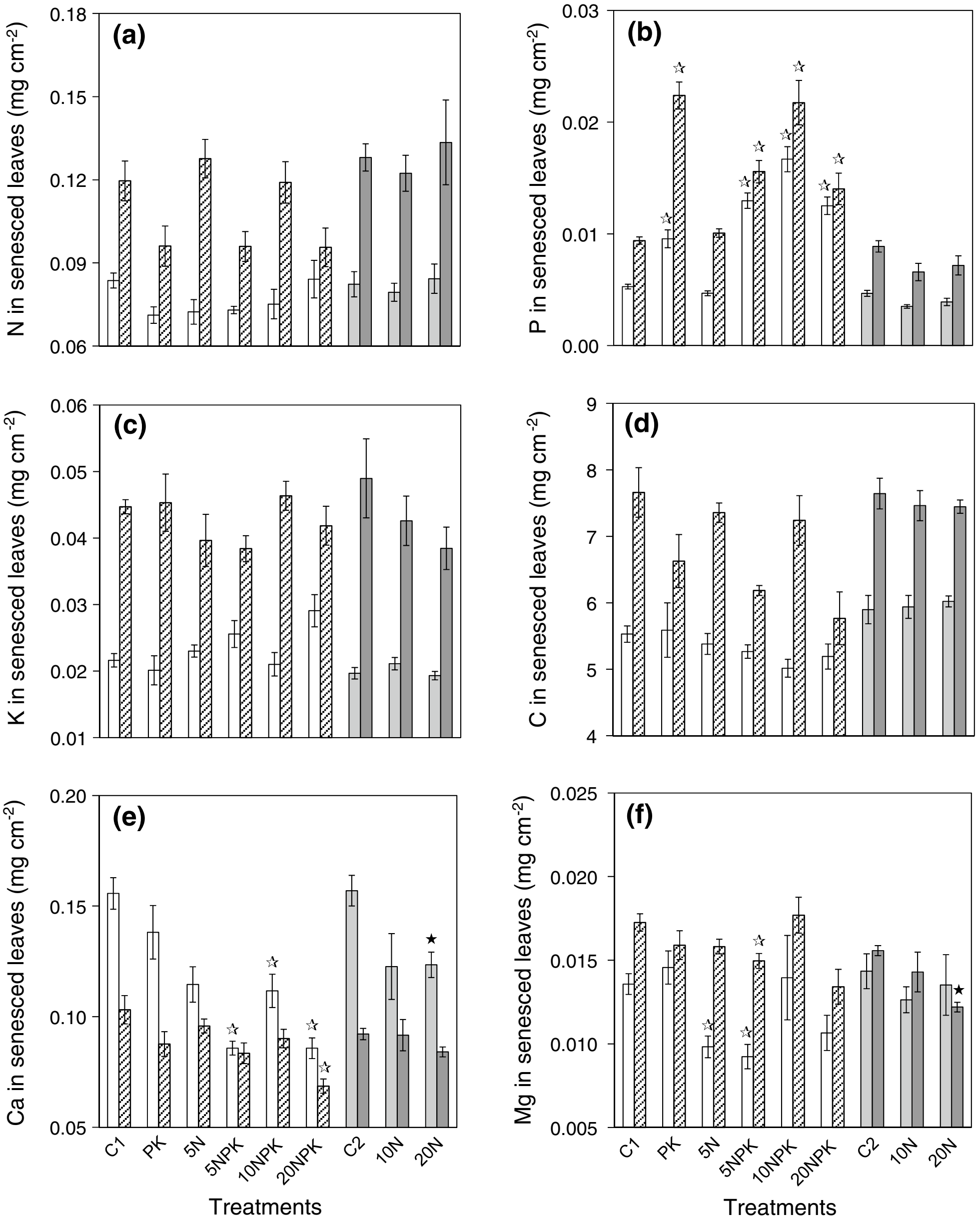

Fig. 1 N, P, K, C, Ca and Mg concentrations (mg cm^{-2}) (**a**–**f**) in senesced leaves of *Chamaedaphne calyculata* (*left bars*) and *Rhododendron groenlandicum* (*right bars*) in response to long-term N, P and K fertilization. Values are mean ± SE ($n = 6$). *Open* and *pattern-filled bars* are treatments in experiment 1, and *light- grey-* and *dark grey-filled bars* are treatments in experiment 2. *Open stars* indicate significant difference between individual treatments and the controls in experiment 1 ($P < 0.05$), *filled stars* indicate significant difference between individual treatments and the controls in experiment 2 ($P < 0.05$). Treatment abbreviations as described in Table 1

All treatments with PK addition (i.e. PK, 5NPK, 10NPK and 20NPK) significantly increased P concentration compared to the control in both species ($P < 0.05$; Fig. 1b). N addition did not affect P concentration ($P > 0.05$).

