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Rebecca E. Drenovsky Nicole Pietrasiak Thomas H. Short

Abstract

Aim: Leaf nutrient resorption is a key nutrient conservation trait, which also influences nutrient cycling rates and pools. Most global biogeochemical models assume that resorption is non-varying at a temporal scale. However, this trait can differ substantially within populations among years. We assessed the commonality of attaining proficient resorption, the factors associated with proficient resorption, as well as the variability of this trait and the factors controlling trait variability.

Location: Global.

Time period: 1965–2009.

Major taxa studied: Plants.

Methods: We compiled multi-year nutrient resorption data from the literature, representing 50 studies, 94 unique study locations, and 141 species from 53 families and 29 orders. We used multiple linear regression to relate resorption data, as well as the variability in this trait, expressed as the coefficient of variation, to environmental factors.

Results: Resource availability was a key driver of resorption, with nutrient-poor soils associated with more complete resorption and lower resorption plasticity. Nitrogen and phosphorus resorption differentially responded to some drivers, such as leaf habit, soil order and mycorrhizal status.

Main conclusions: Overall, environmental and biological factors representing a strong selective force for nutrient conservation, such as nutrient-poor soil orders, semi-arid soil moisture regimes, or lack of plant mutualists, were associated with complete resorption, whereas incomplete resorption was associated with weak selective forces, such as nutrient-rich soil orders, or factors impeding this physiological process (e.g., drought). Inter-annual variability in resorption was common, particularly for phosphorus. This plasticity has implications for ecosystem nutrient cycling and plant productivity, and accounting for this plasticity in dynamic models of nutrient cycling will improve predictions of nutrient limitations and productivity under future climate conditions.

KEYWORDS

leaf litter, nitrogen, nutrient recycling, phosphorus, retranslocation, senesced leaves

1 | INTRODUCTION

Worldwide, soil nutrient availability limits plant performance (Lambers, Chapin, & Pons, 2008; Wang, Law, & Pak, 2010). Soil nutrient limitations arise from a variety of factors, including climate, soil age and

parent material (Huston, 2012) and can act as a strong selective force for plant nutrient conservation traits (Aerts & Chapin, 2000; Anacker, 2011; Drenovsky, Koehler, Skelly, & Richards, 2013). Depending on resource availability, plants deploy leaves that differ strongly in their leaf economy, with nutrient-rich soils selecting for fast-growing species that produce ‘cheap’ tissues (i.e., low in structural and defensive

compounds) and nutrient-poor soils selecting for slow-growing species that produce 'costly' tissues (Wright et al., 2004). Therefore, plants at opposite ends of the leaf economics spectrum differ in tissue longevity and plant nutrient demand. Likewise, nutrient conservation is expected to differ between species from nutrient rich and poor sites, as plant nutrient resorption is one of the most important nutrient conservation traits (Eckstein, Karlsson, & Weih, 1999; Yuan & Chen, 2009). Through the resorption process, biomolecules in senescing tissues are broken down and retranslocated to growing tissues or storage organs (Aerts, 1996; Killingbeck, 1996). Reuse and storage of nutrients from senescing tissues can buffer the plant from variations in inter-annual soil nutrient availability, minimizing plant reliance on soil nutrient supply. Greater resorption has been correlated with greater whole plant nutrient retention (Eckstein et al., 1999) and fitness (Aerts, 1996; May & Killingbeck, 1992), and in some cases, interspecific differences in resorption may have led to niche differentiation (Drenovsky & Richards, 2006) or even conferred a competitive advantage (Fahey, Battles, & Wilson, 1998) under nutrient limiting conditions.

Despite the importance of resorption for whole-plant nutrient conservation and plant performance, significant inter-annual variability in this trait is observed (Drenovsky et al., 2013; Killingbeck, 1996; Nordell & Karlsson, 1995). Killingbeck (2004) proposed that species can differ in their potential resorption (i.e., maximal nutrient translocation for that species) and their realized resorption (i.e., the amount resorbed in any given year). In his model, long-term evolutionary factors such as long-term site fertility and complementary nutrient conservation and acquisition adaptations are drivers of potential resorption. These long-term factors may be represented by characteristics of a system, such as biome, soil moisture regime, or latitude, or by traits of the focal taxon, such as leaf habit, mycorrhizal status or functional group. In contrast, short-term changes in environmental factors, such as inter-annual variability in soil fertility or water availability, or physiological or phenological factors, such as timing of abscission or green leaf nutrient concentrations, are drivers of realized resorption and thus temporal variability in this trait. This distinction between potential and realized resorption is significant, as it suggests that in most years, plants are unlikely to reach their maximum potential resorption due to short-term factors limiting realized resorption (Killingbeck, 2004).

Despite hypothesized differences between realized and potential resorption, few studies have investigated this temporal variability. In a meta-analysis of factors driving resorption, only c. 5% of the included studies were conducted for more than 1 year (Yuan & Chen, 2009). Where data exist, however, inter-annual variation has been significant. For example, data from a 6-year field survey of California chaparral shrubs and trees (Drenovsky et al., 2013) and a 3-year field survey of Great Basin and Mojave Desert shrubs (Drenovsky, James, & Richards, 2010) indicated that the coefficient of variation for N and P resorption proficiency ranged from 13–97% across the 33 taxa studied. Temporal patterns in N and P resorption were not similar among species within these studies, suggesting that variation in N and P resorption may respond to different drivers. Furthermore, variation was

not well correlated with climate (temperature and precipitation), indicating these traits may depend on synergistic effects of multiple factors, including soil properties, climate drivers and plant morphology (Drenovsky et al., 2010). Importantly, all but two species included in these studies had at least one individual attain complete N resorption proficiency (in which 'complete' resorption represents < 7 g/kg leaf litter N and indicates high resorption proficiency, *sensu* Killingbeck, 1996), with similar trends observed for P resorption proficiency. These data underscore the need for multi-year data sets to determine potential resorption. Without multiple years of assessment, potential resorption for many species would have been underestimated. Only through repeated, annual sampling is it possible to determine potential resorption in a species, the range of realized resorption, and the environmental and biological factors driving this process over time.

To address the potential factors influencing realized and potential resorption, we compiled a global data set including only multi-year studies. We posed three main research questions: (a) How common are complete resorption of N and P (i.e., how likely are plants to achieve potential resorption)? (b) are N and P resorption linked to plant nutrient status, each other, or with environmental or biological factors? (c) How plastic are N and P resorption? Based on previous studies, we expected complete resorption to be rarer than incomplete resorption in most years, but that the likelihood of achieving complete resorption would be correlated with poorer plant nutrient status and lower soil nutrient availability.

2 | MATERIALS AND METHODS

2.1 | Data set

We compiled our global data set by searching for studies including two or more years of resorption proficiency data using Web of Science (publication years spanning from 1965 to 2014), and the search terms 'resorption', 'senesced leaf', 'litter' and 'retranslocation'. Published meta-analyses were reviewed for additional citations (e.g., Killingbeck, 1996; Yuan & Chen, 2009). Resorption proficiency was defined as the nutrient concentration in senesced leaf tissue (*sensu* Killingbeck, 1996). Studies were included in our data set if they met the following conditions: (a) ≥ 2 years of senesced leaf N and/or P data were included, (b) leaf nutrient data were reported by species (not community), (c) species identity was available for data reported, (d) data were collected from unfertilized, non-irrigated plants under natural conditions. Our data set represents 50 studies (29 of which were conducted for three or more years), 94 unique study locations, 141 species from 53 families and 29 orders, and most common functional groups (grasses, forbs, shrubs and trees). Most of the studies were conducted in North America and Europe, but most major biomes were represented by the data set (Figure 1). Temperate biomes were most strongly represented in the data set, followed by Mediterranean systems and deserts; tropical, subtropical, taiga, tundra and wetland systems were least represented in the data set (Table 1). No studies included sites from montane grasslands and shrublands. Please see Appendix 1 for resorption data sources.

