

Modest enhancement of nitrogen conservation via retranslocation in response to gradients in N supply and leaf N status

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Abstract Plant nutrient resorption, a ubiquitous mechanism of nutrient conservation, has often been proposed to be more pronounced in infertile than fertile habitats, and in species common to infertile compared to fertile habitats, because of the presumed advantage when nutrients are scarce. However, previous studies provide weak and inconsistent empirical support for these hypotheses, although few have examined intraspecific variation across well-quantified resource gradients. This study addresses intraspecific patterns of nutrient resorption for eight species across two N availability gradients on similar soils in an N-limited oak savanna ecosystem: a long-term fire frequency gradient with a negatively

correlated N fertility gradient and a long-term N fertilization gradient. We hypothesized that both resorption proficiency (the minimum nutrient level retained in a senesced leaf) and efficiency (the proportional change in leaf nutrient concentration) would decrease with increasing soil N availability and plant N status. For the seven non-N fixers, either resorption proficiency or efficiency decreased modestly in treatments with higher N availability. In contrast, the legume *Amorpha canescens* Pursh had higher N levels in green and senesced leaves, and resorbed N much more weakly than the non-fixers, and did not respond in terms of proficiency or efficiency to soil N availability. Across all species and sites in each N fertility gradient, a scaling analysis showed greater resorption efficiency in plants with lower N concentrations. Our data suggest that species can have modest resorption responses reflective of soil nutrient availability and differences in resorption related to their N economy that represent mechanisms of nutrient conservation in nutrient-limited soils.

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Introduction

According to Killingbeck (1996), nutrient retranslocation (or resorption), the mobilization and transfer of nutrients from senescing leaves to storage in perennial tissue (Killingbeck 1986), is a “keystone process” in most ecosystems. At the plant-level, retranslocation represents a major internal nutrient flux by which plants can conserve nutrients (Chapin 1980), increase nutrient use efficiency (Vitousek 1982; Herbert and Fownes 1999), and perhaps increase competitive advantage in nutrient-poor environments (Aerts and Chapin 2000). In a literature review, Aerts (1996) found that plants resorb on average 50% of leaf N and 52% of P, although these patterns vary somewhat with growth form. At the ecosystem-scale, resorption influences the nutrient flux through litterfall and the rate at which those nutrients are cycled through the ecosystem (Aerts 1996, 1997; Cordell et al. 2001). While numerous studies have documented significant effects of plant species or functional groups on ecosystem biogeochemistry (e.g. Melillo et al. 1982; Wedin and Tilman 1990; Gower and Son 1992; Reich et al. 1997; Ferrari 1999; Campbell and Gower 2000; Knops et al. 2002; Lovett et al. 2004), patterns of retranslocation are potentially a mechanism by which ecosystem nutrient dynamics modifies these vegetative effects through the plasticity of both inter- and intraspecific responses to heterogeneity in soil fertility. Two major and distinct questions are whether species adapted to low fertility sites resorb more N than those adapted to greater fertility, and whether individual species demonstrate more effective resorption when growing in less than more fertile habitats. In this report, we address the former question indirectly by assessing whether species differing in plant N status (represented by tissue N concentrations) vary in resorption efficiency and the latter question of intraspecific variation in resorption with respect to soil fertility gradients. It is commonly hypothesized that plants will demonstrate increased resorption efficiency in infertile habitats given that this is described as a mechanism by which plants can increase their fitness in these systems. For example, May and Killingbeck (1992) prevented nutrient resorption through premature foliage removal and found significantly reduced fitness of defoliated plants and suggested that this is especially important for plant fitness in nutrient-poor systems.

What does the evidence show regarding either question regarding resorption effectiveness and fertility gradients? Aerts (1996) concluded that the existing data did not show a clear relationship between nutrient resorption efficiency and soil nutrient availability but argued that these comparisons were problematic. First, the majority of relevant studies investigated interspecific patterns across nutrient gradients; and second, included only a small number of species (Aerts 1996). This precluded conclusions about intraspecific (or phenotypic) responses and confounded species effects (interspecific variation) with site fertility effects.

In a literature review including 89 species, Killingbeck (1996) came to a similar conclusion, suggesting that variation in retranslocation efficiency rates between species may limit conclusions with respect to potential driving factors such as soil fertility. He argued that due to temporal variation and multiple limiting factors (e.g. moisture or light availability, soil fertility, physiological controls), most species rarely achieve maximal resorption. Retranslocation efficiency, defined as the proportional difference in the nutrient content in the leaf prior to and after senescence, is influenced by both green leaf nutrient concentration which can vary considerably and nutrient withdrawal. Killingbeck (1996) suggested then that resorption proficiency (defined as the final nutrient content following senescence) is perhaps a better measure of retranslocation than efficiency, especially in any attempt to measure the extent that plants can minimize nutrient loss through senescence. Killingbeck (1996) argued that in using this measure of proficiency, retranslocation is generally complete when foliar %N is less than 0.7% (or 50 $\mu\text{g N/cm}^2$) and incomplete when leaf %N is more than 1% (or 75 $\mu\text{g N/cm}^2$) remains following senescence.

In contrast to Aerts (1996) and Killingbeck (1996), Kobe et al. (2005) came to a somewhat different conclusion using a similar global data set but an alternative statistical approach. Through original allometric scaling equations, their analysis demonstrated that across a wide and uncontrolled set of species and sites, taxa with higher green leaf N concentrations generally resorb a smaller fraction of their tissue N during senescence than those with lower green leaf N levels, suggesting greater resorption in low fertility environments and/or species with inherently low tissue N status.

