Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants

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Abstract. Nutrient resorption in plants influences nutrient availability and cycling and is a key process in biogeochemical models. Improved estimates of resorption parameters are needed for predicting long-term primary productivity and for improving such models. Currently, most models assume a value of 50% resorption for nitrogen (N) and phosphorus (P) and lack resorption data for other nutrients and for specific vegetation types. We provide global estimates of resorption efficiencies and nutrient concentrations for carbon (C), N, and P and the first global-scale estimates for essential nutrients such as potassium (K), calcium (Ca), and magnesium (Mg). We also examine leaf mass loss during senescence (LML) globally and for different plant types, thus defining a mass loss correction factor (MLCF) needed to quantify unbiased resorption values. We used a global meta-analysis of 86 studies and ~1000 data points across climates for green and senesced leaves in six plant types: ferns, forbs, graminoids, conifers, and evergreen and deciduous woody angiosperms. In general, N and P resorption differed significantly from the commonly used global value of 50% (62.1%, 64.9%, respectively; $P < 0.05$). Ca, C, and Mg showed lower average resorptions of 10.9%, 23.2%, and 28.6%, respectively, while K had the highest resorption, at 70.1%. We also found that resorption of all nutrients except Ca depended on leaf nutrient-status; globally, C, N, P, K, and Mg showed a decrease in resorption with increased nutrient status. On average, global leaf mass loss was 24.2%. Overall, our resorption data differ substantially from commonly assumed values and should help improve ecological theory and biogeochemical and land-surface models.

Key words: *biogeochemical and land-surface models; calcium; carbon; leaf mass loss; magnesium; nitrogen; nutrient resorption efficiency; phosphorus; potassium.*

Introduction

Nutrient availability often constraints plant productivity and the amount of C sequestered in terrestrial ecosystems (e.g., Vitousek and Howarth 1991, Sokolov et al. 2008). Nutrient resorption (NuR) is a key component of nutrient conservation strategies and hence of productivity and elemental cycling in ecosystems. It influences many, if not most, ecosystem processes, including carbon cycling and resource-use efficiency (Aerts and Chapin 2000, Jackson et al. 2000, Franklin and Ågren 2002, Gleason and Ares 2007), plant litter decomposition through changes in litter quality (Berg and McClaugherty 2007, Manzoni et al. 2008, 2010), and plant competition (Eckstein et al. 1999, Yuan et al. 2005). Because NuR can play an important role in nutrient conservation, providing estimates of resorption efficiency is essential for modeling nutrient cycling and

for quantifying biosphere productivity (Jackson et al. 1997, Gordon and Jackson 2000, Chapin et al. 2011). In particular, the new generation of coupled global models of the carbon cycle and climate system include nutrient dynamics (see Table 1 for a list of models), and thus require reliable estimates of nutrient resorption efficiencies (Thornton et al. 2007).

In temperate forests, at least, most nutrients absorbed by plants come from mineralization of organic matter and recycling within ecosystems (e.g., 93%, 89%, 88%, and 65% of the total N, P, K, and Ca, respectively [Chapin 1991]). The availability of P and cations typically decline in old highly weathered soils, as they have been leached out of the system or become bound in unavailable forms (Vitousek and Sanford 1986, Chapin et al. 2011). Under these circumstances, P or relatively mobile cations may limit biological processes and regulate N cycling (Jackson et al. 1990, Chadwick et al. 1999). Nitrogen and other elements are also vulnerable to leaching, requiring plants to develop conservation strategies to limit such losses. These

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TABLE 1. Leaf N and P resorption efficiencies ($\overline{NR}$ and $\overline{PR}$) as represented in ecosystem and global biogeochemical models.

Model name	Source	$\overline{NR}$†	$\overline{PR}$	Notes
PHOENIX	McGill et al. (1981)	0.8		
JABOWA	Pastor and Post (1986)	implicit		
Hurley	Thornley and Verberne (1989)	variable		resorption increases with decreasing leaf N
GEM	Hunt et al. (1991)	0–0.5		resorption increases with increasing leaf N
VEGIE	Aber et al. (1991)	0		
MBL-GEM	Rastetter et al. (1991)	constant		plant-type-specific values
FOREST-BGC	Running and Gower (1991)	0.5		generic value for all ecosystems
TEM	Raich et al. (1991)	implicit		no distinction among leaves, stem, and roots
	Rastetter and Shaver (1992)	variable		resorption increases with decreasing plant N
CASA	Potter et al. (1993)	implicit		litter C:N depends on plant functional type
G'DAY	Comins and McMurtrie (1993)	0		
CENTURY	Parton et al. (1993)	0.5	0	values used in CENTURY 4.0 for tallgrass species
	Aerts and van der Peijl (1993)	0.1–0.17		species-specific values
NICCCE	van Dam and van Breemen (1995)	variable		resorption increases with decreasing leaf N
	Schwinning and Parsons (1996)	0		
TREEDYN3	Bossel (1996)	0.15–0.4		species-specific values
	Tateno and Chapin (1997)	0.3		
HYBRID III	Friend et al. (1997)	0.5		
BIOME-BGC	White et al. (2000)	0.45–0.77		0.55 for deciduous broadleaf and evergreen needle forests, 0.77 for deciduous needle forest, 0.45 for grasses, 0.53 for shrubs
	Daufresne and Loreau (2001)	0		plant C and N turnover rates are equal
	Baisden and Amundson (2003)	0		
RHESSys	Tague and Band (2004)	implicit		
	Wang et al. (2007)	0.5	0.5	
ISAM	Yang et al. (2009)	0.5		
FUN	Fisher et al. (2010)	variable		resorption depends on N availability in the environment and the plant
LM3V	Gerber et al. (2010)	0.4–0.5		plant-type-specific values
O-CN	Zaehle and Friend (2010)	0.5		
NCIM	Esser et al. (2011)	0–0.65		plant-type-specific values

Note: Empty cells indicate that no data are available.
† "Implicit" indicates that resorption efficiency is not prescribed, but is implicitly defined from litter and leaf C:N ratios.

strategies include coordination of plant uptake with peaks of nutrient mineralization, different leaf habits, and, most importantly, nutrient resorption before leaf shedding (Aerts and Chapin 2000, Chapin et al. 2011).

While N and P are the main nutrients limiting plant production globally, basic cations such as Ca, K, and Mg also play important roles in ecosystem processes (Vitousek and Howarth 1991). For instance, cation abundance can limit plant growth in some systems, including the wet tropics, where significant leaching occurs (Cuevas and Medina 1986, 1988). Cation cycling differs substantially among Ca, K, and Mg, however. The dominant source of cations is typically rock weathering, but throughfall is an important source of K for the forest floor in moist tropical forests. In contrast, litterfall often represents the major flux of Ca, and a combination of leaching, resorption, and dry deposition are important for Mg cycling (Parker 1983). Because these nutrients can all limit plant growth, effective resorption before leaves are shed provides an important mechanism for conservation.

Although some studies have examined plant NuR in relation to climate, soil characteristics, and plant traits, mechanistic and global relationships remain difficult to identify because of a lack of available data, especially for essential cations (Chapin and Moilanen 1991, Aerts 1996, Lambers et al. 1998, Kazakou et al. 2007, Yuan

and Chen 2009a). N resorption (NR) generally increases from the tropics to the tundra while P resorption (PR) typically decreases, mirroring increased N-limitation and decreased P limitation toward northern latitudes (Yuan and Chen 2009a). High NuR was predicted to be more common in low-fertility soils, but this relationship has not been universally supported (Aerts 1996, Eckstein et al. 1999, Diehl et al. 2003). Although resorption has been predicted to be higher in plants growing on wetter soils prone to leaching, no correlation between soil moisture and nutrient retention was found in a tree species, *Austrocedrus chilensis* (Buamscha et al. 1998). Much less is known about resorption patterns of other essential nutrients, particularly K, Mg, and Ca, which to our knowledge have not been studied globally.

Results for the relationship of resorption efficiency and plant nutrient status have also been contradictory. While some studies did not find any relationship (Chapin and Moilanen 1991, Reich et al. 1992, Aerts 1996, Lambers et al. 1998, Aerts and Chapin 2000, Kazakou et al. 2007, Yuan and Chen 2009a), other studies have found resorption efficiency to be related to plant nutrient status (Lal et al. 2001, Diehl et al. 2003, Wright and Westoby 2003, Kobe et al. 2005, Cai and Bongers 2007). When nutrient conservation strategies have been related to plant functional type (Aerts 1996, Diehl et al. 2003, Yuan and Chen 2009a), observed

differences across growth forms and functional groups have also typically been small. Those differences that were observed showed that N resorption tends to be higher in deciduous than in evergreen species and in trees than in shrubs (Yuan and Chen 2009b). P resorption is generally higher in graminoids (Aerts 1996) and in evergreen than deciduous species (Yuan and Chen 2009b).