FIGURE 1 Global map of sampling locations. In some cases, small distances between sampling locations led to overlapping symbols. Two sampling locations are located in southern Japan; sixteen in South America; three in New England, USA; four in northern Michigan, USA; six in northeast Spain; four in southern France; and six in Scotland

TABLE 1 Biome representation among study sites. For locations, refer to Figure 1

Biome	No. sites
Boreal forests/taiga	1
Deserts and xeric shrublands	8
Flooded grasslands and savannas	1
Mangroves	2
Mediterranean forests, woodlands and scrub	13
Temperate broadleaf and mixed forests	48
Temperate conifer forests	8
Temperate grasslands, savannas and shrublands	8
Tropical and subtropical dry broadleaf forests	2
Tropical and subtropical moist broadleaf forests	1
Tundra	2
Total	94

For each study, we recorded senesced leaf nutrient concentrations on a mass basis. For a limited number of studies (four), data were presented on an area basis. These values were converted to mass-based values using leaf mass area presented in the paper or

in related papers. In two cases, data were presented as rates of nutrient loss in litterfall. These values were converted to concentrations using the litterfall mass rates reported in the manuscript. Additionally, green leaf N and P concentrations (g/kg), locality (e.g., latitude and longitude), climate (mean annual precipitation, MAP; mean annual temperature, MAT; yearly precipitation; yearly mean annual temperature), elevation, soil chemistry (total soil N, g/kg; extractable soil P, g/kg; soil pH) data were recorded where available. Data from figures were extracted using DATA THIEF v3 (Turners, 2006). Additionally, yearly precipitation and temperature data were obtained from the National Oceanic and Atmospheric Administration Data Climate Center for 44 sites, using data from the closest climate station (38 sites < 25 km from weather station; all sites < 40 km from nearest weather station). For most sites, time since last disturbance was not available, except for some forested sites, in which forest age was reported in the manuscript. Using ArcMAP 10.2 (ESRI, Redlands, CA), we extracted additional environmental data, including soil order, soil temperature regime, soil moisture regime, biome, potential evapotranspiration, soil pH, and elevation (see Appendix 2 for data sources). We applied soil order, soil temperature regime and soil moisture regime definitions and classifications as described by United States Department of Agriculture-Natural Resources Conservation Service

(USDA-NRCS) soil taxonomy (Soil Survey Staff, 2014). Soil temperature regimes represent categorical levels describing the mean annual soil temperature at the upper 50 cm of soil, unless soil is shallower due to the presence of bedrock. In comparison, soil moisture regimes represent categories that define conditions related to the presence or absence of groundwater or the duration of drought conditions in the soils, in which drought is defined as moisture content less than 1500 kPa (Soil Survey Staff, 2014). Thus, these data describe patterns in these abiotic factors, rather than actual values. Biome categorical levels were based on World Wildlife Fund (WWF) classifications (<https://www.worldwildlife.org/biome-categories/terrestrial-ecoregions>). We included these categorical variables because they represent potential synergistic or emergent properties of systems that cannot be represented by mean values. For example, MAP does not encapsulate when soil moisture is biologically available to plants or its variability across years. However, categorical variables, such as soil moisture regime and biome can represent these properties. We assumed the World Geodetic System (WGS) 1984 coordinate system and World Eckert IV projection to process our spatial data. To account for differences in spatial extent of the various studies included, we categorized each study into one of three groups: (a) < 5 km radius, (b) c. 5–10 km radius, and (c) > 10 km radius, and based on the resolution of our maps in these categories. Most of the sites (> 80%) were categorized in the first group, with the smallest spatial extent. Subsequently, we created corresponding buffer zones around the GPS location of each study site using the proximity tool of the ArcMAP analysis toolbox. To extract values of our environmental data that would correspond to each of our study locations we then used the extract and overlay toolset, depending on the data type. Specifically, we applied the extract tool for continuous variables such as elevation and calculated a mean value for each buffer using the raster data of the specific environmental variable. For categorical data such as soil order, biome, soil moisture regime etc., we utilized the overlay tool. In cases in which the buffer zone intersected more than one category type, we reduced the extracted types to one single value for each buffer zone as follows: first, we calculated the area of each category type and then applied the majority rule to obtain the type that best represented the study site.

2.2 | Statistical analysis

Results of statistical tests of significance are accompanied by estimates of effect size, to represent the magnitudes of associations without the confounding influence of sample size. For univariate categorical data, effect size is represented by the odds in favour of the focal outcome (complete resorption). For cross-tabulations of binary categorical variables, effect size is represented by the odds ratio. In multiple linear regression models, effect size is indicated by the values of Type III partial R^2 . These values represent the proportion of variation accounted for by each of the independent variables, including both categorical and continuous predictors.

Following Killingbeck (1996), all N and P resorption proficiency data were coded as either 'complete' or 'intermediate + incomplete'.

We refer to the latter category as 'incomplete'. The proportion of years in which complete resorption occurred per species per study was computed and represents a dependent variable outcome. We used these data to address whether the proportions of years in which N or P complete resorption occurred were correlated. To investigate the factors linked to complete resorption, we used correlation analysis to relate plant nutrient status (as estimated by green leaf N and P) to plant nutrient resorption (as estimated by senesced leaf N and P), as well as N and P resorption to each other, per species per study.

We also examined the relationship between environmental and biological variables and complete resorption (replication for categorical predictor variables reported in Table 2). Principal components analysis (PCA) was applied to the continuous environmental predictor variables (MAP, MAT, latitude, soil pH, potential evapotranspiration, and elevation), resulting in three components that generally represent climate, geography, and soil pH. Site age was not included in our models, as this information was available for < 20% of our sites and was not significantly correlated with senesced leaf N or P at these sites (data not shown). Multiple linear regression models based on the categorical environmental predictor variables and the three principal components – climate, geography and pH – were fit separately to the proportions of years in which complete resorption occurred for N and P. All regression models used weighted least squares to account for differing numbers of years sampled, per species per study. Effect sizes for the linear models are represented by Type III partial R^2 values and three principal components used in the linear models. Non-significant predictors were culled from the linear models using backward elimination strategies.

We also explored the plasticity of N and P resorption, using the coefficient of variation (CV) of this trait within species and study site. The CV for N resorption proficiency was correlated with the CV for P resorption proficiency, per species per study. The CVs were transformed by logarithms (base 10) due to skewness in their distributions. A paired-samples *t* test was used to determine whether the mean variabilities in resorption proficiency (CVs) for N and P were equivalent. Linear models based on the selection from the set of categorical environmental predictor variables and the three principal components were fit separately to the log-transformed CVs for N and P. All data were analysed using sas v9.4 (Cary, North Carolina).

3 | RESULTS

3.1 | How common is complete resorption?