The combination of N and PK addition showed stronger effects on Ca and Mg concentrations than N or PK added separately, but no consistent pattern was observed (Fig. 1e, f).

Resorption efficiency in senesced leaves

The resorption efficiencies of all nutrients were higher in *C. calyculata* than in *R. groenlandicum* under the same treatment ($P < 0.01$; Fig. 2). High levels of N addition (i.e. 10N and 20N treatments) showed a stronger impact on resorption efficiencies than a low level of N addition (i.e. 5N treatment) and PK added alone (i.e. PK treatment). The combinations of N and PK did not affect resorption efficiencies in a consistent way and the effect varied between species.

The N_{RE} was not affected in N-only treatments (i.e. 5, 10 and 20N) compared to controls in either species ($P > 0.05$; Fig. 2a). 5NPK and 20NPK significantly increased N_{RE} compared to the controls in *C. calyculata* and *R. groenlandicum*, respectively ($P < 0.05$). The P_{RE} was significantly increased under 10 and 20N treatments compared to the control in both species ($P < 0.05$; Fig. 2b). However, PK treatment did not affect P_{RE} in either species ($P > 0.05$),

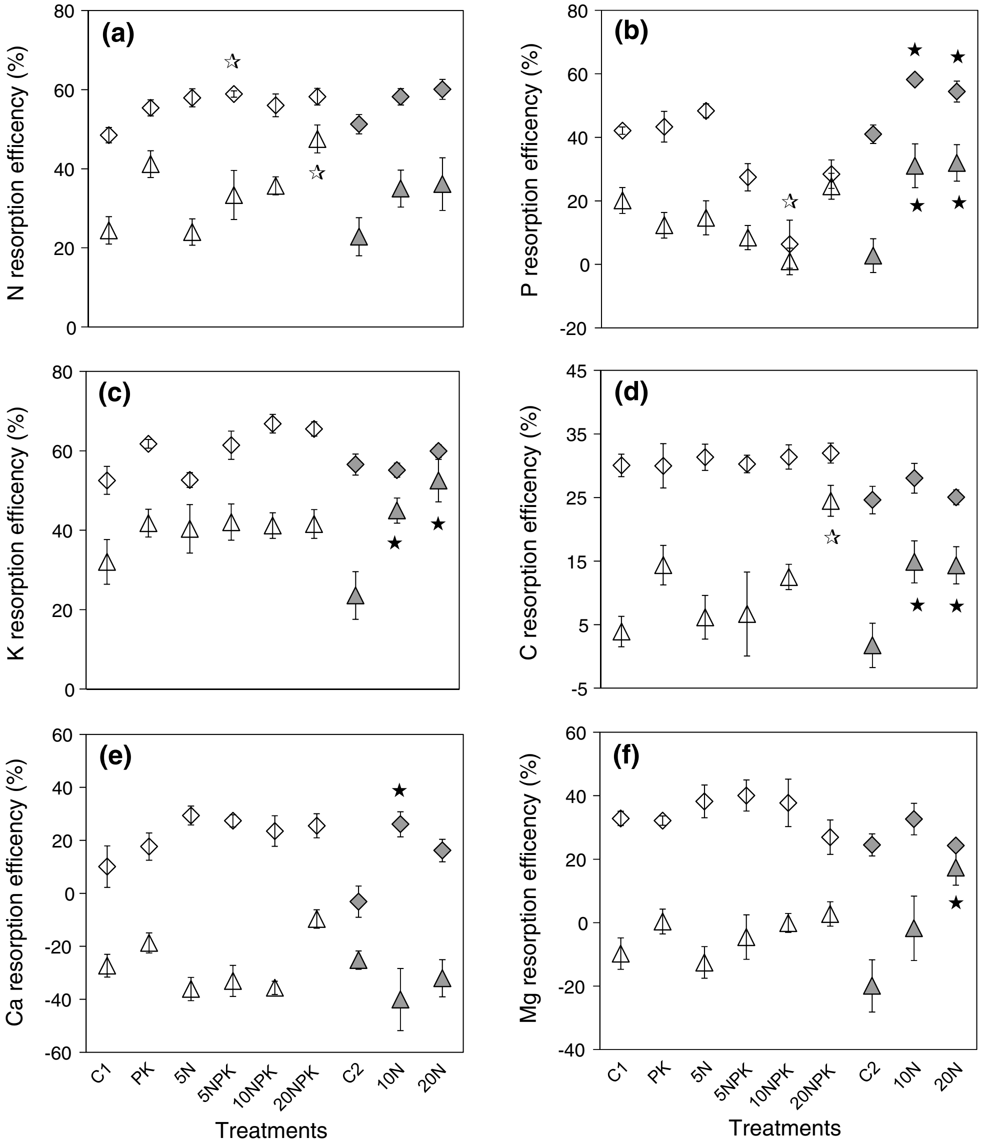

Fig. 2 Nutrient resorption efficiency (RE) of N, P, K, C, Mg and Ca (**a**–**h**) of *C. calyculata* (*diamonds*) and *R. groenlandicum* (*triangles*) in response to long-term N, P and K fertilization. Values are mean ± SE ($n = 6$). *Open stars above the symbols* indicate significant difference between individual treatments and controls in *C. calyculata* in experiment 1, *filled stars above the symbols* indicate significant difference between individual treatments and controls in *C. calyculata* in experiment 2 ($P < 0.05$); *open stars below the symbols* indicate significant difference between individual treatments and controls in *R. groenlandicum* in experiment 1, *filled stars below the symbols* indicate significant difference between individual treatments and controls in *R. groenlandicum* in experiment 2 ($P < 0.05$). Treatment abbreviations as described in Table 1

and 10NPK significantly reduced P_{RE} in *C. calyculata* compared to the control ($P < 0.05$).

N-only treatments did not affect K_{RE} in *C. calyculata* ($P > 0.5$; Fig. 2c); however, both 10 and 20N doubled K_{RE} in *R. groenlandicum* compared to the control ($P < 0.05$). Similar to the pattern observed for P_{RE}, PK treatment did not affect K_{RE} in either species ($P > 0.1$). C_{RE} in *C. calyculata* did not respond to NPK fertilization ($P > 0.05$; Fig. 2d). However, 20NPK treatment significantly increased C_{RE} in *R. groenlandicum* compared to the control ($P < 0.01$) and so did the 10 and 20N treatments ($P < 0.05$).

In general, *C. calyculata* showed positive resorption efficiencies of both Ca (4–30 %) and Mg (29–41 %), while Ca and Mg were accumulated (i.e. negative resorption efficiency) in *R. groenlandicum* (Fig. 2e, f). The effect of N addition on Ca_{RE} and Mg_{RE} in both species was very weak and no significant effect of PK or NPK addition was detected ($P > 0.5$).

Correlations among nutrient concentration, resorption efficiency and stoichiometric ratios