Along with its ecological importance in the field, nutrient resorption parameters are also vital for the accuracy of ecosystem and biogeochemical models. Our analysis of 28 such models shows wide variation in NuR values used in the models, from 0 to 80% of N resorption, with the most commonly used estimate of resorption efficiency being 50% (Table 1). Our model overview also highlights some limitations in current resorption parameterizations. First, ecosystem models tend to neglect P dynamics and do not consider other nutrients. Second, only the most recent models include different resorption parameters for different plant functional types. For these models, a thorough observational base of NuR efficiencies will be valuable to constrain their nutrient cycling parameterization.

Published NuR estimates are strongly affected by differences in measurement approaches. Most analyses express nutrient pools on a leaf-mass basis. One inherent problem is that mass loss occurs during senescence, changing the measurement basis and leading to underestimates of NuR (van Heerwaarden et al. 2003a). Several approaches have been used to avoid this issue. Nutrient pools have been expressed on the basis of leaf area or length, Ca concentration, lignin content, canopy area, and more, presuming that these factors do not change during senescence. However, some changes occur in most cases (e.g., leaf shrinkage) and the only unbiased method to estimate resorption is based on measurement of nutrient pools in the same leaves before and after senescence. Leaf mass loss could lead to an average NuR underestimation of 10% when using leaf mass-based concentrations, while leaf shrinkage could lead to an average underestimation of 6% when using area-based concentrations (van Heerwaarden et al. 2003a). For these reasons, global-scale correction factors are needed that account for changes in leaf mass or area during senescence and that can be used to obtain unbiased estimates of resorption.

The goal of our work was to identify fundamental trends in NuR and element concentrations for different plant functional groups and climatic variables and to determine leaf mass loss during senescence, which affects estimates of NuR. We assembled a global database of nearly 1000 data points from 86 studies to perform a meta-analysis of nutrient contents in mature and senesced leaves. We used the data to address three questions: (1) How do plant functional types and climate interact to alter global patterns of nutrient contents and resorption? (2) How different is resorption for structural and osmotic elements, such as K, Ca, and Mg, compared to the organic elements C, N, and P? and (3) Do nutrient resorption values increase as a nutrient becomes less abundant in leaves and the soil? If the answer to this last question is positive, then nutrient resorption should be higher in nutrient-limited biomes, elements should be resorbed less if leaf nutrient concentrations are high, and N-fixing species should resorb less nitrogen than non-N-fixing species (and potentially resorb proportionally more P). To our knowledge, our analysis also provides the first global estimates of resorption efficiencies for K, Ca, and Mg.

MATERIALS AND METHODS

Data description

We conducted a global meta-analysis of published studies for C, N, P, K, Ca, and Mg concentrations and dry mass of green and senesced leaves to estimate NuR efficiencies and leaf mass loss of terrestrial plants during senescence. We compiled data on nutrient contents in green and senesced leaves from 86 studies in 31 countries on every continent except Antarctica, with the most data points coming from Europe and North America and the fewest from Russia and Africa (Fig. 1). These studies were found using Web of Science and Google Scholar search engines and the following key words: resorption, reabsorption, retranslocation, nutrient resorption, nutrient reabsorption, nutrient retranslocation, nutrient use efficiency, leaf mass loss, and leaf senescence. We also searched for papers citing key work on nutrient resorption by Aerts (1996) and Killingbeck (1996). We collected data from studies that reported or allowed us to calculate mean values of nutrient mass per unit dry mass in mature green and senesced leaves and report nutrient content on a leaf-mass basis. Most of the data for senesced leaves came from newly fallen leaves, with a small subset of data collected from litter-trap studies. In the absence of more specific data, we assume here that leaching between leaf fall and leaf collection was negligible. Although nutrient leaching may occasionally lead to underestimates of nutrient concentrations in senesced leaf litter (Yuan et al. 2005), an intensive leaching experiment for 40 subarctic species supports this assumption; leaching accounted for no more than 1% of the leaf N pool, and less than 0.01% of the leaf P pool, with the average N and P resorption, respectively, 55-fold and >10 000-fold higher than potential N and P leaching losses (Freschet et al. 2010).

We obtained data from major terrestrial vegetation types, including woody (lianas, shrubs, and trees) and non-woody species, grouped in six growth types: ferns, forbs, graminoids, conifers, evergreen woody angiosperms, and deciduous woody angiosperms. We also determined which species were N-fixers, to compare nutrient concentration and resorption properties to those of non-N-fixing species. To focus on more "natural" vegetation, only unfertilized controls from fertilized systems, including annual crops, were included in our database. We obtained mean annual temperature
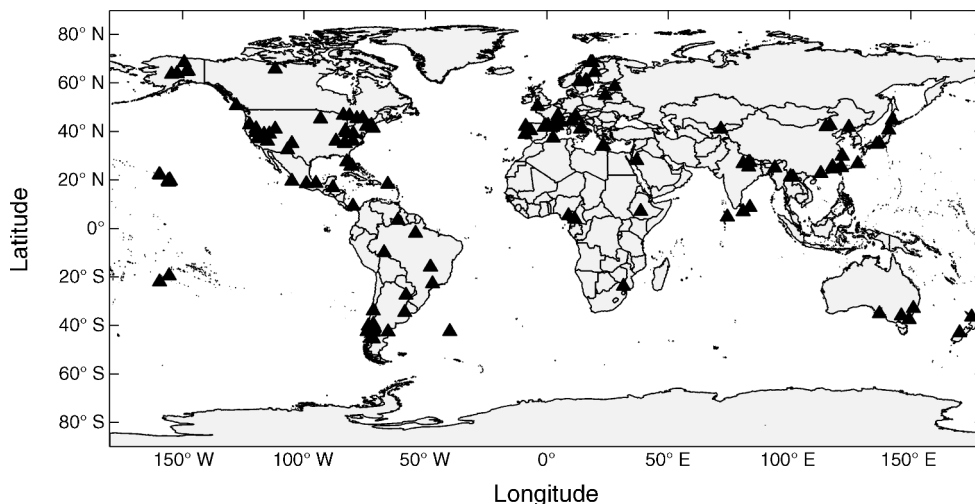
Fig. 1. Global distribution of the nutrient resorption data set.

(MAT) and mean annual precipitation (MAP) data and field characteristics for each site. Across the global data set, site MAT ranged from −8.0° to 31.6°C, MAP ranged from 125 to 5500 mm/yr, and altitude ranged from 0 to 3520 m above sea level. Based on these climatic features we grouped our data according to Koppen's climate classification. This widely used classification links native vegetation to climate by combining average annual and monthly temperatures and precipitation observations (McKnight and Hess 2000, Kottek et al. 2006), resulting in five climatic regions: A, tropical/megathermal; B, dry (arid and semiarid, including desert and steppe climates, where precipitation is less than the potential evapotranspiration); C, temperate/mesothermal (including mediterranean, oceanic, humid subtropical and subpolar oceanic climates); D, continental/microthermal; and E, polar. Overall, 171 data points were available for C concentrations in leaves, with 948 available for N, 669 for P, 207 for K, 150 for Ca, 115 for Mg, and 191 for the leaf mass-loss calculations (see details in the Appendix). Relatively few of the studies provided data on soil attributes, but where possible we compiled data for extractable soil nutrients and texture.

Resorption calculation and data analysis

Resorption data are often presented as NuR efficiency, defined as the proportional withdrawal of a nutrient during senescence (Cartaxana and Catarino 2002, van Heerwaarden et al. 2003a, Wright and Westoby 2003, Cai and Bongers 2007, Yuan and Chen 2009a):

$$\mathrm{NuR} = \left(1 - \frac{\text{mass of nutrient in senesced leaves}}{\text{mass of nutrient in green leaves}}\right) \times 100.$$

(1)

Using nutrient concentrations and leaf mass in green and senesced leaves, Eq. 1 can be written as follows:

$$\mathrm{NuR} = \left(1 - \frac{\mathrm{Nu_{sen}}}{\mathrm{Nu_{gr}}}\mathrm{MLCF}\right) \times 100 \qquad (2)$$

where $\mathrm{Nu_{gr}}$ and $\mathrm{Nu_{sen}}$ are the nutrient concentrations on a mass basis in green and senesced leaves, and MLCF is the mass loss correction factor, specifically the ratio of the dry mass of senesced leaves and the dry mass of green leaves (van Heerwaarden et al. 2003a). In the following analyses, all $\mathrm{Nu_{sen}}$ values have been corrected to account for mass loss during senescence as $\mathrm{Nu_{sen}^*} = \mathrm{Nu_{sen}MLCF}$. The MLCF was calculated directly when data on dry mass were shown for both green and senesced leaves, or estimated as $1 - \mathrm{LML}/100$ when only the percentage of leaf mass loss (LML) was available.

