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Variability and limits of nitrogen and phosphorus resorption during foliar senescence

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ABSTRACT

Foliar nutrient resorption (NuR) plays a key role in ecosystem functioning and plant nutrient economy. Most of this recycling occurs during the senescence of leaves and is actively addressed by cells. Here, we discuss the importance of cell biochemistry, physiology, and subcellular anatomy to condition the outcome of NuR at the cellular level and to explain the existence of limits to NuR. Nutrients are transferred from the leaf in simple metabolites that can be loaded into the phloem. Proteolysis is the main mechanism for mobilization of N, whereas P mobilization requires the involvement of different catabolic pathways, making the dynamics of P in leaves more variable than those of N before, during, and after foliar senescence. The biochemistry and fate of organelles during senescence impose constraints that limit NuR. The efficiency of NuR decreases, especially in evergreen species, as soil fertility increases, which is attributed to the relative costs of nutrient acquisition from soil decreasing with increasing soil nutrient availability, while the energetic costs of NuR from senescing leaves remain constant. NuR is genetically determined, with substantial interspecific variability, and is environmentally regulated in space and time, with nutrient availability being a key driver of intraspecific variability in NuR.

Key words: foliar nutrient resorption, senescence, nitrogen, phosphorus, efficiency, nutrient availability

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RESORPTION OF FOLIAR NUTRIENTS DURING SENESCENCE

Nutrient resorption (NuR), or retranslocation, is a mechanism for conserving nutrients by retrieving them from plant organs, especially leaves, and plays a key role in ecosystem functioning. Most of the N and P used for global net primary productivity (89% N and 98% P) is recycled within ecosystems (Cleveland et al., 2013). NuR partitions the recycling of nutrients between an internal plant pathway and an external ecosystem pathway. Broadly, 35% of N and 41% of P are recycled within plants, and 65% of N and 59% of P are recycled externally by the mineralization of dead plant organic matter in the soil before reentering plants by root uptake (Cleveland et al., 2013). Foliar NuR plays an additional role because it determines the nutritional quality of leaf litter entering the soil, influencing the mineralization rates and thus the release of nutrients in organic matter to plants and soil microbes (Hättenschwiler et al., 2011). Its importance for the N cycle is such that N resorption (NR) (Table 1) accounts for nearly 25% of the variability in the rate of N mineralization, because N-rich leaf litter releases N, whereas N-poor leaf litter immobilizes N (Deng et al., 2018). The significant negative effects on growth and reproduction that result from prevention of resorption offer strong support for the hypothesis that resorption contributes significantly to plant fitness (May and Killingbeck, 1992).

Most of this recycling occurs during the senescence of leaves. Senescing leaves become a source of nutrients to support current new growth (e.g., senescence in evergreens or sequential senescence in herbs), to support future growth (e.g., synchronous developmental senescence in deciduous plants), or to fill seeds to transfer nutrients to the next generation (e.g., entire plant senescence in annuals). A fraction of nutrients can be resorbed from mature green leaves before they senesce, especially in the presence of active sinks (e.g., seasonal growth in evergreens [e.g., Fife et al., 2008] or seed filling). Foliar nutrients are also resorbed during foliar senescence induced by abiotic stress, e.g., drought, when plants reduce canopy size or eliminate non-acclimated or damaged tissues. Nutrients in green

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Abbreviation	Definition	Extra information or definition
NuR	nutrient resorption	
Nu.green	nutrients in green leaves, maximum values	Nu.sen + Nu.res
Nu.sen	nutrients that remain in the senesced leaves	
Nu.res	nutrients that are resorbed	
$[Nu]_{sen}$	concentration of nutrients in senesced leaves	
$[Nu]_{green}$	concentration of nutrients in green leaves	
NuUE	nutrient-use efficiency	
NuRE	nutrient resorption efficiency	Nu.res/Nu.green is the fraction of nutrients present at the nutrient peak in mature leaves that are withdrawn before foliar shedding or death

Table 1. Abbreviations used in this study for variables involved in foliar nutrient resorption during foliar senescence.
Nu can be substituted with N or P for all cases.

leaves (Nu.green) are either resorbed (Nu.res) or remain in the senesced leaves (Nu.sen), so Nu.green = Nu.res + Nu.sen. Reduced C is also retrieved during senescence, and the importance of salvaging C skeletons for maintenance of plant C and energy reserves should not be overlooked, although we are focusing here on nutrients, especially N and P.

Plant ecophysiological studies frequently describe nutrient resorption as an issue of efficiency, likely as a legacy from the concept of nutrient-use efficiency. Nutrient resorption efficiency (NuRE) is the fraction of nutrients present at peak nutrient levels in mature leaves that are withdrawn before foliar shedding or death (i.e., NuRE = Nu.res/Nu.green). NuRE is conveniently used to address relative comparisons of the ability of species to conserve acquired nutrients. NuRE, however, poses problems of interpretation because both terms of the ratio may change.

NuRE has been considered inappropriate for searches for evolutionary patterns because selection to minimize nutrient losses acts on the nutrients remaining in senesced leaves (Nu.sen) rather than on proportional NuR per se (Killingbeck, 1996; Wright and Westoby, 2003). Killingbeck (1996, 2004) has remarked on the importance in evolutionary studies of the proficiency of resorption, defined as the terminal nutrient concentration in senesced leaves ($[Nu]_{sen}$). Nu.sen may thus be more appropriate for studying the dependence of resorption on senescence. Here, we revisit the ideas of Killingbeck (1996, 2004) and other authors on NuR in light of advances in our understanding of the physiology, biochemistry, and regulation of foliar senescence and the regulation of resorption. Ecological studies previously analyzed nutrient pools and plant demands rather than the mechanisms that regulate NuR. These studies, therefore, usually did not differentiate between the influence of species genetic differences in the regulation of NuR and phenotypic differences due to the environmental regulation of resorption (see Figure 1). Overall, environmental and biological factors that represent a strong selective force for nutrient conservation, such as nutrient-poor soil orders, semi-arid soil moisture regimes, or lack of plant mutualists, are associated with complete resorption, whereas incomplete resorption is associated with weak selective forces, such as nutrient-rich soil orders, or with factors that impede this physiological process (e.g., drought). Inter-annual variability in resorption is 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 (Drenovsky et al., 2019).

Here, we examine different mechanisms involved in NuR (Figure 1). We start at the biochemical and subcellular levels to address the mobility of nutrients and how these biochemical and subcellular levels affect the limits to resorption. We examine the existence of limits to the resorption of N and P with a large database of N and P in green and senesced leaves. We then discuss two processes identified as important for NuR: phloem loading and foliar abscission. We next describe the genetic regulation of deployment of NuR mechanisms to further address how the environment regulates their deployment, emphasizing nutrient availability as a driver of the variability in NuR within species. Finally, we introduce the role of sink nutrient demand in NuR.

DIFFERENT MOBILITY OF VARIOUS BIOCHEMICAL AND SUBCELLULAR FRACTIONS OF N AND P

Nutrients can be separated into non-mobilizable and potentially mobilizable fractions, a difference that depends on their subcellular location and biochemistry. To achieve complete resorption, abscission or laminar death must occur after all mobilizable nutrients have been exported and only the non-mobilizable nutrients remain in the senesced leaf. The non-mobilizable compounds determine the limits of potential resorption. NuR will not be complete if the realized resorption is less than the potential resorption, i.e., mobilizable nutrients remain in the senesced leaf (Figure 1).

