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Decreased Temperature with Increasing Elevation Decreases the End-Season Leaf-to-Wood Reallocation of Resources in Deciduous *Betula ermanii* Cham. Trees

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Abstract: Global air temperature has increased and continues to increase, especially in high latitude and high altitude areas, which may affect plant resource physiology and thus plant growth and productivity. The resource remobilization efficiency of plants in response to global warming is, however, still poorly understood. We thus assessed end-season resource remobilization from leaves to woody tissues in deciduous *Betula ermanii* Cham. trees grown along an elevational gradient ranging from 1700 m to 2187 m a.s.l. on Changbai Mountain, northeastern China. We hypothesized that end-season resource remobilization efficiency from leaves to storage tissues increases with increasing elevation or decreasing temperature. To test this hypothesis, concentrations of non-structural carbohydrates (NSCs), nitrogen (N), phosphorus (P), and potassium (K) during peak shoot growth (July) were compared with those at the end of growing season (September on Changbai Mt.) for each tissue type. To avoid leaf phenological effects on parameters, fallen leaves were collected at the end-season. Except for July-shoot NSC and July-leaf K, tissue concentrations of NSC, N, P, and K did not decrease with increasing elevation for both July and September. We found that the end-season leaf-to-wood reallocation efficiency decreased with increasing elevation. This lower reallocation efficiency may result in resource limitation in high-elevation trees. Future warming may promote leaf-to-wood resource reallocation, leading to upward shift of forests to higher elevations. The NSC, N, P, and K accumulated in stems and roots but not in shoots, especially in trees grown close to or at their upper limit, indicating that stems and roots of deciduous trees are the most important storage tissues over winter. Our results contribute to better understand the resource-related ecophysiological mechanisms for treeline formation, and vice versa, to better predict forest dynamics at high elevations in response to global warming. Our study provides resource-related ecophysiological knowledge for developing management strategies for high elevation forests in a rapidly warming world.

Keywords: Alpine treeline; Nitrogen; Non-structural carbohydrates; Phosphorus; Potassium; Remobilization; Storage; Upper limits

1. Introduction

Global air temperature has increased and continues to increase, especially in high latitude and high altitude areas. Climate change such as global warming will inevitably influence tree growth rate [1] via changing resource availability and use efficiency [2], and probably also resource allocation and reallocation. Resources can be recycled through remobilization from senescing leaves to storage tissues

in deciduous trees which enables plants to reuse these resources for regrowth after dormancy [3,4], and for defense and reproduction [5]. Plants remobilize carbon components and nutrients through internal resources cycling from senescing tissues to maximize the resource use efficiency and to minimize the costs [5]. Thus, remobilization is an internal conservation process which can contribute a substantial annual nutrient supply to increase the resource use efficiency [6]. Owing to the importance of resource resorption for plants, differences in patterns of resource remobilization have been exhaustively studied at the intra- and interspecific levels [3,7,8]. The main recycled carbon components in trees are non-structural carbohydrates (NSCs), which are mainly stored in ligneous tissues, particularly in stems and roots [5,8]. Carbohydrate storage is particularly important for deciduous trees that lack photosynthesizing tissues in early spring [9,10]. As a result of greater asynchrony of supply and demand undergone by deciduous species, more carbon compounds are stored in deciduous than in evergreen species [5]. Woody roots or the stems seem to play a crucial role in resource storage of deciduous species [11,12]. Compared to evergreen species that can directly retain resources in over-wintering leaves, rather than translocating them to stems and roots [4], deciduous species recycle resources back to storage tissues before leaf abscission [5]. The resources withdrawn from senescent tissues can be depleted during spring for new growth [13].

Environmental factors have strong impacts on resource remobilization during leaf senescence, because leaf senescence relies most on photoperiod, temperature, precipitation and nutrient availability. For example, resource remobilization efficiency is higher when leaves senesce prematurely as a consequence of low nutrient availability [14–16], indicating an adaptation to infertile habitats [17]. Similarly, recent studies suggested that climatic warming would increase the proficiency of nutrient resorption due to delayed leaf senescence [18]. However, González-Zurdo et al. (2015) studied leaf nitrogen resorption of three evergreen tree species, and concluded that N resorption efficiency was lower when winter temperature was low [19]. Nutrient remobilization efficiency can be lower under water stress, because drought advances leaf abscission [18,20,21]. Current rapid global warming, for example, may result in less water availability in water-limited areas, and warming, in combination with warming-induced changes in water availability, will influence plant ecophysiology such as resource remobilization. Using elevational gradients as a proxy of decreasing temperature, Kutbay and Ok (2003) found that foliar N and P resorption efficiencies did not change in evergreen *Juniperus oxycedrus* L. subsp. *macrocarpa* (Sibth. & Sm.) Ball trees [22]. However, it is unclear how resource remobilization efficiency in deciduous trees responds to low temperature at the alpine treeline and, contrastingly, to future global warming.

We, therefore, studied the effects of elevation on end-season remobilization of carbon and nutrients in deciduous *Betula ermanii* Cham. (Erman's birch) trees grown along an elevational gradient from lower elevation (1700 m a.s.l.) up to the upper limit (2200 m a.s.l.) on Changbai Mountain. We measured tissue NSC, N, P and K concentrations both at the peak shoot growth period and at the end of growing season, and calculated the resource remobilization efficiency of trees along the elevational gradient, to test our hypothesis that the end-season resource remobilization efficiency from leaves to storage tissues in deciduous *B. ermanii* trees increases with increasing elevations, to increase resource use efficiency of trees in a harsh environment.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Natural Reserve, Changbai Mountain (41°59' N, 127°59'–128° E) in northeastern China. The area was not disturbed because of its remoteness and high elevation. The area has a temperate continental climate [23] with mean growing season (late May to late September) temperature of 5.87 °C (ranging from 3.37 to 8.82 °C) [24]. The annual precipitation ranges from 700 to 1400 mm (data from Tian-Chi Meteorological Station located at 2623 m a.s.l.) [25] and the annual frost-free period is about 65 to 70 days [26]. Soils on the Changbai Mountain are classified as mountain

soddy forest soil [25]. The Changbai Mountain has vertical spectra with four vegetation belts [27]: mixed coniferous broad leaved forests distributed from 740 to 1100 m a.s.l., coniferous forests from 1100 to 1700 m a.s.l., birches (*Betula ermanii*) distributed from 1700 to 2200 m a.s.l., with the birch alpine treeline at 2030 m a.s.l., and tundra above 2000 m a.s.l. [22,26].

2.2. Field Sampling

Birch (*B. ermanii*) forests are distributed between 1700 and 2200 m a.s.l. (upper limit) on the Changbai Mt. The *Betula* elevational gradient can be divided by the alpine treeline (2030 m a.s.l.) into two parts, i.e., below the alpine treeline with trees of > 2 m in height and above the alpine treeline with trees of < 2 m in height. We used this elevational gradient as a proxy of environmental change, mainly air warming [1,28]. To compare patterns of remobilization efficiency across environmental gradients from low elevations to high elevations, samples were taken at the peak-growing season and at the end of growing season. We selected end-July (23 July 2017) to collect samples, since for that time the difference in leaf phenology along the elevational gradient was negligible [29] and the physiological processes such as photosynthesis and growth are most active [30]. The end-season samples were collected from the higher elevations downslope to the lower elevations between September 5 and 9, when the nighttime temperature at an elevation dropped to below 0 °C according to a linear model using climate data from Tian-Chi Meteorological Station located at 2623 m a.s.l. and from the Meteorological Station (738 m a.s.l.) of Changbai Mountain Forest Ecosystem Research facility. Five healthy *B. ermanii* trees ($n = 5$) with similar age, height and diameter at breast height (DBH) or basal diameter (2107 and 2187 m a.s.l.) were selected at each of the six elevations, i.e., 1700, 1800, 1900, 2027, 2107 and 2187 m a.s.l. (Table 1). Using a temperature lapse rate of 0.6 °C decrease with 100 m increase in elevation, the annual mean air temperature is 3 °C lower at 2187 m than at 1700 m a.s.l. One-year-old shoots (with bark), main stem sapwood (with bark) and fine roots (< 0.5 cm in diameter, with bark) were collected from each selected tree. For leaf samples, mature green leaves were collected on 23 July (mid-season samples), whereas only freshly fallen leaves were collected from the forest floor close to each sample tree (end-season samples), to minimize difference in leaf phenology among elevations. Also, to minimize the effects of diurnal temperature variation and sunlight on samples, all samples were taken around noon and immediately stored in a cool box [31]. The samples were killed in a microwave oven at 600 W for 40 s to minimize the physiological activities, dried to a constant weight at 65 °C and then ground to fine powder to pass through a 1-mm sieve for analysis. We measured the height and DBH of each tree at the first sampling date (July) (Table 1). For juvenile trees with DBH of < 5 cm, basal diameter of trees (about 1 cm above ground surface) was measured in July. As limitations have been imposed on tree-harvesting within the Changbai Mountain Nature Reserve, we, therefore, only measured the biomass of leaves, shoots, stems, and roots of 5 average trees at the two highest elevations (2107 and 2187 m a.s.l.) in July 2017.