First, we investigated species responses within a study, assessing whether complete resorption occurred in at least one year of the study for either N or P (i.e., did a species ever achieve complete resorption during the study). Based on these data, incomplete and complete N resorption were equally likely to occur, occurring in 54.7 and 45.3% of cases, respectively (odds in favour of complete

TABLE 2 Replication by species and site for significant categorical variables included in regression models

Category	Predictor variable	Replication by species & site (full data set)
Biome		
	Boreal forests/taiga	2
	Deserts and xeric shrublands	19
	Flooded grasslands and savannas	1
	Mangroves	6
	Mediterranean forests, woodlands and scrub	20
	Temperate broadleaf and mixed forests	39
	Temperate conifer forests	32
	Temperate grasslands, savannas and shrublands	31
	Tropical and subtropical dry broadleaf forests	25
	Tropical and subtropical moist broadleaf Forests	3
	Tundra	7
Functional group		
	Fern	1
	Grass	11
	Perennial forb	10
	Shrub	60
	Shrub-tree	3
	Tree	100
Leaf habit		
	Broadleaf	124
	Conifer	61
Mycorrhizal status		
	Arbuscular mycorrhizal	67
	Ectomycorrhizal	68
	Non-mycorrhizal	19
	Other	43
N-fixing status		
	N-fixing	24
	Not N-fixing	161
Soil moisture regime		
	Aridic	20
	Interfrost	10
	Perudic	3
	Udic	74
	Ustic	50
	Xeric	26
Soil order		
	Alfisols	29
	Andisols	14
	Aridisols	5
	Entisols	42
	Histosols	1
	Inceptisols	53
	Mollisols	25
	Oxisols	3

(Continues)

TABLE 2 (Continued)

Category	Predictor variable	Replication by species & site (full data set)
	Spodosols	6
	Ultisols	5
	Vertisols	2
Soil temperature regime		
	Cryic	11
	Cryic/mesic	4
	Frigid	1
	Hyperthermic	2
	Isohypothermic	10
	Isomegathemic	25
	Mesic	75
	Pergelic	10
	Thermic	47

resorption = .83:1, $p = .29$; Table 3). In contrast, incomplete P resorption more commonly occurred than complete P resorption, occurring in 64.9 and 35.1% of cases, respectively (odds in favour of complete resorption = .54:1, $p < .0001$; Table 3). Second, we determined the proportion of years within a study in which complete resorption occurred for a species (i.e., how frequently did a species achieve complete resorption during a study). On average, complete N resorption occurred in approximately one-third of the years studied (32.1%), and complete P resorption occurred in approximately one-quarter of the years studied (25.7%).

3.2 | Are N and P resorption linked to plant nutrient status, each other, or environmental or biological factors?

Particularly for N resorption, plant nutrient status (as evidenced by green leaf nutrient concentration) was positively correlated with senesced leaf nutrient concentrations (Figure 2a,b). As a result, plants with greater green leaf N or P tended to senesce leaves higher in nutrients. However, there was a non-significant relationship between senesced leaf N and P concentrations, suggesting that across values representing the incomplete to complete resorption range, resorption of these nutrients is not strongly linked (Figure 2c). Although

TABLE 3 Cross-tabulations for complete and incomplete N and P resorption proficiency ($N = 148$ observations total). Counts for complete resorption occurred at least once per species per study; counts for incomplete resorption indicate that complete resorption was not measured for a species within the study period

Nitrogen	Phosphorus		Total
	Incomplete	Complete	
Incomplete	60	21	81
Complete	36	31	67
Total	96	52	148

this relationship becomes significant when the six outliers are removed ($r = .32$, $p < .0001$; data not shown), the correlation between senesced leaf N and P is only moderate. Of interest for potential further study, five of the six outliers are ectomycorrhizal species, representing just over 7% of the ectomycorrhizal samples. When we consider the likelihood of complete resorption (a discrete variable), the occurrence of complete N resorption is positively associated with complete P resorption, based on contingency table analysis ($\chi^2_1 = 6.66$; $p = .01$; Phi coefficient = 0.212; Table 3). Likewise, if we investigate the proportion of years in which complete N and P resorption occurred for a species within a study, these proportions are positively correlated ($r = .276$, $p < .001$). Thus, both the occurrence and frequency of complete N and P resorption are positively associated.

Based on multiple regression models, greater frequency of complete N resorption was significantly associated with soil order (partial $R^2 = 15.5\%$, $p = .0003$), biome (partial $R^2 = 14.9\%$, $p = .0003$), soil moisture regime (partial $R^2 = 11.7\%$, $p = .0002$), functional group (partial $R^2 = 9.5\%$, $p = .0011$), N fixing status (partial $R^2 = 4.3\%$, $p = .0032$), leaf habit (broadleaf versus conifer; partial $R^2 = 3.4\%$, $p = .0081$), and 'Geography' (PCA factor 3, partial $R^2 = 3.4\%$, $p = .0079$). Considering sample size and significance within levels of soil order, complete N resorption was predicted to occur most frequently in plants growing on entisols and to occur least frequently in plants growing on andisols (Figure 3a). Although not well replicated in the data set, complete N resorption rates were also high for vertisols and low for ultisols and aridisols. Complete N resorption was predicted to occur most frequently in plants growing in mangroves, and to occur least frequently in plants growing in Mediterranean forests, woodlands and scrublands (Figure 3b). Although not well replicated in the data set, complete N resorption rates were also low for tropical and subtropical moist broadleaf forests, tundra, and deserts and xeric shrublands. Xeric and ustic soil moisture regimes were associated with more frequent complete N resorption, whereas aridic and interfrost soil moisture regimes were associated with less frequent complete N

FIGURE 2 Relationships between N resorption and plant N status ($n = 2-6$ per species) (a), P resorption and plant P status ($n = 2-4$ per species) (b), and N and P resorption ($n = 2-6$ per species) (c). Senesced leaf nutrient concentrations reflect nutrient resorption proficiency. Data are means $\pm$ SE

resorption (Figure 3c). Perudic soils were the most variable, having a standard deviation as great as the mean response. Grasses frequently achieved complete N resorption, whereas perennial forbs were unlikely to attain complete N resorption (Figure 3d). N-fixing plants were less likely to achieve complete resorption than plants

incapable of N fixation (Figure 3e). Furthermore, conifers achieved complete N resorption more frequently than broadleaf plants (Figure 3f). The significant, positive coefficient of the 'Geography' component indicates that greater likelihood of complete resorption was associated with higher elevations and lower latitudes. All of these results are conditional on all of the predictors being in the model simultaneously.

Greater frequency of complete P resorption was significantly associated with biome (partial $R^2 = 13.6\%$, $p = .0019$), soil order (partial $R^2 = 11.3\%$, $p = .0143$) and mycorrhizal status (partial $R^2 = 6.8\%$, $p = .0039$). Although not well replicated in the data set, plants from flooded grasslands and savannas more frequently achieved complete P resorption than plants from other biomes; complete P resorption occurred least frequently in plants from deserts and xeric shrublands (Figure 4a). Complete P resorption rates were also low for plants from temperate coniferous forests, temperate grasslands, savannas and shrublands, and tropical and subtropical dry broadleaf forests. Complete P resorption was predicted to occur most frequently in plants growing on aridisols and to occur least frequently in plants growing on histosols (Figure 4b). Although not well replicated in the data set, complete P resorption rates represented were also high for oxisols and low for spodosols and vertisols. Non-mycorrhizal plants more frequently achieved complete P resorption compared to plants with either arbuscular mycorrhizae or ectomycorrhizae (Figure 4c).

3.3 | How plastic are N and P resorption?

Based on a paired samples t test, P resorption was more variable, on average, than N resorption (t value = 4.45, $p < .001$; Figure 5a). However, species with more variable P resorption also tended to have more variable N resorption ($r = .39$, $p < .001$; Figure 5b). Based on multiple regression analysis ($R^2 = 20.6\%$, $F_{10,149} = 3.87$, $p = .0001$), N resorption plasticity was associated with biome (partial $R^2 = 18.0\%$, $p = .0003$) and leaf habit (broadleaf versus conifer; partial $R^2 = 2.7\%$, $p = .0270$). Based on parameter estimates, plants growing in tropical and subtropical moist broadleaf forests and deserts and xeric shrublands, as well as broadleaf plants, were associated with greater variability in N resorption (Table 4).

Likewise, multiple regression analysis ($R^2 = 61.7\%$, $F_{13,48} = 5.96$, $p < .0001$) indicated that P resorption plasticity was associated with soil order (partial $R^2 = 21.5\%$, $p = .0011$), biome (partial $R^2 = 26.9\%$, $p < .0001$) and 'Geography' (PCA factor 3, partial $R^2 = 7.0\%$, $p = .0048$). According to parameter estimates, plants growing on alfisols and inceptisols, those at lower elevation and higher latitudes, and those growing in tropical and subtropical moist broadleaf forests tended to have more variable P resorption (Table 5).

4 | DISCUSSION

4.1 | How common is complete resorption?