In general, studies included in the above reviews have frequently addressed whether species that inhabit infertile sites or have intrinsically less nutrient-rich tissues are better able to conserve leaf nutrients during senescence than those common to richer sites and/or with more nutrient-rich tissues. Such studies have much less often addressed the plastic response of retranslocation across well defined nutrient availability gradients. Both are specific goals of this study.

A previous study at Cedar Creek Natural History Area, MN, USA (Reich et al. 2001) found that across a fire- and vegetation-associated soil fertility gradient, *Quercus ellipsoidalis* and *Q. macrocarpa* trees had greater N retranslocation efficiency with decreased soil N mineralization. We wanted to further address this issue because of the lack of intraspecific data on retranslocation efficiency rates in relation to soil nutrient availability (Aerts 1996). Therefore, we sought to address the following question: do dominant oak savanna plant species differing by functional group and tissue N status differ in resorption efficiency and/or exhibit a plastic response in resorption efficiency rates across varying levels of soil N availability? Using both that same fertility gradient at Cedar Creek (Reich et al. 2001) and a separate 20-year fertilization gradient at the same location, we examined retranslocation patterns of multiple species representing several growth forms and approximately similar leaf life span. We hypothesized that regardless if green leaf N concentrations vary significantly over fertility treatments, 1) senesced leaf N concentrations (retranslocation proficiency) would demonstrate a sufficiently significant positive relation to fertility and plant green leaf N status to lead to 2) significant differences in resorption efficiency rates that relate inversely to fertility and inherent plant N status. We also asked whether N-fixing and non-fixing species would differ in any of the metrics assessed, because of potentially lesser selection pressure to develop N conservation mechanisms in species capable of fixing their own N.

Methods

Site description

Cedar Creek Natural History Area (Cedar Creek) is a 2300 ha reserve located on the Anoka sandplain in

east central Minnesota (45°25'N, 93°10'W). Upland soils are Entisols derived from a glacial outwash sandplain and are excessively drained, very uniform fine sands (>90% sand) of the Sartell and Zimmerman series (Grigal et al. 1974). Numerous nutrient addition experiments performed in both old fields and native savanna have indicated that nitrogen is the major nutrient limiting plant growth (Tilman 1984, 1987). Cedar Creek has a continental climate and receives on average 79 cm of annual precipitation. The mean July temperature is 22.2°C while the mean January temperature is -10°C. A thorough description of the site including soils, physiography, climate, and vegetation is included in Grigal et al. (1974).

A 210 ha portion of Cedar Creek that was historically oak savanna has been subjected to a prescribed burning treatment since 1964 to investigate the effects of fire frequency on species composition and ecosystem functioning. The sites (3–27 ha in size, mean=14 ha) within this savanna cover a gradient of vegetation types spanning the range found at the prairie–forest border including prairie with sparse oak (*Quercus macrocarpa* Michaux and *Q. ellipsoidalis* E.J. Hill) canopy cover to closed canopy oak forest. Sites were delineated and randomly assigned to a burning regime at the conception of the program. Prescribed (spring burning) fire frequencies range from 0–0.8 fires per year. For the current study, data were collected from 12 permanent plots established in these sites between 1984 and 1995 where there is an existing data set of species composition, above- and belowground production, N mineralization, and litter-fall, among other variables (e.g. canopy coverage, soil respiration, soil moisture and temperature). These 12 plots represented 5 plots of low fire frequency (0–0.11 fires per year), 3 of intermediate fire frequency (0.35–0.49 fires/year) and 4 plots of high fire frequency (0.65–0.81 fires/year). The experimental design has been previously described by Peterson and Reich (2001) and Reich et al. (2001). The fire frequency gradient is strongly negatively related to a gradient in oak canopy cover and net N mineralization rates (Table 1), where the gradient in net N mineralization is a result of both direct fire effects and indirect fire effects on species composition (Reich et al. 2001, Dijkstra et al. 2005).

Within one burn unit (fire frequency=0.65 fires per year), an artificial N gradient, ongoing since 1983, was continued over 9 plots. These 9 plots (20×50 m)

Table 1 Mean soil fertility values (0–20 cm) for treatments in both fire frequency and fertilization gradients

		<i>n</i>	Total soil N Mg N/ha	Mineral N kg N/ha	Net N min. kg N ha ⁻¹ year ⁻¹	Soil water % water
Fire frequency gradient						
2000	Low fire frequency 0–0.11 fires/year	5	2.58	2.74a	58.34a	4.41
	Moderate 0.35–0.49 fires/year	3	2.31	1.98ab	20.76b	3.60
	High 0.65–0.81 fires/year	4	1.89	1.45b	15.53b	2.50
	<i>p</i> -value		NS	0.085	0.038	NS
	<i>R</i> ²			0.42	0.52	
Fertilization gradient						
2001	Control	3	2.04a	6.18	15.81	7.89
	Low fertilization 54 kg N ha ⁻¹ year ⁻¹	3	2.09a	7.95	21.62	8.98
	High 170 kg N ha ⁻¹ year ⁻¹	3	2.75b	9.16	31.06	8.55
	<i>p</i> -value		0.027	NS	NS	NS
	<i>R</i> ²		0.70			

ANOVA statistics with different letters indicating significant differences between treatments ($p \leq 0.05$ by student's *t*). Data from Norris et al. (unpublished).

were randomly assigned one of three fertilization treatments (3 plots of each treatment): unfertilized control, 54 kg N ha⁻¹ year⁻¹, and 170 kg N ha⁻¹ year⁻¹ in the form of granular NH₄NO₃ applied twice each summer. In addition to N, the two fertilized treatments also receive supplemental fertilization to maintain soil nutrient (e.g. cation) status in spite of N fertilization. The same ecosystem variables collected across the fire frequency gradient were repeated here (Table 1) (Avis et al. 2003). This study sampled plant species from 3 plots of each treatment.

