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Original article

Increasing N and P resorption efficiency and proficiency in northern deciduous hardwoods with decreasing foliar N and P concentrations

Benoît Côté*, James W. Fyles and Hamid Djalilvand

Department of Natural Resource Sciences, Macdonald Campus of McGill University, 21,111 Lakeshore,
Ste-Anne-de-Bellevue, QC, H9X 3V9, Canada

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Abstract – The objective of this study was to assess the relationships between pre-senescence leaf N and P concentrations, and resorption efficiency and proficiency of eight deciduous hardwood tree species. Trees were sampled on two sites of contrasting fertility/productivity in southern Quebec. Measured resorption efficiencies ranged from 56 to 71% for N, and from 30 to 78% for P. Linear and exponential models between leaf N and litter N, and between leaf P and litter P were significant. Intercepts of linear models were significantly different from zero. Resorption efficiency and proficiency increased with a decrease in leaf N and P, and the rate of change of resorption efficiency increased with leaf nutrient concentration. Concentrations corresponding to ultimate potential resorption were calculated to be 3.2 mg N g^{-1} and 0.09 mg P g^{-1}. Maximum resorption efficiencies were estimated at 70% for N and 80% for P. The concept of ultimate potential resorption in hardwoods is discussed.

hardwoods / litter / nutrient / resorption / senescence

Résumé – Augmentation de l’efficacité et de la compétence en résorption du N et P foliaire de feuillus nobles nordiques avec la diminution des concentrations foliaires en N et P. L’objectif de cette étude était d’évaluer les relations entre les concentrations foliaires en N et P, et l’efficacité et la compétence de la résorption de huit espèces de feuillus nobles. Les arbres ont été échantillonnés à deux stations de fertilité/productivité contrastante. L’efficacité de résorption a varié de 56 à 71 % pour N et de 30 à 78 % pour P. Les modèles linéaires et exponentiels entre le N des feuilles et le N de la litière, et entre le P des feuilles et le P de la litière étaient significatifs. L’ordonnée à l’origine des modèles linéaires était significativement différente de zéro. L’efficacité et la compétence de la résorption ont augmenté avec une diminution des concentrations en N et P des feuilles, et le taux de changement de l’efficacité de la résorption a augmenté avec la concentration en nutriment des feuilles. Les concentrations correspondant à la résorption potentielle ultime étaient de 3,2 mg N g^{-1} et 0,09 mg P g^{-1}. Les maximums d’efficacité de résorption ont été estimés à 70 % pour N et 80 % pour P. Le concept de résorption potentielle ultime pour les feuillus est discuté.

feuillu / litière / nutriment / résorption / sénescence

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* Correspondence and reprints
Tel. +514 398 7952; Fax. +514 398 7990; e-mail: coteb@nrs.mcgill.ca

1. INTRODUCTION

Autumnal nutrient resorption in broadleaf deciduous tree species is a key component of the nutrient cycle in temperate hardwood forests. This conservation mechanism is particularly important for N and P for which half or more of the maximum leaf content is typically resorbed to other parts of the tree before leaf abscission [1, 5, 11, 14, 15, 23, 31].

Studies on N and P dynamics in senescing leaves have dealt primarily with interspecific differences and the effect of site fertility or nutrient status on nutrient resorption. Many researchers have hypothesized that N and/or P resorption efficiency would be greater on sites low in nutrient availability [25, 26, 29, 30]. A recent review of the literature on N and P resorption in woody plants based on differences in leaf nutrient concentrations did not, however, reveal any relationships between site/plant nutrition and resorption efficiency [1]. Differences in sampling protocols, the confounding effect of genotypic and phenotypic responses to nutrient supply, large annual variation in nutrient resorption efficiency [21], and the possibility that resorption efficiency could respond to nutrient supply over a relatively narrow range [17] may all have contributed to these apparently contradicting results.