Table 1. Characteristics of the plots and the sampling trees *Betula ermanii* Cham. (mean \pm 1 standard deviation; $n = 5$ trees) on the Changbai Mountain (Jilin, NE China).

Site No.	Elevation	Average	Average	Slope Exposure
	(m a.s.l.)	DBH (cm)	Height (m)	
1	2187	1.0 \pm 0.1 ^a	0.9 \pm 0.1	West
2	2107	1.1 \pm 0.1 ^a	1.5 \pm 0.1	West
3	2027	4.7 \pm 0.4	4.2 \pm 0.1	West
4	1900	9.4 \pm 1.0	9.3 \pm 0.4	West
5	1800	9.2 \pm 0.7	9.2 \pm 0.5	West
6	1700	10.9 \pm 0.7	11.2 \pm 0.8	West

^a basal diameter (about 1 cm above ground surface).

2.3. Analysis of NSC

Plant tissue (30 mg) was placed into a 10-mL centrifuge tube and mixed with 5 mL of 80% ethanol. The mixture was incubated at 80 °C in a water shaker (SHA-C, Jintan Jingda Instrument Manufacturing Co., Ltd., Jintan, China) for 30 min, cooled to ambient temperature, and thereafter centrifuged at 4000 rpm for 10 min. The sediments were re-extracted twice with 80% ethanol (Sinopharm Chemical Reagent Co., Ltd., Shanghai, China) to extract the soluble sugars [29]. The ethanol-insoluble pellets were used for starch extraction, and the combined supernatants were retained for soluble sugars analysis by the anthrone method. Glucose was used as a standard. Starch was extracted from the ethanol-insoluble pellets after placing in water at 80 °C to remove the ethanol by evaporation. The ethanol-insoluble residues were boiled with 2 mL of distilled water for 15 min. After cooling to room temperature, 2 mL of 9.2M HClO₄ (Sinopharm Chemical Reagent Co., Ltd., Shanghai, China) was added to hydrolyze the starch for 15 min, 4 mL distilled water was added and mixed thereafter, and then the mixture was centrifuged at 4000 rpm for 10 min. Subsequently, the solid residues were added with 2 mL of 4.6M HClO₄ for one more extraction. Soluble sugars and starch concentrations were both measured at 620 nm using a spectrophotometer (TU-1810, Beijing Purkinje General Instrument Co., Ltd., Beijing, China) [32]. The NSC, soluble sugars and starch concentrations were expressed on a dry matter basis (% d.m.).

2.4. Analysis of Nitrogen, Phosphorus and Potassium

Plant material (0.1 g) was digested in concentrated sulphuric acid and hydrogen peroxide [33]. The digested solutions were used for the determination of nitrogen, phosphorus and potassium. Nitrogen (N) concentration was determined by the idophenol blue colorimetric method on an automatic chemical analyzer (SmartChem 140, AMS-Alliance Instruments, Rome, Italy). Phosphorus (P) was colorimetrically determined by the ammonium molybdate-ascorbic acid method [34] on a spectrophotometer (TU-1810, Beijing Purkinje General Instrument Co., Ltd., Beijing, China). Potassium (K) concentration was measured with a flame photometer (FP6410, Shanghai Precise Scientific Instrument Co., Ltd., Shanghai, China).

2.5. Methods for Evaluating Resource Remobilization

Remobilization efficiency (*R*) was calculated based on differences in concentrations of mobile carbohydrates and nutrients in tissues collected at the peak shoot growth period and at the end season, using the Equation (1):

$$R\% = 100\% \times (C_s - C_j) / C_j = (C_s / C_j - 1) \times 100\% \quad (1)$$

where *C_s* (September) and *C_j* (July) represent concentrations of NSC, N, P or K within each tissue type at the end-season (September) and at the peak shoot growth period (July), respectively. A negative *R*-value (*C_s* < *C_j*) indicates resource reallocation from that tissue, whereas a positive *R*-value (*C_s* > *C_j*) reflects resource accumulation in that tissue at the end-season. A more negative *R*-value indicates higher remobilization efficiency, whereas a more positive *R*-value suggests higher accumulation efficiency.

2.6. Data Analysis

Data (NSC, N, P and K) were confirmed for normality (Kolmogorov-Smirnov test) before statistical analysis. Two-way analyses of variance (ANOVAs) were used to test the effects of elevation, time, and their interactions on the concentrations of NSC, N, P and K in each tissue. Two-way ANOVAs were performed with elevation and tissue type as factors, with random selection of trees as random factor to identify the trends in the remobilization efficiency of NSC, N, P, and K. Differences in the parameters studied among elevations were tested for significance using Tukey's HSD test at $\alpha = 0.05$. Because we

had equal sample size, Duncan's test at $\alpha = 0.05$ was used to analyze the difference for remobilization means next to each adjacent tree among the elevations.

3. Results

3.1. NSC Concentration

Elevation did not affect leaf NSC but significantly affected the NSC concentrations in shoots, stem sapwood, and roots (Table 2). Tissue NSC concentrations varied significantly with time (season), and time interacted with elevation to influence the NSC concentrations in aboveground tissues (leaves, shoots, and stem sapwood) (Table 1). Leaf NSC concentration was higher in July than in September, whereas NSC concentrations in sink tissues (shoots, stem, and roots) were higher in September than in July (Figure 1a–h). Root NSC concentrations seemed to be stable across elevations in both July and September (Figure 1d,h). Apart from this, clear elevational trends in NSC were found only in July shoots where the NSC concentration significantly decreased with increasing elevation (Figure 1b), and in September stem sapwood where the NSC concentrations were significantly higher at higher elevations (Figure 1g).

Table 2. Results of two-way nested ANOVAs with elevation and time as fixed factors. *F* and *p* values are given. NSC = Non-structural carbohydrates.

	NSC		Nitrogen		Phosphorus		Potassium	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Leaves								
Elevations (E)	0.42	0.829	20.15	<0.001	25.57	<0.001	7.21	<0.001
Time (T)	27.80	<0.001	478.52	<0.001	554.96	<0.001	125.46	<0.001
E × T	14.82	<0.001	7.19	<0.001	11.61	<0.001	2.74	0.043
1-year-old-shoots								
Elevations (E)	8.25	<0.001	2.11	0.098	3.96	0.009	8.42	<0.001
Time (T)	253.11	<0.001	301.44	<0.001	222.21	<0.001	465.96	<0.001
E × T	5.77	0.001	5.77	0.001	3.53	0.016	9.37	<0.001
Stem sapwood								
Elevations (E)	23.45	<0.001	206.63	<0.001	215.03	<0.001	22.26	<0.001
Time (T)	36.69	<0.001	306.85	<0.001	113.94	<0.001	28.97	<0.001
E × T	11.69	<0.001	101.70	<0.001	49.27	<0.001	28.55	<0.001
Fine roots								
Elevations (E)	3.63	0.014	7.13	<0.001	10.60	<0.001	5.88	0.001
Time (T)	232.16	<0.001	84.80	<0.001	72.13	<0.001	37.25	<0.001
E × T	1.50	0.228	2.28	0.079	1.21	0.333	0.62	0.688

