N and P resorption as functions of the needle age class in two conifer trees

Zhiyou Yuan[1,2,*], *Xinrong Shi*[1,2], *Feng Jiao*[1,2,*] *and Fengpeng Han*[1,2]

[1] *State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A&F University, Yangling, Shaanxi 712100, China*
[2] *Institute of Soil and Water Conservation, Chinese Academy of Science and Ministry of Water Resource, Yangling, Shaanxi 712100, China*
*Correspondence address. The Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A&F University, Yangling, Shaanxi 712100, PR China. Tel: +86-29-87012411; Fax: +86-29-87012210; E-mail: zyyuan@ms.iswc.ac.cn; jiaof@ms.iswc.ac.cn

Abstract

Aims
Given the importance of resorption in nutrient conservations, nutrient resorption should change with leaf age if resorption depends on nutrient content, and if nutrient content changes with leaf age. However, no study has addressed this issue.

Methods
Here, we measured N and P concentrations of needles of different ages in two woody evergreen conifer species—white spruce (*Picea glauca* Voss.) and balsam fir (*Abies balsamea* Mill.)—to determine the effects of needle aging on nutrient resorption.

Important Findings
For both species, N and P concentrations were higher in newer needles than in older needles. Nutrient resorption efficiency, i.e. percentage of nutrients resorbed during senescence, also declined significantly with needle age from 73 to 22% in these two evergreen conifer species. The difference in nutrient resorption between old and young needles may be attributed to the size of N and P sink tissues, which is likely to decrease with needle age. These results suggest that needle age affects the extent of N and P resorption in these two evergreen conifer species.

Keywords: evergreen conifer, needle age, nutrient resorption, *Picea glauca*, *Abies balsamea*

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INTRODUCTION

Leaf traits play an important role in ecological processes and the variations in different leaf traits tend to be highly correlated (Fajardo and Siefert 2016; Fortunel *et al.* 2009; Poorter and Bongers 2006; Wright *et al.* 2004). Nutrient resorption, a process in which nutrients are withdrawn from senescing leaves and thus conserved, is generally considered to be an essential mechanism of nutrient conservation (Blanco *et al.* 2009; Milla *et al.* 2005; Sabate *et al.* 1995; Scalon *et al.* 2017; Yuan and Chen 2010, 2015) and known to be related to other leaf traits, such as specific leaf mass (mass per unit area of leaf surface) (Killingbeck and Costigan 1988), leaf nutrient concentrations (Yuan *et al.* 2005), leaf position in the canopy (Yasumura *et al.* 2005), leaf longevity (Escudero *et al.* 1992)

and leaf size (i.e. surface area) (Killingbeck and Tainsh 2002). However, we do not know whether nutrient resorption from senescing leaves is related to leaf age (or node position), a fundamental property of leaves for evergreen conifer species. As leaves age, they experience major structural, chemical and functional changes (Field 1983; Niinemets 2016; Warren 2006). These changes are expected to alter nutrient allocation and resorption process. If nutrient content changes with age, the ability of nutrient resorption by plant leaves should also be expected to change over time. For coniferous trees, a green needle retranslocates its nutrients into other plant parts throughout its life and the entire nutrients resorbed from a needle are the sum of its yearly nutrients retranslocated. The nutrients retranslocated from green needles at a specified year, therefore, shall be lower than the total
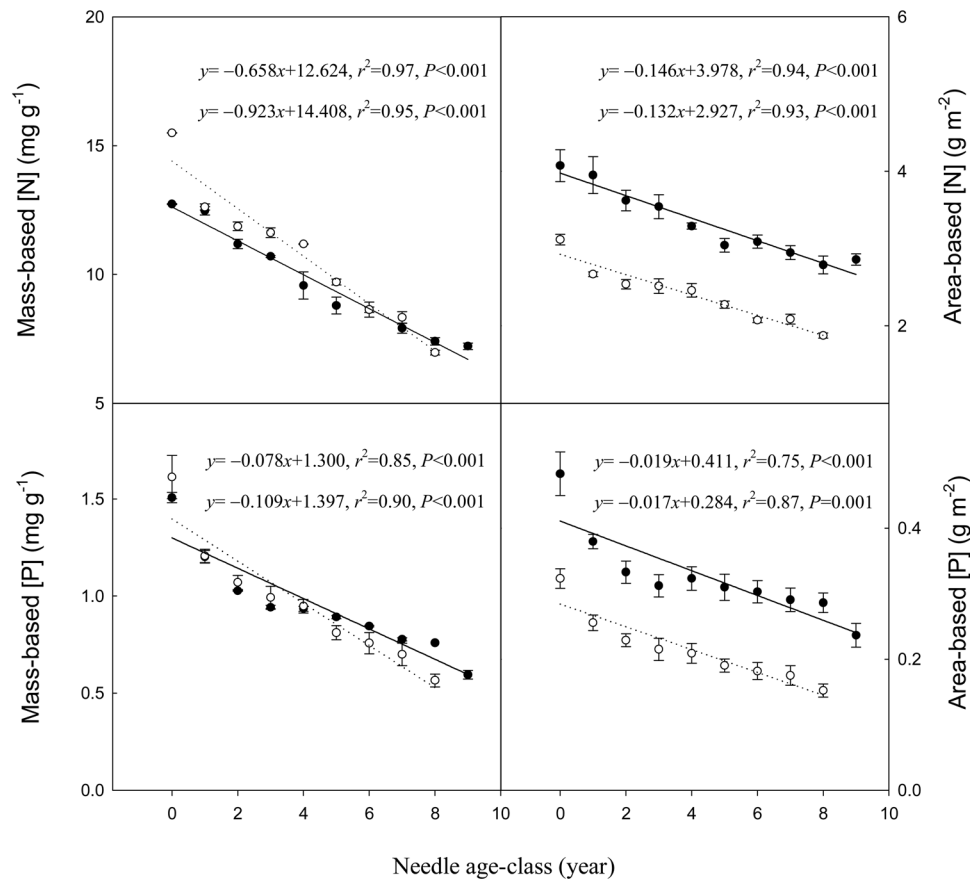
The figure contains four panels with regression equations:

Top-left (Mass-based [N] (mg g⁻¹) vs Needle age-class):
$y = -0.658x + 12.624$, $r^2 = 0.97$, $P < 0.001$
$y = -0.923x + 14.408$, $r^2 = 0.95$, $P < 0.001$

Top-right (Area-based [N] (g m⁻²)):
$y = -0.146x + 3.978$, $r^2 = 0.94$, $P < 0.001$
$y = -0.132x + 2.927$, $r^2 = 0.93$, $P < 0.001$

Bottom-left (Mass-based [P] (mg g⁻¹)):
$y = -0.078x + 1.300$, $r^2 = 0.85$, $P < 0.001$
$y = -0.109x + 1.397$, $r^2 = 0.90$, $P < 0.001$

Bottom-right (Area-based [P] (g m⁻²)):
$y = -0.019x + 0.411$, $r^2 = 0.75$, $P < 0.001$
$y = -0.017x + 0.284$, $r^2 = 0.87$, $P = 0.001$

Figure 1: green-needle N and P concentrations. Evergreen conifer species *Picea glauca* (black circles and solid lines) and *Abies balsamea* (white circles and dashed lines). Data are means of three trees. Bars represent 1 SE. The coefficients of determination (r^2) and *P* are shown in each panel for *P. glauca* (the first line) and *A. balsamea* (the second line).

amount of nutrients retranslocated during the whole life of a needle. The yearly nutrient resorption efficiency indeed shall change at different year, i.e. with needle ages. A pattern of age-related nutrient resorption is thus expected to exist in terms of needle age class. In that sense, the yearly nutrient resorption efficiency for different age class needles reflects the ability to transfer nutrients through the xylem or phloem by live tissues of plants and this ability is expected to decline with needle aging in coniferous trees. A better knowledge of how resorption may change with leaf age is essential for the understanding of plant nutrient conservation strategies. Albeit there are some studies to address how nutrient concentrations in soils and plants change with stand age (Duran *et al.* 2008; Simard *et al.* 2001; Yuan and Chen 2010) or leaf age (Anten *et al.* 1998; Sobardo 1994), and how nutrient resorption changes with nutrient concentrations (Kobe *et al.* 2005; Yuan *et al.* 2005), we still do not know how leaf age affects nutrient resorption.

The purpose of this study was to better understand how nutrient resorption changes with needle age for evergreen conifer trees. We measured N and P content and resorption in needles of different age classes in two evergreen species: white spruce (*Picea glauca* Voss.) and balsam fir (*Abies balsamea* Mill.). During

leaf senescence, nutrients translocation is normally driven by sink activity, such as new leaf growth (Chapin and Moilanen 1991; Hevia *et al.* 1999). Nutrients are translocated not only for simultaneous plant growth, but also for nutrient storage. In some boreal coniferous, evergreen species, such as Scots pine, needles senesce occurs mainly in the autumn after the aboveground growth has ceased. Nutrients are stored mostly in green needles over the dormant winter period and used for new shoot and needle growth the following spring (Proe *et al.* 2000). Given that nutrient resorption is related to nutrient content that changes with age (Ågren 2008; Anten *et al.* 1998; Kuang *et al.* 2007; Yuan *et al.* 2005), we hypothesized that foliar nutrient concentrations and resorption efficiency would decline with increased needle age of these evergreen conifer trees.