We used Eq. 2 to estimate NuR for each data point and species, comparing the values with other leaf traits. MLCFs were estimated for each growth type separately, except for ferns, for which MLCF was estimated from the average LML of the whole data set (24.2%). This choice was motivated by the presence of only one published LML value (20%) for a single fern species (Holub and Tůma 2010), which could not guarantee a statistically robust estimate. We acknowledge that this assumption could be biased due to the fact that ferns and seed plants are different in terms of physiology and anatomy. However, because LML values are fairly consistent across plant groups and the only value for ferns is close to the average LML, this seems a reasonable assumption. Our results also corroborate this assumption in showing no substantial differences in nutrient resorption patterns for ferns compared to the other growth forms.

To calculate mean nutrient resorption ($\overline{\mathrm{NuR}}$) for different functional groups or the global data set as a whole, and to assess the role of plant nutrient status on resorption efficiency, we used power law regressions according to Kobe et al. (2005):

$$\mathrm{Nu}^*_{sen} = \alpha \mathrm{Nu}^\beta_{gr} \qquad (3)$$

where α and β are regression parameters. Eq. (3) corresponds to a linear regression in a logarithmic plot:

$$\log(\mathrm{Nu}^*_{sen}) = \log(\alpha) + \beta \log(\mathrm{Nu}_{gr}). \qquad (4)$$

Combining Eqs. 2 and 3 yields the following expression for $\overline{\mathrm{NuR}}$:

$$\overline{\mathrm{NuR}} = (1 - \alpha \, \mathrm{Nu}^{\beta-1}_{gr}) \times 100. \qquad (5)$$

For Eq. 5, a β value >1 indicates the cases where nutrient resorption efficiency decreases with leaf nutrient status. In other words, when $\beta > 1$, resorption is more efficient in green leaves that have low nutrient concentrations. In contrast, $\beta < 1$ indicates higher resorption efficiency in nutrient-rich fresh leaves. Eq. 3 was used first to assess the mean nutrient resorption ($\overline{\mathrm{NuR}}$) independently of nutrient status, with the β exponent set to 1, resulting in a linear correlation (i.e., $\overline{\mathrm{NuR}} = 1 - \alpha$). Second, we assessed the role of leaf nutrient status by determining β through nonlinear regression. This two-step regression allowed us to compare our results to the $\overline{\mathrm{NuR}}$ values based on linear regression that are typically reported, while also considering, as a second-order approximation, the effect of nutrient status.

In order to calculate $\overline{\mathrm{NuR}}$, the data on nutrient concentration in green and senesced leaves (corrected for mass loss) were log-transformed for statistical analyses to correct for any heteroscedasticity in the data set. We used reduced major axis (RMA) regression analysis (type II regression; Bohonak 2004) with a logarithmic transformation, a common approach in allometric and stoichiometric studies (Seim and Sæther 1983, Kobe et al. 2005, Niklas 2006). According to Niklas (2006), when a predictive relationship is sought, simple ordinary least squares (OLS) regression analysis (also known as type I regression) can be used. However, when the objective is to establish a functional relationship between x and y, as is generally the case, RMA should be used. OLS regression is based on the assumption that x-values are known exactly, while only the y values (dependent variable) are subject to measurement error (Seim and Sæther 1983). In biological data sets, in contrast, x and y values are often subject to measurement errors of comparable magnitude. For purposes of comparison, we proceed with both regression types (I and II) analysis, but results from type II regression are emphasized.

We calculated $\overline{\mathrm{NuR}}$ for each nutrient for the data set as a whole and for each plant growth type and climate group separately using the regression analysis showed above (Eq. 5). To compare mean nutrient resorption efficiencies and nutrient concentrations among growth types and climate groups, we also performed an ANOVA followed by post hoc Duncan test ($P <$
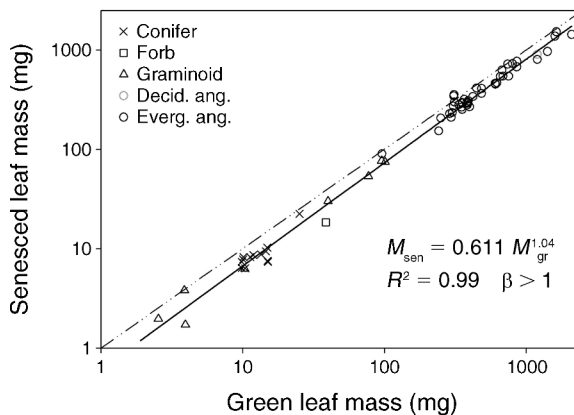

Fig. 2.   Green leaf mass (M_{gr}) vs. senesced leaf mass (M_{sen}) on a log scale, from which leaf mass loss (LML) during senescence is calculated for each plant growth form. Abbreviations are: Decid. ang., deciduous angiosperm; Everg. ang., evergreen angiosperm. The variable β (which is 1.04 in the equation) is the exponent of the regression curve (see Eq. 3).

0.05). In this case, nutrient resorption efficiency was calculated separately for each data point according to Eq. 2, and the averages (by plant types and climates) of those data points were compared. We also used these averages to assess differences from 0% or 50% resorption (t test). To estimate relationships between NuR and climate variables (MAT and MAP) and latitude, we used Pearson correlations and simple as well as stepwise multiple regression analysis.

RESULTS

Leaf mass loss (LML) and mass-loss correction factors (MLCF)

There was a strong relationship between mass in green and senesced leaves for all plant functional types (Fig. 2). On average, leaves lost 24.2% of their mass during senescence (Table 2). Among growth types, LML ranged from 21.6% (deciduous woody angiosperms) to 36.0% (forbs), with forbs showing significantly higher LML than the other growth forms. Within each growth type, no significant differences in LML were found across climate groups, with the exception of woody deciduous angiosperms, where mass loss was significantly higher in Koppen C climates (temperate/mesothermal) than in other climates (Table 3).

The global β value for LML was slightly, but statistically, greater than 1 ($\beta = 1.04$), meaning that lighter leaves lost slightly more mass proportionally than heavier leaves did. Based on the LML data, we calculated MLCF for each plant growth form (Table 2) and used it to correct nutrient resorption estimates for mass loss during senescence (Eq. 2).

Nutrient content and mean resorption efficiency across plant growth types

Across the global data set of C, N, P, K, Ca, and Mg concentrations and plant growth forms, forbs always

TABLE 2. Leaf mass loss (LML), mass loss correction factor (MLCF), and average nutrient content (percentage of dry mass) in green and senesced leaves uncorrected for mass loss, followed by the 95% confidence interval, for the entire data set and for different plant growth types.

Variable	All data	Ferns	Forbs	Graminoids	Conifers	Everg. ang.	Dec. ang.
LML	24.2 ± 2.1		$36.0^b \pm 7.5$	$28.7^{ab} \pm 5.5$	$25.5^a \pm 6.8$	$22.0^a \pm 2.9$	$21.6^a \pm 3.9$
MLCF	0.762		0.640	0.713	0.745	0.780	0.784
n	191		18	18	24	68	63
C							
C_{gr}	44.0 ± 0.7			$44.4^a \pm 2.1$	$49.8^b \pm 9.0$	$44.6^a \pm 1.0$	$43.0^a \pm 1.0$
C_{sen}	43.3 ± 0.8			$41.4^a \pm 2.0$	$54.2^b \pm 10.0$	$44.6^a \pm 1.2$	$41.8^a \pm 1.1$
n	171			15	4	78	74
N							
N_{gr}	1.840 ± 0.050	$1.335^a \pm 0.276$	$2.115^c \pm 0.258$	$1.941^{bc} \pm 0.167$	$1.138^a \pm 0.087$	$1.725^b \pm 0.079$	$2.033^c \pm 0.071$
N_{sen}	0.974 ± 0.033	$0.808^b \pm 0.198$	$1.092^c \pm 0.164$	$0.739^{ab} \pm 0.084$	$0.590^a \pm 0.057$	$1.000^c \pm 0.054$	$1.071^c \pm 0.051$
n	948	22	88	83	81	307	367
P							
P_{gr}	0.143 ± 0.007	$0.136^b \pm 0.030$	$0.158^{bc} \pm 0.033$	$0.191^c \pm 0.043$	$0.096^a \pm 0.013$	$0.125^{ab} \pm 0.011$	$0.155^{bc} \pm 0.011$
P_{sen}	0.077 ± 0.006	$0.065^{ab} \pm 0.017$	$0.078^b \pm 0.022$	$0.060^{ab} \pm 0.018$	$0.045^a \pm 0.014$	$0.073^b \pm 0.009$	$0.092^c \pm 0.009$
n	669	22	58	51	53	222	263
K							
K_{gr}	0.955 ± 0.087		$1.701^d \pm 0.468$	$1.265^c \pm 0.323$	$0.418^a \pm 0.092$	$0.879^b \pm 0.117$	$0.924^b \pm 0.092$
K_{sen}	0.471 ± 0.067		$0.998^d \pm 0.400$	$0.281^{ab} \pm 0.091$	$0.132^a \pm 0.044$	$0.576^c \pm 0.139$	$0.417^{bc} \pm 0.053$
n	207		24	15	30	49	89
Ca							
Ca_{gr}	1.110 ± 0.124		$1.856^c \pm 0.382$	$0.333^a \pm 0.102$	$0.380^a \pm 0.054$	$1.157^b \pm 0.221$	$1.202^b \pm 0.166$
Ca_{sen}	1.318 ± 0.144		$1.907^b \pm 0.503$	$0.311^a \pm 0.105$	$0.518^a \pm 0.128$	$1.491^b \pm 0.241$	$1.462^b \pm 0.198$
n	150		22	16	15	43	54
Mg							
Mg_{gr}	0.336 ± 0.054		$0.506^b \pm 0.116$	$0.099^a \pm 0.015$	$0.078^a \pm 0.011$	$0.367^b \pm 0.087$	$0.398^b \pm 0.130$
Mg_{sen}	0.348 ± 0.059		$0.524^b \pm 0.121$	$0.084^a \pm 0.013$	$0.061^a \pm 0.009$	$0.433^b \pm 0.103$	$0.365^b \pm 0.134$
n	115		22	12	15	36	30