For both species, the nutrient concentrations in mature leaves were positively correlated with those in senesced leaves, except for N (Table 2). In contrast, resorption efficiencies were negatively correlated with the nutrient concentrations in senesced leaves (i.e. positively with resorption proficiency) in both species. In general, resorption efficiencies were significantly correlated with nutrient concentration in both mature and senesced leaves.

In both species, N_{RE}, Ca_{RE} and Mg_{RE} were weakly correlated with the stoichiometric ratios (i.e. N:P, N:K and K:P) considered indicators of the types of nutrient limitation (Table 2). The correlation between nutrient resorption efficiencies and stoichiometric ratios was generally stronger in *C. calyculata* than *R. groenlandicum*: P_{RE} in both species was positively correlated but K_{RE} and C_{RE} were negatively correlated with all three stoichiometric ratios only in *C. calyculata*.

Few significant correlations between resorption efficiencies were observed in *C. calyculata*, whereas in *R. groenlandicum* the resorption efficiencies were significantly correlated with each other, except for Ca_{RE}.

The stoichiometric relationship between N, P and K during leaf senescence

Neither species showed evidence of N being the predominantly limiting nutrient under all treatments, with no samples falling in the N-limited section of the ternary diagram, nor were they primarily N limited even after P and K addition (Fig. 3). The effect of fertilization on N:P:K stoichiometry was more substantial in senesced leaves than in mature leaves. In both species, the addition of P and K drove the symbols to the bottom left, reflecting an increase in the relative P concentration, a decrease in the relative N concentration and little effect on the relative K concentration, compared to the control (i.e. moving parallel to the P-axis) (Fig. 3). If N was added alone, no substantial change was observed. For both species, after fertilization with PK (i.e. PK, 5NPK, 10NPK and 20NPK), leaf senescence generally increased the relative P concentration and decreased the relative N concentration, but did not affect the relative K concentration substantially, similar to the effect of P and K addition compared to the control or N-only treatments (Fig. 3).

Discussion

Resorption efficiency: boreal bog plants in a global context

We used leaf area-based nutrient concentration to derive nutrient resorption efficiency because mass-based data can underestimate the resorption efficiency by up to 10 % (van Heerwaarden et al. 2003a). Mass loss during leaf senescence is likely due to the removal of compounds and carbohydrates (Nordell and Karlsson 1995). The leaves of both evergreen shrubs contained ~54 % C (Online Resource 3) and assuming that leaf shrinkage of both sclerophyllous species during senescence is negligible, we can estimate leaf mass loss based on C_{RE}, which are ~27 and ~3 % in *C. calyculata* and *R. groenlandicum*, respectively, under unfertilized conditions. The leaf mass loss in *C. calyculata* is similar to the global average of evergreen angiosperms (Vergutz et al. 2012), but the small mass loss in *R. groenlandicum* requires further investigation.