MATERIALS AND METHODS

Study species and area

The species selected for the study were white spruce (*P. glauca* Voss.) and balsam fir (*A. balsamea* Mill.), both of which are widely distributed, evergreen coniferous species in the North American boreal forest (Bergeron and Dubuc 1989). Both species retain their needles within a wide range of needle
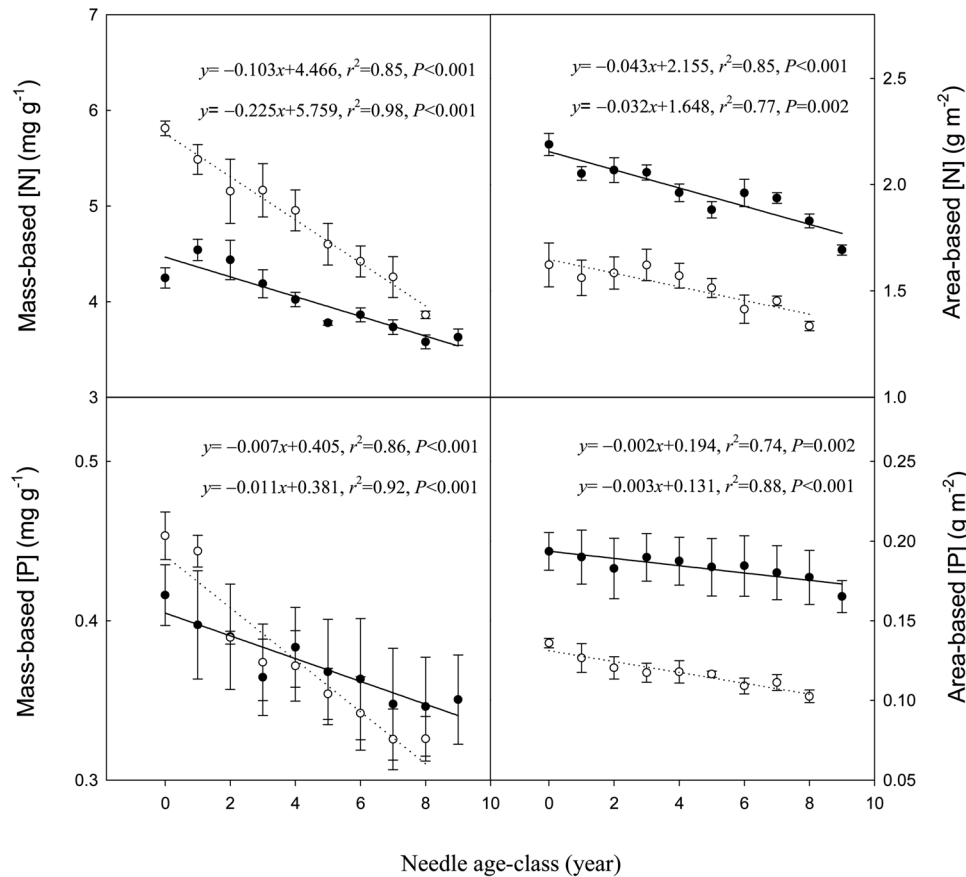
Figure 2: senesced-needle N and P concentrations. Evergreen conifer species *Picea glauca* (black circles and solid lines) and *Abies balsamea* (white circles and dashed lines). Data are means of three trees. Bars represent 1 SE. The coefficients of determination (r^2) and P are shown in each panel for *P. glauca* (the first line) and *A. balsamea* (the second line).

ages, ranging from one to several years, when growing in natural environments.

Both species were sampled in a natural mixed stand, about 5 ha, on the campus of Lakehead University, Ontario, Canada (89°16′W, 48°25′N). We chose to sample these two species in a mixed stand to minimize the differences in microclimate and nutrient availability to which individual trees were exposed. The climate is moderately dry, cool with mean annual temperature and mean annual precipitation being 2.6°C and 710 mm, respectively.

Field methods

Three trees of each species, both about 20-year old, were randomly selected from the even-aged stand, tagged and sampled in 2006. Ten branches with green needle samples were removed from five lateral shoots in the top half of each sampled tree and composited into one sample per tree for each age class. All needles born in one particular year were considered to belong to the same age class. Brown needles in the selected species had been staying on the branches a long time after senescence, and thus brown and finished the resorption processes. Naturally senesced needles were able to be collected from the same branches as green needles in September

2006. Current-year young needles also senesced and turned brown from their tips. It was difficult to collect brown young needles that were much few in branches. Green needles were paired with naturally senesced needles of the same age in calculating resorption efficiency.