In this study, we wanted to understand how commonly complete resorption occurs and the factors associated with it. We addressed

FIGURE 3 Proportion of years in which complete N resorption occurred as related to significant environmental variables, including (a) soil order ($n = 1-42$), (b) biome ($n = 2-30$), (c) soil moisture regime ($n = 3-35$), (d) functional group ($n = 1-36$), (e) N-fixing status ($n = 6-97$), (f) leaf habit ($n = 10-93$). Abbreviations: Bor For = boreal forest; Des Xer Shr = desert and xeric shrublands; Med For Shr = Mediterranean forests and shrublands; Temp Br For = temperate broadleaf forests; Temp Con For = temperate coniferous forests; Temp Sav Gr Shr = temperate savannas, grasslands, and shrublands; Tr Subtr Moist For = tropical and subtropical moist forests. Data are means $\pm$ SE

this question in two ways – first, we asked, did complete resorption ever occur among the years a species was sampled at a given site (a discrete comparison), and second, how frequently did complete resorption occur for a species at a given site (a continuous comparison)? Complete and incomplete N resorption were equally likely outcomes, with complete N resorption occurring in approximately

one-third of the sampled years for species. In contrast, complete P resorption was less likely to occur than incomplete P resorption, and it was observed in only about one-quarter of the years investigated across species and studies. Poorer P resorption may be related to the greater number of temperate studies included in our analysis, relative to other more P-limited systems, such as tropical forests. However,

FIGURE 4 Proportion of years in which complete P resorption occurred as related to significant environmental variables, including (a) soil order ($n = 1-41$), (b) biome ($n = 1-32$) and (c) mycorrhizal status ($n = 13-61$). Abbreviations: AM = arbuscular mycorrhizal fungi; Bor For = boreal forests; Des Xer Shr = desert and xeric shrublands; ECM = ectomycorrhizal fungi; Fl Gr Sav = flooded grasslands and savannas; Med For Shr = Mediterranean forests and shrublands; NM = non-mycorrhizal; Temp Br For = temperate broadleaf forests, Temp Con For = temperate coniferous forests; Temp Sav Gr Shr = temperate savannas, grasslands, and shrublands; Tr Subtr Dry For = tropical and subtropical dry forests, Tr Subtr Moist For = tropical and subtropical moist forests. Data are means $\pm$ SE

even in studies with greater sampling of tropical systems (i.e., those including studies with a single year of data), the median senesced leaf P concentration was 5 g/kg (based on supplemental data from Yuan & Chen, 2009), which is above the complete resorption range for evergreen species and equivalent to the complete resorption range for deciduous species. Furthermore, the 25th quantile for senesced leaf P was 3.5 g/kg, suggesting that our estimate of complete P resorption occurring in approximately one-quarter of cases across biomes is similar to what is observed even in P-limited systems, such as the tropics. Therefore, overall, our data suggest that incomplete N and P resorption is common, even at sites where species can achieve complete resorption in some years.

4.2 | Are N and P resorption linked to plant nutrient status, each other, or environmental or biological factors?

Our results suggest that leaf N and P resorption may respond to different environmental drivers within species, sites and years. In support, we observed that senesced leaf N and P concentrations were not significantly correlated within the same sampling year in our full data set, despite a significant correlation between green leaf N and P concentrations (data not shown). These data were only moderately correlated when outliers, most of which represented ectomycorrhizal species, were temporarily excluded. However, when we

FIGURE 5 Histogram depicting variability in N and P resorption, (a) as indicated by the coefficient of variation (CV) among years within a species and study, and (b) relationship between variability in N and P resorption, as indicated by the CV among years within a species and study

investigated the likelihood of the same species achieving complete N and P resorption within the same study period – although not necessarily the same year – we observed a positive relationship between these two elements. These seemingly contradictory outcomes parallel early research probing the physiological factors limiting nutrient resorption (Brant & Chen, 2015), in which authors uncovered conflicting results regarding the interdependence of N and P resorption (Killingbeck, 1996). We propose that these conflicting results may stem from N and P resorption being independently regulated by biochemical, physiological or environmental limitations in a given year. Only with multiple years of study is it possible to detect patterns in complete N and P resorption. For example, variable access to mutualists, differential need for compatible solute accumulation in response to drought or soil salinity, and disparities in the strength of N or P limitations may differentially impact resorption of one element over the other in a given year (Killingbeck, 2004). In other words, although complete N and P resorption may occur within a species at the same site, they may not occur during the same growing season due to differential drivers for each element.

In general, incomplete N and P resorption were associated with greater plant nutrient status, as indicated by greater green leaf nutrients. These results point to the importance of long-term selective forces, such as site fertility, in driving patterns of potential

resorption (Killingbeck, 2004). In support, complete N resorption was influenced by multiple factors limiting soil nutrient availability. Plants growing on recently developed, N-poor soils, such as entisols, were associated with complete N resorption. Likewise, clay-rich vertisols were associated with complete N resorption. Vertisols tend to tightly fix ammonium to clay minerals due to high negative charges in tetrahedral crystal sheets of smectite clays (Chen, Turner, & Dixon, 1989) while losing nitrogen due to high denitrification rates when saturated (Reid-Soukup & Ulery, 2002). In contrast, plants growing on nutrient-rich andisols, well-developed ultisols or water-limited aridisols were associated with poor N resorption. Plants from higher elevations also tended to be associated with complete N resorption, likely due to poor soil N availability in these geologically young and shallow soils where colder temperatures at higher elevations can limit soil nutrient cycling (Liu et al., 2017; Pierre et al., 2017). Additionally, at high elevations, litterfall rates are lower, and plants from these regions tend to be evergreen (de Sousa-Neto et al., 2017; Lu & Lui, 2012). In contrast to other studies (Kang et al., 2010; Tang, Han, Chen, & Fang, 2013; Yuan & Chen, 2009), lower latitudes were associated with complete N resorption. It may be that our data set was limited by fewer high relative to low latitude sites, precluding our ability to detect stronger trends in latitudinal variation. Alternatively, lower latitudes may be associated with complete resorption due to the highly weathered, and thus nutrient-poor soils, located in these regions, leading to nutrients being tightly held in biomass via internal nutrient recycling processes.

Nitrogen resorption patterns also were related to environmental factors influencing biome distribution. Although plants from nutrient-limited mangroves tended to be associated with complete N resorption (Reef, Feller, & Lovelock, 2010), plants from tundra and desert and xeric shrublands were not. Due to their short growing season and slow growth, tundra plants often exhibit luxury consumption (e.g., van Wijk, Williams, Gough, Hobbie, & Shaver, 2003), raising green leaf nutrient concentrations and potentially limiting resorption. In desert and xeric species, plasticity in senesced leaf N is common (e.g., Killingbeck, 1993; Drenovsky et al., 2010), likely due to inter-annual variation in precipitation and thus soil nutrient availability.

Given the trends observed between complete N resorption and biome, it is not surprising that extremes in soil moisture were less likely to be associated with complete N resorption. Aridic soils, which are dry for at least 90 days per year, likely caused significant drought, leading to incomplete N resorption (Khasanova, James, & Drenovsky, 2013), and perudic soils (in which precipitation exceeds evapotranspiration) may have been sufficiently saturated to disrupt physiological processes necessary for nutrient translocation. For example, low oxygen, flooded soils can lower aerobic root respiration and thus impede ATP production (Lambers et al., 2008), which is required for biomolecule catabolism and transport.

