

## RESORPTION EFFICIENCY DECREASES WITH INCREASING GREEN LEAF NUTRIENTS IN A GLOBAL DATA SET

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**Abstract.** To investigate effects of green-leaf nutrient status on senesced-leaf nutrient concentrations and resorption efficiency, we developed a database of nitrogen (N) and phosphorus (P) concentrations in green and senesced leaves from 92 published studies. We fit power functions (i.e.,  $[\text{nutrient}]_{\text{sen}} = A [\text{nutrient}]_{\text{gr}}^B$ ) separately for N and P. The database encompassed 297 perennial species of different life-forms. Across these divergent species and conditions, a major control on senesced-leaf nutrient concentration was green-leaf nutrient status; nutrient concentrations in senesced leaves were positively associated with green-leaf nutrient concentrations ( $r^2$  values from 51% to 84%). Within-species variation as well as species differences contributed to the overall variation in nutrient concentrations. Moreover, N and P resorption efficiency decreased, respectively, with increased N and P green-leaf status; fitted power functions indicated that a disproportionate amount of nutrient remained in senesced leaves of higher green-leaf nutrient status. Functional relationships between nutrient concentrations in senesced and green leaves were indistinguishable for evergreen and deciduous species, but evergreens tended to have lower concentrations in both senesced and green leaves. General relationships (across species and environments) between senesced- and green-leaf nutrient concentrations and broad, intraspecific variation in nutrient concentrations suggest that variation in resorption efficiency and proficiency could be a result (and not necessarily a cause) of species sorting across fertility gradients.

**Key words:** *deciduous vs. evergreen; fertility gradients; global data sets; nutrient use efficiency; perennial plants; proficiency; resorption; retranslocation; senesced vs. green leaves.*

### INTRODUCTION

Analyses of global ecological data sets have revealed several general principles that hold across contrasting biomes, soils, species, life-forms, and evolutionary histories (Field and Mooney 1986, Reich et al. 1997, Enquist and Niklas 2002). At the leaf level, species' maximum photosynthetic rates are positively related to green-leaf N concentration (Field and Mooney 1986). Reich et al. (1997) extended this analysis and found positive covariance among species' mass-based maximum photosynthetic rates, dark respiration, specific leaf area (leaf surface area per unit mass), and foliar N concentration, all of which covaried negatively with leaf life span.

In contrast, general patterns of foliar nutrient resorption have been elusive (Aerts 1996, Killingbeck 1996, Aerts and Chapin 2000). Resorption is an important mechanism of nutrient conservation (Aerts 1996), recycling ~50% of maximum foliar N and P content in a wide range of perennial life-forms (Aerts

1996). Resorption is typically examined as an efficiency ratio in green (gr) and senesced (sen) leaves:  $([\text{nutrient}]_{\text{gr}} - [\text{nutrient}]_{\text{sen}})/[\text{nutrient}]_{\text{gr}} \times 100\%$ , which varies between <0% (i.e., nutrient concentration increases during leaf senescence) and 90% (e.g., Chapin and Kedrowski [1983], studies reviewed here). The important role of resorption in nutrient conservation has led to general predictions that: (1) species adapted to nutrient-poor environments have higher resorption efficiencies (e.g., Vitousek 1982, Ralhan and Singh 1987) and lower nutrient concentrations in senesced leaves (Killingbeck 1996); and (2) within species, higher leaf nutrient status is associated with lower resorption efficiency (e.g., Lajtha 1987). Although a link between a species' resorption efficiency and its distribution across fertility gradients is intuitively appealing, results of existing studies have been inconsistent. In an unweighted meta-analysis comparison, mean resorption efficiency of evergreen species (47%), assumed to be adapted to low fertility and expected to have high resorption efficiency, was actually lower than that of deciduous species (54%) (Aerts 1996). However, evergreen and deciduous species overlap substantially in foliar nutrient concentrations and distributions across fertility gradients; comparing these groups thus provides coarse resolution to discerning the adaptive significance of resorption efficiency. Nevertheless, within

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sclerophyllous evergreen species, N and P mean resorption efficiencies did not differ between species groups associated with low and high fertility when growing in their native soil types (Wright and Westoby 2003). Within species, resorption efficiency sometimes decreases (e.g., Boerner 1984, Schlesinger et al. 1989), increases (Chapin and Kedrowski 1983, Birk and Vitousek 1986), or does not respond to increased fertility (Knops and Koenig 1997).

In an important review, Killingbeck (1996) emphasized resorption proficiency (the concentration of a nutrient in senesced leaves) over efficiency because proficiency is not subject to temporal variation in nutrient concentration in green leaves and timing of sampling. A species' potential resorption proficiency, the lowest concentration of nutrient in senesced leaves, should reflect biochemical limits of nutrient resorption, which may vary among species adapted to different soil fertilities (Killingbeck 1996). Among a wide range of species, realized resorption proficiency on a mass basis was 0.26–1.9% for N and 0.01–0.21% for P (Killingbeck 1996). Among evergreen sclerophyllous species in their native habitats, concentrations of both N and P in senesced leaves were negatively associated with leaf lifespan (Wright and Westoby 2003), suggesting that selection has minimized nutrient losses through long leaf lifespan and low concentrations of nutrients in senesced leaves, rather than maximizing resorption efficiency. Greater leaf longevity increases nutrient residence times and thus nutrient use efficiency (Berendse and Aerts 1987, Escudero et al. 1992b, Eckstein et al. 1999).

Inconsistent relationships between resorption efficiency and nutrient availability could arise from biological and methodological sources. When gradual, resorption could be constrained by carbon export from leaves; thus, low light (Chapin and Moilanen 1991) or water availability (Escudero et al. 1992a, Minoletti and Boerner 1994) could reduce resorption. Accelerated leaf abscission due to insect damage can influence resorption efficiency in current and future leaf cohorts (May and Killingbeck 1995). Across variation in nutrient status, consistent allocation to various biochemical pools (e.g., enzymes, structural proteins) of differing solubility and potential for being exported could lead to constant resorption efficiency (Chapin and Kedrowski 1983).

Different methodologies also could contribute to inconsistent results. Nutrient concentrations are expressed on both mass and area bases. Mass-based concentrations do not account for changes in soluble carbon and nontarget elements, which can increase or decrease during senescence. Decreases in leaf mass during senescence could underestimate mass-based resorption efficiency by ~20% in that senesced leaves have inflated estimates of terminal concentrations because the translocation of carbon has not been taken into account (van Heerwaarden et al. 2003). Area-based

measures do not confound target element resorption with changes in leaf mass, but leaf area shrinkage also may occur during senescence and can underestimate resorption efficiency by 10% (van Heerwaarden et al. 2003).

Examining resorption as an efficiency ratio poses problems of interpretation and analysis. As in any ratio, a response could be driven by variation in the numerator (i.e.,  $[\text{nutrient}]_{\text{gr}} - [\text{nutrient}]_{\text{sen}}$ ) or denominator ( $[\text{nutrient}]_{\text{gr}}$ ). Thus, plants with low or high nutrient concentrations in both green and senesced leaves could have the same resorption efficiency, even though these leaves would be expected to have contrasting physiologies (Reich et al. 1997). Because resorption efficiency is calculated from green-leaf nutrient concentration, analyses comparing efficiency across variation in green-leaf nutrient concentration violate assumptions of independence in statistical tests.