Vergutz et al. (2012) compiled a global dataset of nutrient resorption efficiency with the averages of N, P, K, C, Ca and Mg for evergreen angiosperms (mainly tree species) being 56, 58, 56, 21, −5 and 12 %, respectively. The N_{RE} and P_{RE} are slightly higher than those reported by Aerts and Chapin (2000) for evergreen species (50 and 55 %, respectively), probably because their study covered a larger proportion of evergreen species in boreal and subarctic ecosystems. Our study indicated interspecific differences under natural conditions: in *C. calyculata*, the C_{RE} (27 %) and Mg_{RE} (29 %) were higher ($P < 0.001$) while N_{RE} (50 %) and P_{RE} (41 %) were lower ($P < 0.001$) than the global average and there was no significant difference for K_{RE} (55 %) and Ca_{RE} (4 %) ($P > 0.5$). In *R. groenlandicum*, the resorption efficiency of all nutrients (N, P, K, C, Ca and Mg: 24, 10, 28, 3, −26 and −16 %, respectively) was significantly lower than the global averages ($P < 0.001$). The N_{RE} and P_{RE} in *R. groenlandicum* were also substantially lower than in a congeneric species, *Rhododendron lapponicum*, in which N_{RE} and P_{RE} were 78–79 and 80–85 %, respectively (Karlsson 1994). As both species are ericoid mycorrhizal evergreen shrubs, mycorrhizal fungi may mediate uptake, reducing dependence on resorption from senesced leaves.

Small (1972) reported the N, P and K concentrations in fresh litters at Mer Bleue were 7.5, 0.3 and 0.3 mg g^{-1} in *C. calyculata* and 4.0, 0.3 and 1.1 mg g^{-1} in *R. groenlandicum* (referred to as *Ledum groenlandicum* in his work), respectively, similar to Killingbeck's (1996) critical values of potential N and P resorption proficiency for evergreen species. Therefore, we consider these N, P and K concentrations in fresh litters as the critical values of potential resorption proficiencies under natural condition in *C. calyculata* and *R. groenlandicum*. *C. calyculata* resorbs N and P proficiently by minimizing nutrient loss through litters (7.4 mg N g^{-1} and 0.4 mg P g^{-1} in unfertilized senesced leaves, Online Resource 4), while *R. groenlandicum* does not (8.4 mg N g^{-1} and 0.6 mg P g^{-1} in unfertilized senesced leaves, Online Resource 4). In contrast, neither species resorbs K proficiently (1.8 and 3.2 mg K g^{-1} in

Table 2 Correlations among leaf area-based N, P, K, C, Ca and Mg concentrations in mature leaves (subscript *m*), senesced leaves (subscript *s*), their nutrient resorption efficiencies (subscript *RE*) and stoichiometric ratios (N:P, N:K and P:K) of *Chamaedaphne calyculata* (*bottom left*) and *Rhododendron groenlandicum* (*upper right*)