Laboratory methods

Needle samples were immediately taken to the laboratory and the branches were separated into annual segments (shoots) of different age classes. After surface areas were measured with a leaf area meter (Li-COR model LI-3000), leaves were dried in oven at 60°C to constant mass, weighed and ground in a Wiley mill to pass a 40-mesh screen to assure adequate sample homogeneity. N and P were extracted from ≈0.20 g samples with a sulfuric acid–hydrogen peroxide wet digestion technique and measured with a Technicon Auto Analyzer II (Technicon Industrial Systems, Tarrytown, NY, USA). Only N and P were measured because these two nutrients are considered the most limiting in terrestrial ecosystems.

Nutrient conservation was characterized by measured nutrient resorption efficiency, which was calculated as the difference in area-based nutrient concentrations between senesced needles and green needles from the same age class (Bothwell
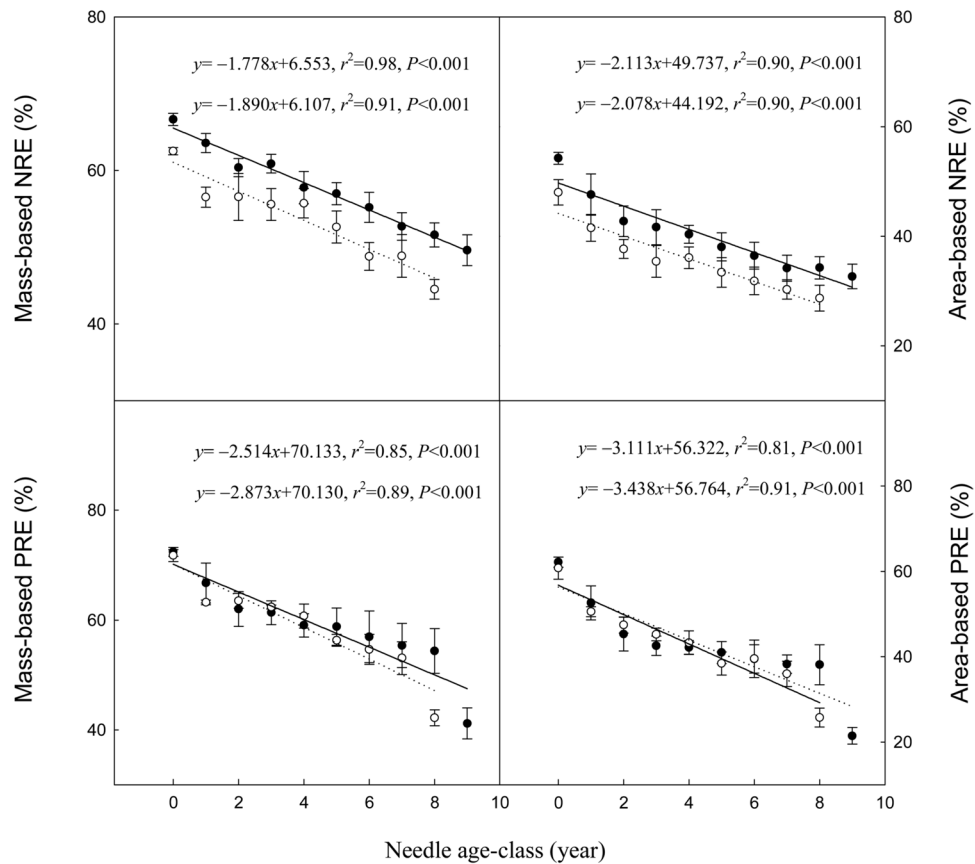
Figure 3: N and P resorption efficiencies. Evergreen conifer species *Picea glauca* (black circles and solid lines) and *Abies balsamea* (white circles and dashed lines). Data are means of three trees. Bars represent 1 SE. NRE = N resorption efficiency (%); PRE = P resorption efficiency (%). The coefficients of determination (r^2) and P are shown in each panel for *P. glauca* (the first line) and *A. balsamea* (the second line).

et al. 2001) and expressed as a percentage. Resorption proficiency was expressed as the concentration of either N or P in senesced needles (Killingbeck 1996).

Needle nutrient concentrations were log-transformed and resorption efficiency data were arcsine-transformed prior to statistical analyses to meet normality and homogeneous variance assumptions, all of which were performed in SYSTAT 12 (SYSTAT, Evanston, IL, USA). Simple linear regression was used to test the relationships between measured variables (nutrient concentrations, resorption and needle age classes).