Resorption proficiency is ultimately a product of green-leaf nutrient concentration and resorption efficiency; we developed analogous mechanistic models to characterize these relationships (Fig. 1). We specified resorption proficiency with a standard allometric equation as:  $[\text{nutrient}]_{\text{sen}} = A ([\text{nutrient}]_{\text{gr}})^B$ , where  $A$  and  $B$  are parameters that are estimated from the data and that govern resorption efficiency. Model development is detailed in the *Methods*; briefly, when  $B$  is not different from 1, then resorption efficiency is  $1 - A$ . When  $B$  is different from 1, then resorption efficiency is dependent upon  $[\text{nutrient}]_{\text{gr}}$ ,  $A$ , and  $B$ . Thus, this modeling approach characterizes resorption efficiency as a mathematical relationship between nutrient concentrations in green and senesced leaves and avoids limitations of statistically analyzing ratios (e.g., not accounting for separate variances of the numerator and denominator, ratio responses driven by either or both the numerator and denominator, potential lack of independence).

We compiled a literature database of green- and senesced-leaf N and P concentrations on mass and area bases, which encompassed both interspecific and inter-environment variation. We then fit variants of our resorption model to characterize effects of nutrient status on resorption efficiency. We used the models and their statistical comparisons to address three primary questions. (1) Does variation in green-leaf nutrient concentrations ( $[\text{nutrient}]_{\text{gr}}$ ) within and among species predict resorption proficiency ( $[\text{nutrient}]_{\text{sen}}$ )? (2) Does a disproportionately greater amount of nutrient remain in senesced leaves of higher nutrient status (i.e., does resorption efficiency generally decrease with higher leaf nutrient status)? (3) Do evergreen and deciduous species diverge in functional relationships between concentrations of nutrients in senesced vs. green leaves?

## METHODS

*Database.*—We compiled a literature database of all publications through August 2002 that: (1) were cited

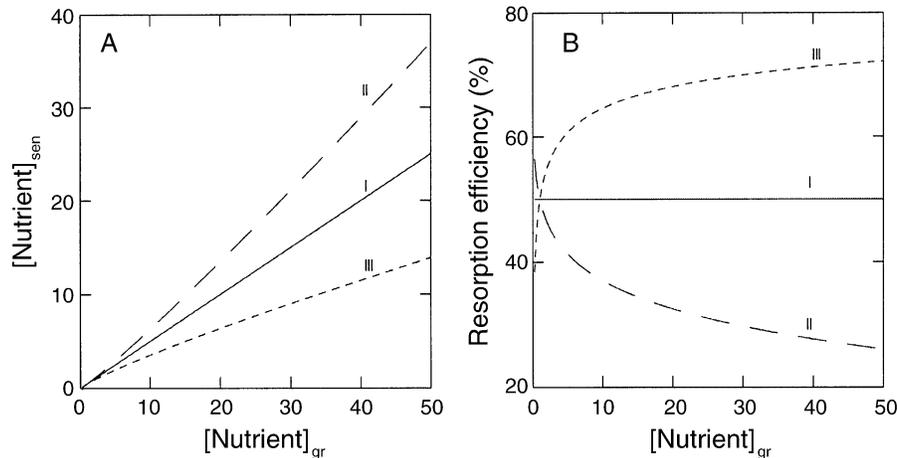


FIG. 1. (A) Theoretical relationships between nutrient concentrations of senesced (sen) and green (gr) leaves using various scenarios (I–III) characterized by the power function (Eq. 2). (B) Relationships in (A) expressed in terms of resorption efficiency vs. green-leaf nutrient concentration. Resorption efficiency is calculated as:  $([\text{nutrient}]_{\text{gr}} - [\text{nutrient}]_{\text{sen}}) / [\text{nutrient}]_{\text{gr}} \times 100\%$ . Units for nutrient concentrations could be either milligrams of nutrient per gram of leaf or micrograms of nutrient per square centimeter of leaf, corresponding with ranges  $N_{\text{mass}}$  and  $P_{\text{area}}$ . Scenario I, *Constant resorption efficiency*: a constant proportion of  $[\text{nutrient}]_{\text{gr}}$  remaining in  $[\text{nutrient}]_{\text{sen}}$  (i.e.,  $[\text{nutrient}]_{\text{sen}} = 0.5 [\text{nutrient}]_{\text{gr}}$ ). Scenario II, *Decreasing resorption efficiency*: an increasing proportion of  $[\text{nutrient}]_{\text{gr}}$  remaining in  $[\text{nutrient}]_{\text{sen}}$  as  $[\text{nutrient}]_{\text{gr}}$  increases (i.e.,  $[\text{nutrient}]_{\text{sen}} = 0.5 ([\text{nutrient}]_{\text{gr}})^{1.1}$ ). Scenario III, *Increasing resorption efficiency*: a decreasing proportion of  $[\text{nutrient}]_{\text{gr}}$  remaining in  $[\text{nutrient}]_{\text{sen}}$  as  $[\text{nutrient}]_{\text{gr}}$  increases (i.e.,  $[\text{nutrient}]_{\text{sen}} = 0.5 ([\text{nutrient}]_{\text{gr}})^{0.85}$ ).

by Aerts (1996) and Killingbeck (1996), the two major reviews to date on nutrient resorption; (2) cited Aerts (1996) or Killingbeck (1996), per the Web of Science Citation Index (Institute for Scientific Information, *available online*);<sup>5</sup> (3) have the key words “resorption,” “retranslocation,” or “reabsorption” per the Web of Science.

We examined each publication in the literature database and recorded data from studies that reported species-specific mean values of N and/or P per unit dry mass or area in both senesced and green fully expanded leaves. For studies reporting mean nutrient concentrations as a time series over the growing season, we used the maximum reported mean value of fully expanded leaves for green-leaf nutrient concentration. We excluded studies that did not use whole leaves for chemical analysis (e.g., Cavender-Bares et al. [2000] took leaf punches to specifically exclude veins) or that were initiated late in the growing season during decreasing day length (e.g., von Firks et al. 2001), which is an important cue for dormancy and resorption. Our final data set was drawn from 92 unique studies encompassing 297 perennial species, ranging across grasses, forbs, shrubs, and trees (Table 1, Appendix A).

**Models and data analysis.**—Our goal was to fit simple mechanistic models with parameters that could be interpreted biologically. First, we fit a simple linear model, which characterized senesced-leaf nutrient concentration as a constant proportion of green-leaf nutrient concentration (for N and P separately):

$$[\text{nutrient}]_{\text{sen}} = A [\text{nutrient}]_{\text{gr}} \quad (1)$$

The parameter  $A$  is the constant fraction of green-leaf nutrients contained in senesced leaves and thus represents “baseline” senesced-leaf nutrient concentration. We also fit simple linear models with a nonzero  $y$ -intercept. However, Eq. 2 (a power function) provided better fits and has parameters with more straightforward biological interpretations than linear models with nonzero intercepts. Thus, we do not report results for the latter models.