In 1996, Killingbeck [16] introduced the concepts of nutrient resorption proficiency and ultimate potential resorption. These concepts offer an alternative measure of resorption as a nutrient conservation mechanism. Nutrient resorption proficiency is defined as the level to which a plant reduces nutrient concentration in senescing leaves whereas ultimate potential resorption corresponds to a minimum threshold concentration that is specific to plant form (e.g. conifers, hardwoods). Ultimate potential resorption is dictated by the physiology and anatomy of the plant tissues. The existence of a minimum threshold concentration in senescing leaves suggests that nutrient resorption efficiency will reach a maximum or decrease at low concentrations as nutrient concentrations in mature leaves are closer to the threshold. The numerous factors that can interfere with nutrient resorption [16, 21] and, therefore, result in incomplete resorption, also suggest that high resorption proficiency is more likely to be achieved in trees with low pre-senescence leaf nutrient concentrations. In this study, we sampled northern deciduous hardwood species on two sites of contrasting fertility/productivity to assess the effect of pre-senescence leaf N and P concentrations on their resorption efficiency and proficiency.

2. MATERIALS AND METHODS

The sites were located in southern Québec at the Morgan Arboretum of McGill University and at the Station de Biologie des Laurentides of University of Montréal. The forest of the Morgan Arboretum is typical of the sugar maple / basswood ecoregion and is composed mainly of sugar maple (*Acer saccharum* Marsh.) , basswood (*Tilia americana* L.), bitternut hickory (*Carya cordiformis* (Wang.) K. Kock.), shagbark hickory (*Carya ovata* (Mill.) K. Kock.), white ash (*Fraxinus americana* L.) and red oak (*Quercus rubra* L.) [12]. Soils are Melanic and Sombric Brunisols with a mull humus type. The forest of the Station de Biologie des Laurentides (SBL) is typical of the sugar maple/yellow birch ecoregion and is composed primarily of sugar maple, red maple (*Acer rubrum* L.), beech (*Fagus grandifolia* Ehrh.), paper birch (*Betula papyrifera* (Marsh.)) and largetooth aspen (*Populus grandidentata* Michx.). Soils are Orthic Ferro-Humic Podzols with a mor humus type. Other site characteristics are provided in *table I*.

Table I. Characteristics of the study sites.

Characteristics	*Station de Biologie des Laurentide*s (SBL)	Morgan Arboretum
Latitude	45° 59’ N	45° 25’ N
Longitude	74° 01’ W	73° 57’ W
Altitude (m)	380	15
Overstory age (yr)	90	50–150
Origin	fire	cut
Basal area (m^2 ha^{-1})	29.1 ± 1.6	20–40
Canopy height (m)	20–25	25–35
Mean July air temperature (°C)	20	20.9
Mean December air temperature (°C)	–10	–6.6
Mean annual precipitation (mm)	1100 (30% as snow)	929 (20% as snow)
Solum depth (cm)	60	100–200
Soil type	Humo-ferric Podzol	Melanic and Sombric Brunisol
Humus type	Moder	Mull
Drainage	Moderate	Moderate

2.1. Sampling

Eight species (American beech, largetooth aspen, sugar maple, red maple, basswood, bitternut hickory, red oak and white ash) were sampled at the Morgan Arboretum. Of these eight species, four were also sampled at the SBL (American beech, largetooth aspen, sugar maple and red maple) while yellow birch was only sampled at the SBL. Ten and nine plots ranging from 300 to 500 m^2 were delineated in the Morgan Arboretum and the SBL, respectively. Sampling of pre-senescence mature leaves was done between 20–30 August 1994 on both sites. Depending on the number of trees per plot, between one and five trees per species were sampled per plot by cutting one to three branches exposed to direct sunlight at mid-crown with a 15-m telescopic pole pruner. The total number of trees sampled per species or combination of species and site ranged from 15 to 32. Sampled leaves were fully developed (i.e. not from the tip of the branch) and were free of disease and insect damage.