Retranslocation sampling

The original species sampling list contained 12 species representing 6 growth forms composed of 2 species each. Although these species were initially found across all plots (green leaves), senesced tissue of several species was scarce and thus several species were not included in the final data set. The final sampling list in both experiments contains *Quercus ellipsoidalis* and *Q. macrocarpa* (trees), *Rosa arkansana* Porter (shrub), *Andropogon gerardii* Vitman and *Sorghastrum nutans* L. Nash (C₄ grasses), *Stipa spartea* Trin. (C₃ grass), *Amorpha canescens* Pursh (legume), and *Smilacena stellata* L. Desf. (forb).

Additionally, *Artemisia ludoviciana* Nutt. (forb) was collected in the fertilization experiment.

In each plot, 4 replicate samples were collected. Each sample consisted of several leaves (typically 2–4) removed from the outer canopy of neighboring plants of each species (within approximately 2 m²) at peak biomass for initial sampling and completely senesced for final sampling. Senesced leaves were either removed directly from the plant or captured during leaf fall. The initial sampling (mature, green tissue) was completed over a 2-week span covering the end of July and beginning of August and the final sampling was done within 1 week of complete senescence (for most plants for each species in each plot). Additional samples were collected biweekly to ensure that the initial sampling occurred at peak biomass. The fire frequency gradient was sampled in 2000, and the fertilization gradient in 2001.

Samples were processed for leaf area and mass. Leaves were scanned using a flat bed scanner and digitized for area using WinDendro (Regent Instruments Inc., Quebec, Canada). Samples were then oven dried to a constant mass (at least 48 h at 60°C) and weighed. Samples were then combined by species and plot and ground for analysis of N content using a Carlo Erba CN Analyzer (Milano, Italy).

Calculations and analysis

From the data collected, we calculated green and senesced leaf nitrogen concentration (resorption proficiency) and resorption efficiency (percent change due to senescence, $((\text{green}-\text{senesced})/\text{green}) \times 100$) where green and senesced refer to the N concentration in green and senesced leaves respectively; N concentrations were expressed on a mass-basis as percent N or on a leaf area basis to account for confounding reduction of leaf mass during senescence. Mean values were calculated for species and plot. Our calculations and inferences assume that foliar leaching was negligible during senescence. These data were analyzed statistically using a two way ANOVA to test for species and treatment (fire frequency or fertilization level) effects and any interaction between the two factors using SAS (SAS Institute, Inc., Cary, NC). When necessary, data were log transformed (green leaf N per leaf area and senesced leaf N) to fit a normal distribution. Contrasts with a Bonferroni correction (maintaining the experimental error rate) were done to examine differences between individual treatments or species. Unless explicitly specified, we present data below on an area-basis which is commonly done to account for changes in mass associated with senescence. We include mass-based measurements only when dissimilar patterns or statistical results were found. Significant results are presented for $P < 0.05$.

A scaling analysis employing a model developed by Kobe et al. (2005) was fitted to the data to explicitly address resorption efficiencies with respect to green leaf nutrient concentrations which are expected to vary with soil fertility. The model is defined as $\log_{10}([\text{nutrient}]_{\text{sen}}) = A' + B \times \log_{10}([\text{nutrient}]_{\text{gr}})$ where $[\text{nutrient}]_{\text{sen}}$ and $[\text{nutrient}]_{\text{gr}}$ are the nutrient concentrations in senesced and green tissues, respectively, on either a mass or area basis. A' is the \log_{10} of A which represents the baseline proportion of $[\text{nutrient}]_{\text{gr}}$ retained in senesced leaves, and B is the log–log scaling slope and indicates whether or not there is a disproportionate effect of $[\text{nutrient}]_{\text{gr}}$ on $[\text{nutrient}]_{\text{sen}}$ where values > 1 indicate decreasing resorption efficiency and $B < 1$ indicates increasing resorption efficiency with increasing $[\text{nutrient}]_{\text{gr}}$. This model was fitted to the data using reduced major axis regression on the $\log_{10} [N]_{\text{sen}}$ by the $\log_{10} ([N]_{\text{gr}})$. All models were computed using JMP (SAS Institute, Inc., Cary, NC).