Leaf P resorption responded to different drivers than leaf N resorption, with complete P resorption most strongly associated with biome, soil order, and mycorrhizal status. Although replication was rather low, plants from flooded grasslands and savannas were more likely to achieve complete P resorption, perhaps due to reduced P

Parameter	Estimate (β)	Standard error	t value	p
Intercept	-0.575	0.192	-2.99	.003
Broadleaf (BL)/conifer (C): BL	0.203	0.091	2.23	.027
Broadleaf/conifer: C	0	-	-	-
Biome: deserts and xeric shrublands	0.156	0.19	0.82	.412
Biome: flooded grasslands and savannas	-0.209	0.449	-0.47	.641
Biome: mangroves	-0.177	0.245	-0.72	.472
Biome: Mediterranean forests, woodlands and scrub	-0.242	0.19	-1.28	.204
Biome: temperate broadleaf and mixed forests	-0.062	0.185	-0.33	.738
Biome: temperate conifer forests	0.053	0.177	0.3	.766
Biome: temperate grasslands, savannas and shrublands	-0.112	0.183	-0.61	.54
Biome: tropical and subtropical dry broadleaf forests	-0.346	0.185	-1.86	.064
Biome: tropical and subtropical moist broadleaf forests	0.218	0.261	0.83	.406
Biome: tundra	0	-	-	-

Note. Significant parameter estimates ($p < .05$) in bold.

TABLE 4 Parameter estimates from multiple regression of log coefficient of variation (CV) senesced leaf N

uptake under flooded conditions (Armstrong & Drew, 2002; Chen, Mendelsohn, Lorenzen, Brix, & Mao, 2005; Kozłowski, 1984). In contrast, complete P resorption occurred less frequently in plants from temperate coniferous forests, where mycorrhizal colonization of plants roots is high. Also, greater mineralization of P relative to N in forested ecosystems (Marklein et al., 2016) may have decreased the selective pressure for proficient P resorption in plants from this biome. Complete P resorption occurred frequently in plants growing on soil types typically limited in P, such as water-limited, alkaline aridisols and highly weathered oxisols. Soils low in soil moisture create a tortuous pathway for soil P movement due to their low effective diffusivity (Marschner & Rengel, 2012), and the alkaline conditions of aridisols and the Al and Fe oxides of oxisols can strongly bind P to minerals, making it unavailable to plants even when soil moisture is available. In contrast, complete P resorption less frequently occurred in plants growing on organic matter-rich histosols.

Not surprisingly, non-mycorrhizal plants more frequently achieved complete P resorption than plants with arbuscular or ectomycorrhizal mutualists. Lacking fungal partners to help non-mycorrhizal plants obtain soil P likely generates a strong selective force for proficient P resorption (Killingbeck, 2004). This same trend was observed on a smaller scale in a study comparing asters and chenopods from the Mojave and Great Basin Deserts (Drenovsky et al., 2010) and another comparing 10 woody species from Andean-Patagonian forests (Diehl, Mazzarino, & Fontenla, 2008). Although data for seven non-mycorrhizal species from these studies were included in this meta-analysis, the trend held when an additional 11 species from nine unique studies were included in the current study.

Overall, we observed consistent patterns in the drivers of complete and incomplete N and P resorption. For both nutrients, complete resorption was commonly associated with low soil nutrient availability, creating a strong selective force for this important nutrient conservation process. Patterns in incomplete resorption, however, were more nuanced. In some cases, incomplete resorption occurred due to factors leading to weak selection for this trait, such as temperate, high nutrient soils or availability of mutualistic partners (i.e., the plants have less 'need' for proficient resorption). In other cases, environmental or other factors limited the physiological mechanisms enabling this process (i.e., the plants were restricted in their ability to achieve proficient resorption). For example, drought can negatively impact plant water balance and thus the export processes required for nutrient resorption out of leaves and into storage tissues (Khasanova et al., 2013), yielding poor resorption proficiency.

4.3 | How plastic are N and P resorption?

Not only was complete N resorption more common than complete P resorption, there was also less plasticity in N resorption than P resorption. N is required in higher concentrations than P to support plant growth and fitness (Hawkesford et al., 2012) and is the most limiting nutrient to plants in many biomes worldwide (Aerts & Chapin, 2000). N resorption plasticity was most strongly associated with leaf habit and biome. In general, N resorption proficiency was less variable in coniferous versus broadleaf plants, similar to results for nutrient resorption efficiency (Aerts & Chapin, 2000), emphasizing the importance of long-lived, evergreen leaves for plants growing on low

TABLE 5 Parameter estimates of log coefficient of variation (CV) senesced leaf P

Parameter	Estimate (β)	Standard error	t value	p
Intercept	0.611	0.55	1.11	.272
Soil order: alfisols	0.476	0.354	1.34	.186
Soil order: andisols	-0.6	0.411	-1.46	.151
Soil order: aridisols	0.069	0.573	0.12	.905
Soil order: entisols	-0.003	0.37	-0.01	.993
Soil order: inceptisols	0.141	0.324	0.44	.665
Soil order: mollisols	-0.048	0.426	-0.11	.911
Soil order: ultisols	-0.876	0.524	-1.67	.101
Soil order: vertisols	0	-	-	-
Biome: deserts and xeric shrublands	0	-	-	-
Biome: mangroves	-0.931	0.465	-2	.051
Biome: Mediterranean forests, woodlands and scrub	-0.694	0.449	-1.55	.129
Biome: temperate broadleaf and mixed forests	-1.437	0.459	-3.13	.003
Biome: temperate conifer forests	-1.289	0.398	-3.23	.002
Biome: temperate grasslands, savannas and shrublands	-1.703	0.555	-3.07	.004
Biome: tropical and subtropical moist broadleaf forests	0	-	-	-
PCA factor 3 'Geography'	-0.34	0.115	-2.96	.005

Note. Significant parameter estimates ($p < .05$) in bold.

nutrient soils. Perhaps due to low replication in the data set, plants from tropical and subtropical moist forests were variable in their N resorption responses. However, in general, highly weathered tropical soils are considered to be more P-limited than N-limited and thus may not present a strong selective force for proficient N resorption. Plants growing in desert and xeric shrublands were also highly variable in their N resorption, with high inter-annual precipitation (Noy-Meir, 1973) potentially limiting N resorption in some years (Khasanova et al., 2013).

Phosphorus resorption plasticity was associated with soil order, biome, and geography. Less weathered inceptisols and nutrient-rich alfisols, as well as soils at lower elevations, were associated with greater plasticity, suggesting these soils do not provide a strong selective force for P resorption and may contribute to variable P resorption plasticity. Plants at high latitudes were also variable in P resorption; this outcome may reflect variation in green leaf P observed in high latitude plants (Reich & Oleksyn, 2004), given the positive correlation between green and senesced leaf P. Surprisingly, plants from typically P-limited tropical and subtropical moist broadleaf forests were variable in P resorption; this outcome may be related to the low replication of tropical sites in our data set and emphasizes the need for more long-term research in these highly threatened ecosystems.

5 | CONCLUSIONS

Overall, our data support the hypothesized drivers for potential and realized resorption proposed by Killingbeck (2004). Nutrient-poor soils, as evidenced by the significance of soil order and environmental factors influencing soil nutrient cycling, typically were associated with complete resorption and less plasticity in this leaf trait. Additionally, soil moisture availability and precipitation patterns influenced complete N resorption and its plasticity. These outcomes highlight the consistent patterns we observed – complete resorption is associated with the 'need' for this process (i.e., strong selective forces for nutrient conservation), whereas incomplete resorption is associated either with poor selective forces for nutrient conservation or factors impeding the ability to complete this process (e.g., drought).

Importantly, our data show strong patterns of resorption plasticity, suggesting complete resorption may not be the norm, particularly for P. Current dynamical models of global ecosystem nutrient cycling do not account for this type of variation, assuming resorption is equivalent across species and environmental conditions (Reed, Townsend, Davidson, & Cleveland, 2012; Vergutz, Manzoni, Porporato, Novais, & Jackson, 2012). Our data suggest that environmental factors, such as nutrient availability and soil moisture,

modulate resorption responses and can, in some cases, increase variation in this trait. However, in contrast to previous assumptions, our data also suggest that N and P resorption may respond differentially to these drivers. Including environmentally related variation in resorption and the potentially unique responses of N and P in dynamical ecosystem models should improve estimates of productivity and nutrient limitation under future global conditions.