Litter sampling was coordinated with the peak of leaf drop for individual species and consisted in collecting falling and recently fallen leaves. In order to reduce the error associated with the sampling of leaf litter that was not restricted to mid-crown position, only falling and fallen leaves that had characteristics of sun leaves in terms of thickness, that were fully developed and that were free of disease and insect damage were collected. A minimum of 50 leaves per species and plot were collected and pooled for analysis Litter sampling was done between 1–15 October 1994 at the Morgan Arboretum, and between 15 September and 15 October 1994 at the SBL. Nutrient resorption efficiency was determined for each combination of species and plot by calculating the percentage change in mean nutrient concentration from leaf maturity to leaf fall according to the following formula:

$$RE = ((a - a') / (a)) * 100$$

where RE is resorption efficiency, a is the mean leaf nutrient concentration (pre-senescence leaves sampled in August; mean of 1 to 5 trees per plot) , and a' is the litter nutrient concentration of the plot. Although not a true measure of nutrient resorption, the percentage decrease in leaf nutrient concentration between pre-senescence and leaf fall has been used extensively to assess nutrient resorption efficiency [16]. The loss of leaf mass during senescence is typically less than 10% [8] which should induce relatively small errors in the determination of resorption efficiency with this approach [1].

2.2. Sample preparation and chemical analysis

Leaves and litter were dried at 65 °C for 48 hours in a forced-air oven before being ground in a mill to pass through a 40-mesh screen. Ground litters were digested according to the procedure of Thomas et al. [28]. Concentrations of N and P in the digest were determined by colorimetry by means of a Technicon AutoAnalyzer.

2.3. Statistical analysis

Mean leaf and litter nutrient concentrations and resorption efficiency of each species or combination of species and site were computed using plots as replicates. The number of replicates was therefore nine and ten for the SBL and the Morgan Arboretum, respectively. To assess the effect of pre-senescence leaf N and P concentrations on resorption efficiency and proficiency, mean leaf and litter nutrient concentrations of all species were fitted with linear and exponential regressions. The probability of having a Y-intercept significantly different from zero was determined with linear regressions. Since any straight line going through zero is a line with constant percentage nutrient resorption efficiency, a Y-intercept significantly different from zero was interpreted as significant change in percentage nutrient resorption efficiency over the range of concentrations measured in mature leaves.

Litter nutrient concentrations corresponding to ultimate potential resorption were estimated by extrapolating the exponential models corresponding to the lowest leaf nutrient concentrations observed in the literature for deciduous broadleaf trees [3, 4, 9, 10, 13, 20, 24, 32]. Maximum resorption efficiency of N and P was estimated by calculating the resorption efficiency isoline that was tangent to the exponential model of each nutrient. All statistics were calculated for a probability level of 5% using Statistica [27].

3. RESULTS

Measured resorption efficiencies ranged from 56% in largetooth aspen to 71% in red maple for N, and from 30% in bitternut hickory to 78% in sugar maple for P (*table II*). Among species that were found on both sites, largest site differences in leaf N and P concentrations were measured in largetooth aspen and beech, and in red maple and sugar maple, respectively (*figure 1*); sugar