In the fit power function, the exponent ( $B$ ) determines the relationship between resorption efficiency and nutrient concentration in green leaves:

TABLE 1. Number of samples distributed across leaf phenology and life-form.

Life-form	$N_{\text{mass}}$	$N_{\text{area}}$	$P_{\text{mass}}$	$P_{\text{area}}$
<b>Deciduous</b>				
Shrub	19	14	18	14
Tree	150	27	118	34
Fern	1		1	
Herb	34	10	25	10
Grass	25	9	18	9
Sedge	20	18	20	18
Subtotal	249	78	200	85
<b>Evergreen</b>				
Shrub	23	2	19	2
Tree	137	5	70	5
Fern	3		3	
Subtotal	163	7	92	7
<b>Total</b>	<b>412</b>	<b>85</b>	<b>292</b>	<b>92</b>

<sup>5</sup> <http://isi4.isiknowledge.com/>

$$[\text{nutrient}]_{\text{sen}} = A ([\text{nutrient}]_{\text{gr}})^B. \quad (2)$$

$B > 1$  indicates decreasing resorption efficiency with increased nutrient status because  $[\text{nutrient}]_{\text{sen}}$  increases more than proportionately with  $[\text{nutrient}]_{\text{gr}}$ . Conversely,  $B < 1$  indicates increasing resorption efficiency with increased nutrient status (see Fig. 1). Eqs. 1 and 2 are equivalent when  $B$  is not different from 1, indicating that  $[\text{nutrient}]_{\text{gr}}$  has no effect on resorption efficiency.  $B$  estimates not different from 0 signify no effect of  $[\text{nutrient}]_{\text{gr}}$  on  $[\text{nutrient}]_{\text{sen}}$ .

Heteroscedasticity in  $N_{\text{mass}}$ ,  $N_{\text{area}}$ , and possibly in  $P_{\text{mass}}$  data sets suggested that the data were distributed as lognormal rather than normal, which was assumed for the previous analyses.  $\log_{10}$  transformation of Eq. 2 yields the linear form

$$\log_{10}([\text{nutrient}]_{\text{sen}}) = A' + B \times \log_{10}([\text{nutrient}]_{\text{gr}}) \quad (3)$$

where  $A'$  and  $B$  are parameters estimated from the data.  $A'$  is essentially  $\log_{10} A$  (from Eq. 2) and  $B$  is the “log–log scaling slope” and retains a similar interpretation as for Eq. 2.

Model I regression used for Eqs. 1 and 2 ascribes error to only the dependent variable ( $[\text{nutrient}]_{\text{sen}}$ ), but  $[\text{nutrient}]_{\text{gr}}$  and  $[\text{nutrient}]_{\text{sen}}$  are both subject to measurement error of similar magnitude. To characterize joint variation of  $[\text{nutrient}]_{\text{gr}}$  and  $[\text{nutrient}]_{\text{sen}}$ , we fit Eq. 3 using major axis regression, the appropriate Model II regression method when both variables are in the same measurement units (Sokal and Rohlf 1981). A Model II regression equation gives the mutual slope of two random variables, but biased estimates of the dependent variable make it inappropriate for prediction, for which Model I regression is more appropriate. For purposes of predicting  $[\text{nutrient}]_{\text{sen}}$ , we report results from fitting Eqs. 1 and 2 with Model I regression. To characterize the mutual slope of  $[\text{nutrient}]_{\text{sen}}$  and  $[\text{nutrient}]_{\text{gr}}$ , we report results of fitting Eq. 3 with major axis regression.

The usual calculation of resorption efficiency

$$\begin{aligned} \text{resorption efficiency} \\ = \frac{[\text{nutrient}]_{\text{gr}} - [\text{nutrient}]_{\text{sen}}}{[\text{nutrient}]_{\text{gr}}} \times 100\% \end{aligned} \quad (4)$$

can be explicitly linked to Eqs. 1 and 2 (and Eq. 3 because it is the log transformation of Eq. 2). Using Eq. 2 to express  $[\text{nutrient}]_{\text{sen}}$  in terms of  $[\text{nutrient}]_{\text{gr}}$ , Eq. 4 becomes:

$$\begin{aligned} \text{resorption efficiency} \\ = \frac{[\text{nutrient}]_{\text{gr}} - A[\text{nutrient}]_{\text{gr}}^B}{[\text{nutrient}]_{\text{gr}}} \times 100\%. \end{aligned} \quad (5)$$

When  $B$  is not different from 1, then resorption efficiency =  $1 - A \times 100\%$ . Otherwise,

$$\text{resorption efficiency} = 1 - \frac{A[\text{nutrient}]_{\text{gr}}^B}{[\text{nutrient}]_{\text{gr}}} \times 100\%. \quad (6)$$

Fig. 1 shows theoretical relationships between nutrient concentrations in senesced and green leaves and resorption efficiency for three different scenarios.

We fit Eqs. 1, 2, and 3 for each of the four data sets:  $N_{\text{mass}}$ ,  $N_{\text{area}}$ ,  $P_{\text{mass}}$ , and  $P_{\text{area}}$  and for the two species for which we had sample sizes  $>12$ . For  $P_{\text{mass}}$ , there were four disjunct data points between 6.5 and 16.9 mg P/g green leaf that could disproportionately influence model fits. Hence, we analyzed  $P_{\text{mass}}$  over the continuous range of 0.009 to 6.5 mg P/g green leaf in addition to analyzing the full data set for Eqs. 1 and 2.  $\log_{10}$ -transformed  $P_{\text{mass}}$  data were continuous without gaps and thus model 3 was not fit to the truncated  $P_{\text{mass}}$  data set.

To assess within- and among-species variation in foliar nutrient concentrations encompassed by our data, we calculated a “grand mean” (i.e., mean of multiple study means) and 95% CI for each species for mass-based senesced- and green-leaf nutrient concentrations for species with a sample size  $\geq 5$ . Species differences were assessed as nonoverlapping 95% confidence intervals; heterogeneous variances precluded ANOVA. Area-based data had fewer species for comparison, showed results similar to those from mass-based data, and thus are not reported. With the exception of two species, low sample sizes precluded fitting models (Eqs. 1, 2, and 3) to individual species. To further assess within-species variation, we tested for correlations between nutrient concentrations in senesced vs. green leaves for species with a sample size  $\geq 5$ .

All statistical analyses were completed in SYSTAT Version 10 (SPSS 2000). We identified best-fit models with likelihood ratio tests (LRTs; Hilborn and Mangel 1997). Coefficients of determination ( $r^2$ ) were calculated as the square of the correlation coefficient between predicted and actual concentrations of nutrients in senesced leaves.

## RESULTS

*Within- and among-species variation.*—Approximately 62% of our data (556 of total 881 points) were drawn from deciduous or evergreen trees. Shrubs, herbs, grasses, and sedges also made substantial contributions to the data set (all with sample sizes  $>61$ ) (Table 1).

Across the divergent species and environmental conditions compiled by our review, increased N and P concentrations in senesced leaves were positively associated, respectively, with N and P concentrations in green leaves. Linear zero-intercept models explained 59–84% of the variation in senesced-leaf nutrient concentration as a simple proportion of green-leaf nutrient concentration (Table 2).