	N_m	P_m	K_m	C_m	Ca_m	Mg_m	N_s	P_s	K_s	C_s	Ca_s	Mg_s	N_{RE}	P_{RE}	K_{RE}	C_{RE}	Ca_{RE}	Mg_{RE}	$N:P_m$	$N:K_m$	$K:P_m$
N_m		−0.14	_0.43*_	_0.77*_	_0.28*_	_0.30*_	0.23	−0.21	−0.01	_0.28*_	0.04	−0.24	_0.35*_	0.19	_0.37*_	_0.38*_	0.05	_0.48*_	_0.45*_	_0.37*_	_0.27*_
P_m	0.06		0.08	−0.11	−0.01	_0.33*_	_−0.42*_	_0.88*_	0.10	_−0.40*_	−0.20	0.27	_0.31*_	_−0.27*_	0.05	0.24	0.25	0.13	_−0.93*_	−0.22	_−0.91*_
K_m	_0.32*_	_0.73*_		_0.43*_	−0.05	0.09	−0.02	0.00	0.15	0.02	−0.08	_−0.32*_	_0.27*_	−0.04	_0.47*_	_0.35*_	−0.14	_0.40*_	0.05	_−0.64*_	0.27
C_m	_0.37*_	_−0.27*_	−0.12		_0.56*_	_0.51*_	_0.29*_	−0.22	0.02	_0.52*_	0.27	0.06	0.15	0.13	_0.33*_	_0.31*_	0.09	_0.44*_	_0.36*_	0.21	_0.27*_
Ca_m	_−0.42*_	_−0.35*_	_−0.55*_	0.20		_0.51*_	0.22	−0.11	0.09	_0.47*_	_0.53*_	_0.33*_	−0.10	−0.02	−0.05	−0.04	0.26	0.11	0.13	_0.34*_	0.02
Mg_m	_−0.40*_	0.16	−0.18	0.03	_0.52*_		−0.03	0.22	−0.12	0.13	0.16	_0.39*_	0.18	−0.01	_0.27*_	_0.28*_	0.10	_0.55*_	−0.18	0.13	−0.26
N_s	0.23	−0.24	−0.22	0.19	0.13	0.06		_−0.29*_	_0.27*_	_0.69*_	0.48	0.18	_−0.54*_	−0.21	−0.12	_−0.31*_	_−0.27*_	−0.13	_0.46*_	_0.27*_	_0.42*_
P_s	−0.10	_0.84*_	_0.65*_	_−0.50*_	_−0.28*_	0.14	−0.09		_0.27*_	_−0.29*_	−0.11	_0.30*_	0.21	_−0.50*_	−0.11	0.11	0.09	0.01	_−0.88*_	−0.19	_−0.86*_
K_s	0.20	_0.28*_	_0.44*_	0.16	_−0.28*_	−0.26	_0.30*_	_0.32*_		_0.31*_	0.20	0.13	−0.24	_−0.40*_	_−0.51*_	−0.25	−0.08	−0.20	−0.10	−0.12	−0.04
C_s	_0.43*_	_−0.46*_	_−0.40*_	_0.51*_	0.09	−0.17	_0.54*_	_−0.52*_	0.08		_0.69*_	_0.45*_	_−0.44*_	−0.11	−0.09	_−0.37*_	−0.23	−0.22	_0.45*_	0.23	_0.42*_
Ca_s	−0.24	_−0.42*_	_−0.63*_	0.13	_0.54*_	_0.29*_	_0.38*_	_−0.34*_	_−0.40*_	_0.49*_		_0.51*_	_−0.47*_	_−0.28*_	−0.15	_−0.45*_	_−0.33*_	_−0.35*_	0.21	0.18	0.19
Mg_s	−0.21	−0.05	_−0.35*_	−0.02	_0.30*_	_0.35*_	0.17	−0.10	_−0.45*_	0.18	_0.68*_		_−0.28*_	_−0.29*_	−0.22	_−0.31*_	−0.15	_−0.40*_	_−0.30*_	0.09	_−0.32*_
N_{RE}	_0.42*_	0.27	_0.45*_	0.07	_−0.44*_	_−0.34*_	_−0.48*_	0.01	−0.05	−0.13	_−0.53*_	−0.25		0.22	_0.42*_	_0.65*_	_0.27*_	_0.48*_	−0.17	−0.02	−0.24
P_{RE}	0.24	_−0.54*_	_−0.43*_	_0.59*_	0.22	−0.06	0.06	_−0.83*_	−0.17	_0.54*_	_0.28*_	0.08	0.09		_0.34*_	_0.32*_	0.14	0.24	_0.32*_	0.16	_0.29*_
K_{RE}	0.22	_0.59*_	_0.57*_	_−0.29*_	−0.23	0.16	−0.19	_0.56*_	−0.15	_−0.42*_	_−0.30*_	0.04	0.26	_−0.38*_		_0.57*_	−0.09	_0.46*_	0.08	−0.22	0.15
C_{RE}	−0.24	_0.33*_	_0.32*_	−0.14	−0.04	0.09	_−0.39*_	_0.32*_	0.09	_−0.67*_	_−0.40*_	−0.20	0.18	−0.21	_0.32*_		0.25	_0.64*_	−0.08	−0.08	−0.11
Ca_{RE}	0.06	0.17	0.26	−0.06	−0.09	−0.10	−0.24	0.12	_0.34*_	_−0.34*_	_−0.48*_	_−0.42*_	0.17	0.05	−0.02	_0.42*_		_0.31*_	−0.18	0.19	_−0.30*_
Mg_{RE}	−0.26	0.19	0.15	−0.02	0.14	_0.28*_	_−0.28*_	0.16	0.18	_−0.32*_	_−0.31*_	_−0.36*_	0.08	−0.08	0.04	_0.33*_	_0.32*_		0.06	−0.02	0.01
$N:P_m$	_0.28*_	_−0.91*_	_−0.64*_	_0.41*_	_0.27*_	−0.23	_0.28*_	_−0.85*_	_−0.28*_	_0.59*_	_0.38*_	0.09	−0.10	_0.62*_	_−0.45*_	_0.40*_	−0.15	_−0.28*_		_0.33*_	_0.91*_
$N:K_m$	0.13	_−0.78*_	_−0.87*_	_0.35*_	_0.42*_	0.03	_0.27*_	_−0.77*_	_−0.40*_	_0.60*_	_0.52*_	0.25	−0.22	_0.62*_	_−0.49*_	_−0.43*_	−0.22	−0.23	_0.85*_		−0.03
$K:P_m$	0.21	_−0.84*_	_−0.34*_	_0.41*_	0.14	_−0.36*_	0.18	_−0.76*_	−0.13	_0.42*_	0.21	−0.07	0.00	_0.52*_	_−0.39*_	−0.23	−0.13	−0.26	_0.85*_	_0.52*_	