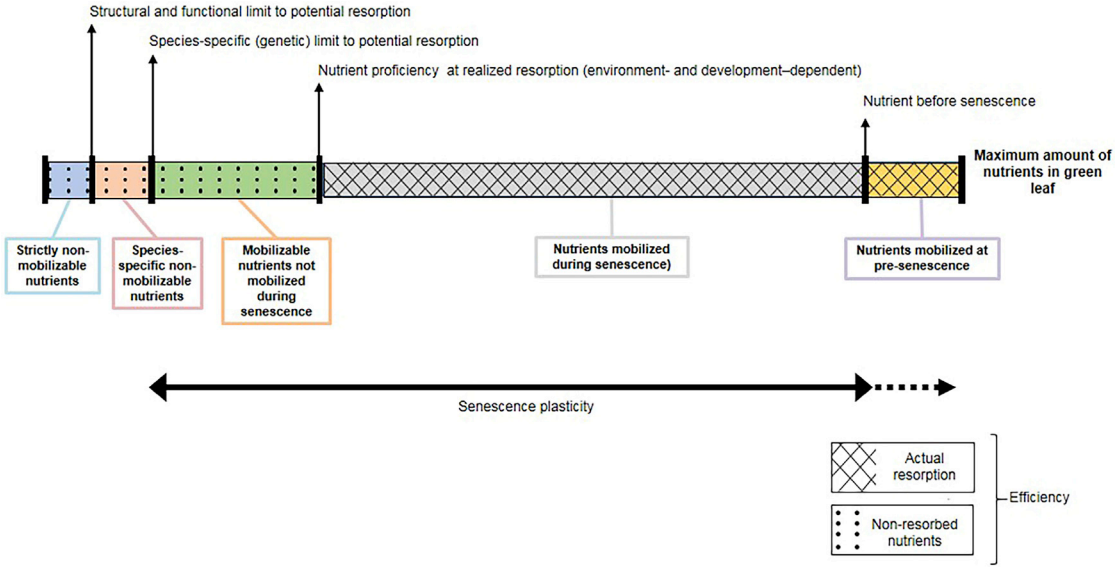

Figure 1. Schematic of foliar nutrient resorption during senescence.

The mobilization of nutrients requires the degradation of macromolecules and their conversion into simple metabolites containing nutrients (Figure 2 and Table 2). Nutrients are transferred from the leaf in these simple metabolites, loaded into the phloem, and transported to sink tissues.

The mechanisms for mobilization depend on the type of nutrient-containing macromolecule. Seventy-five to 85% of foliar N is contained in proteins (Chapin, 1989; Takashima et al., 2004; Yasumura et al., 2006), 9%–15% in nucleic acids (Chapin and Kedrowski, 1983; Evans and Seemann, 1989), and minor amounts (1%–2%) in chlorophylls (Makino and Osmond, 1991), in free amino acids, and as inorganic N (Fischer, 2007). Proteolysis is consequently the main mechanism for mobilizing N.

$[P]_{green}$ in natural ecosystems typically ranges from 0.1 to 3.0 mg g^{-1} (e.g., Vallicrosa et al., 2022). Foliar P is found in inorganic (Pi) or organic (Po) forms. Pi is found in variable amounts that average 58% of the total P pool (Veneklaas et al., 2012). The remaining Po fraction is distributed as 48% in nucleic acids, 31% in lipids and 21% in esters (Sanchez, 2007). P mobilization therefore requires a variety of catabolic pathways.

Two fractions of foliar N were historically considered (Charles-Edwards et al., 1987), one metabolic or labile, assumed to be completely available for resorption, and the other structural, assumed to be non-degradable (e.g., Niinemets and Tamm, 2005). The structural fraction refers to cell-wall proteins, which contain 1.5%–13% of the foliar N (Onoda et al., 2017; Liu et al., 2018) or even as high as 30% (Harrison et al., 2009). The lignocellulosic cell wall is mostly not degraded during senescence, which renders the structural proteins that are crosslinked and tightly bound to the cell wall mostly inaccessible to proteases. About 75%–90% of structural proteins remain undegraded at cell death (Yasumura et al., 2006; Yasumura and Ishida, 2011). Structural proteins have been considered to account for most of the N in litter (McGroody et al., 2004) and to set the lower limit for $[N]_{sen}$ (Yasumura et al., 2006).

Similarly, foliar P can be partitioned into structural or lipidic P (phospholipids), metabolic or easily soluble P (Pi, ATP, and sugar phosphates), and P in nucleic acids and residual components (phosphoproteins and some unidentified residues) (Hidaka and Kitayama, 2011; Tsujii et al., 2017).

N is thus overwhelmingly found in proteins that can be partitioned by their location, solubility, and accessibility. This partitioning allows us to hypothesize about NR. For example, more N allocated to cell walls in evergreen than deciduous species (Takashima et al., 2004) could account for the lower NRE in evergreens. The higher variability in phosphorus resorption (PR) than NR is due to P fractions being more biochemically diverse than N fractions and having a more diverse mobilization.

Nutrients, however, are also harbored in cell organelles other than the cell wall, and they differ in their fate during senescence. A better understanding of the mobility of nutrients can be achieved by taking into account subcellular localization and the functions of the organelles and macromolecules containing the nutrients (Figure 2). A more informative characterization of foliar N considers structural, photosynthetic, respiratory, and so-called storage fractions (Xu et al., 2012; Liu et al., 2018). Alternatively, proteins can be identified by their solubility: insoluble proteins in the cell wall, detergent-soluble proteins in membranes (mostly thylakoid-bound), and water-soluble proteins (mostly in the chloroplast stroma).

Understanding that NuR is actively addressed by cells is important for comprehending the mobility of nutrients during resorption. The requirement of cell machinery for this active task renders impossible the resorption of nutrients embedded in the cellular machinery conducting the mobilization or nutrients in the cellular components essential for maintenance of cell viability. Several decades ago, Charles-Edwards et al. (1987) envisaged that nutrients "involved in maintaining the membrane function and integrity […], and the transport processes by which materials are exported" likely remained in senesced/abscised leaves.

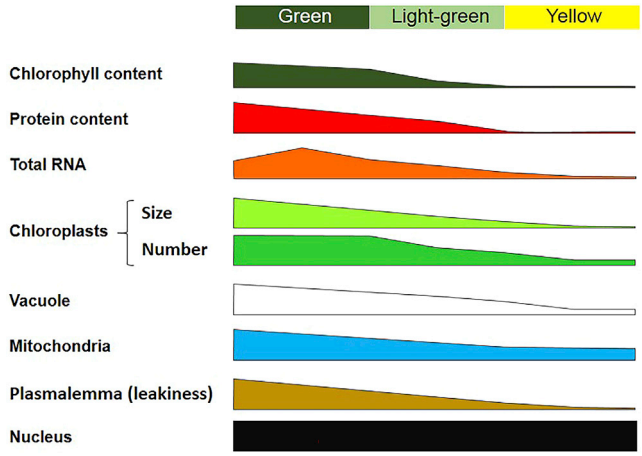

Figure 2. Changes in compounds and organelles during the progression of leaf senescence.
From Keskitalo et al. (2005), Tamary et al. (2019), Bhalerao et al. (2003), Rolny et al. (2011), and Chrobok et al. (2016).