TABLE 2. Parameter estimates and 95% confidence limits for models relating nutrient concentrations in senesced and green leaves.

Nutrient	Model	<i>N</i>	<i>r</i> <sup>2</sup>	<i>A</i> (mean and 95% CL)	<i>B</i> (mean and 95% CL)
a) Model I, nonlinear regression					
<i>N</i> <sub>mass</sub>	Eq. 1	412	0.63	0.58 (0.56, 0.60)	
	<b>Eq. 2</b>	<b>412</b>	<b>0.64</b>	<b>0.43 (0.31, 0.54)</b>	<b>1.10 (1.01, 1.19)</b>
<i>N</i> <sub>area</sub>	<b>Eq. 1</b>	<b>85</b>	<b>0.59</b>	<b>0.55 (0.51, 0.59)</b>	
	Eq. 2	85	0.60	0.30 (−0.31, 0.63)	1.12 (0.91, 1.32)
<i>P</i> <sub>mass</sub> (all)†	Eq. 1	292	0.81	0.65 (0.62, 0.68)	
	<b>Eq. 2</b>	<b>292</b>	<b>0.81</b>	<b>0.58 (0.53, 0.63)</b>	<b>1.07 (1.02, 1.11)</b>
<i>P</i> <sub>mass</sub> (<6.5)‡	Eq. 1	288	0.63	0.62 (0.58, 0.65)	
	<b>Eq. 2</b>	<b>288</b>	<b>0.64</b>	<b>0.51 (0.45, 0.56)</b>	<b>1.22 (1.11, 1.32)</b>
<i>P</i> <sub>area</sub>	Eq. 1	92	0.84	0.76 (0.71, 0.81)	
	<b>Eq. 2</b>	<b>92</b>	<b>0.85</b>	<b>0.29 (0.16, 0.43)</b>	<b>1.28 (1.15, 1.42)</b>
b) Model II (major axis) regression with log <sub>10</sub> transformation (Eq. 3)					
<i>N</i> <sub>mass</sub>		412		−0.63 (−0.73, −0.53)	1.30 (1.22, 1.39)
<i>N</i> <sub>area</sub>		85		−1.21 (−1.69, −0.73)	1.43 (1.20, 1.65)
<i>P</i> <sub>mass</sub> (all)		292		−0.38 (−0.41, −0.35)	1.51 (1.40, 1.61)
<i>P</i> <sub>area</sub>		92		−0.88 (−1.04, −0.72)	1.54 (1.41, 1.68)

Notes: (a) Model I, nonlinear regression with parameters estimated through maximum likelihood. Boldface text indicates the best fit and most parsimonious model by likelihood ratio tests ( $P < 0.05$ ). (b) Major axis regression parameter estimates for the model:  $\log_{10}([\text{nutrient}]_{\text{sen}}) = A' + B \times \log_{10}([\text{nutrient}]_{\text{gr}})$ . Parameter *A* represents the baseline fraction of  $[\text{nutrient}]_{\text{gr}}$  contained in senesced leaves. Parameter *B* represents disproportionate effects of  $[\text{nutrient}]_{\text{gr}}$  on  $[\text{nutrient}]_{\text{sen}}$ ;  $B > 1$  indicates decreasing resorption efficiency, and  $B < 1$  indicates increasing resorption efficiency with higher  $[\text{nutrient}]_{\text{gr}}$ . *A'* arises from the log<sub>10</sub> transformation of Eq. 2.

† Analysis with all data, including four outliers of very high phosphorus (>6.5 mg P/g green leaf).

‡ Analysis excluded four outlying data points of very high phosphorus (>6.5 mg P/g green leaf).

The positive relationship between senesced- and green-leaf nutrient concentrations among combined species and environments also held within species (Table 3). Nutrient concentrations in senesced and green leaves were positively correlated ( $P < 0.05$ ) in 12 of 16 species for *N*<sub>mass</sub> and in 8 of 11 species for *P*<sub>mass</sub> (Table 3), indicating substantial within-species variation in green-leaf nutrient concentrations that generally explained variation in senesced-leaf nutrient concentrations.

Mean nitrogen concentration in green leaves ( $[\text{N}]_{\text{gr}}$ ) varied substantially within most species, but species effects also were apparent. A grand mean  $[\text{N}]_{\text{gr}}$  value of 15 mg N/g leaf delimited two major species groups with 95% confidence intervals above this threshold for eight species, below for 12 species, and overlapping for seven species (Fig. 2A). Species effects were less pronounced for mean nitrogen concentration in senesced leaves ( $[\text{N}]_{\text{sen}}$ ), with 13 of 17 species generally overlapping in 95% confidence intervals between 5 and 10 mg N/g leaf. The N-fixing *Alnus glutinosa* had significantly higher concentrations of N in senesced leaves than did all other species. *Austrocedrus chilensis* (all from Buamscha et al. [1998]), *Pinus thunbergii* (all from Enoki and Kawaguchi [1999]), and *Metrosideros polymorpha* generally had lower concentrations of N in senesced leaves than did most other species (Fig. 2B).

Contrary to expectation, species differences in grand mean P concentrations were weak (Fig. 2C and D). 95% confidence intervals of P concentrations in green leaves overlapped for most of the 20 species examined, except that *Molinia caerulea* tended to have higher concentrations and *Pinus taeda* had lower concentrations. Among 14 species for P concentrations in senesced leaves, most overlapped in 95% confidence intervals, except that *Betula papyrifera* tended to have higher and *Salix glauca* (all from Bowman and Conant [1994]) lower concentrations.

These species comparisons overestimated species differences and underestimated within-species variation because an individual data point here already represents a species (or a species–treatment) mean from a study. Furthermore, within-species variation in nutrient concentration was underestimated for studies using extant plants that have restricted distributions across fertility gradients.

*Variation in resorption with leaf nutrient status.*—Across species and environments, disproportionately more nutrient remained in senesced leaves as the green-leaf nutrient concentration increased. The power function with exponent (*B*) significantly greater than 1 provided better fits than the simple proportion model ( $P < 0.05$ , LRT) for *N*<sub>mass</sub>, *P*<sub>mass</sub> (for full and restricted data sets), and *P*<sub>area</sub>. For *N*<sub>area</sub>, the *B* estimate was nonsignificantly greater than 1 (Table 2). Consistent with

TABLE 3. Species-specific correlations between nutrient concentrations in green and senesced leaves for N and P.