Notes: The same letters after values on the same row indicate no significant difference (Duncan's test; $P < 0.05$). Key: n, number of observations for each nutrient; Nu_{gr}, nutrient content (%) in green leaves for nutrients C, N, P, K, Ca, and Mg; Nu_{sen}, nutrient content (%) in senesced leaves (uncorrected for mass loss); LML, leaf mass loss during senescence (%); and MLCF, mass loss correction factor (i.e., senesced leaf mass/green leaf mass). Empty cells indicate that no data are available.

had the highest or among the highest nutrient concentrations for both green and senesced leaves. In contrast, conifers generally had the lowest C and nutrient contents in both green and senesced leaves (Table 2).

Mean nutrient resorption estimates differed substantially among nutrients, growth forms, and climates (Fig. 3, Table 3). Mean N and P resorptions ($\overline{NR}$, $\overline{PR}$) globally were 62.1% and 64.9%, respectively, and statistically greater than the typically assumed value of 50% (t test; $P < 0.05$; Fig. 3). Graminoids tended to have the highest $\overline{NuR}$ values for all nutrients, whereas evergreen woody angiosperms typically had the lowest or close to lowest $\overline{NuR}$ (Fig. 4). Regarding N resorption, graminoids had the highest $\overline{NR}$ (74.6%) while evergreen woody angiosperms and ferns had the lowest values (56.1% and 59.2%, respectively; Fig. 4). For $\overline{PR}$, evergreen and deciduous woody angiosperms had the lowest resorption (58.4% and 58.5%, respectively; Fig. 4), whereas graminoids again showed the highest $\overline{PR}$ (82.1%).

Average nutrient resorption for K ($\overline{KR} = 70.1\%$) was the highest for all nutrients examined (Fig. 3). As for N and P, graminoids showed the highest $\overline{KR}$ (84.9%; Fig. 4), whereas evergreen woody angiosperms had the lowest ($\overline{KR} = 56.1\%$). In contrast, C, Ca, and Mg

showed lower average resorption efficiencies (23.2%, 10.9%, and 28.6%, respectively) globally compared to the other nutrients (Fig. 3), but none of the three showed evidence of enrichment during senescence. $\overline{MgR}$ was found to be the most conservative and was statistically indistinguishable among all growth types except for evergreen woody angiosperms, which had the lowest resorption (11.7%). $\overline{CaR}$ was statistically indistinguishable from 0% resorption for all woody species (t test; $P < 0.05$; Fig. 4), but not for graminoids and forbs, which showed a $\overline{CaR}$ of 32.5% and 36.9%, respectively. Graminoids showed the highest mean C resorption (33.6%) and conifers and evergreen woody angiosperms had the lowest, 18.9% and 20.8%, respectively (Fig. 4).

Nutrient content and mean nutrient resorption for N-fixers and non-N-fixers.

Nitrogen contents in both green and senesced leaves were one-third and one-half higher in N-fixers than in non-N-fixers (Table 4), a result consistent with previous studies (Killingbeck 1996, Killingbeck and Whitford 2001, Wright and Westoby 2003). In contrast, we did not find statistically significant differences in the

TABLE 3. Comparison among climate groups (Koppen) of mean leaf mass loss (LML) and resorption efficiencies within each growth type.

Variable	Koppen	Conifers	Ferns	Forbs	Gram.	Dec. Ang.	Ev. Ang.
LML (%)	A						22.6[a] (31)
	B				25.2[a] (4)		
	C	27.5[a] (4)		39.0[b] (14)	29.6[a] (10)	29.1[b] (32)	20.8[a] (34)
	D	24.9[a] (18)			29.9[a] (4)	12.8[a] (21)	
	E	26.9[a] (2)		16.7[a] (3)		15.9[a] (9)	32.0[a] (2)
$\overline{CR}$ (%)	A						18.1[a] (11)
	B				33.6[a] (8)		
	C	18.7 (4)			33.8[a] (6)	23.8 (72)	20.9[a] (66)
	D						
	E						
$\overline{NR}$ (%)	A		53.6[ab] (4)	61.1[a] (22)	67.5[a] (2)	44.0[a] (31)	49.5[a] (112)
	B			69.1[ab] (16)	69.7[a] (17)	62.0[bc] (32)	60.6[bc] (11)
	C	56.0[a] (43)	47.8[a] (9)	69.7[ab] (15)	75.2[a] (35)	57.6[b] (222)	55.3[ab] (174)
	D	67.7[b] (38)	66.7[b] (7)	73.4[b] (24)	72.9[a] (12)	64.2[bc] (82)	61.5[bc] (10)
	E			70.0[ab] (6)	73.3[a] (7)	67.9[c] (9)	69.5[c] (6)
$\overline{PR}$ (%)	A		62.9[a] (4)	77.4[b] (22)	79.1[a] (2)	54.5[a] (30)	59.3[a] (98)
	B			81.6[a] (8)		64.5[a] (4)	
	C	68.0[a] (29)	63.8[a] (9)	64.0[a] (14)	79.0[a] (22)	54.1[a] (175)	52.3[a] (135)
	D	71.6[a] (26)	75.3[a] (7)	76.8[b] (12)	83.3[a] (4)	57.5[a] (64)	71.2[b] (8)
	E			76.0[b] (6)	79.7[a] (7)	66.0[a] (8)	70.6[b] (5)
$\overline{KR}$ (%)	A			61.6[a] (19)		45.3[a] (11)	51.9[a] (19)
	B				86.9[b] (8)		
	C	30.9[a] (7)			84.8[b] (3)	61.2[ab] (59)	40.7[a] (33)
	D	78.7[b] (24)		91.9[b] (2)		77.3[b] (22)	87.0[b] (5)
	E			73.6[ab] (3)	77.2[a] (4)	48.9[a] (3)	58.1[a] (3)
$\overline{CaR}$ (%)	A			30.7[a] (19)		11.4[a] (8)	0.9[b] (20)
	B				41.6[b] (8)		
	C				50.7[b] (4)	5.3[a] (46)	−0.1[b] (28)
	D	0.4 (15)					
	E			18.3[a] (3)	−31.5[a] (4)	−9.1[a] (3)	−64.8[a] (3)
$\overline{MgR}$ (%)	A			31.2[a] (19)		14.2[a] (8)	14.5[a] (17)
	B				42.2[a] (8)		
	C					31.7[b] (18)	−6.6[a] (16)
	D	39.3 (15)					
	E			34.0[a] (3)	31.5[a] (4)	12.9[a] (3)	43.5[b] (3)

Notes: The value in parentheses is the number of data points, and different letters within each growth type mean that the values are significantly different (Duncan's test; $P < 0.05$). Variables $\overline{CR}$, $\overline{NR}$, $\overline{PR}$, $\overline{KR}$, $\overline{CaR}$, and $\overline{MgR}$ are resorption efficiencies of C, N, P, K, Ca, and Mg, respectively. Empty cells indicate that no data are available.

contents of C and other nutrients in green and senesced leaves of N-fixers compared to non-N-fixers (Table 4).

Overall, both $\overline{NR}$ and $\overline{KR}$ were significantly lower in N-fixers than in non-N-fixers ($P < 0.05$; Table 4). However, this pattern did not hold for all plant growth types, with forbs showing no difference in $\overline{NR}$ for N-fixers and non-N-fixers, and deciduous woody angiosperm being the only growth type showing statistically higher $\overline{KR}$ for non-N-fixers. Regarding the dependence of $\overline{NuR}$ on leaf nutrient status, β values were mostly statistically indistinguishable from 1 (no dependence) for N-fixers, except $\overline{PR}$. For non-N-fixers species, β values were significantly higher than 1 for almost all of them, except $\overline{CaR}$ and $\overline{MgR}$ ($P < 0.05$; Table 4).

Resorption efficiency and plant nutrient status

Based on the power law regression equation (Eq. 3), we tested whether nutrient resorption was affected by nutrient concentrations in green leaves, by analyzing for nonlinear relationships between nutrient concentrations in green and senesced leaves (i.e., β ≠ 1; Fig. 5). Across the data set, every nutrient except Ca showed β > 1 (i.e., greater resorption efficiency in fresh leaves with lower nutrient concentrations; $P < 0.05$). The β value for Ca did not differ statistically from one, suggesting no evidence for a relationship with nutrient status (Fig. 5).