The plasmalemma is maintained to preserve cell integrity until final cell collapse. Previously, it was considered to increase in leakiness from early stages of senescence onwards (Thompson et al., 1998), but detailed studies showed that the integrity of the plasmalemma extends to later stages (Rolny et al., 2011). Although the lipidic P fraction has been considered "structural" (e.g., Hidaka and Kitayama, 2011), deterioration of the plasmalemma is a consequence of the partial degradation of phospholipids, the main components of the cell membrane (Borochov et al., 1982). Phospholipid hydrolysis and replacement by galactolipids and sulfolipids during leaf senescence is an important strategy by which plants can improve phosphorus use efficiency without compromising membrane integrity or function, especially in the case of phosphorus deficiency. The plasmalemma also contains transport proteins that are required to export the mobilized nutrients to the apoplast and for their import into companion cells through apoplastic phloem loading (Tegeder, 2014). To accomplish this key role, several membrane transporters are induced during senescence, some exclusively at this stage (Have et al., 2017), suggesting that they remain among the undegraded phospholipids until the end of senescence and are unlikely to be resorbed.

The vacuole is a key organelle for storing nutrients and energy during final major recycling at foliar senescence (Yang et al., 2017). During the cell's lifespan, the vacuole acts as a compartment for storing metabolites and nutrients (Tan et al., 2019). The vacuole stores P that exceeds the requirements of cellular metabolism as Pi (Pratt et al., 2009), which under a non-limiting P supply may represent a large proportion of cellular P (Veneklaas et al., 2012). The vacuole has a central role in the degradation of proteins and RNA because it receives macromolecules from the cytoplasm and organelles and because it contains most of the cellular hydrolytic enzymes (Müntz, 2007; Yang et al., 2017). The vacuole remains intact for a long time during foliar senescence, although by the end of the process, it may end up in such a degraded state that it cannot be distinguished from the cytoplasm (Keskitalo et al., 2005). Most nutrients have already left the vacuole at this stage, although we lack information on the fate of the hydrolytic enzymes.

Vacuoles receive components of the chloroplast for degradation. Senescing cells can obtain energy from the catabolic activity of the mitochondria (see Chrobok et al., 2016), rendering chloroplasts non-essential for short-term cellular survival. Chloroplasts contain large amounts of water-soluble proteins for carboxylation in the stroma, such as Rubisco, and thylakoid-bound proteins for electron transfer and light capture. The high N concentration of chloroplasts, about 50%–60% of foliar N (Mostowska, 2005) or even up to 80% (Makino and Osmond, 1991), especially in mesophyll cells (Peoples and Dalling, 1988), renders their dismantling key for NuR.

Chloroplasts degrade and break down before other organelles through processes that take place within and outside them. Chloroplasts decrease in size during foliar senescence by transfer of their Rubisco-containing bodies toward the vacuole. Chloroplasts also often decrease in number by vacuolar autophagy of entire chloroplasts (Ishida and Makino, 2018; Izumi and Nakamura, 2018; Buet et al., 2019). The chloroplasts remaining at the final stages of senescence have been transformed into gerontoplasts after losing their ultrastructure and thylakoid membrane system (Krupinska, 2007; Fulgosi et al., 2012), and chloroplasts can sometimes disappear completely (Sorin et al., 2015). The degree of degradation and disappearance determines the proportion of chloroplastic nutrients that remain at the end of senescence.

Mitochondria, despite their high concentrations of nutrients, must remain functional to provide cells with energy and C skeletons until the end of senescence. Mitochondria are constituted of a protein-rich matrix with circulating P-esters and a very protein-rich inner membrane made of phospholipids (Horvath and Daum, 2013). The number of mitochondria can decrease during senescence, with declines ranging from 30% to 75% of pre-senescence concentrations (Keech et al., 2007; Ruberti et al., 2014; Chrobok et al., 2016). Cells contain whole mitochondria (Keskitalo et al., 2005) that contain transcripts for the catabolism of amino acids and fatty acids and that maintain respiratory metabolism until the advanced stages of senescence (Chrobok et al., 2016). Large amounts of mitochondrial nutrients can consequently remain in senesced leaves.

Nucleic acids are the most important pool of Po. The nucleus, containing DNA and nuclear proteins, is required to govern senescence by the provision of transcripts and is maintained until final degradation at cellular death. By contrast, chloroplastic DNA is degraded during chloroplast dismantling (Fulgosi et al., 2012). Eighty percent of the P in nucleic acids is contained in RNA, mostly as ribosomal RNA (Veneklaas et al., 2012). Pi can be resorbed earlier without altering cellular function, but P in ribosomes may be required for the synthesis of proteins for reprogramming senescence. Ribophagy, the autophagy of ribosomes, leads to the degradation of vacuolar rRNA and its associated proteins (Floyd et al., 2015). RNAses are common during senescence, and total RNA levels decrease rapidly (Chapin and Kedrowski, 1983; Bhalerao et al., 2003), with clear initial decreases in chloroplastic rRNAs and cytoplasmic rRNAs followed by decreases in cytoplasmic mRNAs and tRNAs (Lim and Nam, 2007).

	Function during senescence	Content	Period of activity during senescence
Vacuole	recycling (degradation of proteins and RNA) and storage of nutrients	hydrolytic enzymes	until the end of senescence
Chloroplast	source of nutrient-containing macromolecules	Rubisco-containing bodies and thylakoid-bound proteins for electron transfer and light capture (degraded during senescence)	disappearance during senescence
Mitochondrion	provide energy	transcripts for the catabolism of amino acids and fatty acids (not degraded during senescence)	until the end of senescence
Nucleus	governs senescence	DNA and nuclear proteins (transcripts)	until the end of senescence

Table 2. Functions and activities of key organelles involved in foliar senescence.

Nutrient pools recalcitrant to export depend on the organelle and its function. For example, nutrients embedded in the enzymatic machinery responsible for mobilization are difficult to export (Killingbeck, 2004). The many proteases upregulated during senescence are candidates for retention (Avice and Etienne, 2014), but we are not aware of details on the final fates of the many hydrolytic enzymes. Enzymes that are upregulated late and that remain until the late stages of senescence, such as the cysteine protease SAG12 present in vacuoles associated with senescence (Avice and Etienne, 2014), are more likely to remain in senesced leaves. Other candidates with activity in the late stages of senescence are the cytosolic glutamine synthetase GS1 and asparagine synthetase, which recycle ammonia from protein degradation to produce glutamine and asparagine, respectively (Avila-Ospina et al., 2015).

Limits to NuR

Scaling down to the subcellular level exposes the constraints on NuR imposed by cell physiology. Cellular components other than the cell wall also remain in leaves after senescence has ended, along with the nutrients they contain (see Figure 2). In addition to the nutrients embedded in the cell wall, those required to maintain metabolic activity (mitochondria) and cellular integrity (plasmalemma), those required to regulate the cell (nucleus), those in the enzymatic machinery for mobilizing nutrients or in transporters for phloem loading, and those in undegraded parts of the vacuoles and chloroplasts will also remain. These nutrients, which are not recycled in most plants, determine the physiological limits to NuR (e.g., Killingbeck, 2004; Tully et al., 2013). Figure 1 represents the strictly non-mobilizable nutrients that delimit NuR as a small part of the total nutrients available for resorption.