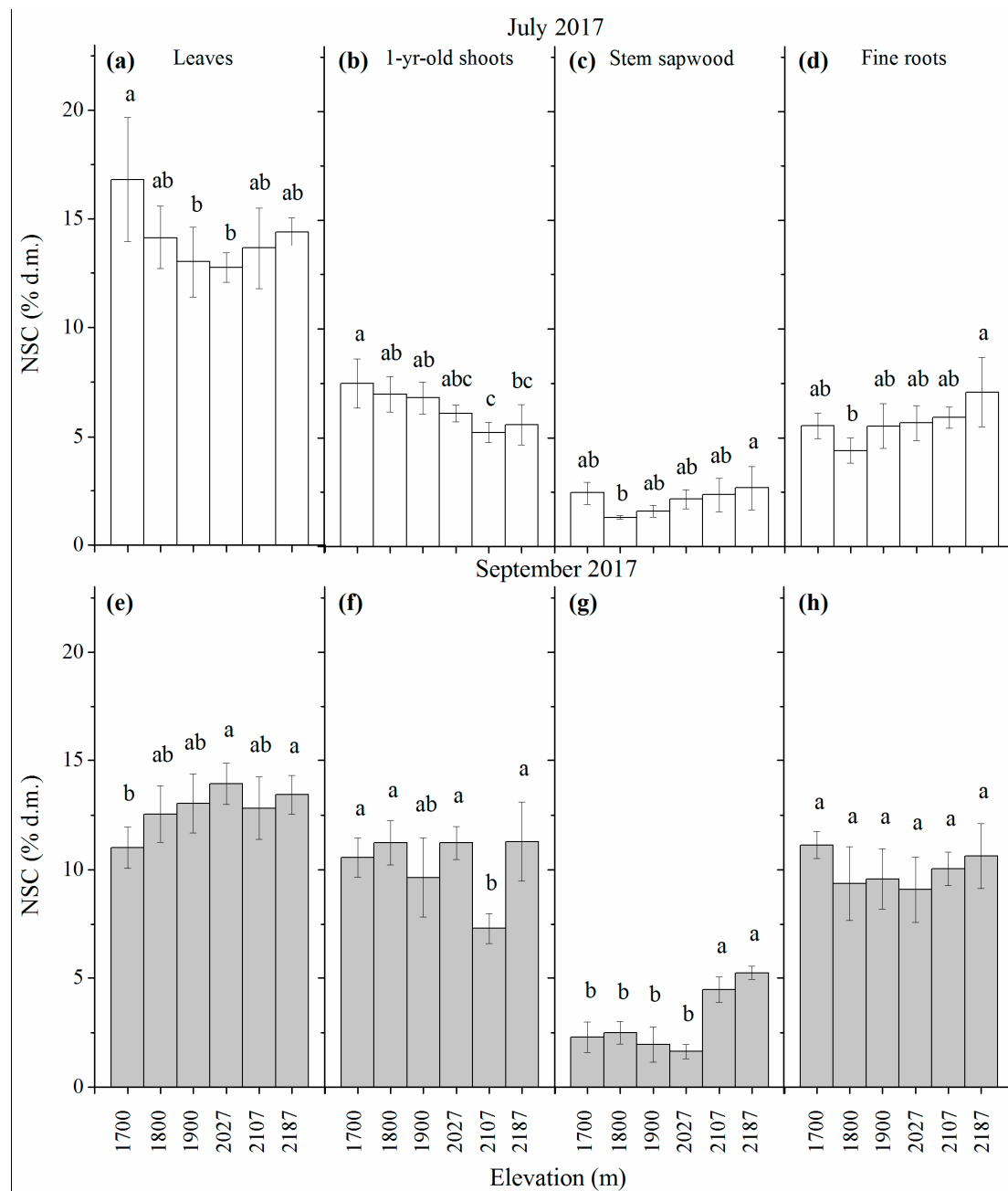


Figure 1. Seasonal tissues concentration (Mean \pm 1SD; % of dry matter) changes in non-structural carbohydrate (NSC) compounds of *Betula ermanii* Cham. trees along elevational gradients in Changbai Mountain ($n = 5$ for each elevational site and tissue type). Different letters display significant differences at the 0.05 level among elevations as determined by Tukey's HSD test.

3.2. N Concentration

Elevation significantly affected the N concentrations in leaves, stem sapwood, and roots but not in shoots (Table 2). Tissue N concentrations changed significantly with time (season), and the interaction between time and elevation was significant for N concentrations in aboveground tissues (leaves, shoots, and stem sapwood) (Table 2). Stem N concentration was higher in September than in July, whereas N concentrations in other tissues (leaves, shoots, and roots) were higher in July than in September (Figure 2a–h). In both July and September, trees at higher elevations had higher N concentrations in tissues, except the N concentrations in shoots and roots did not change with elevation in July (Figure 2a–h).

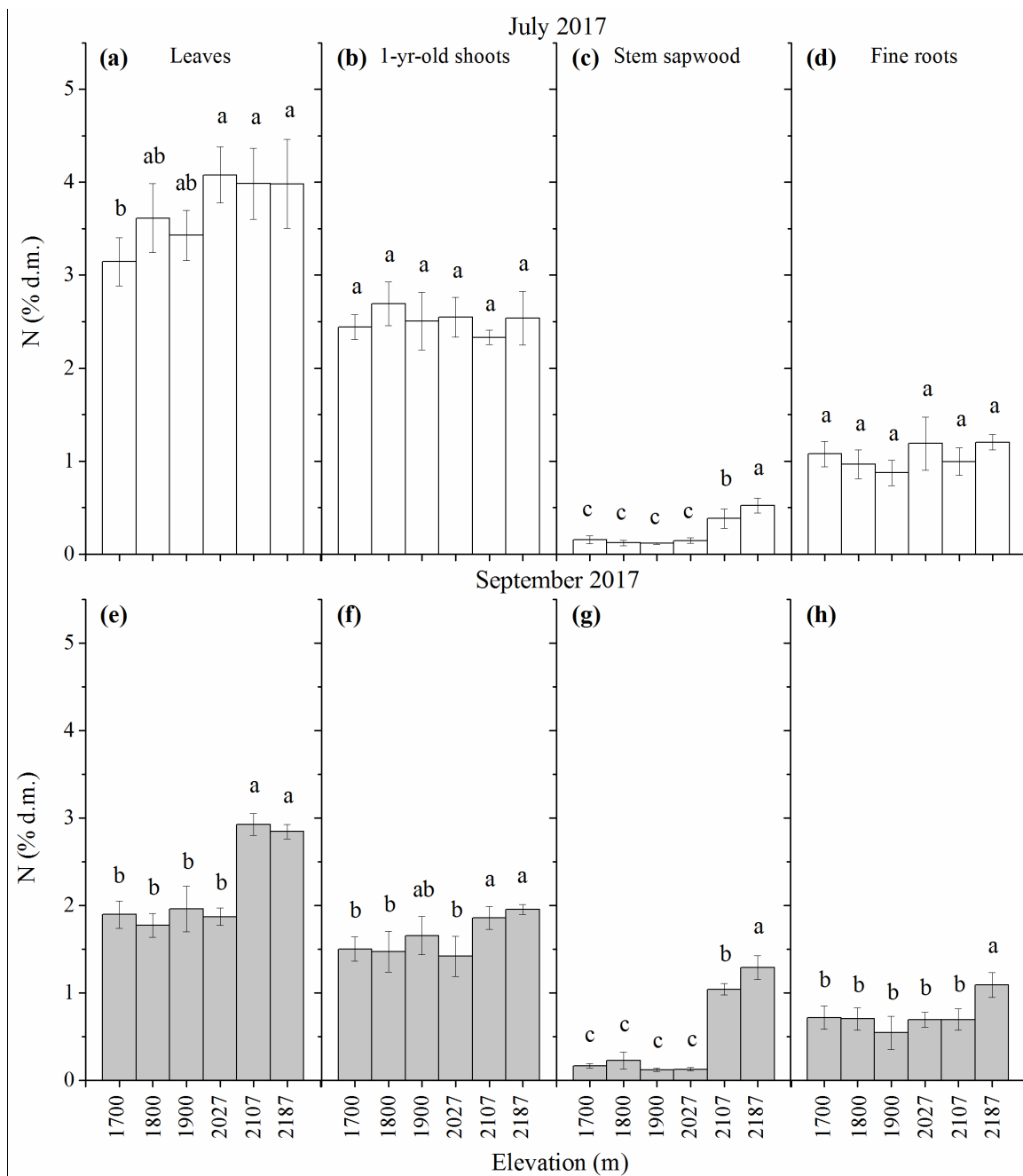


Figure 2. Seasonal tissues concentration (Mean \pm 1SD; % of dry matter) changes in total nitrogen (N) of *Betula ermanii* trees along elevational gradients in Changbai Mountain ($n = 5$ for each elevational site and tissue type). Different letters display significant differences at the 0.05 level among elevations as determined by Tukey's HSD test.