Spearman's correlation coefficients ($n = 54$) are shown

Asterisk indicates significant results, which are also highlighted in *italic*

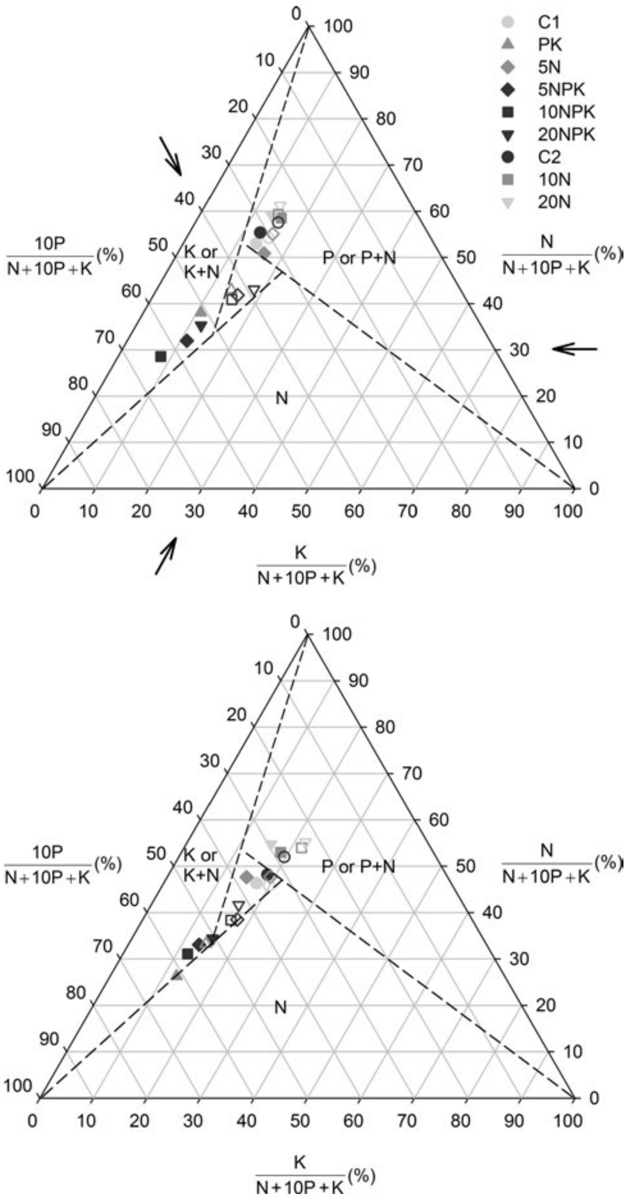

Fig. 3 Ternary diagram showing the stoichiometric relationship of N, P and K in the mature and senesced leaves of *C. calyculata* (*upper*) and *R. groenlandicum* (*bottom*) in response to long-term N, P and K fertilization. *Open symbols* indicate mature leaves, *filled symbols* indicate senesced leaves. *Dashed lines* indicate the critical ratios of N:P (14.5), N:K (2.1) and K:P (3.4) (Olde Venterink et al. 2003). These lines divide the plot into four parts, and three of them indicate N limitation (N section), P or P, N-co-limitation (P or P + N section) and K or K, N-co-limitation (K or K + N section), respectively. For the *central triangle section*, the stoichiometric ratio cannot be used to determine the type of nutrient limitation or this is non-NPK limitation. For visual reasons, the P concentration is multiplied by a factor of 10. *Arrows* show the direction in which the axes should be read. Treatment abbreviations as described in Table 1

unfertilized senesced leaves of *C. calyculata* and *R. groenlandicum*, respectively). The general trend of lower nutrient concentration, or higher resorption proficiency, in the senesced leaves of *C. calyculata* than *R. groenlandicum*, apart from Ca, suggests that *C. calyculata* adapts to nutrient deficiency better than *R. groenlandicum*, by minimizing nutrient loss. The two species did not show differences in SLA of mature leaves (Online Resource 1) but the difference appeared in the senesced leaves. A larger SLA in senesced leaves contributes little to changes in leaf life span or morphological adjustment (Shipley et al. 2005), but reflects mass loss during leaf senescence.