When the amount of N in senesced whole leaves is greater than the amount in structural proteins in the cell walls of green leaves, this means that N other than that in the cell walls remains in senesced leaves. Alternatively, remnants of chloroplastic N in senesced leaves are unequivocal when NRE is lower than the percentage of N allocated to the photosynthetic apparatus, which may account for 30% in evergreens and 40% in deciduous plants (Takashima et al., 2004). Killingbeck (1996) proposed that, after "complete" resorption, $[Nu]_{sen}$ attains concentrations <0.7% (7 mg g^{-1}) for N and <0.05% (0.5 mg g^{-1}) for P in deciduous plants and <0.04% (0.4 mg g^{-1}) in evergreens. He therefore suggested that concentrations >1.0% (10 mg g^{-1}) N and 0.08%/0.05% (0.8/0.5 mg g^{-1}) P (deciduous/evergreen) corresponded to incomplete resorption. Killingbeck did not advocate for a common value of potential $[Nu]_{sen}$ for all species but for a range of values. Hättenschwiler et al. (2008) later hypothesized that interspecific differences in $[Nu]_{green}$ should converge in $[Nu]_{sen}$, but the existence of a common minimum $[P]_{sen}$ was not supported in a neotropical rainforest where $[P]_{sen}$ was much more variable than $[P]_{green}$, likely because the dataset included many values of incomplete resorption.

Incomplete resorption is not rare (Drenovsky et al., 2019) and hinders the elucidation of the limits of NuR. Quantile regression of $[Nu]_{sen}$ on $[N]_{green}$ has been used to delimit the limits of NuR, an approach that allows the limits to vary with $[Nu]_{green}$. Ratnam et al. (2008) used the 0.10 quantile regression on a database of savanna grasses and broadleaved species, but the slope obtained did not differ from zero, and the intercept values yielded $[N]_{sen}$ and $[P]_{sen}$ similar but slightly lower than those from Killingbeck (1996) (5 and 8 mg g^{-1} N for grasses and broadleaved trees, respectively, and 0.3 mg g^{-1} P for both functional groups).

Here, we present the limits to NuR using a database of N and P in green and senescent leaves including circa 1800 and 1500 points for N and P, respectively (see Figure 3 for a description of the database). We estimated the limits to NuR using the 0.05 quantile regression on this database. The regression indicates that the limits to NuR increase as $[Nu]_{green}$ increases in a similar way for both N (slope = 0.181 ± 0.012, p = 0.0000) and P (slope = 0.203 ± 0.0168, p = 0.0000). The increase in the limits with $[Nu]_{green}$ indicates either that the absolute amount of nutrients in non-resorbable fractions (i.e., the strictly non-mobilizable nutrients in Figure 1) is larger when $[Nu]_{green}$ is more concentrated or that species adapted to nutrient impoverished environments (and with lower $[Nu]_{green}$) have mechanisms that enable them to scour leaf nutrients more deeply (i.e., in Figure 1 the species-specific limit approaches the structural and functional limits of NuR). The limits of resorption are clear for N even at the lowest $[N]_{green}$ because the intercept of the regression is clearly positive (intercept = 1.593 ± 0.162, p = 0.0000). This is not the case for P, whose limits of resorption blur at very low $[P]_{green}$ values, leading to a negative intercept of the quantile regression (intercept = −0.023 ± 0.006, p = 0.0000).

Differential effects of environmental conditions on the timing and strength of N-mobilization versus P-mobilization processes may

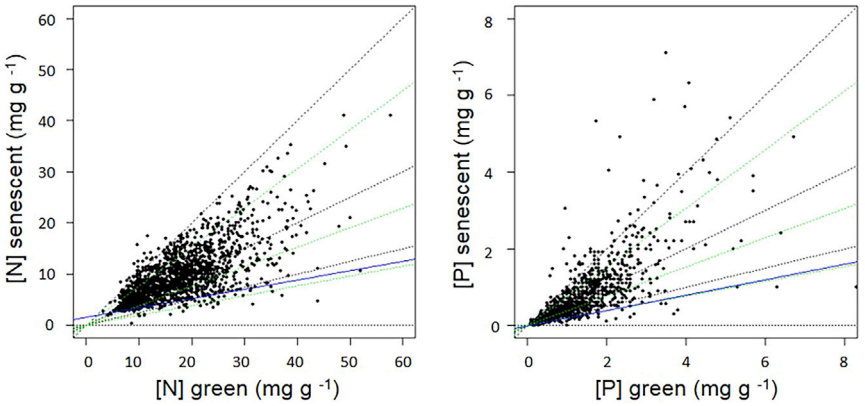

Figure 3. $[Nu]_{sen}$ versus $[Nu]_{green}$ for foliar N and foliar P.

Top black dotted lines represent the points where $[Nu]_{sen}$ is 100% of $[Nu]_{green}$ (i.e., NuRE = 0%), the middle line where it is 50% (i.e., NuRE = 50%), and the lower line where it is 25% (i.e., NuRE = 75%). Vergutz et al. (2012) suggested using a mass loss correction factor (MLCF) of 0.784, 0.780, and 0.745 to account for leaf mass loss during leaf senescence due to resorption processes in deciduous broadleaf, evergreen broadleaf, and coniferous species, respectively. The MLCF decreases the value of $[Nu]_{sen}$ and increases estimates of NuRE. We chose not to introduce such correction for individual entries in the database because we found it likely that individual values for mass loss vary depending on the actual performance of the senescence process. However, for orientation purposes, green and orange lines in the plots represent NuRE values of 0%, 50%, and 25% after correction for leaf mass loss using an MLCF of 0.763 obtained by averaging the values for broadleaves and conifers suggested by Vergutz et al. (2012). The blue line represents the 0.05 conditional quantile regression line to the data and delineates the lower 5th percentile of the points. We used this line to define the limits of NuR. The data presented correspond to our merging of four databases (Vergutz et al., 2012; Hayes et al., 2014; Sohrt et al., 2018; Jiang et al., 2019). Data from Freschet et al. (2010) were excluded from the database of Vergutz et al. because the values were anomalously low for the two elements and the two leaf stages. The final database included 1773 entries for $[N]_{green}$ and $[N]_{sen}$ and 1417 entries for $[P]_{green}$ and $[P]_{sen}$.

alter the coordination of relationships between these two elements. For example, N fertilization weakens the relationship between $[N]_{green}$ and $[P]_{green}$ but does not weaken the relationship between $[N]_{sen}$ and $[P]_{sen}$ (You et al., 2018), suggesting that $[Nu]_{sen}$ can be anchored to a lower limit of non-mobilizable nutrients but that $[Nu]_{green}$ mostly depends on nutrient uptake and has less-strict limits that can even increase dramatically after luxury uptake.

$[P]_{green}$ is more variable than $[N]_{green}$ (e.g., Rejmánková,2005; Hättenschwiler et al., 2008; Vallicrosa et al., 2022). $[P]_{sen}$ is also more variable than $[N]_{sen}$ (e.g., Aerts et al., 2012), perhaps reflecting differences in the mobilization potentials of N- and P-containing molecules (i.e., Han et al., 2013). Higher variabilities of $[P]_{green}$ and $[P]_{sen}$ lead to higher variability of PRE (phosphorus resorption efficiency) compared with NRE (Hättenschwiler et al., 2008; Han et al., 2013), with PRE reported to vary two-fold with moderate variation in $[P]_{green}$ (Kobe et al., 2005). This variability may explain discrepancies in studies of the relationships of $[P]_{green}$ with PR. Tsujii et al. (2017) predicted a strong correlation between $[P]_{green}$ and $[P]_{sen}$ because they hypothesized that a constant PRE would be expected if the relative amount of mobile P was a function of total foliar P. Another study, however, reported that the variability in PR among species was independent of $[P]_{green}$ (Hättenschwiler et al., 2008).