Species	Family	Life-form	Nut.	<i>n</i>	<i>r</i>	<i>P</i>	Source†
<i>Acer rubrum</i>	Aceraceae	decid. tree	N	6	0.94	0.006	7, 20, 29
<i>Alnus glutinosa</i>	Betulaceae	decid. tree	N	9	0.71	0.033	13, 14, 15, 33, 38
<i>A. glutinosa</i>	Betulaceae	decid. tree	P	6	0.94	0.006	13, 14, 38
<i>Austrocedrus chilensis</i>	Cupressaceae	ever. tree	N	8	0.56	0.15	9
<i>Betula papyrifera</i>	Betulaceae	decid. tree	N	12	0.62	0.033	11, 21
<i>Calamagrostis canadensis</i>	Poaceae	grass	N	10	0.95	<0.001	12, 36
<i>C. canadensis</i>	Poaceae	grass	P	10	0.94	<0.001	12, 36
<i>Carex lacustris</i>	Cyperaceae	sedge	N	18	0.94	<0.001	36
<i>Fraxinus uhdei</i>	Oleaceae	decid. tree	N	6	0.97	0.002	3
<i>F. uhdei</i>	Oleaceae	decid. tree	P	6	0.98	<0.001	3
<i>Larrea tridentata</i>	Zygophyllaceae	decid. shrub	P	8	0.62	0.104	26
<i>Liquidambar styraciflua</i>	Hamamelidaceae	decid. tree	N	5	0.93	0.028	20, 10, 29, 32
<i>Lonicera maackii</i>	Caprifoliaceae	decid. shrub	P	12	0.86	<0.001	16
<i>Lyonia lucida</i>	Ericaceae	ever. shrub	P	8	0.51	0.198	42
<i>Metrosideros polymorpha</i>	Myrtaceae	ever. tree	N	32	0.74	<0.001	39, 41
<i>M. polymorpha</i>	Myrtaceae	ever. tree	P	11	0.96	<0.001	41
<i>Molinia caerulea</i>	Poaceae	grass	P	6	-0.22	0.674	1, 2, 5, 30
<i>Pinus monophylla</i>	Pinaceae	ever. tree	P	5	0.98	0.005	35
<i>P. taeda</i>	Pinaceae	ever. tree	N	9	0.54	0.176	6, 20, 23
<i>P. thunbergii</i>	Pinaceae	ever. tree	N	5	0.98	0.004	17
<i>Populus deltoides</i>	Salicaceae	decid. tree	N	5	0.93	0.023	4, 13, 14, 31
<i>P. deltoides</i>	Salicaceae	decid. tree	P	7	0.96	0.001	4, 13, 14, 27, 31
<i>P. tremuloides</i>	Salicaceae	decid. tree	N	8	-0.12	0.778	21, 25, 40
<i>P. tremuloides</i>	Salicaceae	decid. tree	P	9	0.93	<0.001	21, 24, 37, 40
<i>Quercus ilex</i>	Fagaceae	ever. tree	N	5	0.84	0.038	18, 28
<i>Q. pyrenaica</i>	Fagaceae	decid. tree	N	6	-0.23	0.658	19, 22, 34
<i>Salix glauca</i>	Salicaceae	decid. shrub	P	6	-0.04	0.94	8
<i>Typha latifolia</i>	Typhaceae	herb	N	10	0.68	0.033	36

Notes: Abbreviations are: decid., deciduous; ever., evergreen; nut., nutrients nitrogen and phosphorus. The Pearson correlation coefficient (*r*) and *P* values (*P*) are shown. For each species, data were gathered from named source studies (*n* is the total number of data lines drawn from all studies).

† 1, Aerts (1989); 2, Aerts and Berendse (1989); 3, Ares and Fownes (2001); 4, Baker and Blackmon (1977); 5, Berendse et al. (1987); 6, Birk and Vitousek (1986); 7, Boerner (1984); 8, Bowman and Conant (1994); 9, Buamscha et al. (1998); 10, Burke et al. (1999); 11, Chapin and Moilanen (1991); 12, Chapin and Shaver (1989); 13, Cote and Dawson (1986); 14, Cote et al. (1989); 15, Dawson and Funk (1981); 16, Demars and Boerner (1997); 17, Enoki and Kawaguchi (1999); 18, Escudero et al. (1992a); 19, Escudero et al. (1992b); 20, Finzi et al. (2001); 21, Flanagan and Van Cleve (1983); 22, Gallardo et al. (1999); 23, Grizzard et al. (1976); 24, Killingbeck et al. (1989); 25, Killingbeck et al. (1990); 26, Lajtha and Klein (1988); 27, Lodhiyal et al. (1994); 28, Mayor and Roda (1992); 29, Moorhead and McArthur (1996); 30, Morton (1977); 31, Negi and Singh (1993); 32, Nelson et al. (1995); 33, Rodriguez-Barrueco et al. (1984); 34, Santa Regina et al. (1997); 35, Schlesinger et al. (1989); 36, Shaver and Melillo (1984); 37, Small (1972); 38, Stachurski and Zimka (1975); 39, Treseder and Vitousek (2001); 40, Verry and Timmons (1976); 41, Vitousek (1998); 42, Walbridge (1991).

Model I regression, *B* estimates from major axis regression were significantly greater than 1 for all data sets, ranging from 1.3 to 1.54 (Fig. 3, Table 2).

We fit species-specific models for the two species for which we had sample sizes >12:  $N_{\text{mass}}$  for *Carex lacustris* ( $n = 18$ ) and *Metrosideros polymorpha* ( $n = 32$ ). For *C. lacustris*, the power function (Eq. 2) provided a significantly better fit than the simple proportion model ( $P < 0.05$ , LRT), with  $B = 1.256$  (95% CL 1.031, 1.481); *B* estimated from major axis regression was 1.33 (95% CL 1.02, 1.64). For *M. polymorpha*, *B* was nonsignificantly greater than 1 (Model I regression,  $B = 1.124$ ; 95% CL 0.78, 1.47; major axis regression  $B = 1.46$ , 95% CL 0.91, 2.01) and the power function did not provide an improved fit over Eq. 1 ( $P > 0.05$ , LRT).

Simple calculations illustrate the magnitude of the change in resorption efficiency with increases in nutrient concentrations (also see Fig. 1). For example, at 5  $\mu\text{g P/cm}^2$  green leaf, the power function (Table 2;  $A$

= 0.294 and  $B = 1.283$ ) predicts 2.32  $\mu\text{g P/cm}^2$  senesced leaf, a resorption efficiency of ~54%. In contrast, intermediate nutrient concentrations of 30  $\mu\text{g P/cm}^2$  green leaf would result in 23.1  $\mu\text{g P/cm}^2$  senesced leaf, a resorption efficiency of 23%. Thus P resorption efficiency could vary twofold with moderate variation in green-leaf P concentration.