3.3. P Concentration

Both elevation and time (season) significantly affected the tissue P concentrations, and the elevation \times time interaction was significant for P concentrations in aboveground tissues (leaves, shoots, and stem sapwood) (Table 2). Leaf and shoot P concentrations were higher in July than in September, whereas stem and root P concentrations were higher in September than in July (Figure 3a–h). Tissue P concentrations were higher in trees at higher elevations in both July and September, except for P in leaves and shoots in July (Figure 3a–h).

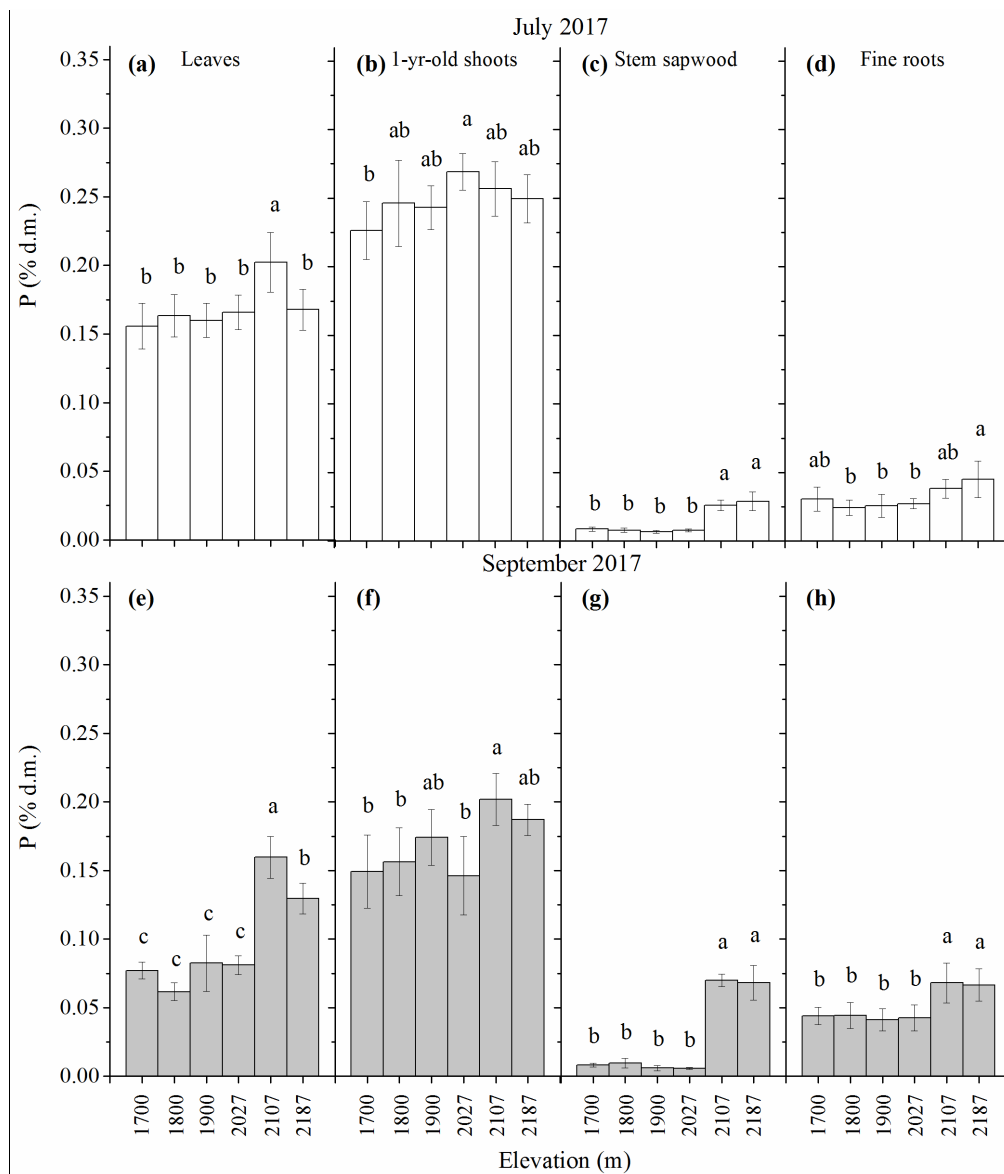


Figure 3. Seasonal tissues concentration (Mean \pm 1SD; % of dry matter) changes in total phosphorus (P) of *Betula ermanii* trees along elevational gradients in Changbai Mountain ($n = 5$ for each elevational site and tissue type). Different letters display significant differences at the 0.05 level among elevations as determined by Tukey's HSD test.

3.4. K Concentration

Tissue K concentrations were significantly affected by both elevation and time (season) (Table 2). The interaction between elevation and time was significant for K concentrations in leaves, shoots and stem sapwood (Table 2). Leaf and shoot K concentrations were higher in July than in September, whereas stem and root K concentrations were higher in September than in July (Figure 4a–h). Stem and root K concentrations in July, as well as leaf, shoot and root K in September remained stable among trees at different elevations (Figure 4c,d,f,h). Apart from those, leaf K concentrations significantly decreased but shoot K significantly increased with increasing elevation in July (Figure 4a,b), and stem sapwood had higher K concentrations in trees close to their upper limit in September (Figure 4g).

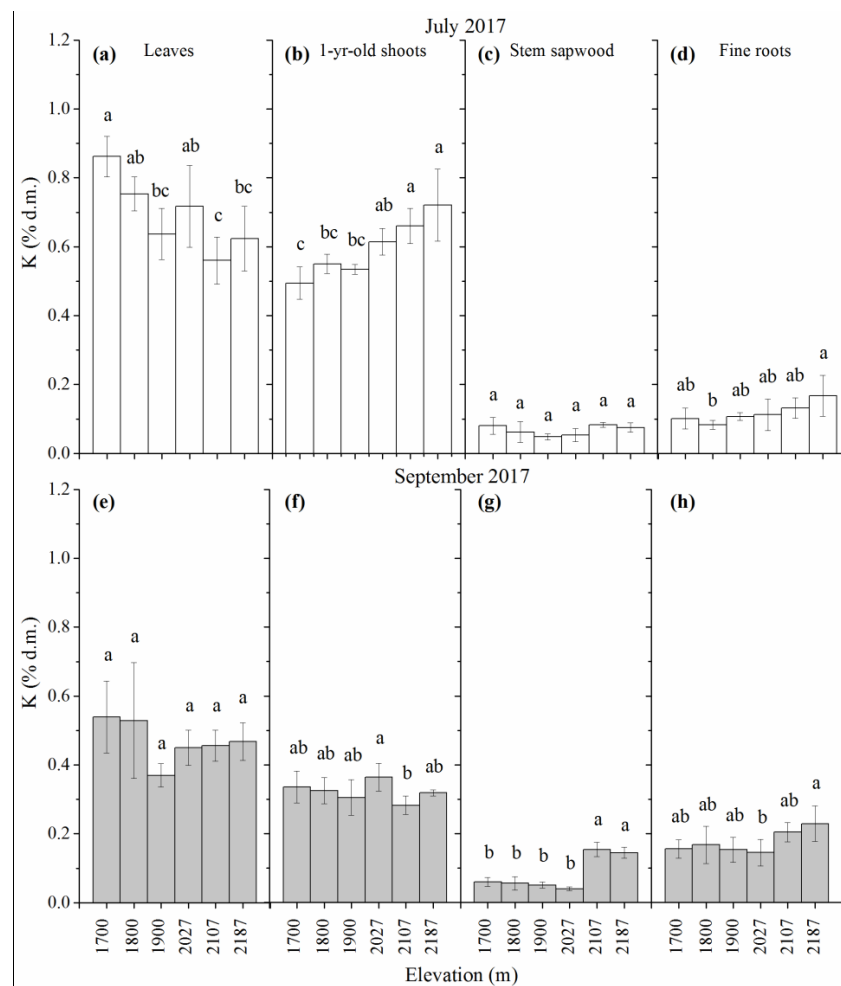


Figure 4. Seasonal tissues concentration (Mean \pm 1SD; % of dry matter) changes in total potassium (K) of *Betula ermanii* trees along elevational gradients in Changbai Mountain ($n = 5$ for each elevational site and tissue type). Different letters display significant differences at the 0.05 level among elevations as determined by Tukey's HSD test.