Results

Fire frequency gradient

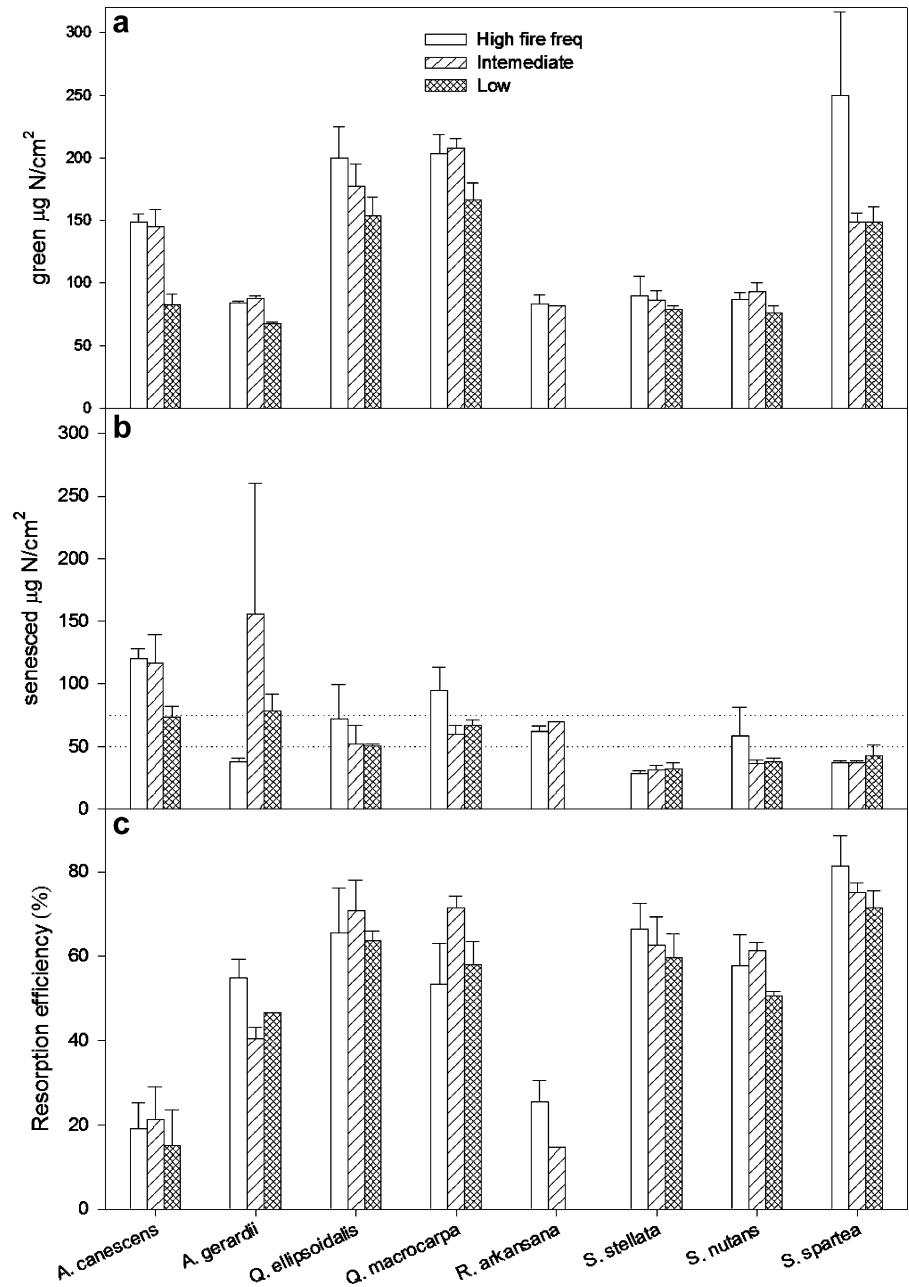
In most species, green leaf N concentrations (mass-based) increased with increased soil N availability and decreasing fire frequency ($P = 0.0310$, data not shown). Plants in low fire frequency plots (higher soil N availability) had greater leaf N concentrations than in higher fire frequency plots. In contrast, green leaf N contents expressed per unit leaf area were opposite to what was expected. There was less N per cm^2 with decreasing fire frequency ($P < 0.0001$) and increasing soil N for most species (Fig. 1A). This occurred in spite of N concentrations on a mass basis trending in the opposite direction, which was due to an increase in specific leaf area with decreasing fire frequency. In both analyses (area- and mass-based), there were also significant species effects but no treatment \times species interaction.

Resorption proficiency, the N remaining following leaf senescence, did not demonstrate consistent patterns across the fire frequency treatment ($P > 0.05$), although several species increased senesced leaf N per cm^2 with decreasing fire frequency (Fig. 1B). As was found for concentrations in green leaves, resorption proficiency on a mass basis increased with decreasing fire frequency and increasing soil N availability ($P < 0.0001$) and post-hoc contrasts showed that the low fire frequency plots had statistically greater senesced leaf %N than either the intermediate or high plots. There were also significant differences between species by both metrics (mass- and area-based, $P < 0.0001$, nonsignificant treatment \times species interaction term) due largely to *A. canescens* which had the greatest N concentrations.

Patterns of proficiency were also examined using the minimum (rather than the mean) amount that each species reduced leaf N to during senescence (Table 2). This analysis found that the species generally decreased resorption proficiency with increasing soil N availability and half of these species exhibited complete resorption ($< 0.7\% \text{N}$ or $< 50 \mu\text{g N}/\text{cm}^2$) (Killingbeck 1996) under conditions of low soil N.