Effects of fertilization on resorption proficiency and efficiency

Resorption proficiency and efficiency complement each other and are often used together to investigate nutrient resorption. We found there was a strong negative correlation between nutrient resorption efficiency and the nutrient concentration in senesced leaves (Table 2), indicating that, in general, resorption efficiency and proficiency respond to nutrient addition identically.

We found the addition of N or PK only weakly affected resorption directly (hypothesis 1) and stoichiometric interactions played a more important role, given the significant positive effect of N addition on P and K resorption (hypothesis 2). We found an inconsistent effect of fertilization on Ca and Mg resorption and the two species resorbed Ca and Mg in different ways: *C. calyculata* resorbed both Ca and Mg while *R. groenlandicum* resorbed neither (hypothesis 3). In general, the response of nutrient resorption to NPK addition depended on the types of nutrient limitation.

As expected, after a decade of N addition combined with atmospheric N deposition (0.8 g N m^{-2} $year^{-1}$), P was the predominant limiting nutrient or at least co-limited with N (Fig. 3). Contrary to our first hypothesis, the addition of N did not affect N resorption, regardless of the level of addition (1.6, 3.2 or 6.4 g N m^{-2} $year^{-1}$), supporting the argument of possible N saturation in this ecosystem (Bubier et al. 2011). To maintain a balanced N:P:K stoichiometry, we anticipated an increase in P and K resorption in response to N addition, especially under P-(co)limited condition: we found P_{RE} of both species was increased by high levels of N addition (3.2 and 6.4 g N m^{-2} $year^{-1}$) which also increased K_{RE} of *R. groenlandicum*. This positive response of P resorption to N addition follows the general anticipation that in a P-(co)limited ecosystem, the conservation of P will be stimulated to meet the requirement of P when the availability of N is increased (Rejmánková 2005).

A difference in resorption proficiency response to increasing nutrient availability among species affects the role of vegetation in ecosystem nutrient cycling (van Heerwaarden et al. 2003b), through a feedback between soil fertility and plant economics. Raising soil fertility usually has positive effects on plant leaf nutrient concentration, increasing the amount of nutrients returning to the soil. Increasing abundance of *C. calyculata* over *R. groenlandicum* after a decade with the highest N level together with PK (i.e. 20NPK) (Bubier et al. 2011) suggests further attention should be paid to the relationship between nutrient resorption and changes in species composition in bog ecosystems. The interspecific divergence in nutrient resorption can mediate ecosystem nutrient cycling through stoichiometric interactions with consumers and decomposers along the food webs (Sterner and Elser 2002). For example, the higher resorption proficiency in *C. calyculata* than *R. groenlandicum* would further decrease litter decomposition by exacerbating the mismatch of C:element ratios between plants and decomposers.

After the addition of PK alone for 12 years, P-(co)limitation was compensated but not yet shifted into N limitation and the shrubs were on the margin of K limitation (Fig. 3). This may be related to K leaching through the peat owing to the high mobility of K under acidic conditions in this ecosystem (Rydin and Jeglum 2006) and the lack of response of K resorption to PK addition goes against our first hypothesis. The dominance of co-limitation by N and PK is supported by changing shrub abundance in response to fertilization: the abundances of *C. calyculata* and *R. groenlandicum* under N- or PK-only treatments were not significantly different from controls, whereas their abundances increased by ~50 % under 10NPK and 20NPK treatments (Larmola et al. under review). There was a strong correlation between mature and senesced leaves' P concentration (Spearman's $r = 0.9$), and the addition of PK increased the P concentration in mature and senesced leaves to a similar extent, leading to a higher P resorption proficiency but unchanged efficiency. This response of resorption proficiency over efficiency to nutrient addition has been discussed in subarctic bog species (van Heerwaarden et al. 2003b), mangroves (Feller et al. 2003; Rejmánková 2005) as well as in a perennial herb (Anderson and Eickmeier 2000). Contrary to our second hypothesis, PK addition did not significantly increase N resorption. The weak trend of increasing N resorption efficiency and proficiency in response to PK addition in both species implies that the increase in N resorption cannot keep pace with the increasing P concentration, leading to an ultimate shift in nutrient limitation.

There was no general, strong interactive effect among N, P and K resorption, contrary to our expectation, and the few significant effects are mainly due to the cumulative rather than the interactive effect of N and PK. For example, although 5N, 20N and PK can increase N_{RE} substantially but insignificantly (from a statistical perspective), their combination showed a significant increase of N_{RE} in 5NPK and 20NPK treatments in *C. calyculata* and *R. groenlandicum*, respectively.