When data were grouped by plant type or climate, however, the effect of nutrient status differed by nutrient (Table 5). N and P resorption had β > 1 for all growth types and climates ($P < 0.05$). P resorption showed the highest β values in the data set, 2.08 and 2.54 for conifers and Koppen B (dry climates), respectively. In contrast, C resorption had an overall β > 1 for the entire data set (Fig. 5), but the relationship was driven primarily by results in Koppen C climates. For K, Ca, and Mg, responses in β were intermediate and depended on the specific climate and vegetation types (Table 5).

Resorption efficiency along climatic gradients

C, N, P, K, and Mg resorption efficiencies were positively correlated with latitude because of significant negative relationships with mean annual temperature and/or precipitation (Appendix: Figs. A1, A2, and A3). CR was negatively correlated only with precipitation ($P < 0.001$) but not with temperature. The opposite was true for MgR, which showed a negative relationship
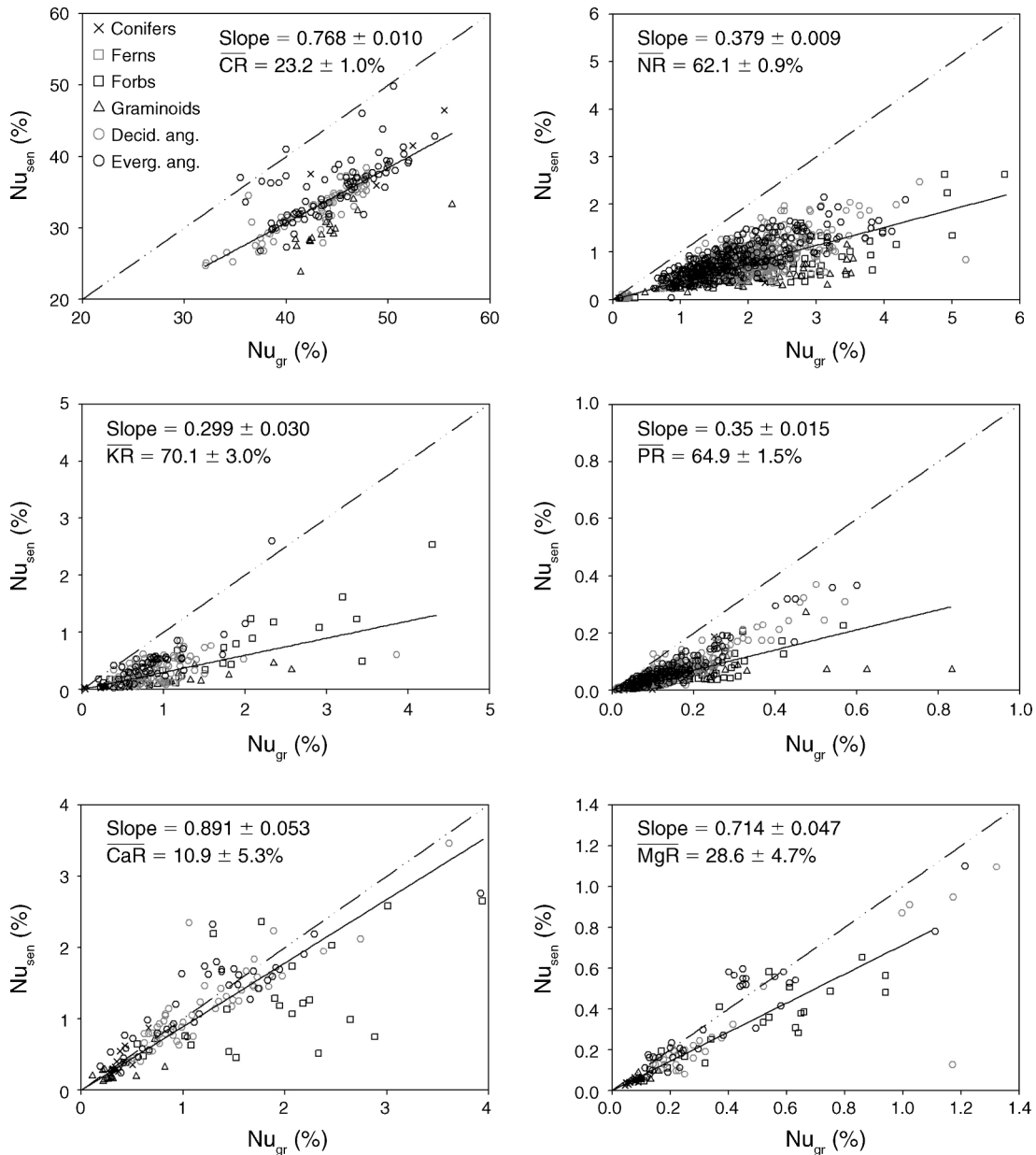
FIG. 3. Linear regressions of nutrient content in green (Nu_{gr}) vs. senesced (Nu_{sen}) leaves (corrected for mass loss) for the global data set. Nutrient content is measured as percentage of dry mass. The dash-dotted line is the reference line set to a unitary slope, defining zero resorption. Variables $\overline{CR}$, $\overline{NR}$, $\overline{KR}$, $\overline{PR}$, $\overline{CaR}$, and $\overline{MgR}$ are resorption efficiencies of C, N, K, P, Ca, and Mg, respectively.

with temperature ($P < 0.001$), but no correlation with precipitation. CaR was the only variable to show a positive correlation with latitude, which was driven by a positive correlation with temperature ($P < 0.05$). Regarding the joint influence of latitude (LAT), mean annual temperature (MAT), and mean annual precipitation (MAP) on NuR, MAT had more influence on NuR than LAT and MAP had (Table 6). Eleven out of the 15 equations involve MAT, with MAT being the only predictor variable in nine of them.

Among the studied climatic groups, dry climates (Koppen B) tended to have the highest $\overline{NuR}$ for most nutrients, while tropical climates (Koppen A) had the lowest, except for Ca (Fig. 4). Usually, NuR correlated positively with latitude and negatively with MAT and MAP (except again for Ca; see the Appendix). Latitude, MAT, and MAP also showed strong and statistically significant correlations with green leaf mass (−0.66, 0.62, and 0.57, respectively; $P < 0.001$), which in turn correlated negatively with NR, KR, CaR, and MgR
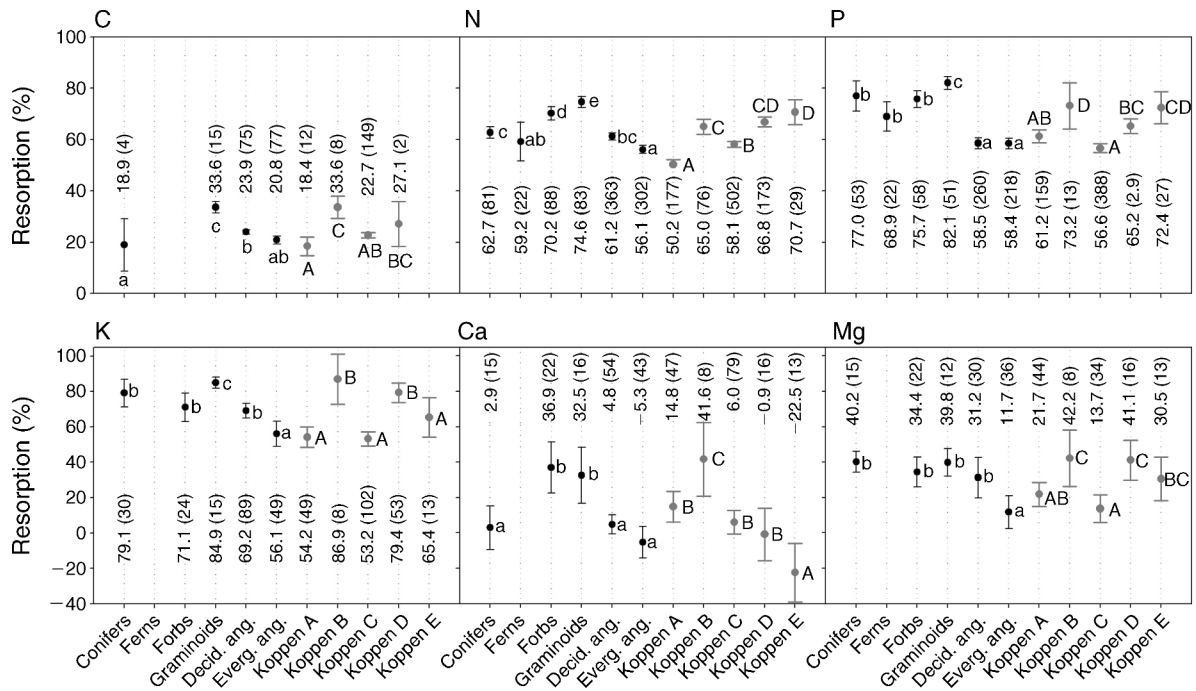
FIG. 4.   Mean nutrient resorption by growth type and climates (Koppen classification) for all studied nutrients. Values under or above symbols are the mean nutrient resorption for each given growth type or climate, with the number of observations within parentheses. Different letters beside the points represent the differences on resorption efficiency among growth types according to Duncan's test ($P < 0.05$). Lowercase letters compare growth types (black symbols) and uppercase letters compare climates (gray symbols).