Evergreen and deciduous species shared a common functional relationship between senesced- and green-leaf nutrient concentrations on a mass basis (Table 4), with evergreen species occupying lower ranges (Fig. 3, Appendix B). For  $N_{\text{mass}}$ , *B* estimates from major axis regression were identical (1.35) for the two groups and were significantly different from 1. Model I regression yielded similar *A* and *B* estimates (Eq. 2) for evergreen and deciduous groups and respective 95% confidence intervals overlapped broadly, but each group-specific *B* estimate was not significantly different from 1. It is likely that combining subsets yielded  $B > 1$  through increasing sample size/power and enhancing variability in  $N_{\text{mass}}$ ,

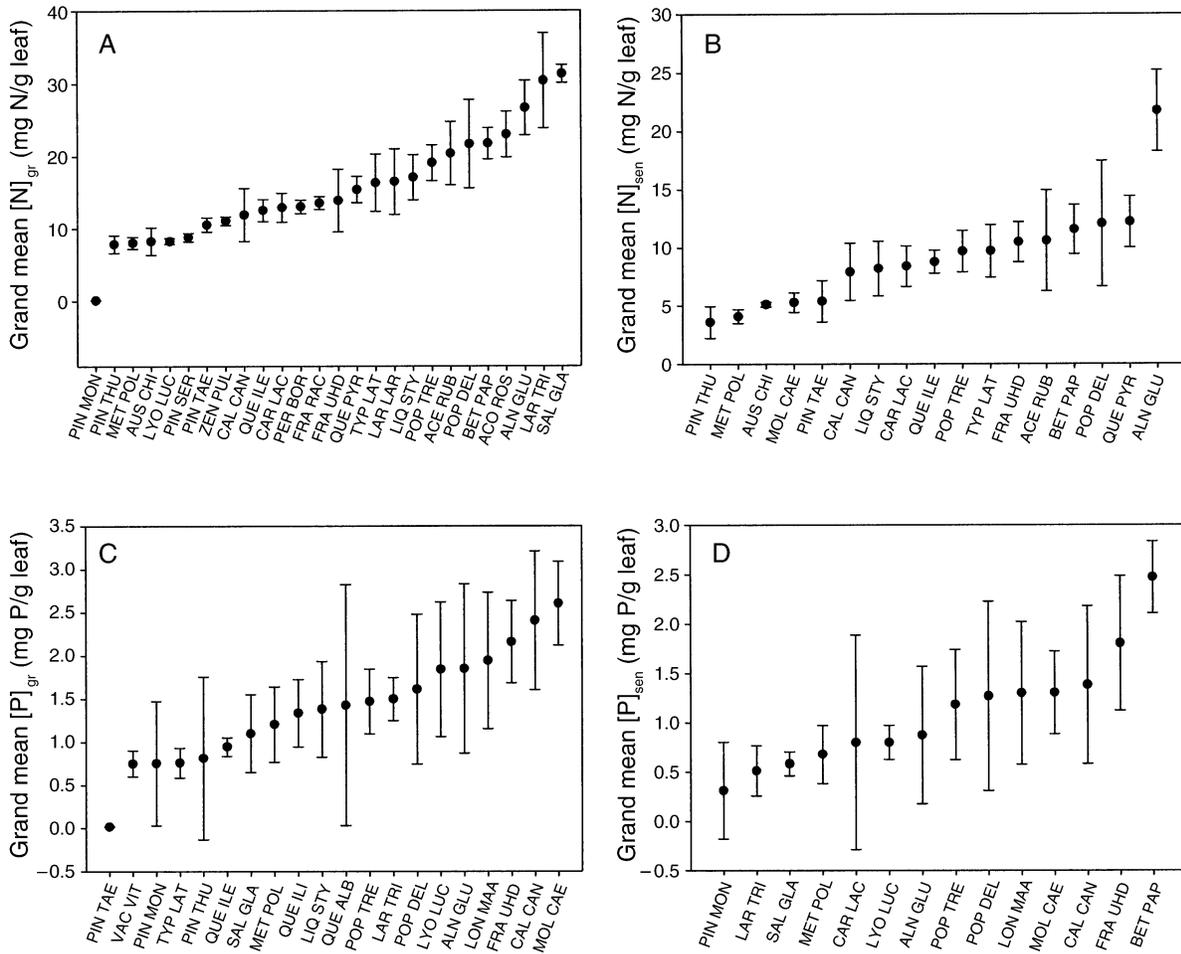


FIG. 2. Species-specific grand means and 95% confidence intervals for nutrient concentrations: (A) N in green leaves; (B) N in senesced leaves; (C) P in green leaves; and (D) P in senesced leaves. Species abbreviations are based on the first three letters of the genus and species. Abbreviations of species not listed in Table 3 are as follows: ACO ROS, *Acomastylis rossii*; CYR RAC, *Cyrilla racemiflora*; LAR LAR, *Larix laricina*; PER BOR, *Persea borbonia*; PIN SER, *Pinus serotina*; QUE ALB, *Quercus alba*; QUE ILI, *Quercus ilicifolia*; VAC VIT, *Vaccinium vitis-idaea*; and ZEN PUL, *Zenobia pulverulenta*.

because evergreen and deciduous species tended to occupy different N ranges. In the simple proportion model (Eq. 1), evergreens and deciduous species also did not differ in  $A$  (slope) estimates (Table 4).

For  $P_{\text{mass}}$ ,  $A$  and  $B$  estimates (Eq. 2) were similar for evergreen and deciduous groups (Table 4) and  $B$  estimates were significantly greater than 1 based on both Model I and II regression. To avoid disproportionate leverage of one evergreen and three deciduous outlying points, Model I regression of original scale data used the restricted  $P_{\text{mass}}$  data while Model II regression of log-transformed data used the full range. There were inadequate area-based evergreen data (Table 1) to develop separate evergreen and deciduous models.

Using mass vs. area-based concentrations did not have consistent effects on estimated models. If soluble carbohydrates were to be translocated out of leaves during senescence, then mass-based nutrient concen-

tration in senesced leaves should be overestimated relative to green-leaf nutrient concentration. Comparing the same models, parameter estimates for  $N_{\text{mass}}$  vs.  $N_{\text{area}}$  were broadly overlapping (Table 2). Contrary to expectation,  $A$  (Eq. 1, simple proportion model) was higher for  $P_{\text{area}}$  than  $P_{\text{mass}}$ , indicating lower P resorption efficiency calculated on an area basis. The power function for  $P_{\text{area}}$  also suggests lower resorption efficiency because of its higher  $B$  estimate in comparison to the  $P_{\text{mass}}$  model.

#### DISCUSSION

Our analytical approach integrated resorption proficiency (nutrient concentration in senesced leaves; Killingbeck [1996]) as the response variable, green-leaf nutrient concentration as the predictor variable, and resorption efficiency as the functional relationship between them. Both resorption efficiency and proficiency