3.5. Elevational Effects on Resource Remobilization

Both elevation and tissue type, and their interaction had significant effects on the remobilization efficiency of NSC, N, P and K (Table 3). At the end of the growing season, leaves reallocated NSC, N, P, and K to other tissues (Figure 5a,e,i,m), and the remobilization efficiency tended to decrease with increasing elevation, and even for an NSC accumulation at 1900 and 2027 m a.s.l. (Figure 5a). Shoots accumulated NSC but remobilized N, P, and K (Figure 5b,f,j,n), and the NSC accumulation (Figure 5b) and K reallocation (Figure 5n) tended to increase but N reallocation (Figure 5f) seemed to decrease with increasing elevation. Stems in trees close to the upper limit accumulated NSC, N, P and K (Figure 5c,g,k,o). Roots accumulated NSC, P and K, but reallocated N to other tissues (Figure 5d,h,l,p). The root NSC accumulation efficiency decreased with increasing elevation (Figure 5d). At the two highest elevations (i.e., 2107 and 2187 m a.s.l.), for example, both the amount of resource reallocation (less negative values at 2187 m compared to 2107 m) and accumulation (positive values) decreased with increasing elevation (Table 4). The mean reallocation efficiency of resources from leaves to other tissues was significantly lower in trees above the alpine treeline than in trees below the treeline (Table 5), and the mean efficiency across the entire transect was 40% (N), 42% (P), 31% (K), and 8% (NSC) (Table 5).

Table 3. Results of two-way nested ANOVAs with elevation and tissue types as fixed factors. The *F* and *p* values are given. R refers to remobilization rate.

	R NSC		R Nitrogen		R Phosphorus		R Potassium	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Elevations (E)	8.67	<0.001	17.20	<0.001	10.72	<0.001	3.49	0.016
Tissue types (T)	287.57	<0.001	42.36	<0.001	79.04	<0.001	84.44	<0.001
E × T	5.73	<0.001	2.50	0.005	3.22	<0.001	2.50	0.005

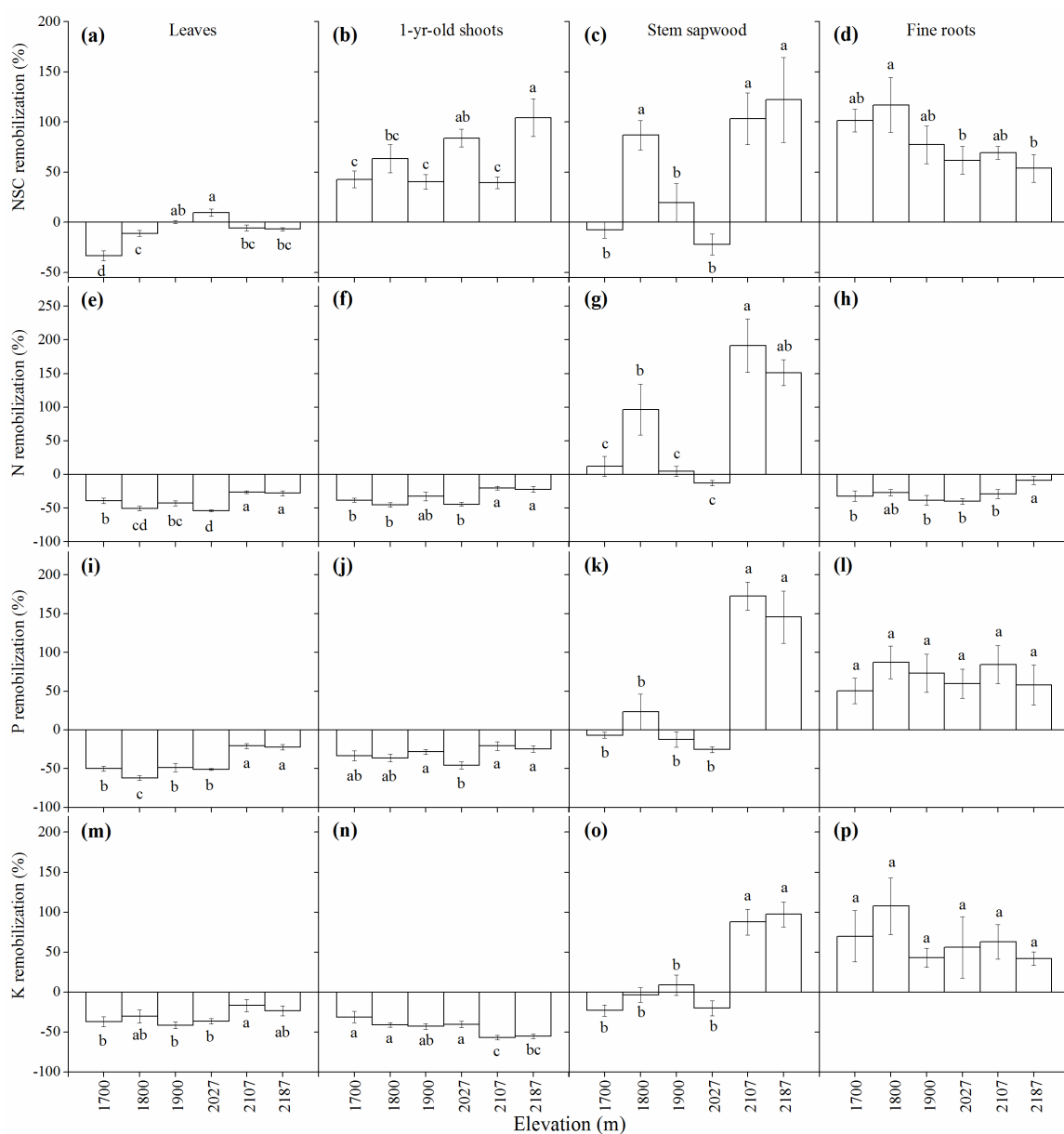


Figure 5. Carbohydrates, N, P and K remobilization efficiency (Mean ± 1SE) (R%) in *Betula ermanii* trees along the altitudinal gradients in Changbai Mountain (*n* = 5 for each elevational site and tissue type). Different letters display significant differences at the 0.05 level among elevations as determined by Duncan’s test (A negative *R*-value indicates resource translocation, whereas a positive *R*-value reflects resource accumulation).

Table 4. End-season resource reallocation (mean value \pm 1 standard deviation; $n = 5$ trees; calculated using biomass \times reallocation rate) for *Betula ermanii* trees at 2187 m (upper limit of distribution) and 2107 m a.s.l. on Changbai Mt. Different letters display significant differences at the 0.05 level among elevations as determined by Tukey’s HSD test. Negative values (dark-highlighted) indicate resource “loss” due to resource reallocation, and positive values indicate resource “gain” because of accumulation.

Elevation (m a.s.l.)	NSC (g)	N (g)	P (g)	K (g)
		Leaves		
2187	−1.4 \pm 0.4 ^a	−5.8 \pm 1.5 ^b	−4.3 \pm 0.8 ^b	−5.3 \pm 1.9 ^a
2107	−3.0 \pm 1.3 ^a	−12.9 \pm 2.7 ^a	−10.5 \pm 2.8 ^a	−4.7 \pm 3.6 ^a
		1-year-old shoots		
2187	31.1 \pm 8.3 ^a	−7.0 \pm 2.3 ^a	−7.6 \pm 2.2 ^a	−17.4 \pm 4.0 ^a
2107	26.6 \pm 9.9 ^a	−17.1 \pm 7.0 ^a	−18.2 \pm 8.1 ^a	−43.7 \pm 16.3 ^a
		Stem sapwood		
2187	63.0 \pm 21.2 ^b	77.5 \pm 10.8 ^b	76.7 \pm 20.1 ^b	49.8 \pm 7.6 ^b
2107	240.4 \pm 72.6 ^a	391.5 \pm 65.1 ^a	369.6 \pm 50.5 ^a	193.4 \pm 43.3 ^a
		Fine roots		
2187	22.0 \pm 6.7 ^b	−4.1 \pm 2.2 ^b	22.3 \pm 8.8 ^a	17.0 \pm 4.7 ^a
2107	85.1 \pm 15.1 ^a	−36.7 \pm 13.1 ^a	102.7 \pm 34.7 ^a	59.3 \pm 26.5 ^a

Table 5. Mean end-season reallocation rate (%) of resources (NSC, N, P, K) from leaves to other tissues in *Betula ermanii* trees grown at higher elevations (2107 and 2187 m a.s.l.) and lower elevations (1700, 1800, 1900, and 2027 m), separated by the alpine treeline located at 2030 m a.s.l. on the Changbai Mt., northeastern China.