(-0.27 [$P < 0.05$], -0.81 [$P < 0.001$], -0.47 [$P < 0.05$], and -0.86 [$P < 0.001$], respectively; Appendix: Table A2).

Resorption efficiency differed by climate (Koppen) within individual growth forms (Table 3). In general, $\overline{NR}$ within growth forms varied the most across the five climates, whereas values of $\overline{PR}$ were more similar among climates. Conifers in Koppen D had significantly higher $\overline{NR}$ and $\overline{KR}$ than those in Koppen C. Graminoids showed the smallest influence of climate on nutrient resorption, with no significant differences among climate groups except for $\overline{KR}$ and $\overline{CaR}$ in Koppen D (Table 3). For deciduous and evergreen woody angiosperms, $\overline{NR}$ varied among climate groups, with the lowest $\overline{NR}$ occurring in Koppen A climates and the highest $\overline{NR}$ in Koppen E. $\overline{PR}$ did not differ among climate groups in deciduous species, but in evergreen species PR was 70% or more in Koppen D and E habitats.

Regarding the dependence of NuR to nutrient status within climate groups, temperate and continental climates (Koppen C and D, respectively) showed $\beta > 1$ for all nutrients except Mg (Table 5). In contrast, tropical, dry, and polar climates (Koppen A, B, and E, respectively) showed $\beta > 1$ only for N and P resorption ($P < 0.05$). The high β value of 2.54 for P resorption in dry climates (Koppen B) shows that resorption depends strongly on green-leaf P status in this more arid environment.

DISCUSSION

Global patterns of nutrient resorption efficiency

Our results build upon earlier work (Aerts 1996, van Heerwaarden et al. 2003b, Kobe et al. 2005, Yuan and Chen 2009a, b) to offer new insights on C, N, and P resorption and to provide, to our knowledge, the first global estimates for K, Ca, and Mg resorption. Our work is also unique in developing unbiased estimates of resorption (by correcting for mass loss; see the following section), in extensively comparing resorption for plant growth forms and climates (see *Nutrient content and resorption efficiency for different plant growth types*), and analyzing nutrient resorption across different nutrient availabilities (see *Resorption efficiency and leaf nutrient status*).

Mass loss during senescence

Unlike the often-cited 50% $\overline{NR}$ and $\overline{PR}$ found in the literature (Aerts 1996, Yuan et al. 2005, Huang et al. 2007, Yuan and Chen 2009a, Kilic et al. 2010), we estimate that $\overline{NR}$ and $\overline{PR}$ for terrestrial plants in general are 62.1% and 64.9%, respectively (Fig. 3). One major difference between our estimates and this 50% value arises from taking into account mass loss (and thus the change in measurement basis) that occurs during senescence. Ignoring mass loss leads to an underestimation of nutrient resorption by ~10% (van Heerwaarden et al. 2003a). Mass loss can be caused by several

TABLE 4. Average nutrient content (percentage of dry mass) in green and senesced leaves (uncorrected for mass loss), resorption efficiencies (corrected for mass loss), regression exponent β values, and number of observations (*n*) for nitrogen fixers and non-fixers.

Parameter	All		Forbs		Decid. ang.		Everg. ang.	
	Fixers	Non-fixers	Fixers	Non-fixers	Fixers	Non-fixers	Fixers	Non-fixers
C								
C_{gr}	44.89^a	43.75^a			44.23^a	42.84^a		44.54
C_{sen}	43.15^a	43.26^a			42.63^a	41.67^a		44.59
$\overline{CR}$	24.4^a	21.9^a			24.4^a	23.7^a		20.3
β	1.11ns	1.17*			1.19 ns	1.08 ns		1.16 ns
n	10	142			8	66		75
N								
N_{gr}	2.44^b	1.87^a	3.04^b	2.02^a	2.37^b	2.00^a	2.35^b	1.70^a
N_{sen}	1.55^b	1.00^a	1.55^a	1.05^a	1.52^b	1.02^a	1.65^b	0.97^a
$\overline{NR}$	49.9^a	58.5^b	67.3^a	67.8^a	49.5^a	59.7^b	41.8^a	54.5^b
β	1.14 ns	1.29*	1.71 ns	1.23*	1.20 ns	1.30*	0.99 ns	1.30*
n	61	701	8	80	37	326	14	288
P								
P_{gr}	0.14^a	0.14^a		0.15	0.13^a	0.16^a	0.15^a	0.12^a
P_{sen}	0.074^a	0.084^a		0.078	0.072^a	0.095^a	0.078^a	0.073^a
$\overline{PR}$	60.0^a	57.0^a		75.4	59.6^a	54.5^a	57.4^a	55.6^a
β	1.33*	1.31*		1.25*	1.32*	1.28*	1.43 ns	1.29*
n	47	496		55	30	230	13	205
K								
K_{gr}	0.81^a	1.05^a		1.70	0.67^a	0.96^b	1.13^a	0.85^a
K_{sen}	0.51^a	0.56^a		1.00	0.40^a	0.42^a	0.76^a	0.56^a
$\overline{KR}$	48.6^a	61.0^b		71.1	52.1^a	65.0^b	41.0^a	51.3^a
β	1.77 ns	1.61*		1.42	2.25 ns	1.80*	1.87 ns	1.83*
n	16	146		24	11	78	5	44
Ca								
Ca_{gr}	1.31^a	1.31^a		1.86		1.17		1.15
Ca_{sen}	1.77^a	1.53^a		1.91		1.38		1.48
$\overline{CaR}$	-9.1^a	4.7^a		36.9		6.3		5.6
β	1.18 ns	0.92 ns		1.08 ns		0.95 ns		0.94 ns
n	14	105		22		45		38
Mg								
Mg_{gr}	0.52^a	0.40^a		0.51		0.36		0.35
Mg_{sen}	0.54^a	0.42^a		0.52		0.31		0.42
$\overline{MgR}$	13.9^a	20.9^a		34.4		34.9		10.9
β	0.88 ns	1.10 ns		0.95 ns		0.98 ns		1.25 ns
n	11	77		22		24		31

Notes: The β coefficients followed by ns are not statistically different from 1, while those followed by asterisks are significantly different from 1 ($P < 0.05$). Different letters indicate significant differences between N fixers and non-fixers within each plant growth type based on ANOVA ($P < 0.05$). Empty cells indicate that no data are available.

processes, including resorption, leaching, and in situ decomposition (between senescence and collection of the fallen leaves). The main cause of mass loss is likely the resorption of C and nutrients, while leaching and decomposition probably play a secondary role. On a mass basis, C concentrations are much higher than any other nutrient (Table 2) and hence even small C resorption efficiencies can cause substantial decreases in the total mass of the leaf. This explanation seems supported by the similar LML and $\overline{CR}$ values that we found (Table 3).

Leaching removes organic and inorganic compounds from leaves and other organs, particularly in wetter climates. Of the inorganic nutrients leached from plants, K, Ca, and Mg are often leached in the greatest quantities (Tukey 1970). Nonetheless, rates of leaching tend to be lower than resorption during the relatively short period of leaf senescence, likely not affecting resorption calculations appreciably (Freschet et al. 2010). Our data, for instance, show no relationship between mean annual precipitation, which would be expected to correlate with leaching rates, and CaR and MgR; this correlation was even negative for CR, NR, PR, and KR (Appendix: Fig. A3). Leaching does not appear to be significantly affecting resorption efficiency of the nutrients we examined, at least at the large scales investigated here.