COST OF RESORPTION

The link between plant economy and nutrient partitioning among compounds has been used as a benchmark to account for the variability in NuR among species based on the costs of resorption. The process of nutrient resorption requires energy consumption, for example, the process of loading nutrients from the source organ to the phloem through the symplastic transport pathway and then unloading from the phloem to the sink organ. Wright and Westoby (2003) hypothesized that the trade-off between nutrients resorbed and those taken up by roots depended on the relative cost of obtaining nutrients from each source. One implication of the hypothesis is that NuRE decreases as soil fertility increases, as does its competitive advantage, because the relative costs of acquiring nutrients from soil decrease as concentrations of soil nutrients increase, but the energetic costs of NuR from senescing leaves remain constant.

The diversity of nutrient-containing compounds and organelles, larger for P than for N, may add heterogeneity to the costs of resorption. For example, proteins were the source of 87% of the N removed during senescence, whereas 45% and 32% of resorbed P came from nucleic acids and phospholipids, respectively, in several Alaskan trees (Chapin and Kedrowski, 1983). Overall support for the hypothesis of costs is provided by stronger mobilization of nutrients from recalcitrant compounds in nutrient-poor soils (Hidaka and Kitayama, 2011; Tsujii et al., 2017).

The variety of P fractions and differences in their degradation pathways have been suggested to underlie the variability among species in PR associated with gradients of soil P availability. Hidaka and Kitayama (2011) reported that metabolic P and P in nucleic acids decreased across species as the availability of P decreased, whereas PR increased. The amount of P resorbed by species in P-poor soils exceeded the metabolic-P fraction, indicating that a high PR requires resorption from immobile fractions (Hidaka and Kitayama, 2011). Another study found that PR was proportionally higher from the lipid and nucleic acid P fractions than from the easily soluble and residual P fractions and that lower $[P]_{sen}$ and higher PRE were associated with greater degradation of the residual fraction in species growing where P is scarce (Tsujii et al., 2017).

Easily soluble simple compounds are already mobile, and their resorption therefore has a minor additional cost; according to the hypothesis, they should be completely resorbed. For example, the resorption of Pi, the main form of P in the phloem (Młodzińska and Zboińska, 2016), only requires the action of membrane transporters (Versaw and Garcia, 2017). The

presence of Pi and free amino acids in senesced leaves suggests that they are resorbed less than predicted (see phloem loading for an extended discussion), which is in apparent contradiction with the cost hypothesis. However, these compounds are also obtained from the degradation of macromolecules and are found in leaves while transiting toward export; they can be trapped in leaf litter if abscission occurs before complete resorption, but this does not contradict the cost hypothesis.

We believe that a more detailed assessment of the economy of resorption is needed to update the ideas proposed by Wright and Westoby (2003). We have to incorporate not only the nutrients, but also the energy and C concentrations of the resorbed compounds that would be wasted when leaves fall if the compounds were not resorbed. We also have to take into account that energy for resorption can be supplied by catabolizing compounds whose energy would be lost if they remained non-catabolized in fully senesced leaves.

TWO ADDITIONAL KEY STEPS FOR NUTRIENT RESORPTION: PHLOEM LOADING AND FOLIAR ABSCISSION

The final outcome of NuR could potentially be affected by phloem loading and foliar abscission. Phloem loading of mobile metabolites is the final step of resorption after nutrients are mobilized. Mobilized nutrients should ideally be completely exported, but simple metabolites, such as Pi and amino acids, may be an important fraction of $[Nu]_{sen}$ (Chapin and Kedrowski, 1983; Da Ros and Mansfield, 2020), raising the possibility that NuR may be limited by low phloem loading (Chapin and Moilanen, 1991). This possibility led Yasumura et al. (2006) to propose that $[N]_{sen}$ >25% accounted for by proteins was due to accumulation of free amino acids. Similarly, low PR and accumulation of Pi in senesced leaves under abundant P was suggested to indicate a limitation in the rate of Pi export by transporters at the vacuole (Da Ros and Mansfield, 2020).

The suggested role of phloem loading as a bottleneck for NuR has not been demonstrated. Low NR in the crop *Brassica napus* was attributed to limited N phloem loading, but this was not supported by evidence from the dynamics of amino acids in the leaves or the phloem or by the expression of amino acid permeases (Tilsner et al., 2005). Low NR in one cultivar was instead attributed to delayed proteolysis and hence delayed N mobilization and export (Girondé et al., 2015a, 2015b). However, studies must be extended phylogenetically beyond the brassicas to resolve the importance of loading for NuR. Studies of deciduous species with synchronous senescence throughout the canopy, in which large amounts of mobile metabolites are in the phloem when resorption is intense, would emphasize the importance of loading. Studies during synchronous senescence could resolve whether high concentrations of mobile metabolites in laminar cells are required until late senescence to maintain gradients with the phloem. If so, this would increase the probability of nutrient permanence in the litter if abscission is not finely coordinated with senescence.

Foliar abscission is another important step for NuR. Leaves abscise at the end of senescence in many plant species, although not in the intensely studied *Arabidopsis* and cereals. Abscission truncates phloem transport and hence NuR. Leaves detach at the abscission zone, a few layers of cells at the base of the petiole that differentiate long before the onset of senescence (Primka and Smith, 2019). Detachment occurs after dissolution by enzymatic hydrolysis of the pectin in the middle lamella that binds cells. This dissolution is ultimately triggered (Patharkar and Walker, 2018) and progresses with the progression of laminar senescence.

Leaf lifespan is genetically determined by a hormonally governed process, although the process may be regulated by external factors and stresses. Both foliar abscission and laminar senescence are stimulated by ethylene and inhibited by auxin, facilitating their coordination. Leaves that are shed when completely yellow contain living laminar cells and are often assumed to have completed senescence and hence NuR, although the last step in foliar cell senescence is programmed cell death. Abscission and laminar senescence, however, can be uncoordinated, e.g., in marcescent trees that maintain attached leaves after death of the laminar cells. The opposite may occur in non-marcescent trees when events in the abscission zone progress faster than the senescence of the lamina and leaves containing chlorophyll are shed, for example, because of drought (Rentería et al., 2005; Rentería and Jaramillo, 2011).

Abscission before the completion of senescence could underlie the higher $[Nu]_{sen}$ in leaves that fall earlier in winter in deciduous plants (Niinemets and Tamm, 2005; See et al., 2015). For example, NuR in a winter deciduous clone (*Populus tremuloides*) was lower in leaves that abscised earlier within individual ramets and was also lower in older ramets senescing earlier than in younger ramets senescing later (Killingbeck et al., 1990). NuR in the same clone was also lower for 3 consecutive years when abscission occurred 1 week earlier, likely owing to drought during the preceding summer (Killingbeck et al., 1990). The importance of abscission, however, cannot be ascertained from this type of field data, because the timing of the onset of senescence and its rate of progression must be known in order to determine whether premature abscission or the effect of stress on nutrient mobilization is the cause of low NuR. The longer the period between the onset of senescence and abscission, the more likely it is that resorption will be complete. Truncating NuR before the completion of senescence notably reduces the resorption of all nutrients, producing a signal resembling the coordination of resorption among nutrients.