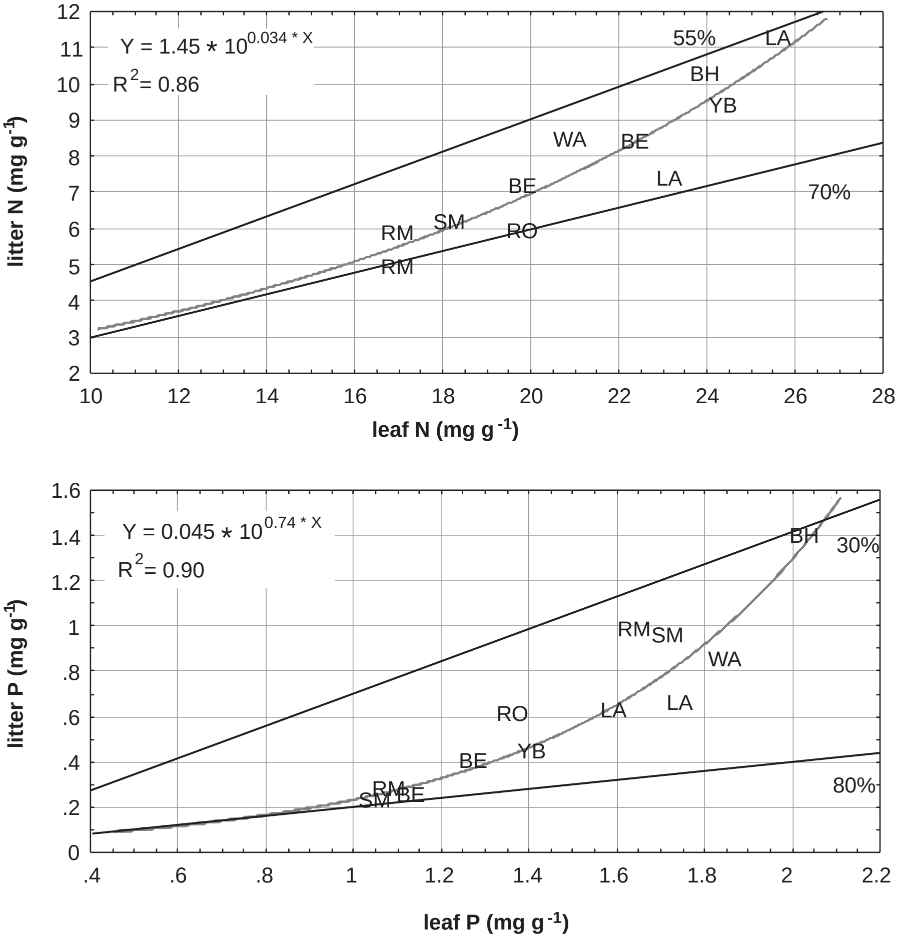

Figure 1. Exponential regressions between leaf N and litter N, and leaf P and litter P concentrations. Solid lines are isolines of maximum and minimum resorption efficiencies measured in this study. Beech (BE), bitternut hickory (BH), largetooth aspen (LA), red maple (RM), red oak (RO), sugar maple (SM), white ash (WA), yellow birch (YB).

maple and red maple had higher leaf P at the Morgan Arboretum whereas beech and largetooth aspen had lower leaf N at the Morgan Arboretum. Resorption efficiencies for these combinations of species and elements were lower at the Morgan Arboretum for leaf P in red and sugar maple but similar in beech and higher in largetooth aspen for leaf N (*table II*).

Both linear and exponential models were significant but exponential models had higher R^2 values (*table III*). Intercepts of linear models were significantly different from zero (*table III*). Minimum and maximum resorption efficiencies calculated with the exponential models over the range of observed leaf nutrient concentrations were 58 and 68% for N, and 30 and 75% for P (*figure 1*). Exponential models yielded ultimate potential resorption values of 3.2 mg N g^{-1} and 0.09 mg P g^{-1}, respectively (*figure 1*).

4. DISCUSSION

The negative intercepts associated with the linear regressions between leaf N and litter N, and leaf P and litter P for hardwoods of eastern Canada indicate that resorption efficiency and proficiency generally increased with a decrease in leaf N and P. The better fit of the exponential model, particularly for P, indicates, however, that the rate of change of resorption efficiency increases with leaf nutrient concentration and that the increase is more pronounced for leaf P. Our results suggest maximum resorption efficiencies of about 70% for N and 80% for P in broadleaf deciduous species for concentrations in pre-senescence leaves in the range of 10 to 16 mg N g^{-1} and 0.4 to 1.0 mg P g^{-1}, respectively. These maximum resorption efficiencies and leaf nutrient concentrations associated

Table II. Resorption efficiencies of species on both sites (mean ± SE).