Resorption efficiency, the percentage of N in green leaves that is withdrawn prior to senescence, showed no significant differences among fire frequency treatments (Fig. 1C). There were significant species effects as *A. canescens* (the lone legume in this study)

Fig. 1 Patterns of foliar N on an area basis ($\mu\text{g N}/\text{cm}^2$) in green leaves (A), senesced leaves (resorption proficiency) (B), and resorption efficiencies, proportional change in foliar N concentrations due to senescence (C) across a fire frequency gradient. For each species, *open bars* represent the mean values for high fire frequency (corresponding to low fertility), *dashed bars* are intermediate fire frequency plots, and the *hatched bars* are low fire frequency (relatively high soil fertility). *Error bars* are standard errors. In panel B, *dashed lines* represent complete (0.7%N or $50 \mu\text{g N}/\text{cm}^2$) and incomplete resorption (1.0%N or $75 \mu\text{g N}/\text{cm}^2$) following Killingbeck (1996). There was a significant treatment (fire frequency) effect in green leaf N (A, $P < 0.0001$) but not on resorption proficiency (B) or efficiency (C). In a separate analysis, the seven non-legumes did exhibit significantly decreased resorption efficiency with increasing soil N availability ($P = 0.0312$). In each panel, there were significant species effects ($P < 0.001$) but no significant interaction term (fire frequency \times species)



had lower resorption efficiency rates than six of the other seven species and *Stipa spartea* generally had greater resorption than the other species. When the N-fixer *A. canescens* (with potentially less selection pressure to develop N conservation mechanisms) was removed from the analysis, fire frequency effects on resorption efficiency were significant ($P = 0.0312$) with resorption increasing with increasing fire frequency (Fig. 2A). There were trends towards greater

fractional resorption with increasing fire frequency in each of *A. gerardii*, *R. arkansas*, *S. spartea*, *S. stellata*, and perhaps *S. nutans* (Fig. 1C).

Fertilization gradient

Green leaf N contents (Fig. 3A) generally increased with fertilization ($P = 0.0166$) with the clear exception of *A. canescens*. Plants in the control and low N plots

Table 2 Resorption proficiency (minimum senesced foliar N concentrations) for both natural and artificial fertility gradients

	<i>Amorpha canescens</i>	<i>Andropogon gerardii</i>	<i>Artemisia ludoviciana</i>	<i>Quercus ellipsoidalis</i>	<i>Quercus macrocarpa</i>	<i>Rosa arkansana</i>	<i>Smilacena stellata</i>	<i>Sorghastrum nutans</i>	<i>Stipa stellata</i>	Mean (\pm SE)
Fire frequency gradient										
Senesced %N										
Fire frequency										
High	1.80	0.41		0.63	0.60	0.79	0.31	0.34	0.31	0.65 (0.18)
Intermed	1.78	0.50		0.61	0.79	1.22	0.39	0.37	0.28	0.74 (0.18)
Low	1.64	0.40		0.69	0.91	1.61	0.32	0.43	0.38	0.80 (0.19)
Senesced μ g N/cm ²										
Fire frequency										
High	97.2	31.2		37.6	45.8	53.7	26.4	26.6	35.5	44.2 (8.3)
Intermed	90.0	48.6		36.6	45.2	70.0	26.4	32.5	35.3	48.1 (7.6)
Low	59.7	34.5		45.7	53.7	82.6	13.3	31.8	28.5	43.7 (7.6)
Fertilization gradient										
Senesced %N										
Fertilization										
Control	1.77	0.99	0.95	0.70	1.41	0.41	0.83	0.54	0.55	0.90 (0.15)
Low N	1.93	0.76	1.41	0.78	1.43	0.46	0.74	0.64	0.48	0.96 (0.17)
High N	2.35	1.04	1.62	0.71	1.59	0.50	1.25		0.57	1.20 (0.22)
Senesced μ g N/cm ²										
Fertilization										
Control	105.4	72.2	69.7	46.1	117.8	24.1	38.7	32.7	44.0	61.2 (10.9)
Low N	93.7	41.1	72.9	42.6	85.9	26.8	30.1	40.4	41.2	52.7 (8.2)
High N	94.4	66.7	125.1	56.9	122.1	28.8	54.6		61.5	76.3 (12.1)