VARIABILITY IN NuR: NuR IS GENETICALLY DETERMINED (NOW THIS, NOW THAT) AND ENVIRONMENTALLY REGULATED (MORE THIS, LESS THAT)

Genetic regulation

Beyond the contribution of abscission, the regulation of senescence is the main source of variation in NuR. Foliar senescence lasts from days to a few weeks and progresses by an ordered succession of molecular, biochemical, physiological, and cellular events that unfold over time in a highly regulated manner (Jansson and Thomas, 2008). The regulation of events associated with NuR during foliar senescence involves controls at the

genetic, developmental, and environmental levels (Brant and Chen, 2015). The genetics of regulation sets the species-specific limits for NuR (Figure 1). In practice, the external environment and internal plant conditions regulate the deployment of genetically determined steps for NuR during senescence. Environmental regulation likely prevents NuR from reaching species-specific limits, and a fraction of mobilizable nutrients are not mobilized and remain in senesced leaves (Figure 1).

Leaves follow an ontogenetic and age-dependent developmental pathway toward senescence that is assumed to transit through three phases (Jibran et al., 2013; Schippers, 2015). Leaves first pass through the young growth phase, when they do not respond to senescence-inducing factors, and then through the mature phase, when they become sensitive to internal and external senescence-inducing factors, i.e., they are able to senesce. Senescence is the last phase. The ability to senesce is acquired through changes associated with age and increases with age.

Foliar senescence reprograms the transcriptome (Breeze et al., 2011; Stigter and Plaxton, 2015) and affects the expression of thousands of genes to shift cellular metabolism from anabolic to catabolic (Guo, 2013). This shift is achieved by downregulating many genes, such as those involved in photosynthesis, and upregulating the so-called senescence-associated genes (Lim et al., 2007; Breeze et al., 2011; Kim et al., 2018). The upregulated genes follow a coordinated schedule to turn on the physiological and cellular mechanisms and establish the metabolic machinery for the mobilization of nutrients.

The developmental pathway to senescence is controlled by the interplay between plant hormones and incorporates signals from reactive oxygen species and sugars (Lim et al., 2007). Phytohormones regulate the activation or repression of genes encoding transcription factors, which initiate the signaling cascades that affect gene expression (Woo et al., 2013). The onset of senescence is regulated by transcription factors from different families (NAC, MYB, AP2, and WRKY) (Luoni et al., 2019). The NAC family, which includes the well-known transcription factors ORE1 and AtNAP and some microRNAs for post-transcriptional regulation, plays a central role in foliar senescence (Kim et al., 2018).

Intergenotypic/interspecific variability

The overall variability in NuR across plants is also partly due to genetically determined species-specific differences in the regulation of senescence and the mechanisms that control NuR (Figure 1). Foliar senescence is highly conserved. The details of deployment of the program are genetically differentiated (Chrobok et al., 2016). Different aspects of this differentiation have been detected, e.g., in the timing of foliar senescence, as described in cotton lines, likely caused by differences in the expression of genes associated with hormones and transcription factors (Kong et al., 2013), in pigment dynamics by senescence, as described in trees differing in shade tolerance (Garcia-Plazaola et al., 2003), or in the mechanisms of dismantling chloroplasts, as described for barley cultivars (Krupinska et al., 2012).

Genetic differences in foliar senescence also affect nutrient mobilization and export. Many studies have emphasized the importance of genetics for NuR (Chapin and Moilanen, 1991; Minoletti and Boerner, 1994; Killingbeck, 2004), even considering that genetic factors are stronger determinants of NR patterns than are environmental factors (Stewart et al., 2008). Fittingly, NuR and $[Nu]_{green}$, especially for N but also for P, have been reported to be rooted within phylogenetic lines (e.g., Tsujii et al., 2017).

Genetic differences produced during crop breeding provide useful systems for studying the regulatory mechanisms that control NuR. Oilseed rape (*B. napus*), which has been intensively studied because of its low NRE during the vegetative phase (Avice and Etienne, 2014), has provided enlightening information. For example, genotypes with a higher NRE under N limitation break down more soluble protein and have higher activities of serine and cysteine proteases (Girondé et al., 2015a, 2015b), perhaps due to the higher hormonal ratio ([salicylic acid] + [abscisic acid])/([cytokinins]) during foliar senescence (Poret et al., 2017). The different rates of amino acid export that underlie genotypic variability in the NR response to N availability may also depend on differences in the regulation of amino acid transporters (Girondé et al., 2015a, 2015b).

In observational studies, genetic differences may underlie differences in NuR among populations (Staaf and Stjernquist, 1986) and even individuals (Nordell and Karlsson, 1995). Certainty is achieved with controlled and common garden experiments that allow us to discern the genetic basis of differences in NuR performance, e.g., among poplar clones (Harvey and van den Driessche, 1999), among populations of *Pinus sylvestris* (Oleksyn et al., 2003) or *Metrosideros polymorpha* (Treseder and Vitousek, 2001), or among *Helianthus* species (Rea et al., 2018).

Differences in NuR in the field among sympatric species in the same environment, e.g., as reported in a neotropical rainforest (Hättenschwiler et al., 2008), clearly indicate differences in either the environmental or genetic regulation of NuR. An obvious example is a subtropical deciduous tree species that extends its foliar lifespan into winter, with leaves in a senescence-like state with reduced chlorophyll and accumulation of anthocyanins. This tree species has higher NRE and PRE than coexisting deciduous trees that have no anthocyanin and do not extend foliar lifespan (Zhang et al., 2013). NuR differs in many coexisting species, e.g., in forests (Hättenschwiler et al., 2008) and shrublands (Drenovsky et al., 2010). For instance, Figure 4 shows that, along an altitudinal gradient, a deciduous shrub and a grass have very different patterns of NR as a function of $[N]_{green}$, with the grass being able to scour both N and P more deeply during NuR.

Species and genotypes generally differ in how tightly they deploy and activate the machinery for NuR and in the sensitivity of deployment to external factors. Genetic differences in NuR under natural conditions are assumed to be determined by evolutionary history (Killingbeck and Whitford, 2001). Constitutively high NuR leads to high NuUE, which is advantageous and thus an adaptation to nutrient-poor habitats (Vitousek, 1982). The strong selection of traits to minimize nutrient loss in nutrient-poor habitats (Killingbeck, 1996; Aerts, 1999) would accordingly lead to genotypic differentiation and species-specific programs of foliar senescence and nutrient transport mechanisms (Kim et al., 2016).

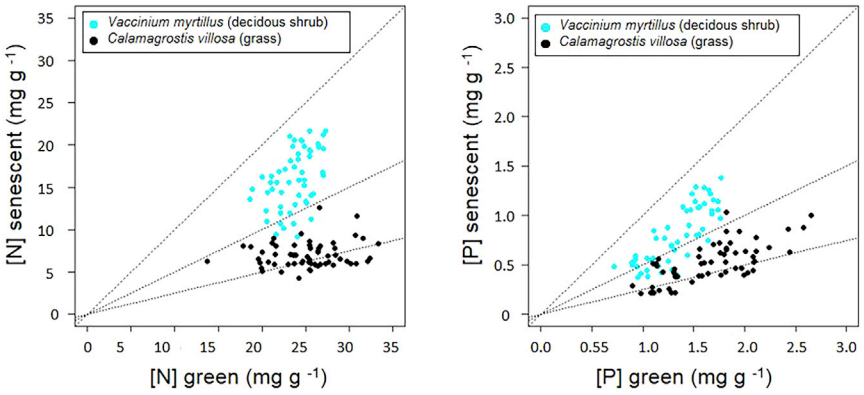

Figure 4. Values from two contrasting species (a deciduous evergreen and a grass) sampled along a 1000-m altitudinal gradient on two different bedrock types.
Note wider $[N]_{green}$ in the grass than in the deciduous evergreen but wider $[N]_{sen}$ in the deciduous evergreen than in the grass. The top dotted line indicates where $[Nu]_{sen}$ is 100% of $[Nu]_{green}$ (i.e., NuRE = 0%), the middle line where it is 50% (i.e., NuRE = 50%), and the lower line where it is 25% (i.e., NuRE = 75%). Data are from Gerdol et al. (2019).