Site/Species	Resorption efficiency (%)	
	N	P
Station de Biologie des Laurentides (SBL)		
Beech	62 ± 3	77 ± 5
Largetooth aspen	56 ± 4	62 ± 3
Red maple	65 ± 4	74 ± 4
Sugar maple	66 ± 3	78 ± 3
Yellow birch	61 ± 5	68 ± 5
Morgan Arboretum		
Beech	64 ± 6	68 ± 7
Largetooth aspen	68 ± 7	60 ± 8
Red maple	71 ± 5	40 ± 5
Sugar maple	66 ± 6	44 ± 7
Bitternut hickory	57 ± 7	30 ± 9
Red oak	70 ± 5	55 ± 6
White ash	59 ± 8	54 ± 7

Table III. Parameters and statistics of regressions between leaf N and litter N, and leaf P and litter P ($N = 12$).

Nutrient/ regression	Model		Parameters	
	Prob.	R^2	Intercept[1]	Prob.
Nitrogen				
Linear	< 0.001	0.84	–4.9	0.01
Exponential	< 0.001	0.86	3.2	N.A.
Phosphorus				
Linear	< 0.001	0.83	–0.86	0.002
Exponential	< 0.001	0.90	0.09	N.A.

[1] Intercept for the exponential model is the litter nutrient concentration corresponding to the lowest leaf nutrient concentration observed in broadleaf deciduous trees based on a review of the literature [3, 4, 8, 9, 12, 19, 23, 31].
N.A., not applicable.

with them are consistent with values observed in the literature for broadleaf deciduous trees [1].

Larger interspecific differences in resorption efficiency were observed for leaf P than leaf N in our study. Based on the literature, leaf N and leaf P in broadleaf deciduous trees can range from about 10 to 40 mg N kg^{-1} compared to 0.4 to 2 mg P kg^{-1} [2, 3, 9, 10, 13, 20, 24, 32]. The range of concentrations observed in our study relative to the absolute range for broadleaf deciduous tree species was, therefore, much smaller and more restricted to intermediate values for N than P, the latter encompassing intermediate and high leaf P concentrations. If indeed pre-senescence leaf nutrient concentration affects nutrient resorption efficiency, and if the effect is more pronounced at high leaf nutrient concentrations, then sampling a wider range of leaf nutrient concentrations and/or sampling in the upper range of leaf nutrient concentrations should increase the likelihood of measuring larger differences in resorption efficiencies. This would be consistent with the results of a study of resorption efficiency in Alaskan birch (*Betula papyrifera* var *humilis* (Reg.)) in which lower P resorption efficiency was only observed for trees growing in a very fertile lawn [7]. The suggestion of Lajtha [17] that resorption efficiency could be maximum in plants of intermediate nutrient status is also consistent with our results that showed increased resorption efficiency from high to intermediate leaf nutrient concentration with no additional decrease below intermediate concentrations.

Evidence exists to suggest that the efficiency of nutrient resorption may be determined primarily either by soil nutrient availability [6, 22] or plant nutrient status [4, 18, 19]. The relationships established in our study between pre-senescence leaf N and P and their respective litter concentrations using the means of species found on both sites or all species pooled together appear, however, to be consistent with the dominant effect of plant nutrient status. Indeed, tree species growing on common sites and, therefore, with similar soil fertility level, had different pre-senescence leaf nutrient concentrations which in turn was correlated negatively with resorption efficiency. Moreover, only when trees of the same species that were grown on both sites showed differences in leaf nutrient concentrations did they show differences in resorption efficiency.