RESULTS

For the two studied species, N and P concentrations based on both needle mass and needle area in green needles decreased with increasing needle age (Fig. 1). The area-based N concentrations in green needles ranged from 2.9 to 4.1 g m^{-2} for *P. glauca* and 1.9 to 3.1 g m^{-2} for *A. balsamea*. The area-based P concentrations ranged from 0.24 to 0.48 g m^{-2} and 0.15 to 0.32 g m^{-2} for *P. glauca* and *A. balsamea*, respectively. N and P concentrations, although gradually declining with needle age, remained at 50–70% of the maximum values in the oldest

needle age classes. *Picea glauca* had higher N and P concentrations in green needles (on average, 3.4 and 0.33 g m^{-2} for N and P, respectively) than *A. balsamea* (on average, 2.4 g m^{-2} and 0.22 g m^{-2} for N and P, respectively) ($P < 0.001$). N and P proficiencies, the concentrations in senesced needles, also decreased with increasing needle age for the two species (Fig. 2). Both grand mean N and P concentrations in senesced needles were higher in *P. glauca* than in *A. balsamea* ($P < 0.001$).

The resorption of N and P for both species also gradually declined with needle age (Fig. 3). *Picea glauca* retranslocated 33–54% of N and 22–63% of P from green needles during senescence. *Abies balsamea* retranslocated 29–48% of N and 26–61% of P from green needles prior to senescence. *Picea glauca* had higher average N resorption efficiency (42%) than *A. balsamea* (36%) ($P < 0.05$). However, P resorption efficiency did not significantly differ between two species ($P = 0.804$). For both species, resorption efficiency increased with the N and P concentrations in green needles (Fig. 4) and those in senesced needles (Fig. 5). Both N and P concentrations in green needles were positively associated with those in senesced needles (Fig. 6).
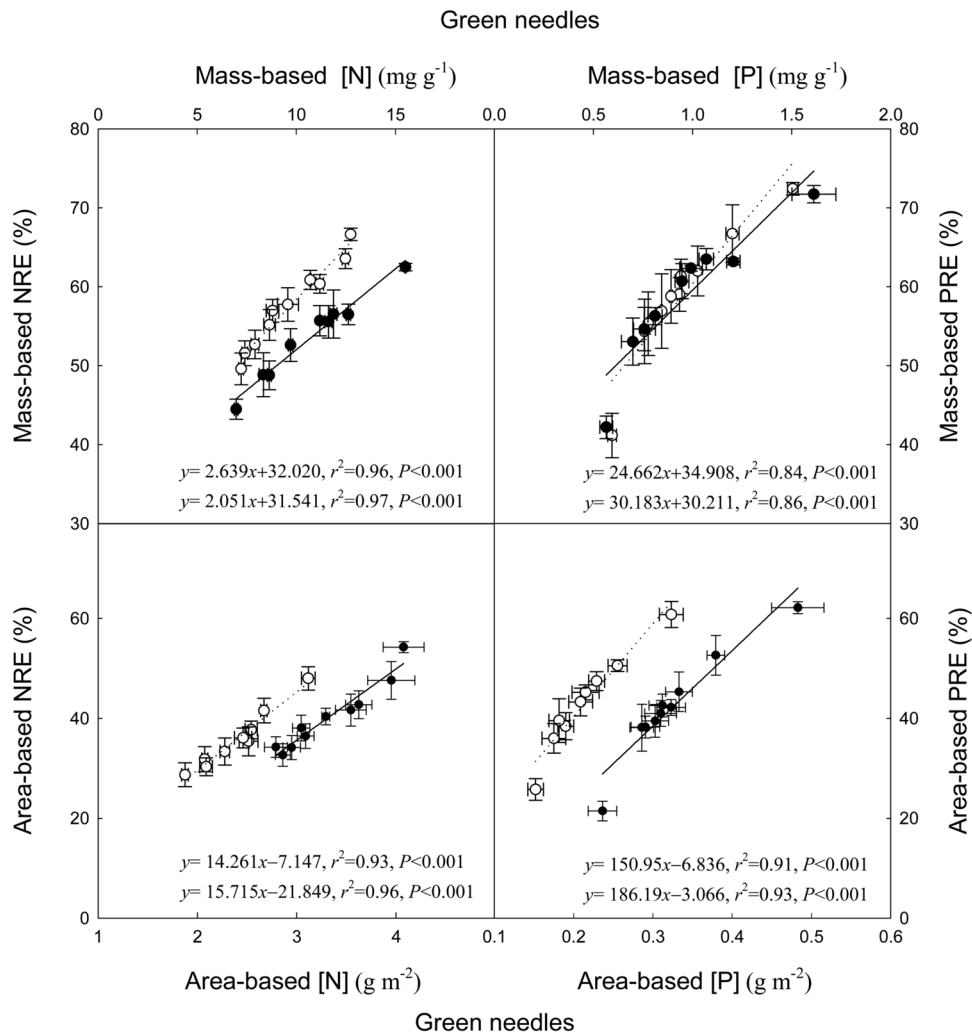
Green needles

Figure 4: N and P resorption efficiencies in relation to green-needle nutrient concentrations. Evergreen conifer species *Picea glauca* (black circles and solid lines) and *Abies balsamea* (white circles and dashed lines). Data are means of three trees. Bars represent 1 SE. NRE = N resorption efficiency (%); PRE = P resorption efficiency (%). The coefficients of determination (r^2) and P are shown in each panel for *P. glauca* (the first line) and *A. balsamea* (the second line).