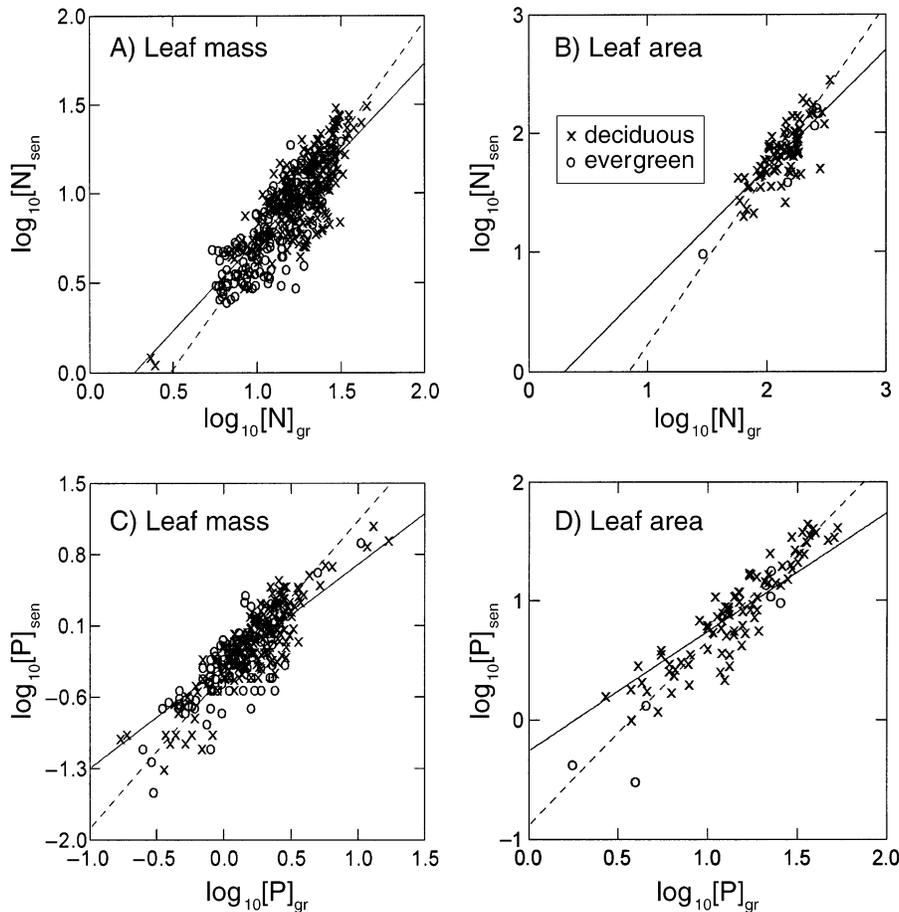


FIG. 3. Fits of the allometric scaling equation (Eq. 3) using major axis regression (dashed lines) for  $\log_{10}$ -transformed nutrient concentrations in senesced vs. green leaves for: (A) N on a mass basis, measured as mg N/g leaf; (B) N on an area basis, measured as  $\mu\text{g N}/\text{cm}^2$  leaf; (C) P on a mass basis, measured as mg P/g leaf; and (D) P on area basis, measured as  $\mu\text{g P}/\text{cm}^2$  leaf. All slope estimates were significantly greater than 1 (dashed lines), indicating that proportionately less nutrient was withdrawn prior to leaf senescence as green-leaf nutrient concentrations increased. Models assuming that resorption is constant with green-leaf nutrient status (i.e., slope = 1) were also fit and are shown with solid lines for comparison.

varied with green-leaf nutrient concentration, among and within species across variation in climate, soils, fertilization treatments, life-forms, evolutionary histories, and methodologies. Within species, as well as across species and environmental variation, our results suggest that an important determinant of senesced-leaf nutrient concentration is green-leaf nutrient concentration. Higher concentrations of N or P in green leaves were associated with higher levels of N or P in senesced leaves, consistent with previously documented intraspecific variation (e.g., Staaf 1982, Birk and Vitousek 1986, Killingbeck and Costigan 1988). In addition, resorption efficiency declined with increases in green-leaf nutrient concentration for both N and P.

Evergreen and deciduous species shared a common functional relationship between nutrient concentrations in senesced and green leaves for N and P, respectively, and major axis regression parameter estimates for the two species groups were nearly identical (Table 4). In

general, evergreens occupied lower ranges in the functional relationships, consistent with evergreens having lower concentrations of P and nonsignificantly lower concentrations of N in senesced leaves (Killingbeck 1996). Occupying a lower range on the functional relationship between nutrient concentrations in senesced and green leaves is associated with higher resorption efficiency (as encapsulated by  $B$  estimates  $>1$ ). However, our results suggest that lower nutrient concentrations in senesced leaves of evergreens may largely reflect lower green-leaf nutrient concentrations resulting from low environmental availability of nutrients, rather than necessarily demonstrating a greater ability by evergreens to draw down leaf nutrient levels prior to abscission as an adaptation to low fertility (cf. Killingbeck 1996, Wright and Westoby 2003).

Consistency among species and environments in the functional relationship between nutrient concentrations in senesced and green leaves could reflect general bio-

TABLE 4. Estimates of parameters *A* and *B* (mean and 95% CI) for models fit separately to evergreen and deciduous species.

Life-form	<i>A</i>	<i>B</i>	<i>n</i>	<i>r</i> <sup>2</sup>
a) Maximum likelihood estimation, Eqs. 1 and 2				
<i>N</i> <sub>mass</sub>				
Deciduous				
Eq. 2	0.42 (0.25, 0.60)	1.10 (0.97, 1.23)	249	0.56
Eq. 1	0.59 (0.56, 0.61)			0.55
Evergreen				
Eq. 2	0.47 (0.30, 0.64)	1.06 (0.94, 1.19)	163	0.65
Eq. 1	0.56 (0.53, 0.59)			0.65
<i>P</i> <sub>mass</sub> (<6.5)				
Deciduous (<6.5)				
	0.54 (0.46, 0.61)	1.19 (1.07, 1.31)	197	0.65
Evergreen (<6.5)				
	0.45 (0.35, 0.54)	1.23 (1.01, 1.46)	91	0.50
b) Major axis regression of log <sub>10</sub> -transformed data				
<i>N</i> <sub>mass</sub>				
Deciduous				
	-0.70 (-0.87, -0.53)	1.35 (1.22, 1.48)	249	
Evergreen				
	-0.66 (-0.83, -0.50)	1.35 (1.20, 1.50)	163	
<i>P</i> <sub>mass</sub> (all data)				
Deciduous				
	-0.37 (-0.41, -0.33)	1.43 (1.33, 1.53)	200	
Evergreen				
	-0.37 (-0.43, -0.32)	1.53 (1.28, 1.78)	92	

chemical and/or biophysical constraints. For example, a positive linear relationship between nutrient concentrations in senesced and green leaves could arise if nutrient allocation to various biochemical pools (e.g., enzymes, structural proteins) is constant with increased green-leaf nutrient concentration and if pools differ in solubility and/or phloem mobility. Evergreen and deciduous species can have similar proportions of N fractions (Chapin and Kedrowski 1983) and the ratio of soluble to insoluble N is related to N resorption efficiency, at least within evergreen species (Pugnaire and Chapin 1993). Divergence from linearity ( $B > 1$ ) in the relationship between senesced- and green-leaf nutrient concentrations represents decreasing resorption efficiency with increasing green-leaf nutrient concentration, which might be explained by the possibility that, under higher fertility, nutrients may be relatively less expensive to acquire from soil than breaking down foliar compounds, and loading, transporting, and storing breakdown products (see the hypothetical scenario represented by Fig. 3A in Wright and Westoby [2003]). However, the relative energy costs of nutrient resorption vs. uptake from the environment are unknown.

Nutrient concentrations in green and senesced leaves often covary with species distributions across fertility gradients, with lower concentrations occurring in species that are presumably adapted to low fertility (Aerts and Berendse 1989, Aerts 1996, Wright and Westoby 2003). However, as Aerts (1996) points out, responses of nutrient concentrations to soil fertility and inherent interspecific differences in nutrient concentrations are often confounded because many studies compare "low-" and "high-" fertility species in their native soils (that is, a comparison of extant species growing in high-fertility habitats with extant species growing

in low-fertility habitats) (e.g., Wright and Westoby 2003). Aerts (1996) attempted to correct this deficiency by comparing evergreen and deciduous species, but the tendency of evergreen species to occupy environments of lower fertility presents the same potential for confounding species and environment. Although it is reasonable to expect that low nutrient concentrations in green and senesced leaves and associated higher nutrient use efficiency are species adaptations to low fertility, confounding species and environment precludes inference of cause-effect relationships.