	Trees across the Entire Transect	Trees below the Alpine Treeline	Trees above the Alpine Treeline
Non-structural carbohydrates (NSC)	8	9	6
Nitrogen (N)	40	47	27
Phosphorus (P)	42	52	22
Potassium (K)	31	36	20

4. Discussion

4.1. Tissue- and Resource-Dependent Reallocation or Accumulation

At the end of season, NSC reallocated from leaves to woody tissues (Figure 5a–d) and N accumulated only in stems (Figure 5g), whereas P and K seemed to store in stems and roots (Figure 5k,l,o,p), indicating tissue- and resource-dependent reallocation or accumulation (Table 4). *B. ermanii* leaves reallocated NSC to other tissues (Figure 5a; Table 4), leading to decreases in leaf NSC (Figure 1e vs. Figure 1a) but increases in NSC concentrations in shoots (Figure 1f vs. Figure 1b), stem sapwood (Figure 1g vs. Figure 1c), and roots (Figure 1h vs. Figure 1d), and thus an NSC accumulation in those storage tissues (Figure 5b–d). In line with previous studies, our results confirmed that leaf carbon compounds in deciduous trees were reallocated and stored in ligneous tissues, particularly in stems and roots [5,8]. Leaf carbon components recycled through remobilization from leaves to storage tissues before leaf senescence are particularly important for regrowth of new leaves in a leafless state of deciduous trees in early spring [5,9,10]. We found that the NSC remobilization efficiency of *B. ermanii* leaves ranged from 6% at high elevation to 33% at low elevation (Figure 5a). Chapin et al. (1990) proposed a carbon remobilization efficiency of ~10% based on an assumption that the loss of leaf weight was a direct result of carbon remobilization [5]. Similarly, Eckstein et al. (1998) proposed a carbon remobilization efficiency of 6%–13% for deciduous species [35].

Nitrogen (N) is the most important stored compound [36], paralleling to carbohydrates in supporting growth and reproduction [37]. Our results indicated that all tissue types decreased in N concentration during leaf senescence except stems (Figure 5e–h), suggesting that stems participated in the N accumulation rather than N translocation. Our results agreed with previous studies,

showing that N remobilized from senescing tissues (e.g., leaves and shoots) for storage prior to leaf abscission [3,37,38]. As previously reported for *Betula pendula* Roth., the deciduous broadleaf tree tended to store N in roots and stem [11,12]. Our findings differ from coniferous evergreen species, which store N in the youngest age class of needle [11,13]. N stored in specific tissues with an individual species, dependent on leaf habit [37]. In addition, the mean leaf N remobilization efficiency of 40% (Table 5) was lower than that value reported by Aerts (1996) for deciduous shrubs and trees (mean 54%) [3]. In another study, Vergutz et al. (2012) showed that, based on a leaf mass loss correction, average nutrient resorption was 62% for N during senescence [39].

Apart from mobile carbohydrates and nitrogen (N), plants also store and remobilize macronutrients such as phosphorus (P) and potassium (K) [38,40]. By the process of leaf senescence, P and K is reallocated from leaves and shoots to and stored in roots and stems (Figure 5i–p). The mean efficiency of P remobilized from senescing leaves was 42% (Table 5), which is lower than that reported by Aerts (1996) for deciduous shrubs and trees (50% for N) [3]. Vergutz et al. (2012) even suggested that, in general, leaf average P resorption value was 65%, after correction for leaf mass loss [39]. Similar results were found for K. As K occurs in ionic form but not in macromolecule form [18], K is thus highly mobile and has been transferred to storage tissues (i.e., stems and roots) before leaf abscission. However, our remobilization efficiency from senescing leaves of 31% (Table 5) was much lower than published resorption efficiency. Chapin et al. (1990) and Vergutz et al. (2012) proposed 50 and 70%, respectively [5,39].

As previously reported for deciduous species, carbohydrate remobilization took place in the leaves, indicating that carbon components recycled from senescing leaves (Figure 5a) are used as a carbon source for new growth [5,41]. But unlike carbohydrates, nitrogen was recycled from senescing leaves (Figure 5e), shoots (Figure 5f) and roots (Figure 5h) to support new leaf and shoot growth, showing that senescing tissues play an important role as potential supplier of nitrogen. Besides, our findings were in agreement with other studies that demonstrate N storage in roots and stems in broad-leaved deciduous species [11,12]. P and K were reallocated from leaves and shoots to stems and roots at the end-season (Figure 5i–p), although these patterns differed from those of NSC and N mentioned above (Table 4). In *B. ermanii* trees, 6%–33% of the leaf mobile carbohydrates was recycled at the end-season. However, about half the N and P was remobilized from senescing leaves before leaves were shed, and 36% of the leaf K was resorbed during leaf senescence. Our results support the fact that resource remobilization is composed of a large storage of nutrients but a small storage of carbohydrates [5].

4.2. Elevational Effects on Resource Remobilization

In the present study, we calculated the remobilization efficiency using the resource concentration within the same tissue type measured at two time points (end-season vs. peak growth season), which may provide insights into resource remobilization processes during leaf senescence. This calculation revealed that the end-season remobilization efficiency of NSC, N, P, and K from leaves to storage tissues tended to decrease with increasing elevation (Figure 5a,e,i,m), which does not support our hypothesis that expected an increase in remobilization efficiency at higher elevations, especially at the upper limit. In our previous study [25], we calculated the remobilization efficiency using the end-season difference in the resource concentrations between leaves (source) and shoots (sink), and found that the remobilization efficiency from leaves to shoots increased with increasing elevation. Using that method [25], we re-calculated the end-season remobilization efficiency from leaves to shoots for the present study and found that NSC remobilization efficiency had a bimodal curve of R% with a bigger remobilization efficiency (smaller R% value) at the upper distribution limit (Figure 6a). Leaf to shoot K reallocation efficiency did not show any response to elevational gradients (Figure 6d), and leaf to shoot N and P reallocation efficiency tended to be lower above the treeline compared to below the treeline (Figure 6b,c). This comparison suggests that a standard method for calculating the remobilization efficiency and thus for understanding the reallocation processes

of resources is urgently needed. Previous studies proposed that resource remobilization efficiency can be higher at low nutrient availability or in low temperature condition [14,16], representing an adaptation to stress environment [17]. However, Kutbay and Ok (2003) have demonstrated that the absolute and proportional N and P resorption efficiency did not change significantly along elevational gradients [22,29,31,42]. Many reports have revealed the importance of temperature on regulating leaf senescence and fall [18]. For example, leaf senescence and fall were delayed, in response to warmer temperature [43–45]. The timing or phenology of leaf abscission is considered as one of the reasons leading to altered resorption patterns of nutrients. To minimize such leaf phenological effects on resource remobilization, we did not collect end-season leaves from trees, instead, we collected the fallen leaves as end-season samples in the present study. However, *B. ermanii* in low temperature at the upper limit may have less time to complete nutrient resorption from leaves, which may result in a lower resorption of resources [18], as discussed in our previous study [25].

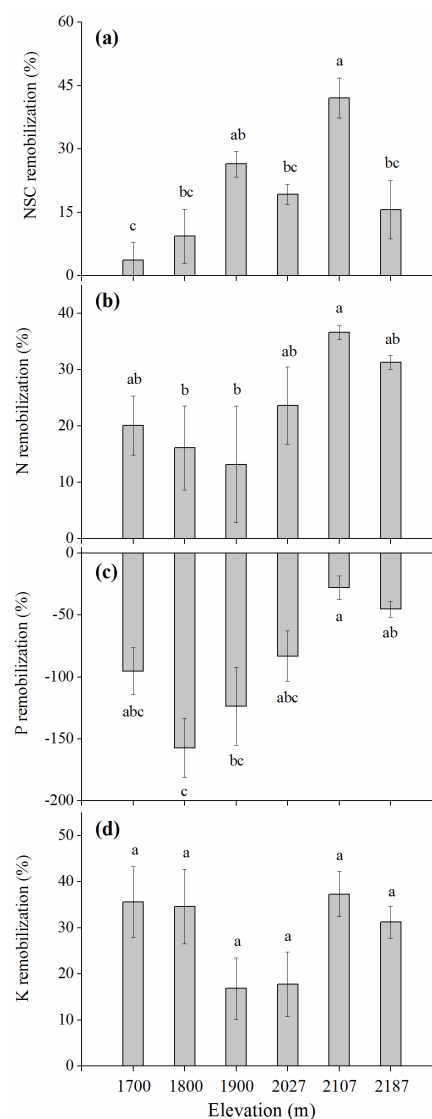


Figure 6. Carbohydrates, N, P and K remobilization efficiency (Mean \pm 1SE) (R%) in *Betula ermanii* trees along the altitudinal gradients in Changbai Mountain ($n = 5$ for each elevational site). R% was calculated using $R\% = ((C_l - C_s)/C_l) \times 100\% = (1 - C_s/C_l) \times 100\%$, where C_l and C_s represent concentrations in leaves and shoots at the end of growing season, respectively. Different letters display significant differences at the 0.05 level among elevations as determined by Tukey's HSD test (The larger the R-value, the lower the remobilization efficiency is).