We also identified gaps in the resorption literature that require future study. We observed that some biogeographic locations have been more intensely studied than others, with few studies of multi-year resorption patterns conducted in the Southern Hemisphere or wetland or flooded systems (including mangroves), and to our knowledge, no multi-year studies have been conducted in montane systems. Surprisingly, few multi-year studies have been carried out on heavily weathered soils such as oxisols and ultisols or strongly nutrient-limited systems such as tropical forests, boreal forests, and taiga. Given the anthropogenic pressures on these systems due to global climate change, it is imperative to understand the links between abiotic drivers, resorption, and ecosystem nutrient cycling and productivity in these regions.

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DATA ACCESSIBILITY

Resorption data were extracted from the manuscripts included in appendix 1, and geospatial data were extracted from the sources included in appendix 2.

REFERENCES

- Aerts, R. (1996). Nutrient resorption from senescing leaves of perennials: Are there general patterns? *Journal of Ecology*, 84, 597–608.
- Aerts, R., & Chapin, F. S. III (2000). The mineral nutrition of wildland plants revisited: A re-evaluation of patterns and processes. *Advances in Ecological Research*, 30, 1–66.
- Anacker, B. L. (2011). Phylogenetic patterns of endemism and diversity. In S. Harrison & N. Rajakaruna (Eds.), *Serpentine: The evolution and ecology of a model system* (pp. 49–70). Berkeley, CA: University of California Press.
- Armstrong, W., & Drew, M. C. (2002). Root growth and metabolism under oxygen deficiency. In Y. Waisel, A. Eshel, & U. Kafkafi (Eds.), *Plant roots: The hidden half* (pp. 1111–1169). Boca Raton, FL: CRC Press.
- Brant, A. M., & Chen, H. Y. H. (2015). Patterns and mechanisms of nutrient resorption in plants. *Critical Reviews in Plant Sciences*, 34, 471–486. <https://doi.org/10.1080/07352689.2015.1078611>
- Chen, C. C., Turner, F. T., & Dixon, J. B. (1989). Ammonium fixation by high-charge smectite in selected Texas Gulf coast soils. *Soil Science Society of America Journal*, 53, 1035–1040. <https://doi.org/10.2136/sssaj1989.03615995005300040008x>
- Chen, H., Mendelssohn, I. A., Lorenzen, B., Brix, H., & Mao, S. (2005). Growth and nutrient responses of *Eleocharis cellulosa* (Cyperaceae) to phosphate level and redox intensity. *American Journal of Botany*, 92, 1457–1466.
- de Sousa-Neto, E. R., Lins, S. R. M., Martins, S. C., de Cassia Piccolo, M., Ferreira, M. L., de Camargo, P. B., ... Martinelli, L. A. (2017). Litterfall mass and nutrient fluxes over an altitudinal gradient in the coastal Atlantic Forest, Brazil. *Journal of Tropical Ecology*, 33, 261–269. <https://doi.org/10.1017/S0266467417000207>
- Diehl, P., Mazzarino, M. J., & Fontenla, S. (2008). Plant limiting nutrients in Andean-Patagonian woody species: Effects of interannual rainfall variation, soil fertility and mycorrhizal infection. *Forest Ecology and Management*, 255, 2973–2980. <https://doi.org/10.1016/j.foreco.2008.02.003>
- Drenovsky, R. E., James, J. J., & Richards, J. H. (2010). Variation in nutrient resorption in desert shrubs. *Journal of Arid Environments*, 74, 1564–1568.
- Drenovsky, R. E., Koehler, C. E., Skelly, K., & Richards, J. H. (2013). Potential and realized nutrient resorption in serpentine and non-serpentine chaparral shrubs and trees. *Oecologia*, 171, 39–50. <https://doi.org/10.1007/s00442-012-2396-7>
- Drenovsky, R. E., & Richards, J. H. (2006). Low leaf N and P resorption contributes to nutrient limitation in two desert shrubs. *Plant Ecology*, 183, 305–314. <https://doi.org/10.1007/s11258-005-9041-z>
- Eckstein, R. L., Karlsson, P. S., & Weih, M. (1999). Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytologist*, 143, 177–189. <https://doi.org/10.1046/j.1469-8137.1999.00429.x>
- Fahey, T. J., Battles, J. J., & Wilson, G. F. (1998). Responses of early successional northern hardwood forests to changes in nutrient availability. *Ecological Monographs*, 68, 183–212. [https://doi.org/10.1890/0012-9615\(1998\)068\[0183:ROESNH\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1998)068[0183:ROESNH]2.0.CO;2)
- Hawkesford, M., Horst, W., Kichey, T., Lambers, H., Schjoerring, J., Skrumsager Møller, I., & White, P. (2012). Functions of macronutrients. In P. Marschner (Ed.), *Marschner's mineral nutrition of higher plants* (pp. 135–190). Cambridge, MA: Academic Press.
- Huston, M. A. (2012). Precipitation, soils, NPP, and biodiversity: Resurrection of Albrecht's curve. *Ecological Monographs*, 82, 277–296. <https://doi.org/10.1890/11-1927.1>
- Kang, H., Xin, Z., Berg, B., Burgess, P. J., Liu, Q., Liu, Z., ... Liu, C. (2010). Global pattern of leaf litter nitrogen and phosphorus in woody plants. *Annals of Forest Science*, 67, 811. <https://doi.org/10.1051/forest/2010047>
- Khasanova, A., James, J. J., & Drenovsky, R. E. (2013). Drought impacts plant water relations and nitrogen nutrition in aridland perennial grasses. *Plant and Soil*, 372, 541–552.
- Killingbeck, K. T. (1993). Nutrient resorption in desert shrubs. *Revista Chilena Historia Natural*, 66, 345–355.
- Killingbeck, K. T. (1996). Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. *Ecology*, 77, 1716–1727. <https://doi.org/10.2307/2265777>
- Killingbeck, K. T. (2004). Nutrient resorption. In L. D. Noodén (Ed.), *Plant cell death processes* (pp. 215–226). Amsterdam, the Netherlands: Elsevier.
- Kozłowski, T. T. (1984). Plant responses to flooding of soil. *BioScience*, 34, 162–167. <https://doi.org/10.2307/1309751>
- Lambers, H., Chapin, F. S. III, & Pons, T. L. (2008). *Plant physiological ecology*. New York, NY: Springer-Verlag.
- Liu, Y., Wang, C., He, N., Wen, X., Gao, Y., Li, S., ... Yu, G. (2017). A global synthesis of the rate and temperature sensitivity of soil nitrogen mineralization: Latitudinal patterns and mechanisms. *Global Change Biology*, 23, 455–464. <https://doi.org/10.1111/gcb.13372>