In addition to leaching, mass loss may also be caused by photo-degradation and decomposition. Photochemical mineralization of organic material can cause the loss of up to 60% of mass in high-irradiance water-limited ecosystems (Austin and Vivanco 2006, Austin and Ballaré 2010). However, photo-degradation is a relatively slow process when compared to leaf senescence
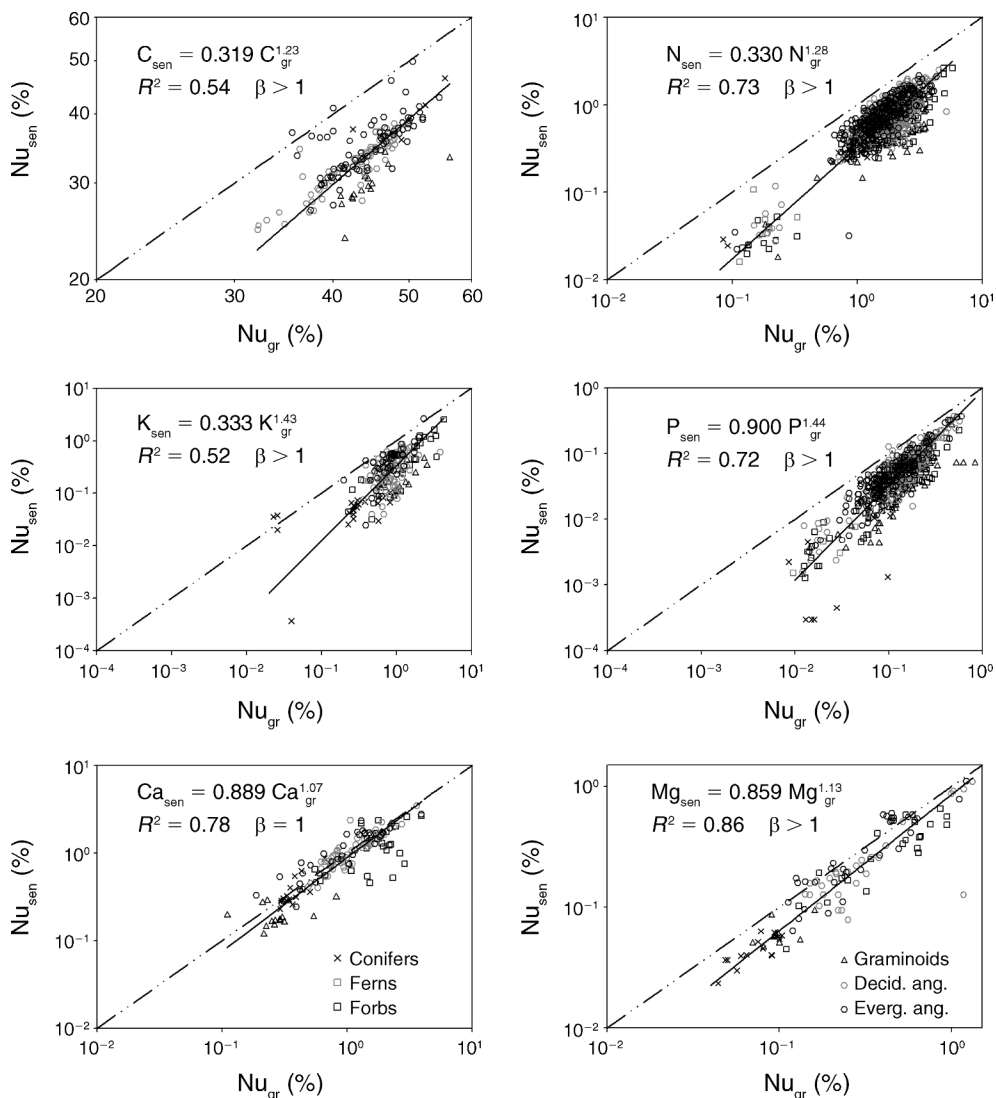
Fig. 5. Power law regression analysis (Eq. 3) of nutrient content in green vs. senesced leaves (corrected for mass loss) for the global data set on a log scale. A value of β different from 1 means that the relationship between Nu_{sen} and Nu_{gr} is nonlinear, with $\beta > 1$ indicating decreased resorption efficiency with increasing leaf nutrient status.

TABLE 5.   Table entries are β coefficients for different plant growth types and Koppen climates.

Variable	Plant growth type						Koppen climate				
	Ferns	Forbs	Graminoids	Conifers	Everg. ang.	Decid. ang.	A	B	C	D	E
$\overline{CR}$			1.08 ns	1.06 ns	1.15 ns	1.08 ns	1.11 ns	1.37 ns	1.16*		
$\overline{NR}$	1.29*	1.23*	1.24*	1.18*	1.31*	1.30*	1.23*	1.39*	1.30*	1.22*	1.24*
$\overline{PR}$	1.26*	1.24*	1.23*	2.08*	1.34*	1.30*	1.45*	2.54*	1.62*	1.37*	1.50*
$\overline{KR}$		1.42*	1.20 ns	1.18 ns	1.77*	1.83*	1.11 ns	0.66 ns	1.24*	1.54*	1.11 ns
$\overline{CaR}$		1.10 ns	0.87 ns	1.65*	1.02 ns	0.95 ns	0.88 ns	1.00 ns	1.25*	1.46*	0.86 ns
$\overline{MgR}$		1.00 ns	1.01 ns	0.99 ns	1.07 ns	1.19*	0.99 ns	0.71 ns	1.28 ns	0.75*	0.94 ns

Notes: These β coefficients were obtained from the power law regression of Eq. 3. A value of β different from 1 means that the relationship between Nu_{sen} and Nu_{gr} is not linear, with $\beta > 1$ indicating greater nutrient resorption efficiency in leaves with lower nutrient concentrations. Empty cells indicate that no data are available.

* $P < 0.05$ (β coefficients are significantly different from 1); ns, β coefficients are not significantly different from 1.

TABLE 6. Stepwise multiple regressions between C, N, P, K, Ca, and Mg resorption and mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), and latitude (LAT).

Growth type	Equation	R^2
CR		
All data	$y = 28.6 - 0.073\text{LAT}^{***}$ $- 0.0032\text{MAP}^{***}$	0.24
Everg. ang.	$y = 10.9 + 0.462\text{MAT}^{**}$	0.13
NR		
All data	$y = 69.0 - 0.483\text{MAT}^{***}$ $- 0.0024\text{MAP}^{***}$	0.18
Conifers	$y = 63.1 + 0.097\text{LAT}^{**}$ $- 0.628\text{MAT}^{***}$	0.42
Forbs	$y = 71.9 - 0.374\text{MAT}^{***}$	0.14
Decid. ang.	$y = 66.9 - 0.637\text{MAT}^{***}$	0.15
Everg. ang.	$y = 58.1 - 0.0023\text{MAP}^{***}$	0.05
PR		
All data	$y = 69.1 - 0.571\text{MAT}^{***}$	0.10
Decid. ang.	$y = 62.5 - 0.468\text{MAT}^{***}$	0.06
KR		
All data	$y = 77.0 - 1.08\text{MAT}^{***}$	0.20
Conifers	$y = 95.9 - 4.45\text{MAT}^{***}$	0.44
Decid. ang.	$y = 81.4 - 1.35\text{MAT}^{***}$	0.29
Everg. ang.	$y = 40.2 + 0.375\text{LAT}^{**}$	0.16
CaR		
All data	$y = 13.2 - 0.263\text{LAT}^{***}$	0.07
MgR		
All data	$y = 36.9 - 0.791\text{MAT}^{***}$	0.14

Notes: Some specific growth types are not shown here, due to low number of data or because the regression was not statistically significant. Empty cells indicate that no data are available.

** $P < 0.01$; *** $P < 0.001$ for the preceding regression coefficient.

and abscission. Similarly, although decomposers can start to degrade high quality, nutrient-rich leaves, especially in wetter habitats, this process also is likely to be slower than resorption in most systems (Palm and Sanchez 1990, Berg and McClaugherty 2007).

Nutrient content and resorption efficiency for different plant growth types

Since the predominance of evergreens in low fertility soils was first documented (Monk 1966), numerous papers have discussed the adaptive significance of evergreens in low-nutrient conditions (Chapin 1980, Aerts 1990, 1996, Killingbeck 1996, Lambers et al. 1998, Yuan and Chen 2009*a*). Nutrient concentrations and resorption efficiencies, as estimated here and by other researchers, can be used to assess such adaptations. Aerts (1996) found that N resorption was significantly lower in evergreen species and forbs than in deciduous species and graminoids. Recently, Yuan and Chen (2009*a*) also showed that N, but not P, resorption is lower in evergreen than in deciduous species. Other studies have observed consistent differences in leaf traits between evergreen and deciduous species, although such analyses may also include systematic differences in leaf life-spans (Reich et al. 1992, Hobbie and Gough 2002).

We found that nutrient contents in green and senesced leaves differed between evergreen and deciduous species only for N_{gr} and P_{sen} (Table 2), which were higher in deciduous species. However, deciduous species showed higher $\overline{NR}$, $\overline{KR}$, and $\overline{MgR}$ compared to evergreens, with no differences for $\overline{CR}$, $\overline{PR}$, and $\overline{CaR}$ (Fig. 4). Our results confirm that there are indeed important differences in nutrient concentrations and resorption, but these differences are not universal.

Although Aerts (1996) concluded that there were only minor differences in nutrient resorption efficiencies between plant growth types, our results show that these differences can be large, particularly for K (Fig. 4). In fact, graminoids had among the highest K resorption, followed by conifers and forbs. The largest differences observed were for N, P, and K, where graminoids had 74.6% $\overline{NR}$, 82.1% $\overline{PR}$, and 84.9% $\overline{KR}$, much higher than the average of 50% typically assumed in most terrestrial models for N and P (Table 1) and reported by Yuan and Chen (2009*a*) for conifers and broadleaf species. Among all plant growth types, only ferns showed values of $\overline{NR}$ that were statistically indistinguishable from 50% ($P > 0.05$ for each).