Stem and shoot NSC accumulation increased but root NSC accumulation decreased with increasing elevation (Figure 5b–d). Given that the NSC accumulation increased in stems and shoots up to the upper limit, this process may act to resist the harsh cold alpine environment for survival in winter [46], because soluble sugars participate in cell osmotic regulation and prevent intracellular ice formation by decreasing the freezing point of the cytoplasm [47]. Moreover, accumulation of soluble sugars would prime stems for recovery after the stress is alleviated, and stem is an important organ not only for long-distance carbon transport, but also for the regulation of the tree's carbon balance [48].

Similarly, our results showed that N, P, and K were also accumulated in stems, especially in trees grown close to or at their upper limit (Figure 5g,k,o). Oleksyn et al. (1998) and Körner (1999) have reported that nutrient accumulation and conservation are adaptive responses that enhance metabolic activity and growth rates in harsh cold environment [49,50]. In such situations, the tree would internally store more recycling nutrients to recover from harsh environment because of losses in respiration. The reserve storage is a risk-aversion function to minimize risk of catastrophic loss [5]. The greater the risk (high frequency or large losses), the more the tree should invest in internally stored reserves.

5. Conclusions

Many studies have stated that the end-season resource remobilization is strategic since it supports growth at the beginning of bud break in deciduous species [18,49,50]. Except for July-shoot NSC and July-leaf K, tissue concentrations of NSC, N, P, and K did not decrease with increasing elevation for both July and September. Our results partly supported our hypothesis that resources (i.e., mobile carbohydrates, N, P, and K) were reallocated from leaves to storage tissues at the end of growing season in deciduous *B. ermanii* trees. In an economic view, shoots should be an important storage tissue for resources to reduce the transport costs at both the end-season and early growing season. However, our study indicates that stems and roots of deciduous *B. ermanii* trees at high elevations are the most important storage tissues for resources over winter. Inconsistent with our initial hypothesis, we found trees had lower end-season reallocation efficiency of NSC, N, P, and K from leaves to woody tissues at the higher elevations above the alpine treeline compared to lower elevations (Table 5; Figure 5a,e,i,m), and this may result in a resource limitation in high-elevation trees and further limit tree growth at high elevations. Our results contribute to better understand the resource-related ecophysiological mechanisms for treeline formation, and vice versa, to better predict treeline dynamics in response to global warming. Our study provides resource-related ecophysiological knowledge for developing management strategies for high elevation forests in a rapidly warming world. To more closely explore carbon and nutrient remobilization mechanisms, further studies are needed to estimate the pool size of resources remobilized (concentration \times biomass, see Table 4) [51] and their stoichiometry [52]. Furthermore, stable isotope labeling experiments would be taken into account (e.g., ^{13}C , ^{15}N) to accurately evaluate carbon and N remobilization from senescing tissues, and to determine which tissues contribute to the most internal resource remobilization [13].

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References

- Li, M.; Yang, J. Effects of elevation and microsite on growth of *Pinus cembra* in the subalpine zone of the Austrian Alps. *Annu. For. Sci.* **2004**, *61*, 319–325. [[CrossRef](#)]
- Bhattacharya, A. *Changing Climate and Resource use Efficiency in Plants*; Academic Press: London, UK, 2018.
- Aerts, R. Nutrient resorption from senescing leaves of perennials: Are there general patterns? *J. Ecol.* **1996**, *84*, 597–608. [[CrossRef](#)]
- Cherbuy, B.; Joffre, R.; Gillon, D.; Rambal, S. Internal remobilization of carbohydrates, lipids, nitrogen and phosphorus in the Mediterranean evergreen oak *Quercus ilex*. *Tree Physiol.* **2001**, *21*, 9–17. [[CrossRef](#)] [[PubMed](#)]
- Chapin, F.; Schulze, E.; Mooney, H. The ecology and economics of storage in plants. *Annu. Rev. Ecol. Syst.* **1990**, *21*, 423–447. [[CrossRef](#)]
- Li, Y.; Lan, G.; Xia, Y. Rubber Trees demonstrate a clear retranslocation under seasonal drought and cold stresses. *Front. Plant Sci.* **2016**, *7*. [[CrossRef](#)] [[PubMed](#)]
- Chapin, F.; Kedrowski, R.A. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* **1983**, *64*, 376–391. [[CrossRef](#)]
- Millard, P. Ecophysiology of the internal cycling of nitrogen for tree growth. *Zeitschrift für Pflanzenernährung Bodenkunde* **1996**, *159*, 1–10. [[CrossRef](#)]
- Marchi, S.; Sebastiani, L.; Gucci, R.; Tognetti, R. Changes in sink-source relationships during shoot development in olive. *J. Am. Soc. Hortic. Sci.* **2005**, *130*, 631–637. [[CrossRef](#)]
- Marchi, S.; Sebastiani, L.; Gucci, R.; Tognetti, R. Sink-source transition in peach leaves during shoot development. *J. Am. Soc. Hortic. Sci.* **2005**, *130*, 928–935. [[CrossRef](#)]
- Millard, P.; Hester, A.; Wendler, R.; Baillie, G. Interspecific defoliation responses of trees depend on sites of winter nitrogen storage. *Funct. Ecol.* **2001**, *15*, 535–543. [[CrossRef](#)]
- Millard, P.; Wendler, R.; Hepburn, A.; Smith, A. Variations in the amino acid composition of xylem sap of *Betula pendula* Roth. trees due to remobilization of stored N in the spring. *Plant Cell Environ.* **1998**, *21*, 715–722. [[CrossRef](#)]
- Millard, P.; Proe, M.F. Storage and internal cycling of nitrogen in relation to seasonal growth of *Sitka spruce*. *Tree Physiol.* **1992**, *10*, 33–43. [[CrossRef](#)] [[PubMed](#)]
- Bridgham, S.D.; Pastor, J.; McClaugherty, C.A.; Richardson, C.J. Nutrient-use efficiency: A litterfall index, a model, and a test along a nutrient-availability gradient in North Carolina peatlands. *Am. Nat.* **1995**, *145*, 1–21. [[CrossRef](#)]
- Maillard, A.; Diquélou, S.; Billard, V.; Lainé, P.; Garnica, M.; Prudent, M.; Garcia-Mina, J.-M.; Yvin, J.-C.; Ourry, A. Leaf mineral nutrient remobilization during leaf senescence and modulation by nutrient deficiency. *Front. Plant Sci.* **2015**, *6*, 317. [[CrossRef](#)] [[PubMed](#)]
- Pugnaire, F.I.; Chapin, F.S. Environmental and physiological factors governing nutrient resorption efficiency in barley. *Oecologia* **1992**, *90*, 120–126. [[CrossRef](#)] [[PubMed](#)]
- Dissanayaka, D.M.S.B.; Maruyama, H.; Nishida, S.; Tawarayama, K.; Wasaki, J. Landrace of japonica rice, Akamai exhibits enhanced root growth and efficient leaf phosphorus remobilization in response to limited phosphorus availability. *Plant Soil* **2017**, *414*, 327–338. [[CrossRef](#)]
- Estiarte, M.; Peñuelas, J. Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: Effects on nutrient proficiency. *Glob. Chang. Biol.* **2015**, *21*, 1005–1017. [[CrossRef](#)]
- González-Zurdo, P.; Escudero, A.; Mediavilla, S. N resorption efficiency and proficiency in response to winter cold in three evergreen species. *Plant Soil* **2015**, *394*, 87–98. [[CrossRef](#)]
- Killingbeck, K.T. Nutrient Resorption. In *Plant Cell Death Processes*; Academic Press: San Diego, CA, USA, 2004; pp. 215–226.
- Etienne, P.; Diquélou, S.; Prudent, M.; Salon, C.; Maillard, A.; Ourry, A. Macro and micronutrient storage in plants and their remobilization when facing scarcity: the case of drought. *Agriculture* **2018**, *8*, 14. [[CrossRef](#)]
- Kutbay, H.; Ok, T. Foliar N and P resorption and nutrient levels along an elevational gradient in *Juniperus oxycedrus* L. subsp. *macrocarpa* (Sibth. & Sm.) Ball. *Ann. For. Sci.* **2003**, *60*, 449–454.
- Du, H.; Liu, J.; Li, M.-H.; Büntgen, U.; Yang, Y.; Wang, L.; Wu, Z.; He, H.S. Warming-induced upward migration of the alpine treeline in the Changbai Mountains, northeast China. *Glob. Chang. Biol.* **2018**, *24*, 1256–1266. [[CrossRef](#)] [[PubMed](#)]