- Lu, S., & Liu, C. (2012). Patterns of litterfall and nutrient return at different altitudes in evergreen hardwood forests of Central Taiwan. *Annals of Forest Science*, 69, 877–886. <https://doi.org/10.1007/s13595-012-0213-4>
- Marklein, A. R., Winbourne, J. B., Enders, S. K., Gonzalez, D. J. X., van Huysen, T. L., Izquierdo, J. E., ... Houlton, B. Z. (2016). Mineralization ratios of nitrogen and phosphorus from decomposing litter in temperate versus tropical forests. *Global Ecology and Biogeography*, 25, 335–346.
- Marschner, P., & Rengel, Z. (2012). Nutrient availability in soils. In P. Marschner (Ed.), *Marschner's mineral nutrition of higher plants* (pp. 315–330). Cambridge, MA: Academic Press.
- May, J. D., & Killingbeck, K. T. (1992). Effects of preventing nutrient resorption on plant fitness and foliar nutrient dynamics. *Ecology*, 73, 1868–1878. <https://doi.org/10.2307/1940038>
- Nordell, K. O., & Karlsson, P. S. (1995). Resorption of nitrogen and dry matter prior to leaf abscission: Variation among individuals, sites, and years in the mountain birch. *Functional Ecology*, 9, 326–333. <https://doi.org/10.2307/2390581>
- Noy-Meir, I. (1973). Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics*, 4, 25–51. <https://doi.org/10.1146/annurev.es.04.110173.000325>
- Pierre, S., Hewson, I., Sparks, J. P., Litton, C. M., Giardina, C., Groffman, P. M., & Fahey, T. J. (2017). Ammonia oxidizer populations vary with nitrogen cycling across a tropical montane mean annual temperature gradient. *Ecology*, 98, 1896–1907. <https://doi.org/10.1002/ecy.1863>
- Reed, S. C., Townsend, A. R., Davidson, E. A., & Cleveland, C. C. (2012). Stoichiometric patterns in foliar nutrient resorption across multiple scales. *New Phytologist*, 196, 173–180. <https://doi.org/10.1111/j.1469-8137.2012.04249.x>
- Reef, R., Feller, I. C., & Lovelock, C. E. (2010). Nutrition of mangroves. *Tree Physiology*, 30, 1148–1160. <https://doi.org/10.1093/treephys/tq048>
- Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academies of Sciences USA*, 101, 11001–11006. <https://doi.org/10.1073/pnas.0403588101>
- Reid-Soukup, D. A., & Ulery, A. L. (2002). Smectites. In J. B. Dixon & D. G. Schulze (Eds.), *Soil mineralogy with environmental applications* (SSSA Book Series 7, pp. 501–526). Madison, WI: Soil Science Society of America.
- Soil Survey Staff. (2014). *Keys to soil taxonomy* (12th ed.). Washington, DC: USDA-Natural Resources Conservation Service.
- Tang, L., Han, W., Chen, Y., & Fang, J. (2013). Resorption proficiency and efficiency of leaf nutrients in woody plants in eastern China. *Journal of Plant Ecology*, 6, 408–417. <https://doi.org/10.1093/jpe/rtt013>
- Tummers, B. (2006). DataThief III. Retrieved from <http://datathief.org/>
- van Wijk, M. T., Williams, M., Gough, L., Hobbie, S. E., & Shaver, G. R. (2003). Luxury consumption of soil nutrients: A possible competitive strategy in above-ground and below-ground biomass allocation and root morphology for slow-growing arctic vegetation? *Journal of Ecology*, 91, 664–676.
- Vergutz, L., Manzoni, S., Porporato, A., Novais, R. F., & Jackson, R. B. (2012). Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecological Monographs*, 82, 205–220. <https://doi.org/10.1890/11-0416.1>
- Wang, Y. P., Law, R. M., & Pak, B. (2010). A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences*, 7, 2261–2282. <https://doi.org/10.5194/bg-7-2261-2010>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827. <https://doi.org/10.1038/nature02403>
- Yuan, Z., & Chen, H. Y. H. (2009). Global trends in senesced-leaf nitrogen and phosphorus. *Global Ecology and Biogeography*, 18, 532–542. <https://doi.org/10.1111/j.1466-8238.2009.00474.x>

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APPENDIX 1. RESORPTION DATA SOURCES

- An, Y., Wan, S., Zhou, X., Subedar, A. A., Wallace, L. L., & Luo, Y. (2005). Plant nitrogen concentration, use efficiency, and contents in a tall-grass prairie ecosystem under experimental warming. *Global Change Biology*, 11, 1733–1744.
- Berg, B., Ekbohm, G., Johansson, M. B., McClaugherty, C., Rutigliano, F., & Vizo De Santo, A. (1996). Maximum decomposition limits of forest litter types: A synthesis. *Canadian Journal of Botany*, 74, 659–672.
- Blanco, J. A., Imbert, J. B., & Castillo, F. J. (2008). Nutrient return via litterfall in two contrasting *Pinus sylvestris* forests in the Pyrenees under different thinning intensities. *Forest Ecology and Management*, 256, 1840–1852.
- Briggs, S. V., & Maher, M. T. (1983). Litter fall and leaf decomposition in a River Red Gum (*Eucalyptus camaldulensis*) Swamp. *Australian Journal of Botany*, 31, 307–316.
- Callaway, R. M., & Nadkarni, N. L. (1991). Seasonal patterns of nutrient deposition in a *Quercus douglasii* woodland in central California. *Plant and Soil*, 137, 209–222.
- Chapin, F. S. III, & Kedrowski, R. A. (1983). Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology*, 64, 376–391.
- Chapin, F. S. III, & Moilanen, L. (1991). Nutritional controls over nitrogen and phosphorus resorption from Alaskan birch leaves. *Ecology*, 72, 709–715.
- Covelo, F., Ávila, J. M., & Gallardo, A. (2011). Temporal changes in the spatial pattern of leaf traits in a *Quercus robur* population. *Annals of Forest Science*, 68, 453–460.
- Covelo, F., Durán, J., & Gallardo, A. (2008). Leaf resorption efficiency and proficiency in a *Quercus robur* population following forest harvest. *Forest Ecology and Management*, 255, 2264–2271.
- Diehl, P., Mazzarino, M. J., & Fontenla, S. (2008). Plant limiting nutrients in Andean-Patagonian woody species: Effects of interannual rainfall variation, soil fertility and mycorrhizal infection. *Forest Ecology and Management*, 255, 2973–2980.
- Drenovsky, R. E., James, J. J., & Richards, J. H. (2010). Variation in nutrient resorption in desert shrubs. *Journal of Arid Environments*, 74, 1564–1568.
- Drenovsky, R. E., Koehler, C. E., Skelly, K., & Richards, J. H. (2013). Potential and realized nutrient resorption in serpentine and non-serpentine chaparral shrubs and trees. *Oecologia*, 171, 39–50.