Given that resorption efficiency is affected by plant traits that differ among growth forms, one key factor likely causing variation in nutrient resorption is differences in the size of the non-leaf nutrient pool (Kull and Kruijt 1999). Because nutrient resorption efficiency depends on the transfer of nutrients between leaf and other plant pools, the size of those pools may play an important role in the variation of nutrient resorption we observed among different plant types. For instance, the smaller non-leaf pools in graminoids could lead to a greater need for nutrient resorption compared to other growth forms such as deciduous and evergreen woody angiosperms (Table 3).

As a structural element in plants, particularly in cell walls, Ca tends to be resorbed less during senescence than most other elements (Tukey 1970, Lambers et al. 1998, Kazakou et al. 2007). Previous research has suggested that Ca is generally conserved in leaves (van Heerwaarden et al. 2003*a*). Our data showed, on average, a modest 10.9% $\overline{CaR}$ during senescence (Fig. 3). While conifers and both deciduous and evergreen woody angiosperms showed a $\overline{CaR}$ statistically indistinguishable from zero, forbs and graminoids showed 36.9% and 32.5% $\overline{CaR}$, respectively (*t* test, $P < 0.05$; Fig. 4). Hence, these results show that Ca is not always retained in leaves and thus cannot reliably be used to obtain unbiased estimates of resorption efficiencies.

Resorption efficiency and leaf nutrient status

Although correlations between NuR and nutrient status have not always been observed (Chapin and Moilanen 1991, Aerts 1996, Lambers et al. 1998, Aerts and Chapin 2000, Kazakou et al. 2007, Hättenschwiler et al. 2008, Yuan and Chen 2009*a*), Kobe et al. (2005) showed that N and P resorption efficiencies generally

declined with increasing leaf nutrient status. General patterns may emerge using data sets that span a range of climatic conditions and plant growth forms. The power-law regression analysis we performed reveals a broad-scale dependence of resorption on green-leaf nutrient status for all elements except Ca, with resorption being more efficient in green leaves that have low nutrient concentrations ($\beta > 1$; Fig. 5). Consistent with this pattern of increased resorption as nutrient availability decreases (based on foliar nutrients) we also found lower N resorption in most N-fixer growth types (Table 4), as has already been shown elsewhere (Killingbeck 1993, Eckstein et al. 1999, Norris and Reich 2009). Overall, these results suggest that resorption may be an adaptive trait with considerable flexibility.

Other elements showed differences among or across plant growth forms. Perhaps surprisingly, carbon showed increased resorption overall in C-poor leaves ($\beta > 1$; Fig. 5), even though this relationship did not hold for any singular growth form (Table 5). If relative changes in leaf C concentrations were due mainly to different concentration of nonstructural carbohydrates (NSC) (our $\overline{CR}$ estimates are indeed consistent with the amount of C stored in NSC; see Körner and Miglietta 1994, Körner 2003), C resorption would be expected to be correlated with NSC content, and β would be <1 because NSC are relatively easily resorbed. For N and P resorption, $\beta > 1$ held for all plant types and climates, suggesting that resorption increases in relatively N- and P-poor leaves globally. For the other nutrients, β values varied among plant types and climates, either being equal to or greater than one. In only one case was β negative: Mg resorption in continental climates. From a leaf economics perspective, all nutrients for which uptake from the soil is more energy-demanding than resorption might be expected to show $\beta > 1$ (Franklin and Ågren 2002).

Resorption efficiency and climate

Our analysis contrasts with some of the conclusions of Yuan and Chen (2009a), who found that resorption of N increased with latitude but decreased with MAT and MAP, whereas for P resorption the opposite relationships were true. In contrast, we found similar, statistically significant climate trends for N and P. Both nutrients were negatively correlated with MAT and MAP, and positively correlated with latitude (Appendix: Figs. A1, A2, and A3). We found this pattern of negative relationships between NuR and MAT and MAP, and a positive relationship between NuR and latitude, across almost all climates and growth types.

Regarding climate and soil fertility, tropical soils are generally considered to be older and relatively less fertile than are soils in most other regions. From the standpoint of leaf economics, the low nutrient availability of tropical soils, especially for P availability, would be expected to lead to a generally higher $\overline{NuR}$, and improved ecosystem nutrient recycling in general (Vi-

tousek 1984, Aerts 1997, Aerts and Chapin 2000). However, as observed in other studies (Reich et al. 1995, Aerts 1996, Diehl et al. 2003), our results do not always show higher $\overline{NuR}$ in low-fertility soils (e.g., tropical climates in Fig. 4). In fact, tropical sites (Koppen A) were always among the climates with the lowest $\overline{NuR}$, except for $\overline{CaR}$. This lack of a relationship may be due to strong heterogeneity in tropical soils (Richter and Babbar 1991) that leads to a range of nutrient conditions, or to the fact that plants in the tropics have adopted other nutrient conservation strategies, such as longer leaf life spans (Aerts and Chapin 2000).

Implications for terrestrial ecosystem modeling

The $\overline{NuR}$ estimates we obtained should be useful for parameterizing and improving ecosystem and biogeochemical models (e.g., Falkowski et al. 2000). NuR plays an important role in determining nutrient concentrations in litter, and litter nutrient and lignin concentrations are two of the main controlling factors of decomposition rates (Aerts 1997, Berg and McClaugherty 2007). Moreover, litter nutrient concentrations control the balance of net mineralization and immobilization during decomposition, with nutrient-rich residues releasing nutrients sooner than nutrient-poor ones (Parton et al. 2007, Manzoni et al. 2008, 2010). Because the quality of leaves after senescence, the final step of nutrient cycling in leaves, is the initial condition for litter decomposition, our $\overline{NuR}$ parameters provide important data for bridging plant and soil carbon and nutrient cycling.

In the broader context of ecosystem models, nutrient resorption is also a key parameter for defining nutrient requirements and litter quality, with feedbacks to all model components. Because N is considered the most limiting nutrient for most terrestrial ecosystems, most ecosystem models consider N alone, with a few models also describing P dynamics explicitly (Parton et al. 1993, Wang et al. 2007). In general, a greater resorption efficiency used in a model results in more nutrient storage for growth in the following year. Thus, prescribing accurate NuR values for models is important for predicting the temporal changes in biomass under limiting nutrient conditions. In some models, resorption efficiency is assumed to be constant for a given species or functional group (Table 1), with values obtained from specific observations or published data sets. In other models, resorption efficiency is modeled implicitly based on leaf nutrient status, which depends on nutrient availability in the environment, and on prescribed nutrient concentrations in litter (Table 1). Hence, in these models resorption efficiency is not defined a priori as an intrinsic plant property but instead changes to accommodate constant nutrient conditions in the litter. Our results, however, show that nutrient resorption depends on leaf nutrient status before senescence, differently than assumed in most models. The lack of

this important feedback may lead to overestimated litter nutrient concentrations in nutrient-poor sites and underestimated concentrations in nutrient-rich ones, with consequences for simulated long-term ecosystem development and nutrient cycling.

Conclusions

Our new global database of nutrient contents in green and senesced leaves allowed us to compute resorption efficiencies across plant types and climates, accounting for mass loss during senescence. We showed a consistent pattern of leaf mass loss during senescence in terrestrial plants and how neglecting it can lead to underestimating nutrient resorption. Based on our global database, overall C, N, P, K, and Mg resorption depends on nutrient-status, with relatively more nutrients resorbed at lower leaf nutrient concentrations, in agreement with a leaf-economics perspective. Based on the relative amount of element resorbed during senescence, the elements studied here can be split into two groups: $\overline{NR}$, $\overline{PR}$, and $\overline{KR}$ had the highest global resorption efficiencies (62.1%, 64.9%, and 70.1%, respectively) and $\overline{CaR}$, $\overline{CR}$, and $\overline{MgR}$ had the lowest (10.9%, 23.2%, and 28.6%, respectively). We also found that resorption efficiencies clearly differed among plant growth types, with graminoids resorbing relatively more nutrients and evergreen woody angiosperms resorbing relatively less. In regard to climate, our results indicate that the same growth form growing in different climates can show different resorption efficiencies and that the climate characteristic with the greatest influence on NuR is mean annual temperature. Overall, our new global estimates for nutrient concentrations and resorption efficiencies should improve models that explicitly represent the cycling of C and nutrients, particularly N and P. They should also allow the modeling community to represent the coupling of other nutrient cycles more explicitly within plants and ecosystems.

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Supplemental Material

Appendix

Tables and figures reporting correlations between nutrient concentrations and resorption efficiencies and climatic variables (altitude, mean annual temperature, and mean annual precipitation) (*Ecological Archives* M082-008-A1).

Data Availability

Data associated with this paper have been deposited in the Oak Ridge National Laboratory Distributed Archive Center (ORNL DAAC): http://daac.ornl.gov