Regulation of senescence by environmental conditions including nutrient availability

Phytohormones are key regulators of senescence. Cytokinins, auxins, and gibberellins are hormones that repress senescence, and jasmonic acid, abscisic acid, salicylic acid (SA), and ethylene are hormones that promote senescence. Hormones (auxin and brassinosteroids, but also ethylene) in young leaves may indirectly affect the timing of senescence by changing the timing of modifications associated with age. Hormones such as SA regulate the progression of senescence after it is initiated (Jibran et al., 2013; Schippers, 2015).

Plants suffer stress from many physical factors, including heat, cold, drought, salinity, strong light, and nutrient limitation, and from biotic factors such as pathogenic infection. Plants synthesize phytohormones to adjust their physiology to resist these stresses (Luoni et al., 2019). Phytohormones also integrate stress signals into the developmental program, which may accelerate senescence or, if the leaves are old enough, lead to stress-induced senescence. If the leaves are immature, or if the stress is too weak to trigger the onset of senescence in mature leaves, only physiological changes associated with the stress are induced, not senescence changes, although such changes may activate mechanisms for nutrient mobilization. The signals from radical oxygen species generated under stress may also alter changes associated with age (Khanna-Chopra, 2012) or regulate the timing of senescence in mature leaves (Pintó-Marijuan and Munné-Bosch, 2014). Radical oxygen species generated early in senescence can regulate the progression of senescence after it is initiated (Khanna-Chopra, 2012).

Cells can reprogram themselves to cope with stress, making some proteins unnecessary after the reprograming. The cellular machinery to remove these proteins and to eliminate molecules damaged by stress mostly overlaps with the machinery required to degrade molecules to mobilize nutrients for NuR (e.g., Simova-Stoilova et al., 2010). Similarly, the upregulation of genes encoding proteases and mobilization mechanisms is a response common to several stresses and to foliar senescence (e.g., Simova-Stoilova et al., 2010), and many transcription factors that regulate age-induced senescence are therefore also involved in plant stress tolerance (i.e., Sade et al., 2018). For example, 28 of the 43 genes encoding transcription factors induced during senescence in *Arabidopsis* are also induced by stress (Chen et al., 2002).

How changes in the timing and progression of senescence induced by stress affect NuR is not yet known. The interaction between age and stress regulates deployment of mobilization mechanisms as stress-induced foliar senescence progresses and may affect NuR; this likely underlies part of the intraspecific variability in NuR. How stress-induced changes in leaves before senescence alter NuR is even less well understood.

Environmental regulation is responsible for part of the phenotypic variability in NuR (Figure 1) reported in observational studies (Drenovsky et al., 2019). Variability in NuR in naturally grown individuals and populations across years has been observed in records of environmental variability (e.g., *Acer saccharum* [Pregitzer et al., 2010], *Fagus sylvatica* [Khanna et al., 2009], deciduous and evergreen shrubs [Drenovsky et al., 2013], *Quercus robur* [Covelo et al., 2008], and *Populus tremuloides* [Killingbeck et al., 1990]).

Light has been described as a factor affecting NuR (i.e., Garcia-Plazaola et al., 2003; Brunel-Muguet et al., 2013), although this is not always the case (Yasumura et al., 2006). Both drought and temperature have direct effects on NuR that are also associated with effects on the phenology of foliar senescence, as has been reviewed for deciduous trees (Estiarte and Peñuelas, 2015). The overall effect of water stress is a reduction in NuR, whereas the effects of warming on NuR in winter deciduous species have not been elucidated. The effects of temperature are intertwined with those of water stress in climates with dry seasons, and higher resorption during wet years has been reported in dry deciduous species (Rentería et al., 2005; Rentería and Jaramillo, 2011). An example of differences in $[Nu]_{sen}$ among years that differ in the amount and distribution of precipitation can be seen in Figure 5.

The connection between senescence and nutrient stress is obvious: foliar senescence is the terminal mechanism for nutrient recycling across organs, and plants recycle nutrients when they are nutrient limited. Not surprisingly, the expression of genes for recycling before senescence mostly overlaps with their expression during early senescence. For example, genes for degrading proteins (Comadira et al., 2015) and genes for autophagy (Safavi-Rizi et al., 2018) under N limitation are expressed before senescence is triggered. The overall overlap has been documented in *Arabidopsis*, where 38% of the genes upregulated under P deficit

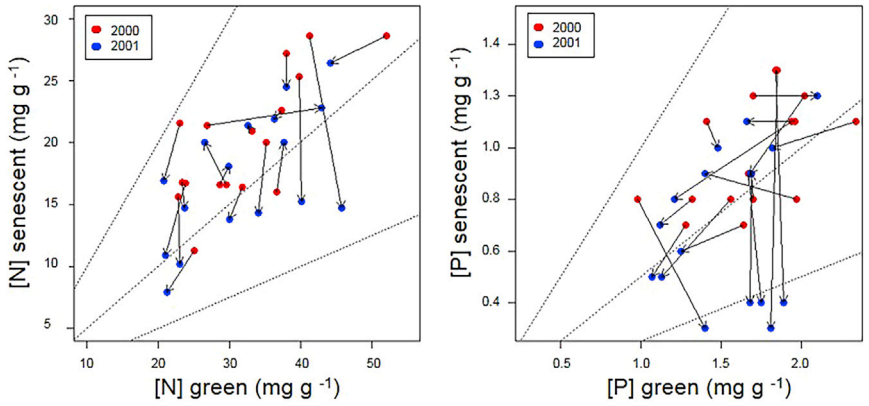

Figure 5. Mean values of 3–8 individuals from 17 mostly dry deciduous species from a tropical dry deciduous forest in 2 consecutive years that differed in precipitation.
The top dotted line indicates where $[Nu]_{sen}$ is 100% of $[Nu]_{green}$ (i.e., NuRE = 0%), the middle line where it is 50% (i.e., NuRE = 50%), and the lower line where it is 25% (i.e., NuRE = 75%). Data are from Rentería and Jaramillo (2011). Note how, for many species, $[N]_{green}$ values that were similar between both years ended up with very different $[N]_{sen}$ values between years, likely because of differences in the amount and seasonality of precipitation. The pattern for $[P]_{sen}$ had some similarities, although not for all species.

are also upregulated during senescence, and the overlap also encompasses 40% of the downregulated genes (Stigter and Plaxton, 2015).

The regulatory relevance is clear after the advance in the timing of senescence under nutrient stress (Cote et al., 1989). The relevance is even clearer when senescence is reversed by relieving nutrient limitation, e.g., in barley leaves, in which N supply reversed the regulation of many of the nearly 2000 genes associated with the induction of premature senescence by N limitation (Schildhauer et al., 2008; Fataftah et al., 2018).