DISCUSSION

In this study, we found that both N and P concentrations based on needle mass were lower in older needles than those in younger needles of both species (Figs 1 and 2). This reduction with needle age was not simply due to the dilution of N and P in a larger needle mass per area, as the area-based N and P concentration changed significantly with leaf age. Thus, this result indicated that N and P could be retranslocated from needles with low productivity and allocated to new needles of high productivity. The high N and P concentrations in young needles may be due to the higher metabolic levels found in the young tissues where there is active synthesis and growth (Chapin and Kedrowski 1983; Hom and Oechel 1983; Kitajima *et al.* 2002). Also, higher P levels in young tissues may be related to phospholipids, which increase frost tolerance in non-hardened tissues (Chapin and Kedrowski 1983). These results suggested that nutrient retranslocation may occur from all needle age classes in our two studied species. In fact, previous studies have shown that evergreen conifer tree species can retranslocate nutrients from 1-year-old needles to current-year needles (age class 0) (Nambiar and Fife 1987; Wyka *et al.* 2016). Pensa *et al.* (2007) found that Scots pine (*Pinus sylvestris*) had higher concentrations of N and P in current-year needles than older needles. All needle cohorts, including non-senescing needles in two species, are likely to be involved in resorption processes. However, Pasche *et al.* (2002) found that there was no net nutrient translocation from old to new developing needles in *Rhododendron* species, suggesting that the process of nutrient remobilization from senescing needles to new needles and shoots might vary between species and this process is not necessarily a general characteristic of all evergreen species.
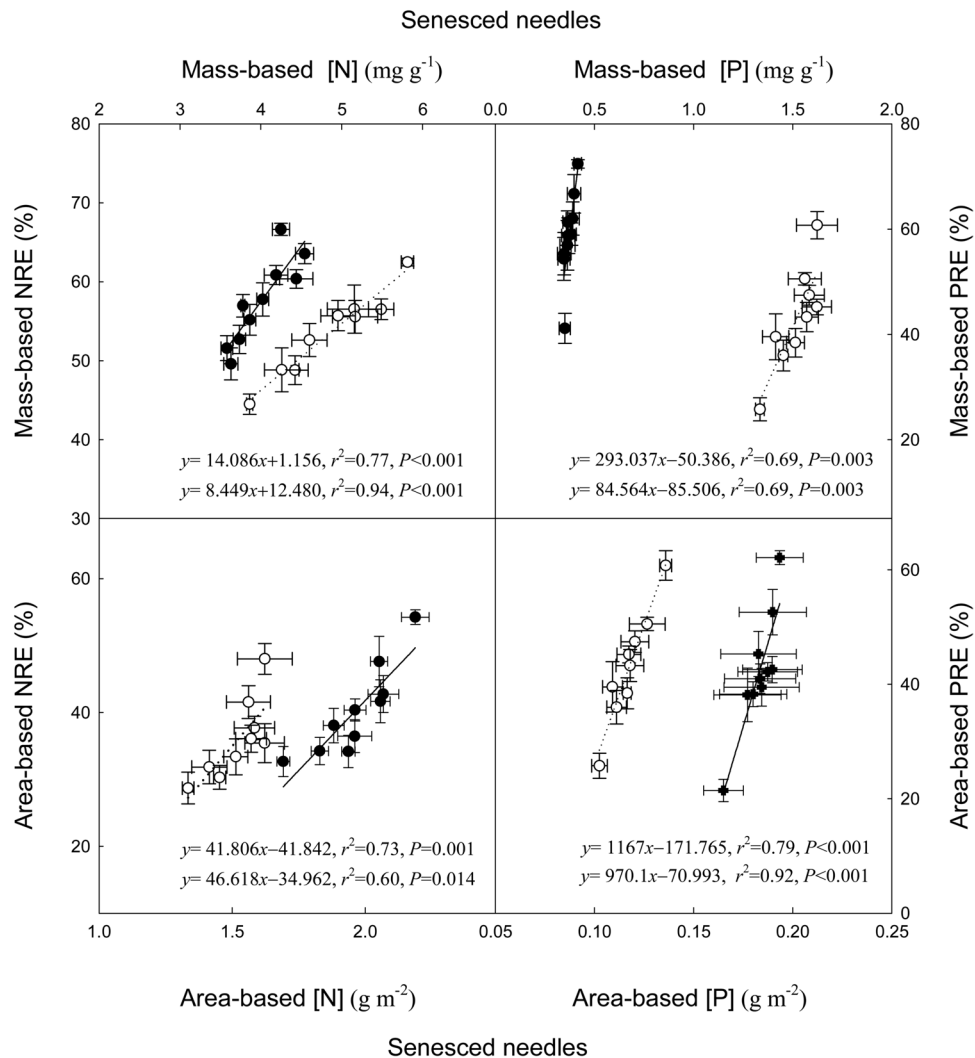
Senesced needles