Based on the small number of papers published on the topic of nutrient resorption in the last few years, it could be said that the two major essays of Aerts [1] and Killingbeck [16] have settled the debate relative to the factors controlling nutrient resorption and particularly nutrient resorption efficiency. In the former study [1], it was concluded that there was no clear evidence of nutritional controls on nutrient resorption efficiency. Our study provides ground to challenge this conclusion at least for broadleaf deciduous species of northeastern North America. In contrast to the study of Aerts [1] that was derived from eight different studies encompassing 12 species of deciduous shrubs and trees dispersed over a large area, our study was characterized by a uniform sampling protocol performed during the same year for all combinations of species and sites, by very similar climatic conditions provided by the close proximity of the study sites, and by a wide range of leaf N and P concentrations provided by the relatively large number of combinations of species and sites (12). The approach used in our study is likely to have decreased the effect of the numerous non-nutritional factors known to affect nutrient resorption [16, 17, 21] and, therefore, to have increased the likelihood of detecting significant relationships between tree nutritional status and resorption efficiency.

In contrast to the concept of resorption efficiency that did not provide general patterns of nutrient resorption [1], the concept of resorption proficiency developed by Killingbeck [16] provided strong generalities about the factors involved in nutrient resorption as well as insights about the evolution of this process through selection pressures. Although in general agreement with the concept of resorption proficiency, our study provides new insights about the concept and its applications. For one, the concentrations of N and P corresponding to ultimate potential resorption in woody perennials are supported by our study. According to Killingbeck [16], the range of concentrations corresponding to ultimate potential resorption and complete resorption, the latter being defined as the 39th percentile of litter N or P of the 88 species surveyed, is from 3.0 to 7.0 mg N g^{-1} and from 0.1 to 0.4 mg P g^{-1}. The estimates of ultimate potential resorption of 3.2 mg N g^{-1} and of 0.09 mg P g^{-1} determined in the present study are therefore close to the estimates of Killingbeck [16]. The low litter nutrient concentrations measured in red maple, sugar maple and red oak for N, and in red maple, sugar maple and beech for P are characteristic of species capable of complete resorption according to Killingbeck's criteria. These low litter nutrient concentrations likely contributed to the similarity of estimates obtained in the two studies.

Interestingly, only species with low foliage nutrient concentrations were capable of complete resorption, implying that the likelihood of achieving maximum resorption decreased as leaf nutrient concentration increased. If all species had a similar range of litter concentrations at complete resorption, and if species were adapted to at least approach ultimate potential resorption under normal senescence conditions, it would have been expected that some of the observations in *figure 1* with high nutrient concentrations would have been near the ultimate potential resorption concentration for hardwoods. The data suggest that species with high foliage nutrient concentrations either have higher ultimate potential resorption concentrations, or have a lower likelihood of achieving complete resorption. If the processes controlling resorption proficiency are phenotypic as well as genotypic, as Killingbeck [16] suggests, repeated sampling of individual species on the same site will be required to distinguish these two possibilities.

In Killingbeck's study [16], multiple examples were provided to demonstrate the complementarity of the two approaches (efficiency vs. proficiency). Such examples can also be found in our data by examining partial sets of data points. For example, largetooth aspen at the poor site achieved average resorption proficiency while having relatively high resorption efficiency. Such discrepancy between approaches disappeared, however, when linear and/or exponential models were computed with the whole data set with resorption efficiency and proficiency increasing with decreasing leaf N and P. This suggests that the multifaceted approach prescribed by Killingeck [16] would be particularly advantageous for the study of resorption processes and their implications for tree nutrition and fitness when comparing species and/or group of species (e.g. deciduous vs. evergreen, N_2-fixing plants), sites or nutritional levels.

Within a relatively narrow range of site conditions, it would appear that both nutrient resorption efficiency and proficiency of hardwoods of eastern Canada increase with a decrease in pre-senescence leaf nutrient concentration. Whether similar relationships can be established for other groups of plants or across plant groups (e.g. plant form, N_2-fixing) still has to be demonstrated. Future attempts at determining general patterns of nutrient resorption should consider both concepts as well as using an approach that would provide a uniform sampling protocol, close proximity of the study sites, and a wide range of pre-senescence leaf N and P concentrations.

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