An equally plausible explanation of the association between species occurrence under low fertility and low foliar nutrient concentrations is that species sort across soil fertility gradients due to other mechanisms, and that nutrient concentrations in green and senesced leaves follow environmental nutrient availability. Two results here support this view. First, there was substantial within-species variation in nutrient concentrations (Fig. 2). With a few exceptions (e.g., higher N concentrations in N-fixing species), within-species variation made it difficult to ascribe a particular green or senesced nutrient concentration to a given species. The majority of species with sample sizes  $>5$  had sufficient variation in foliar nutrient concentration to result in strong positive relationships between green- and senesced-leaf nutrient concentrations. Second, we found common functional relationships between senesced-leaf and green-leaf nutrient concentrations within and among evergreen and deciduous species; within and among grasses, forbs, shrubs, and trees; across biomes; and all across a range of nutrient environments. An implication of the common functional relationships is that a "high-fertility" species in a low-fertility environment is likely to have low green- and senesced-leaf

nutrient concentrations and higher resorption efficiency. Conversely, common models would predict that a "low-fertility" species in a high-fertility environment would have high green- and senesced-leaf nutrient concentrations and lower resorption efficiency.

In addition to facets of nutrient use efficiency (e.g., nutrient concentrations in green and senesced leaves, leaf longevity), access to and storage of resources are other classes of mechanisms that could lead to species sorting across resource gradients. For example, tree species distributions across soil resource environments in northern Michigan are consistent with an interspecific trade-off between seedling growth under high fertility vs. survivorship under low fertility (Schreeg et al. 2005). Species associated with high-fertility sites have high specific root area that enables high nutrient uptake and that could confer higher growth rates (Reich et al. 1998, Wright and Westoby 1999, Comas et al. 2002). Species associated with low-fertility sites have traits that favor survivorship, including deeper roots that could enable greater access to water (Nicotra et al. 2002) and higher allocation to root mass and stored carbohydrates that could enable plants to survive periods of resource limitation (Kobe 1997; M. Iyer, R. K. Kobe, M. B. Walters, and J. M. Kunkle, *unpublished manuscript*).

Because of disproportionate relationships between senesced- and green-leaf nutrient concentrations (as characterized by  $B$  estimates  $>1$ ), there are important implications of occupying different ranges in this functional relationship, whether for individuals of the same or different species. Lower green-leaf nutrient concentration results in lower senesced-leaf nutrient concentration; as a consequence, individuals under low-fertility environments should have lower terminal nutrient concentrations, which is consistent with the predictions of Killingbeck (1996). Unless species and environmental effects are distinguished, however, this could lead to the potentially erroneous conclusion that lower senesced-leaf nutrient concentration is a species adaptation to low fertility. Similarly, a comparison of two widely spaced points (whether different species or environments) along the senesced- vs. green-leaf nutrient concentration relationship will show higher resorption efficiency in the region of lower nutrient status. Again, however, if species and environmental effects are not distinguished, one might erroneously conclude that species typically occupying low-fertility environments are adapted to these conditions through higher resorption efficiency.

Even though we used many of the same data papers, our results conflict with an important and comprehensive literature review (Aerts 1996), which concludes that there are no nutritional controls on resorption efficiency. Counter to expectations, Aerts (1996) found lower N resorption efficiency in evergreen vs. deciduous species, a surprising result considering that evergreens are assumed to be adapted to low nutrient

conditions. However, our data suggest that foliar nutrient concentrations vary continuously and overlap substantially between deciduous and evergreen species; therefore, a categorical comparison offers fairly coarse resolution to assessing the functional significance of resorption efficiency. Also supporting Aerts' (1996) conclusion was his result that variation in N and P resorption efficiencies were poorly explained by regressions against green-leaf nutrient concentrations for most life-forms. We built on the regression analysis of Aerts (1996) to arrive at a novel mechanistic framework for examining resorption as a functional relationship between senesced- vs. green-leaf nutrient concentrations. The modeling approach developed here avoids confounding senesced- and green-leaf concentrations in an efficiency index (i.e., resorption efficiency) that could be driven by changes in either or both variables. Note that with increases in green-leaf nutrient concentration, even though an increasing proportion of green-leaf nutrient remains in senesced leaves, the index of resorption efficiency loses sensitivity (Fig. 1). Furthermore, conceptualizing resorption efficiency as a relationship between two variables enabled the use of independent axes in analyses. In contrast, resorption efficiency is calculated from, and thus is not independent of, green-leaf nutrient concentration, invalidating the assumptions of regression. Finally, use of a ratio such as resorption efficiency as the response variable in ANOVA (as is often done in ecological studies) leads to an increased probability of committing a Type II error (Anderson and Lydic 1977).

Based on both intra- and interspecific variation, our analysis adds senesced-leaf nutrient concentration to the suite of leaf traits that covary with green-leaf nutrient concentration at a global scale. Although we found more than twofold variation in N and P concentrations within species, previous analyses of leaf traits used a single value for a given species to conclude that species with high foliar N levels are associated with higher mass-based maximum photosynthetic rates, specific leaf area, and shorter leaf longevity (Field and Mooney 1986, Reich et al. 1997). However, these studies used extant plants in their native habitats, potentially confounding species and environmental effects. Thus the covarying leaf traits documented previously (Field and Mooney 1986, Reich et al. 1997) probably arise from both species and environmental variation.

### Conclusions

Based on our global database, a disproportionate amount of N and P remained in senesced leaves as green-leaf N and P status increased. Thus, resorption efficiency generally declined with increasing leaf nutrient status, both within and among species. In addition, there was a common relationship between senesced- and green-leaf nutrient concentrations across species, environments, and investigators. Even though evergreen and deciduous species are often contrasted in

assessing adaptations to nutrient environments, our results suggest that evergreen and deciduous species share common functional relationships between senesced and green-leaf nutrient concentrations and simply occupy different ranges of the relationship. Biochemical (e.g., solubility of different compounds of which N or P are a constituent) or biophysical (e.g., phloem loading) constraints to resorption could lead to the strong positive linear relationship between senesced and green-leaf nutrient concentrations. Divergence from linearity (i.e.,  $B > 1$ ) would be consistent with lower relative costs of nutrient uptake than costs of resorption in high-fertility environments, but the energetic costs of uptake vs. resorption are unknown. Our results suggest that interspecific variation in resorption efficiency and proficiency is not necessarily a cause of species sorting across soil resource gradients, but rather that variation among species in resorption processes is equally likely to be the result of species sorting across soil resource environments that originate from other mechanisms.

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#### APPENDIX A

A list of the studies from which data were obtained is available in ESA's Electronic Data Archive: *Ecological Archives* E086-150-A1.

#### APPENDIX B

A table showing descriptive statistics for nutrient concentrations in green and senesced leaves is available in ESA's Electronic Data Archive: *Ecological Archives* E086-150-A2.