Figure 5: N and P resorption efficiencies in relation to senesced-needle nutrient concentrations. Evergreen conifer species *Picea glauca* (black circles and solid lines) and *Abies balsamea* (white circles and dashed lines). Data are means of three trees. Bars represent 1 SE. NRE, N resorption efficiency (%); PRE, P resorption efficiency (%). The coefficients of determination (r^2) and P are shown in each panel for *P. glauca* (the first line) and *A. balsamea* (the second line).

For both species, average resorption efficiency was around 37% for N and 43% for P. There are no other studies of the same species to allow for comparison of results. Salifu and Timmer (2001) reported that the seedlings of black spruce (*Picea mariana*) can retranslocate 50% of N. The values of nutrient resorption for our studied species were lower than Chinese fir seedlings (*Cunninghamia lanceolata*) (Xu and Timmer 1999), radiata pine (*Pinus radiata*) (Nambiar and Fife 1987), white pine (*Pinus strobus*) (Munson *et al.* 1995) and other evergreen conifer species in the view of a global dataset presented by Yuan and Chen (2009). In this study, white spruce had higher N but similar P resorption efficiency as balsam fir, both of which changes with needle age. N and P resorption proficiency also differed between our two studied species. Both N and P resorption proficiencies were lower than reported in other studies for these species (Ferrari 1999;

Gordon *et al.* 2000; Taylor *et al.* 1989). These differences seem to support that nutrient resorption capacity may differ within and between species (Keenan *et al.* 1995; Yuan *et al.* 2005, 2007, 2011).

In agreement with our expectations, nutrient resorption decreased with aging in needles older than 1 year (Fig. 3). A reduced resorption efficiency implies that a higher percentage of nutrients will be lost when the needles are shed. The reason for this reduction could be due to the change in the size of nutrient sink associated with needle age. Because nutrients in plant tissues are distributed in either the mobile or structurally bound forms, the actively growing new leaves are strong nutrient sink in plants and these plants generally have high resorption efficiency at the time of leaf senescence (Lambers *et al.* 2008). Nutrients in the old leaves tend to be more structurally bound (Chapin and Moilanen 1991). Therefore, young
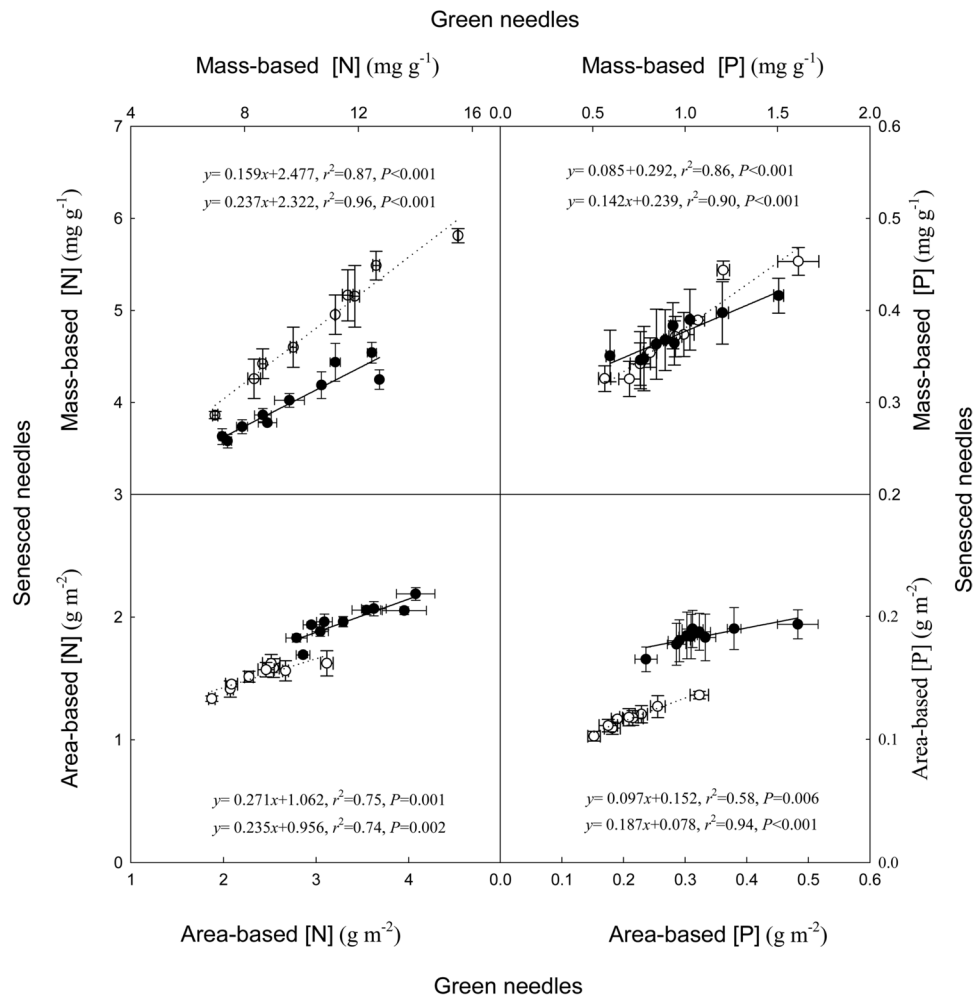
Green needles