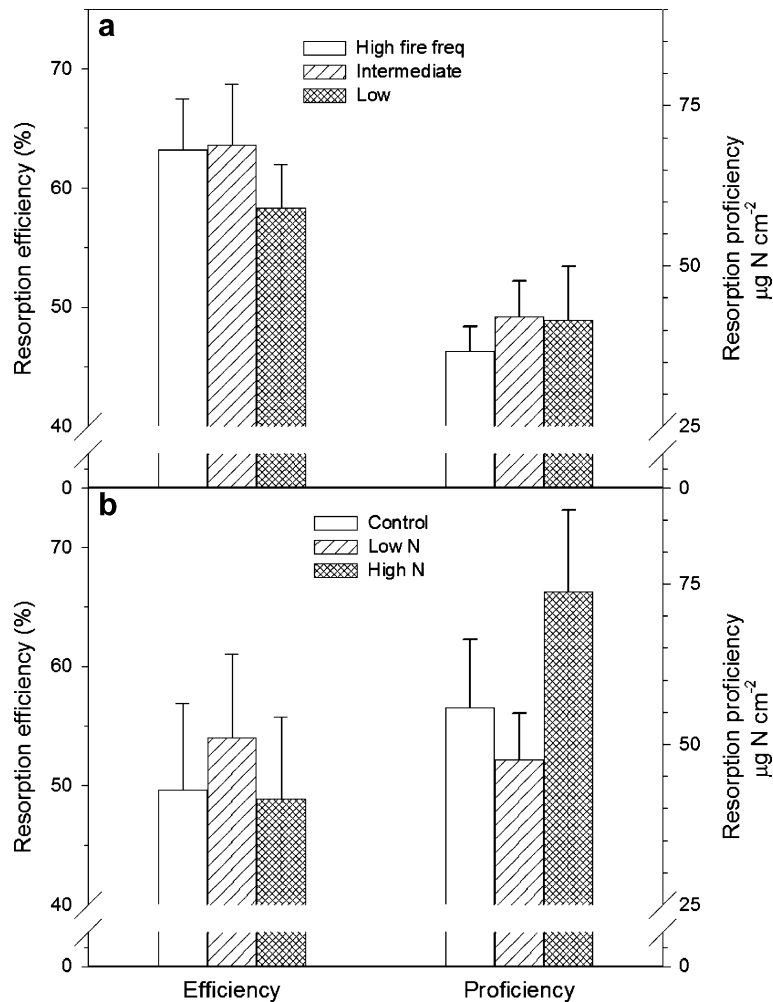


Fig. 2 Mean resorption efficiencies and proficiencies (minimum senesced leaf N) on an area basis across all species excluding the legume in the fire frequency gradient (**A**) and the fertilization gradient (**B**). Decreasing fire frequency and associated increased in soil N availability significantly reduced

resorption efficiency ($p=0.0312$) but did not significantly impact resorption proficiency. In the fertilization gradient, decreasing soil N availability significantly reduced resorption proficiency ($P<0.0001$) but not efficiency

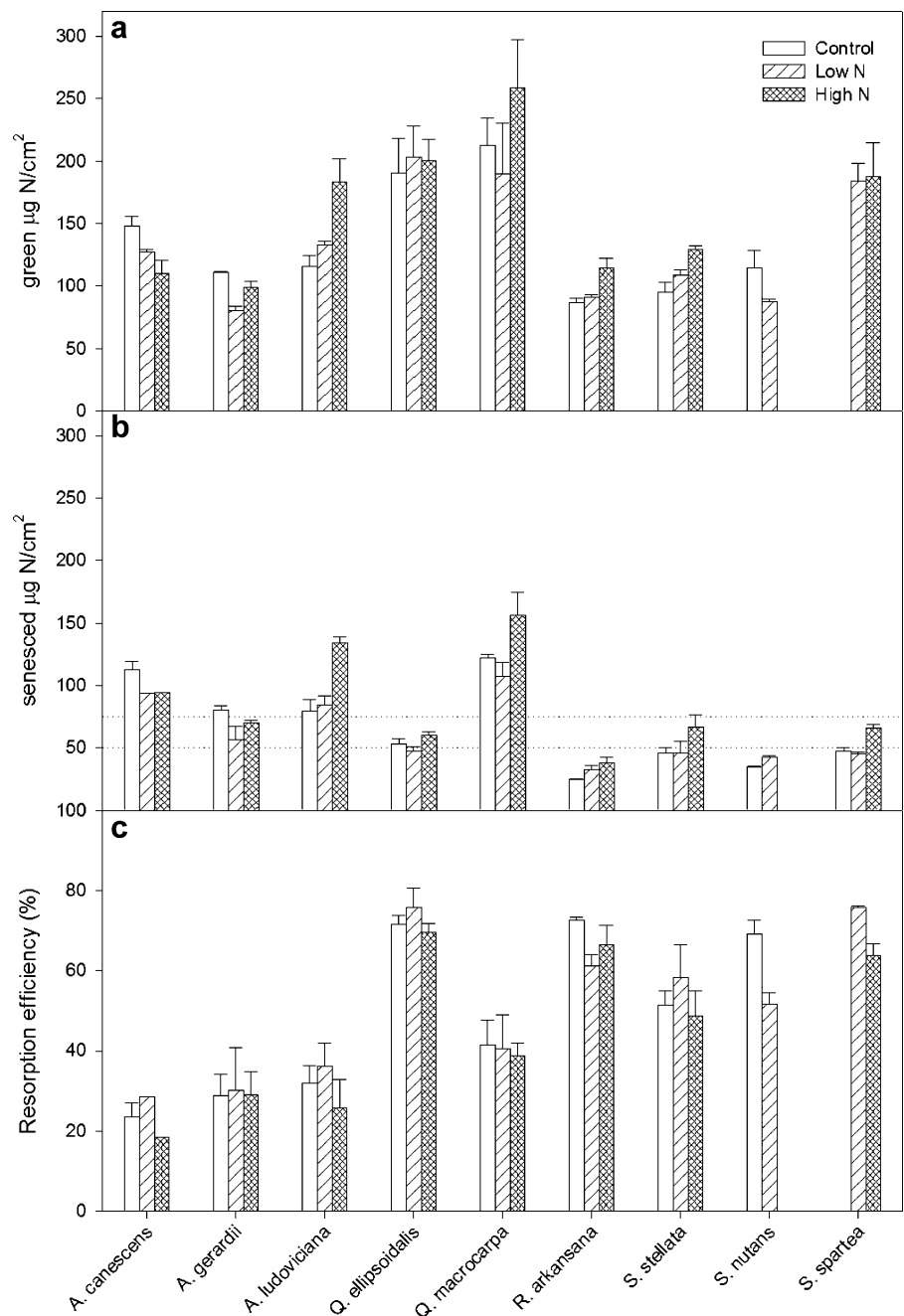
did not differ significantly from each other but had statistically lower leaf N than the high fertilized treatment. There were significant species effects ($P<0.0001$) and also a significant species \times treatment interaction ($P=0.0067$) that disappears with the exclusion of *A. canescens*.