24. Zong, S.; He, H.; Liu, K.; Du, H.; Wu, Z.; Zhao, Y.; Jin, H. Typhoon diverged forest succession from natural trajectory in the treeline ecotone of the Changbai Mountains, Northeast China. *For. Ecol. Manag.* **2018**, *407*, 75–83. [[CrossRef](#)]
25. Cong, Y.; Wang, A.; He, H.; Yu, F.; Tognetti, R.; Cherubini, P.; Wang, X.; Li, M.H. Evergreen *Quercus aquifolioides* remobilizes more soluble carbon components but less N and P from leaves to shoots than deciduous *Betula ermanii* at the end-season. *iForest* **2018**, *11*, 517–525. [[CrossRef](#)]
26. Yu, D.; Wang, Q.; Liu, J.; Zhou, W.; Qi, L.; Wang, X.; Zhou, L.; Dai, L. Formation mechanisms of the alpine Erman's birch (*Betula ermanii*) treeline on Changbai Mountain in Northeast China. *Trees* **2014**, *28*, 935–947. [[CrossRef](#)]
27. Liu, Q.-J.; Li, X.-R.; Ma, Z.-Q.; Takeuchi, N. Monitoring forest dynamics using satellite imagery—A case study in the natural reserve of Changbai Mountain in China. *For. Ecol. Manag.* **2005**, *210*, 25–37. [[CrossRef](#)]
28. Li, M.; Yang, J.; Kräuchi, N. Growth responses of *Picea abies* and *Larix decidua* to elevation in subalpine areas of Tyrol, Austria. *Can. J. For. Res.* **2003**, *33*, 653–662. [[CrossRef](#)]
29. Li, M.; Jiang, Y.; Wang, A.; Li, X.; Zhu, W.; Yan, C.-F.; Du, Z.; Shi, Z.; Lei, J.; Schönbeck, L.; et al. Active summer carbon storage for winter persistence in trees at the cold alpine treeline. *Tree Physiol.* **2018**, *38*, 1345–1355. [[CrossRef](#)]
30. Yamaguchi, D.P.; Nakaji, T.; Hiura, T.; Hikosaka, K. Effect of seasonal change and experimental warming on the temperature dependence of photosynthesis in the canopy leaves of *Quercus serrata*. *Tree Physiol.* **2016**, *36*, 1283–1295. [[CrossRef](#)]
31. Li, M.; Xiao, W.-F.; Shi, P.; Wang, S.-G.; Zhong, Y.-D.; Liu, X.-L.; Wang, X.-D.; Cai, X.-H.; Shi, Z.-M. Nitrogen and carbon source–sink relationships in trees at the Himalayan treelines compared with lower elevations. *Plant Cell Environ.* **2008**, *31*, 1377–1387. [[CrossRef](#)]
32. Wang, X.; Xu, Z.; Yan, C.; Luo, W.; Wang, R.; Han, X.; Jiang, Y.; Li, M.-H. Responses and sensitivity of N, P and mobile carbohydrates of dominant species to increased water, N and P availability in semi-arid grasslands in northern China. *J. Plant Ecol.* **2017**, *10*, 486–496. [[CrossRef](#)]
33. Parkinson, J.A.; Allen, S.E. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. *Commun. Soil Sci. Plant Anal.* **1975**, *6*, 1–11. [[CrossRef](#)]
34. Murphy, J.; Riley, J.P. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* **1962**, *27*, 31–36. [[CrossRef](#)]
35. Eckstein, R.L.; Karlsson, P.S.; Weih, W. The significance of resorption of leaf resources for shoot growth in evergreen and deciduous woody plants from a subarctic environment. *Oikos* **1998**, *81*, 567–575. [[CrossRef](#)]
36. Millard, P.; Sommerkorn, M.; Grelet, G.A. Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. *New Phytol.* **2007**, *175*, 11–28. [[CrossRef](#)] [[PubMed](#)]
37. Millard, P.; Grelet, G.-A. Nitrogen storage and remobilization by trees: ecophysiological relevance in a changing world. *Tree Physiol.* **2010**, *30*, 1083–1095. [[CrossRef](#)] [[PubMed](#)]
38. Nambiar, E.K.S.; Fife, D.N. Nutrient retranslocation in temperate conifers. *Tree Physiol.* **1991**, *9*, 185–207. [[CrossRef](#)]
39. Vergutz, L.; Manzoni, S.; Porporato, A.; Novais, R.F.; Jackson, R.B. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecol. Monogr.* **2012**, *82*, 205–220. [[CrossRef](#)]
40. Villar-Salvador, P.; Uscola, M.; Jacobs, D.F. The role of stored carbohydrates and nitrogen in the growth and stress tolerance of planted forest trees. *New For.* **2015**, *46*, 813–839. [[CrossRef](#)]
41. Gessler, A.; Treydte, K. The fate and age of carbon—Insights into the storage and remobilization dynamics in trees. *New Phytol.* **2016**, *209*, 1338–1340. [[CrossRef](#)]
42. Körner, C. The nutritional status of plants from high altitudes. A worldwide comparison. *Oecologia* **1989**, *81*, 379–391. [[CrossRef](#)]
43. Chung, H.; Muraoka, H.; Nakamura, M.; Han, S.; Muller, O.; Son, Y. Experimental warming studies on tree species and forest ecosystems: A literature review. *J. Plant Res.* **2013**, *126*, 447–460. [[CrossRef](#)] [[PubMed](#)]
44. Gunderson, C.A.; Edwards, N.T.; Walker, A.V.; O'Hara, K.H.; Campion, C.M.; Hanson, P.J. Forest phenology and a warmer climate—growing season extension in relation to climatic provenance. *Glob. Chang. Biol.* **2012**, *18*, 2008–2025. [[CrossRef](#)]
45. Xu, Z.; Hu, T.; Zhang, Y. Effects of experimental warming on phenology, growth and gas exchange of treeline birch (*Betula utilis*) saplings, Eastern Tibetan Plateau, China. *Eur. J. For. Res.* **2012**, *131*, 811–819. [[CrossRef](#)]

46. Sheen, J.; Zhou, L.; Jang, J.-C. Sugars as signaling molecules. *Curr. Opin. Plant Biol.* **1999**, *2*, 410–418. [[CrossRef](#)]
47. Morin, X.; Améglio, T.; Ahas, R.; Kurz-Besson, C.; Lanta, V.; Lebourgeois, F.; Miglietta, F.; Chuine, I. Variation in cold hardiness and carbohydrate concentration from dormancy induction to bud burst among provenances of three European oak species. *Tree Physiol.* **2007**, *27*, 817–825. [[CrossRef](#)] [[PubMed](#)]
48. Furze, M.E.; Trumbore, S.; Hartmann, H. Detours on the phloem sugar highway: Stem carbon storage and remobilization. *Curr. Opin. Plant Biol.* **2018**, *43*, 89–95. [[CrossRef](#)] [[PubMed](#)]
49. Oleksyn, J.; Modrzyński, J.; Tjoelker, M.G.; Z-ytkowski, R.; Reich, P.B.; Karolewski, P. Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Funct. Ecol.* **1998**, *12*, 573–590. [[CrossRef](#)]
50. Körner, C. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*; Springer: Berlin, Germany, 1999.
51. Li, M.; Kräuchi, N.; Dobbertin, M. Biomass distribution of different-aged needles in young and old *Pinus cembra* trees at highland and lowland sites. *Trees* **2006**, *20*, 611–618. [[CrossRef](#)]
52. Wang, A.; Wang, X.; Tognetti, R.; Lei, J.-P.; Pan, H.-L.; Liu, X.-L.; Jiang, Y.; Wang, X.-Y.; He, P.; Yu, F.-H.; et al. Elevation alters carbon and nutrient concentrations and stoichiometry in *Quercus aquifolioides* in southwestern China. *Sci. Total Environ.* **2018**, *622*, 1463–1475. [[CrossRef](#)] [[PubMed](#)]



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