Figure 6: the relationships of N and P concentrations between green and senesced needles. Evergreen conifer species *Picea glauca* (black circles and solid lines) and *Abies balsamea* (white circles and dashed lines). Data are means of three trees. Bars represent 1 SE. NRE, N resorption efficiency (%); PRE, P resorption efficiency (%). The coefficients of determination (r^2) and *P* are shown in each panel for *P. glauca* (the first line) and *A. balsamea* (the second line).

needles tend to have more nutrients than old needles due to the fact that nutrients are higher in functional than in structural materials.

Active growth of young needles could result in a strong sink for carbohydrates and nutrients in plants, and consequently high resorption efficiencies. Previous studies have shown that nutrient resorption from old needles increased with the size of new sink (new shoots) in radiata pine (Nambiar and Fife 1987), and that the removal of catkins reduced resorption in Alaskan birch (*Betula papyrifera*) (Chapin and Moilanen 1991). Similarly, reducing the source of photosynthate by shading senescing leaves has been found to lower the amount of nutrients recovered from these leaves (Chapin and Moilanen 1991). Therefore, delaying needle abscission could be advantageous to enhance production as it retains more nutrients in the canopy. Since photosynthetic capacity is generally proportional to leaf nutrients, especially N (Evans 1989; Field and Mooney 1986; Hikosaka 2004) and leaf aging reduces

photosynthetic N use efficiency (Kitajima *et al.* 2002; Sobardo 1994), nutrients resorbed from old leaves may be used to increase the photosynthetic rate and biomass, thus enhancing the nutrient use efficiency of young leaves. Then the loss of nutrients in senesced needles and the energy costs of new needle construction would be offset by this mechanism.

Another reason for the decreasing resorption with aging could be due to the cause of needle senescence, which could influence resorption. Furthermore, greater proportion of N and P are bound in structural components in older needles and this would contribute to the decreasing resorption efficiency with age. Young needles with greater dry weight contain a greater portion of mobile carbohydrates that can be retranslocated, whereas in old needles more of the substances is tightly bound in the needle structure (Helmisaari 1992). Although both N and P resorption efficiencies were low in old needles in our study, this did not mean that old needles were not useful for the tree growth. In fact, old needles are

still likely making a contribution to photosynthesis and nutrient residence time which influence nutrient use efficiency (Wendler *et al.* 1995; Zude and Ludders 1997).

In our study, nutrient resorption efficiency showed a positive correlation with nutrient concentration in green needles (Fig. 4), suggesting that green needles with higher nutrient concentrations are capable of withdrawing a higher percentage of nutrients. The significantly positive correlation between nutrient resorption efficiency and nutrient concentration in green needles observed in our study was consistent with those reported in previous studies (Bollmark *et al.* 1999; Yuan *et al.* 2006) and our study extends previous findings on different plants to different needles with varying ages.

In conclusion, needle age did influence N and P resorption in the two woody evergreen conifer species. Young needles were more efficient in resorbing N and P than old needles. We can attribute the difference to changed nutrient sink size, which likely decreases with needle age. For young needles, many nutrients are required for construction of new tissues, which accelerates senescence in old leaves (Nambiar and Fife 1987). The absence of a strong nutrient sink prior to needle abscission may further reduce nutrient resorption in evergreen conifer trees. These results support the idea that the demand for nutrients from growing tissues may drive nutrient resorption and senescence of older leaves (Grubb *et al.* 2014; Killingbeck and Whitford 2001). Our findings indicate that the ability to resorb nutrients by leaves changes over time albeit the total amount of nutrients resorbed for a leaf during its life may be the same as other leaves. Further studies need to consider the time scale governing the mechanism of nutrient resorption.

FUNDING

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