The lack of correlation between mature and senesced leaves' N concentration to a certain extent supports the argument that a large portion of N in mature leaves is probably stored as amino acids. These are easy to transport when resorbed (Chapin and Kedrowski 1983) and reduce the risk of toxic effects of NH_4^+ through excess N availability (Bubier et al. 2011).

Contrary to our third hypothesis, there was interspecific divergence in Ca and Mg resorption, with Ca accumulation in *R. groenlandicum* and Mg resorption in *C. calyculata* during leaf senescence. However, *C. calyculata* can resorb Ca as reported in grasslands and alpine forests (Ralhan and Singh 1987; Peri and Lasagno 2010), while *R. groenlandicum* did not conserve Mg through resorption (i.e. resorption efficiency ≤ 0). The positive resorption of Ca and Mg in *C. calyculata* is attributable to the conservation of these two important cations in bogs, and might facilitate the growth of *C. calyculata* in an acidic ombrotrophic environment where the available Ca and Mg are extremely low and benefit its competitive advantage over *R. groenlandicum*.

Stoichiometric relationships and the implications for bogs

Bogs, covering ~700,000 km^2 in Canada, are generally poor in nutrients, dominated by evergreen shrubs and mosses, and nutrient retention and recycling by plants play an important role in the functioning of these peatland ecosystems, one process being the resorption of nutrients from senescent leaves. Elevated rates of atmospheric deposition of nutrients, especially N, and global warming (Rustad et al. 2001) have increased nutrient availability. Thus, determining shrub nutrient resorption and the effect of added nutrients are important with regard to the future of these important C-sequestering ecosystems. Our results illustrate that, although *C. calyculata* and *R. groenlandicum* share the same habitat and have a similar leaf life span and N and P concentrations in mature leaves, they have different resorption characteristics.

Under natural conditions, substantial portions of N, P and K were resorbed (10–55 %) during leaf senescence in the two shrubs, though Ca and Mg resorption was lower and *R. groenlandicum* showed a gain in Ca and Mg in some treatments during senescence. Fertilization with PK (i.e. PK, 5NPK, 10NPK and 20NPK) drove the trend of increasing relative concentration of P, decreasing N and not affecting K in both mature and senesced leaves in the ternary diagram. A similar pattern was observed during leaf senescence (i.e. difference between mature and senesced leaves) under PK treatments, suggesting that litter decomposition could become more N limited after P and K fertilization. By resorbing nutrients proficiently, the shrubs maintain a low nutrient concentration in the litter, with likely slower decomposition rates, thereby linking the leaf economy and soil processes and imposing a feedback on nutrient cycling.

The lack of correlation between N_{RE} and the resorption efficiency of other nutrients, especially P, confirms that N and P resorption are not always coupled, as the hydrolysis processes of N and P during leaf senescence are regulated by independent mechanisms (Rejmánková 2005). The N_{RE} showed no correlation with the types of nutrient limitation, as indicated by the stoichiometric ratios (Table 2). In contrast, P_{RE} in general positively correlated with N:P and K:P ratios, which appears to counter the argument that there is no relationship between nutrient resorption and the types of nutrient limitation among wetland graminoids (Güsewell 2005). However, our results indirectly confirmed the conclusion from Rejmánková (2005) that P resorption was significantly higher in P-limited plots, facilitating adaptation to nutrient limitation. This may be an important strategy of these two shrubs in Mer Bleue bog, which adapt to increased N deposition (from ~0.2 to ~0.8 g m^{-2} $year^{-1}$).

C. calyculata and *R. groenlandicum* are two dominant shrubs in boreal peatlands and appear similar in many characteristics including leaf-level photosynthetic capacity, leaf chemistry and morphology (Bubier et al. 2011), yet resorbed nutrients in different ways during the long-term fertilization: *C. calyculata* showed a greater ability to resorb nutrients than *R. groenlandicum* by embracing a higher SLA in senesced leaves. Other physiological controls of the interspecific difference in terms of resorption efficiency and proficiency in response to the increased soil N, P and K availability remain unknown, but observed changes in species composition can have a strong impact on nutrient cycling through nutrient resorption. Recent reviews of nutrient resorption have established broad patterns, mainly in forests and grasslands (Yuan and Chen 2009a, b; Vergutz et al. 2012). Our study advances the understanding of the stoichiometric interactions of multiple limiting nutrients in bog ecosystems, showing the large variation between species within plant functional types in nutrient resorption (Nordell and Karlsson 1995; Aerts 1996; Eckstein et al. 1998; Aerts and Chapin 2000). Changes in species composition through changing nutrient limitation, owing to nutrient enrichment or global warming, could mediate ecosystem nutrient cycling in bog ecosystems.

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