Resorption proficiency expressed as mean N in senesced leaves decreased with fertilization (Fig. 3B). There was a significant treatment effect ($P<0.0001$) as the control and low fertilization plots (which did not differ) had lower senesced leaf N concentrations than high fertilized plots. Minimum N concentration

values in senesced tissue indicated the ability for greater leaf N reduction without fertilization as most species were less proficient under high fertilization (Table 2). By Killingbeck's (1996) index, *R. arkansana*, *S. nutans*, and *S. spartea* were the only species to exhibit complete resorption.

Resorption efficiency was not significantly affected by fertilization treatment (Fig. 3C). Statistical differences were again found among species due to four species (*Q. ellipsoidalis*, *R. arkansana*, *S. stellata*, and *S. spartea*) being more efficient than other species and the N-fixer *A. canescens* being the least efficient.

Fig. 3 Patterns of foliar N on an area basis ($\mu\text{g N}/\text{cm}^2$) in green leaves (A), senesced leaves (resorption proficiency) (B), and resorption efficiencies, proportional change in foliar N concentrations due to senescence (C) across a N fertilization gradient. For each species, *open bars* represent the mean values for the control plots (corresponding to lowest relative fertility), *dashed bars* are plots fertilized with $5.4 \text{ g N m}^{-2} \text{ year}^{-1}$, and the *hatched bars* are plots fertilized with $17 \text{ g N m}^{-2} \text{ year}^{-1}$. Error bars are standard errors. In panel B, *dashed lines* represent complete (0.7%N or $50 \mu\text{g N}/\text{cm}^2$) and incomplete resorption (1.0%N or $75 \mu\text{g N}/\text{cm}^2$) following Killingbeck (1996). There was a significant treatment (fertilization) effect in green leaf N (A, $P=0.002$) and resorption proficiency ($P<0.0001$) but not resorption efficiency (C) regardless of the inclusion of the legume *Amorpha canescens*. In each panel, there were significant species effects ($P<0.001$) but no significant interaction term (fire frequency \times species) except in green leaf N ($P=0.0067$)



As was done for the fire frequency gradient, *A. canescens* was removed from the analyses but with no impact on results (Fig. 2B).

Scaling analysis

Across species and treatments in both experimental fertility gradients, there were significant relationships

between green and senesced foliar N concentrations and contents (Fig. 4). Using the model defined as $\log_{10}([\text{nutrient}]_{\text{sen}}) = A' + B \times \log_{10}([\text{nutrient}]_{\text{gr}})$ where $[\text{nutrient}]_{\text{sen}}$ and $[\text{nutrient}]_{\text{gr}}$ are the nutrient concentrations in senesced and green tissues, respectively, on either a mass or area basis, A' is the baseline proportion of $[\text{nutrient}]_{\text{gr}}$ retained in senesced leaves, and B represents the disproportionate effects of

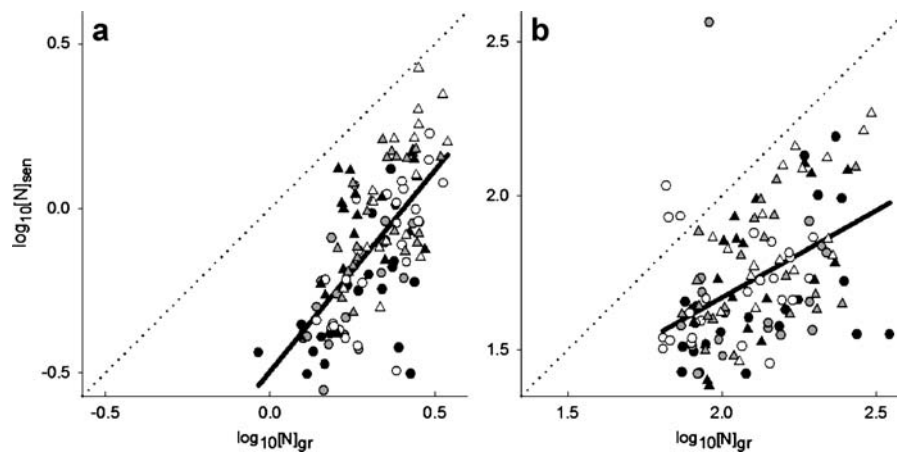


Fig. 4 The relationship between green and senesced foliar N concentrations using combined data from the fire frequency gradient and the fertilization gradient is a significant linear relationship for mass based data (**A**, $R^2=0.44$, $P<0.0001$) and by leaf area (**B**, $R^2=0.20$, $P<0.0001$). The slopes of these lines (**B**) are 1.23 (although not significantly different than 1) and 0.56, respectively. Individual symbols represent the mean

[nutrient]_{gr} on [nutrient]_{sen} where values >1 indicate decreasing resorption efficiency and $B<1$ indicates increasing resorption efficiency with increasing [nutrient]_{gr} (Kobe et al. 2005). Fitting this model to our mass-based data including all species except *A. canescens*, we found B to be equal to 1.06 and 1.11 in the fire frequency and fertilization gradients, respectively, indicating decreasing resorption efficiency with increasing green leaf N concentration. Results based on area-based N contents yielded B values of 0.35 and 0.79 in the fire frequency and fertilization gradients, respectively. In each of the above cases, the relationship between green and senesced leaf N was significant ($p<0.0001$); however, the slopes (B) were not statistically different from 1 with the exception of the area-based analysis in the fire frequency gradient which was less than 1. Combining data from these two gradients results in an increased sample size and using these data, the value of B for the mass-based data equals 1.23 ($p<0.0001$, $R^2=0.44$) (95% confidence interval: 0.97, 1.48) and 0.56 ($p<0.0001$, $R^2=0.20$) (95% confidence interval: 0.36, 0.77) for the leaf area-based measurements (Fig. 4). If B is examined by data analyzed by individual treatments, B generally increases with increasing soil N status (in 3 of the 4 scenarios of mass or area-based measurements in the fire frequency or fertilization gradient) suggest-

ing that as soil N status decreases, resorption efficiency increases; however, these values were not statistically different from one another.