The overlap is obvious at the post-transcriptional level because many mechanisms for scavenging nutrients that act before the onset of senescence also act during the early stages of senescence. For example, one of many *Arabidopsis* purple acid phosphatases that predominate in the vacuole and cell wall for P recycling under P deficit also predominates during senescence, when its role is so important that PR is greatly impaired in deficient mutants (Robinson et al., 2012). Overlap between the responses to nutrient limitation and senescence suggests that a senescence program deployed on top of the signal for starvation of a nutrient is reinforced in mechanisms that mobilize that nutrient. Evidence supporting such a reinforcement includes, for instance, that nitrate nutrition regulates expression of genes encoding glutamate synthases and asparagine synthetases during senescence, which are key enzymes for the synthesis of phloem-transported amino acids (Avila-Ospina et al., 2015), or that autophagy is induced in old leaves approaching senescence and under N starvation because autophagy is needed for N remobilization under both limiting and ample supplies of nitrate (Guiboileau et al., 2012). Similarly, RNAses become more abundant during senescence, as they do under P deprivation (Morcuende et al., 2007).

Reports on the dependence of nutrient efficiency on plant nutrient status suggest differential regulation of the degree of resorption and therefore of senescence. Plant nutrient status, and hence soil nutrient availability, are assumed to exert a key control on NuR in accordance with the nutrient conservation function of foliar senescence. Identification of the phenotypic effects of nutrient availability on NuR, however, has produced mixed results that have revealed no clear pattern (e.g., van Heerwaarden et al., 2003), despite widespread claims of higher resorption under nutrient limitation.

A metanalysis of a large number of fertilization experiments (Yuan and Chen, 2015) revealed increasing $[N]_{sen}$ and $[P]_{sen}$ and decreasing NRE and PRE in response to fertilization with the respective nutrients and decreasing NRE and PRE in response to combined N and P fertilization. The increases in $[Nu]_{sen}$ occurred after a 27% increase in $[N]_{green}$ and a 73% increase in $[P]_{green}$ with N and P fertilization, respectively (Yuan and Chen, 2015), consistent with the positive relationship between $[Nu]_{green}$ and $[Nu]_{sen}$ reported at the intraspecific level for both N and P (Kobe et al., 2005; Mao et al., 2015).

A lack of clear patterns in some experiments are likely to have been caused by the effects of nutrients on growth and sink nutrient demands (see next) but also by the distortion in NuR caused by abiotic and biotic stresses under field conditions.

THE OTHER SIDE: SINK NUTRIENT DEMAND

Nutrients used to supply primary growth and reproductive sinks are provided mainly by internal reserves. Nutrients stored in twigs, stems, or roots of deciduous trees during the leafless season provide nutrients for the seasonal growth of shoots. In growth forms other than deciduous trees, many of the nutrient reserves are contained in leaves; they provide nutrients for sequential growth of leaves in herbs, seasonal growth of shoots in many evergreens, and seed filling in many species of monocarpic plants.

Nutrients retrieved from leaves to directly meet sink demand can be retrieved from green leaves but also often from senescing leaves. NuR of evergreens from seasonal climates was hypothesized to be driven by shoot growth (Nambiar and Fife, 1991) because NuR from both senescing and mature green leaves is nearly concurrent with shoot growth (Miyazawa et al., 2004; Pornon and Lamaze, 2007; Fife et al., 2008).

Sink demand can also account for changes in NuR with plant development. Nutrient demands change with ageing because of changes in productivity, growth, and allocation (e.g., Brant and Chen, 2015) and may therefore lead to changes in NuR. For

example, higher NR in adults than in juvenile stages of deciduous trees is due to the larger N sink in adults (e.g., *Fagus crenata*, Yasumura et al., 2005). Shifts in the controls of internal nutrients in response to increasing sink size in a chronosequence of a deciduous conifer were also proposed to underlie the increase in NR associated with age when $[N]_{green}$ increased but $[N]_{sen}$ decreased, and the availability of soil N tended to decrease as the stand aged (Sun et al., 2016). Similarly, difficulties in resolving the apparent inconsistencies in the variation in NuR under fertilization (i.e., Peng et al., 2019) may be due to interactions with changes in plant size and nutrient demand.

The relationship between sink nutrient demand and NuR has been hypothesized to underlie differences in nutrient conservation patterns, e.g., to account for the low NuR in slowly growing evergreen shrubs in Patagonia compared with the higher NuR of faster growing perennial grasses with a higher sink strength (Carrera et al., 2000). Similar reasoning has also led to the speculation that plants under continuous tropical growth would continuously have a strong sink and consequently a high NuR (Rejmánková, 2005).

Beyond vegetative growth, reproductive efforts impose an additional demand with the potential to deplete nutrients from the leaves of reproductive trees (Pakonen et al., 1988, May and Killingbeck, 1992; Tully et al., 2013) and hence affect NuR. For example, reproductive efforts regulated the nutrient response of a tropical N-fixing tree that flushes leaves and flowers throughout the year. Foliar $[N]_{sen}$ and $[P]_{sen}$ are lower in trees with larger short- and long-term reproductive demands than in trees with smaller demands (Tully et al., 2013).

The shift toward the reproductive stage in short-lived plants with sequential senescence is often accompanied by an increase in NuR (Malagoli et al., 2005). Optimal resorption in annual plants is also considered to require close synchronization between sink formation and senescence of the source organ (Pottier et al., 2014). For example, the low sink capacity before pod filling in the annual crop *B. napus* has been proposed to be the main bottleneck for foliar NR at this stage, and NR accordingly improved when the sink increased at the filling stage (Tilsner et al., 2005). Similarly, NR decreased in oilseed rape and soybean in the absence, or after the removal, of seeds to fill (Malagoli et al., 2005; Htwe et al., 2011).

These examples indicate that sink nutrient demands add an additional layer of variability to NuR, a layer that also adds interactions with environmental cues that directly affect both sink size and NuR.

FINAL REMARKS

NuR is a key component of plant nutrient use and hence of productivity and elemental cycling in ecosystems. The data and processes described here improve our understanding of NuR and should thus help to improve ecological theory and biogeochemical and Earth system models. However, at the same time, these data and processes warrant further research to reveal the still poorly understood complex genetic, physiological, and ecological processes involved and their effects on most ecosystem processes, including carbon cycling, plant litter decomposition through changes in litter quality, and plant competition. Study of model plant species, such as beech, which has a broad distribution under various climatic and soil conditions and has also been well studied genetically, would enable deeper investigation of the mechanisms of nutrient resorption in terms of ecology, physiology, biochemistry, metabolomics, and genetics. Meanwhile, we can conclude that (1) foliar nutrient resorption (NuR) plays a key role in ecosystem functioning and plant nutrient economy, (2) nutrients are transferred from the leaf in simple metabolites that can be loaded into the phloem, (3) proteolysis is the main mechanism for N mobilization, whereas P mobilization requires the involvement of different catabolic pathways, making the dynamics of P in leaves more variable than those of N before, during, and after foliar senescence, (4) the biochemistry and fate of organelles during senescence impose constraints that limit NuR, (5) the efficiency of NuR decreases, especially in evergreen species, as soil fertility increases, which is attributed to relative costs of soil nutrient acquisition decreasing with increasing soil nutrient availability, while the energetic costs of NuR from senescing leaves remain constant, and (6) NuR is genetically determined, with substantial interspecific variability, and environmentally regulated in space and time, with nutrient availability being a key driver of variability in NuR within species.

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AUTHOR CONTRIBUTIONS

M.E and J.P. designed the review. M.E. gathered and analyzed the data and wrote the first draft. M.E., M.C., M.M., and J.P. contributed to the analyses and interpretation of the results and to the revision and improvement of the text.

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