- Eckstein, R. L., & Karlsson, P. S. (2001). The effect of reproduction on nitrogen use-efficiency of three species of the carnivorous genus *Pinguicula*. *Journal of Ecology*, 89, 798–806.
- Holub, P., & Tůma, I. (2010). The effect of enhanced nitrogen on aboveground biomass allocation and nutrient resorption in the fern *Athyrium distentifolium*. *Plant Ecology*, 207, 373–380.
- Housman, D. C., Killingbeck, K. T., Evans, R. D., Charlet, T. N., & Smith, S. D. (2012). Foliar nutrient resorption in two Mojave Desert shrubs exposed to Free-Air CO₂ Enrichment (FACE). *Journal of Arid Environments*, 78, 26–32.
- Inagaki, Y., Sakai, A., Kuramoto, S., Kodani, E., Yamada, T., & Kawasaki, T. (2008). Inter-annual variations of leaf-fall phenology and leaf-litter nitrogen concentration in a hinoki cypress (*Chamaecyparis obtusa* Endlicher) stand. *Ecological Research*, 23, 965–972.
- Inagaki, Y., Kamo, K., Miyamoto, K., Titin, J., Jamalung, L., Lapongan, J., & Miura, S. (2011). Nitrogen and phosphorus retranslocation and N:P ratios of litterfall in three tropical plantations: luxurious N and efficient P use by *Acacia mangium*. *Plant and Soil*, 341, 295–307.
- Killingbeck, K. T. (1993). Inefficient nitrogen resorption in genets of the actinorhizal nitrogen-fixing shrub *Comptonia peregrina*: Physiological ineptitude or evolutionary trade-off? *Oecologia*, 94, 542–549.
- Killingbeck, K. T. (1996). Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. *Ecology*, 77, 1716–1727.
- Killingbeck, K. T. (2008). Can zinc influence nutrient resorption? A test with the drought-deciduous desert shrub *Fouquieria splendens* (ocotillo). *Plant and Soil*, 304, 145–155.
- Killingbeck, K. T., May, J. D., & Nyman, S. (1990). Foliar senescence in an aspen (*Populus tremuloides*) clone: The response of element resorption to interramet variation and timing of abscission. *Canadian Journal of Forest Research*, 20, 1156–1164.
- Kim, C., Sharik, T. L., & Jurgensen, M. F. (1996). Litterfall, nitrogen and phosphorus inputs at various levels of canopy removal in oak and pine stands in northern lower Michigan. *American Midland Naturalist*, 135, 195–204.
- Li, Y., Jing, C., Mao, W., Cui, D., Wang, X., & Zhao, X. (2014). N and P resorption in a pioneer shrub (*Artemisia halodendron*) inhabiting severely desertified lands of Northern China. *Journal of Arid Lands*, 6, 174–185.
- Lockaby, B. G., & Taylor-Boyd, J. E. (1986). Nutrient dynamics in the litter fall and forest floor of an 18-year-old loblolly pine plantation. *Canadian Journal of Forest Research*, 16, 1109–1112.
- May, J.D. & Killingbeck, K.T. (1992). Effects of preventing nutrient resorption on plant fitness and foliar nutrient dynamics. *Ecology*, 73, 1868–1878.
- Milla, R., Castro-Díez, P., Maestro-Martínez, M., & Montserrat-Martí, G. (2005). Does the gradualness of leaf shedding govern nutrient resorption from senescing leaves in Mediterranean woody plants? *Plant and Soil*, 278, 303–313.
- Milla, R., Gimenez-Benavides, L., Escudero, A., & Reich, P. B. (2009). Intra- and interspecific performance in growth and reproduction increase with altitude: A case study with two *Saxifraga* species from northern Spain. *Functional Ecology*, 23, 111–118.
- Miller, J. D., Cooper, J. M., & Miller, H. G. (1996). Amounts and nutrient weights in litterfall, and their annual cycles, from a series of fertilizer experiments on pole-stage Sitka spruce. *Forestry*, 69, 289–302.
- Minoletti, M. L., & Boerner, R. E. J. (1994). Drought and site fertility effects on foliar nitrogen and phosphorus dynamics and nutrient resorption by the forest understorey shrub *Viburnum acerifolium* L. *American Midland Naturalist*, 131, 109–119.
- Nelson, L. E., Shelton, M. G., & Switzer, G. L. (1995). The influence of nitrogen applications on the resorption of foliar nutrients in sweetgum. *Canadian Journal of Forest Research*, 25, 298–306.
- Norby, R.J., & Iverson, C. M. (2006). Nitrogen uptake, distribution, turnover, and efficiency of use in a CO₂-enriched sweetgum forest. *Ecology*, 87, 5–14.
- Nordell, K. O., & Karlsson, P. S. (1995). Resorption of nitrogen and dry matter prior to leaf abscission: Variation among individuals, sites and years in the mountain birch. *Functional Ecology*, 9, 326–333.
- Ohmart, C. P., Stewart, L. G., & Thomas, J. R. (1983). Leaf consumption by insects in three eucalyptus forest types in Southeastern Australia and their role in short-term nutrient cycling. *Oecologia*, 59, 322–330.
- Pavón, N. P., Briones, O., & Flores-Rivas, J. (2005). Litterfall production and nitrogen content in an intertropical semi-arid Mexican scrub. *Journal of Arid Environments*, 60, 1–13.
- Pregitzer, K. S., Zak, D. R., Talhelm, A. F., Burton, A. J., & Eikenberry, J. R. (2010). Nitrogen turnover in the leaf litter and fine roots of sugar maple. *Ecology*, 91, 3456–3462.
- Rapp, M. (1969). Litter production and mineral element supply to soil in two mediterranean ecosystems—*Quercus ilex* forest and *Quercus coccifera* garrigue. *Oecologia Plantarum*, 4, 377–410.
- Rejmánková, E. (2001). Effect of experimental phosphorus enrichment on oligotrophic tropical marshes in Belize, Central America. *Plant and Soil*, 236, 33–53.
- Rejmánková, E., & Snyder, J. M. (2008). Emergent macrophytes in phosphorus limited marshes: do phosphorus usage strategies change after nutrient addition. *Plant and Soil*, 313, 141–153.
- Renteria, L. Y., & Jaramillo, V. J. (2011). Rainfall drives leaf traits and leaf nutrient resorption in a tropical dry forest in Mexico. *Oecologia*, 165, 201–211.
- Renteria, L. Y., Jaramillo, V. J., Martínez-Yrizar, A., & Pérez-Jiménez, A. (2005). Nitrogen and phosphorus resorption in trees of a Mexican tropical dry forest. *Trees*, 19, 431–441.
- Shaw, M. R., & Harte, J. (2001). Control of litter decomposition in a sub-alpine meadow-sagebrush steppe ecotone under climate change. *Ecological Applications*, 11, 1206–1223.
- Silla, F., & Escudero A. (2006). Coupling N cycling and N productivity in relation to seasonal stress in *Quercus pyrenaica* Willd. saplings. *Plant and Soil*, 282, 301–311.
- Steinberger, Y. (1991). Litter fall and nitrogen reabsorption in *Zygophyllum dumosum* in the Negev Desert. *Israel Journal of Botany*, 40, 33–39.
- Stewart, J. R., Kennedy, G. J., Landes, R. D., & Dawson, J. O. (2008). Foliar-nitrogen and phosphorus resorption patterns differ among nitrogen-fixing and nonfixing temperate-deciduous trees and shrubs. *International Journal of Plant Sciences*, 169, 495–502.
- Taylor, B. R., & Parkinson, D. (1988). Annual differences in quality of leaf litter of aspen (*Populus tremuloides*) affecting rates of decomposition. *Canadian Journal of Botany*, 66, 1940–1947.
- Troxler-Gann, T., Childers, D. L., & Rondeau, D. (2005). Ecosystem structure, nutrient dynamics, and hydrologic relationships in tree islands of the southern Everglades, Florida, USA. *Forest Ecology and Management*, 214, 11–27.
- Vitousek, P. M., Porder, S., Houlton, B. Z., & Chadwick, O. A. (2010). Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications*, 20, 5–15.
- Vogel, C. S., & Dawson, J. O. (1993). Changes in tissue nitrogen and phosphorus and foliar free amino acids in autumn olive, black locust, American sycamore, and honey locust during autumn. *Canadian Journal of Forest Research*, 23, 665–672.
- Weand, M. P., Arthur, M. A., Lovett, G. M., Sikora, F., & Weathers, K. C. (2010). The phosphorus status of northern hardwoods differs by species but is unaffected by nitrogen fertilization. *Biogeochemistry*, 97, 159–181.
- Yasumura, Y., Hikosaka, K., & Hirose, T. (2006). Resource allocation to vegetative and reproductive growth in relation to mast seeding in *Fagus crenata*. *Forest Ecology and Management*, 229, 228–233.

APPENDIX 2. GEOSPATIAL DATA SOURCES

- FAO-UNESCO. (2005). Soil map of the world, digitized by ESRI. Soil Climate map, Washington D.C.: USDA-NRCS, Soil Science Division, World Soil Resources.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978.
- Global Soil Data Task. 2000. Global Soil Data Products CD-ROM (IGBP-DIS). CD-ROM. International Geosphere-Biosphere Programme, Data and Information System, Potsdam, Germany. Available from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A. [<http://www.daac.ornl.gov>].
- USDA-NRCS. (1999b). Soil temperature regimes. Washington D.C.: USDA-NRCS, Soil Science Division, World Soil Resources.
- USDA-NRCS. (2000). Major biomes. Washington D.C.: USDA-NRCS, Soil Science Division, World Soil Resources.
- Willmott, C. J., & Matsuura, K. (2001). Terrestrial water budget data archive: Monthly time series (1950–1999). Available at: http://climate.geog.udel.edu/~climate/html_pages/README.wb_ts2.html
- Further information on geospatial data sources can be accessed at: https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/use/?cid=nrcs142p2_054010. Soil pH and potential evapotranspiration data: Used by permission of The Center for Sustainability and the Global Environment, Nelson Institute for Environmental Studies, University of Wisconsin-Madison.