Discussion

In contrast to a previous review of the topic (Aerts 1996), our results provide some evidence that soil fertility modestly influences nutrient resorption patterns. Our data largely support the hypothesis that senesced foliar N would demonstrate a significant intra-specific positive relationship to fertility. Patterns of resorption proficiency show that within a species, plants under lowest soil fertility (with respect to fire or fertilization) generally reduce N in senesced foliar tissue to a lower amount, on either a mass or area basis, than that of plants at higher fertility (Table 2), possibly due either to lower green leaf N or greater resorption efficiency. Similarly, a regional scale analysis of Scots pine also suggested greater N resorption for plants in increasingly N-limited conditions (Oleksyn et al. 2003).

Our results also provide some limited support for the hypothesis that resorption efficiency should decrease with increasing N supply and increasing plant N status. There was increased N resorption with decreasing N availability across the fire frequency

gradient for the seven non-fixers (Fig. 2A) but not with decreasing N fertilization (Fig. 2B). Also, a modeling approach showed decreasing resorption efficiency with increasing green tissue N concentrations (Fig. 4).

This study is rare amongst related literature in that it provides a direct comparison of plant species that occur over a range of measured soil nitrogen availability on similar soils. Despite suggesting that plants do not respond to soil fertility through retranslocation efficiency, Aerts (1996) suggested that many of the reviewed experiments were problematic as a test of the hypothesis that plants decrease resorption efficiency rates with elevated nutrient availability as they did not explicitly compare intraspecific variation across levels of soil nutrient availability. In our data, there are three arguments suggesting that we should not disregard retranslocation as a means of nutrient conservation differences along soil fertility gradients or among species with different N status. First, there is a trend in many species, at least in the fire frequency gradient, that resorption efficiency declines with increasing soil N (Figs. 1C and 2A). Second, species do respond significantly to increased soil fertility through reduced resorption proficiency (Figs. 3B, and 2B). These data add credence to Killingbeck's (1996) conclusion that resorption efficiency and proficiency are not inherently linked and may be indicative of different processes or selective pressures. However, in a simple linear regression (not shown), proficiency and efficiency were significantly related ($P < 0.0001$) although the model explained relatively little of the variation ($R^2 = 0.24$). It appears in this study that severe limitation by N (Tilman 1984, 1987) allows mature green foliar N concentrations to respond positively to increased soil N fertility (Figs. 1A and 3A) perhaps masking substantial reductions in resorption if green N concentrations are more variable than resorption efficiency.

The third argument for meaningful ecological differences in resorption patterns is found in the scaling analysis fitting the models developed by Kobe et al. (2005) to our data. Their conclusion based on a global meta-analysis suggested that variation in resorption efficiency across fertility gradients may result from species sorting across gradients. When we applied the model to our data, values of B (the disproportional effect of green leaf N

concentration on resorption) were also >1 (based on the mass-based measurements), indicating that resorption efficiency decreased with increasing plant N status (Fig. 4A). Given that the vast majority of the variation in green and senesced N values in our study were due to species and not treatments, this indicates that species with intrinsically lower N tissues, presumed to be better adapted to less fertile sites (Aerts and Chapin 2000), had greater resorption efficiency. The fact that this pattern was not seen in the area-based measurements (Fig. 4B) is likely due at least in part to decreasing green leaf N with increasing soil N availability in the fire frequency gradient which is likely attributed to a corresponding increase in specific leaf area. Additionally, although there is a statistically significant correlation, the green leaf N explains relatively little of the variation in senesced leaf N contents ($R^2 = 0.20$).

For each measure of foliar N concentration and retranslocation, there were significant differences between species (but not significantly different responses of species across fertility gradients). We could not address whether these differences could be attributed to plant growth form or photosynthetic pathway given our sample size. One consistent pattern amongst the species is that the legume *Amorpha canescens* had relatively high foliar N concentrations and low resorption efficiencies, regardless of fertility level, which is consistent with the idea that legumes should have less selective pressure to maximize resorption efficiency. Removing this species from the analysis only altered the statistical results in one case, resorption efficiency in the fire frequency gradient, presumably due to interspecific variation between the remaining species.

In conclusion, retranslocation is a mechanism by which all plants conserve N in N-poor oak savanna habitats at Cedar Creek as in many other systems, with some evidence that this conservation is enhanced when soil N availability is low and in species with intrinsically low tissue N levels. Our data, along with previous syntheses and reviews (Aerts 1996; Killingbeck 1996; Kobe et al. 2005), indicate that there remains a need to better understand differences in patterns and mechanisms of plastic versus interspecific variation in N conservation during tissue senescence.

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