

Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species

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Summary

1. Most plants withdraw nutrients from leaves as they age, and redeploy them elsewhere in the plant. The proportion of nutrients resorbed and the residual nutrient concentration in senesced leaves are different but complementary indices of nutrient conservation via this process. A major spectrum of strategic variation runs from plant species with typically long leaf lifespan (LL), high leaf mass per area (LMA), low leaf nutrient concentrations, and low photosynthetic capacity, to species with the opposite characteristics. It is unknown to what extent either facet of resorption covaries with the LL–LMA spectrum.

2. Green-leaf and senesced-leaf N and P concentrations were quantified for 73 evergreen species from four sites in eastern Australia (nutrient-rich and nutrient-poor sites in each of two rainfall zones). Leaf nutrient concentrations in green and senesced leaves were negatively correlated with LL across all species and at most sites, especially if N₂-fixing species were excluded from analyses involving leaf N.

3. Proportional resorption did not differ with soil nutrients, as has been found elsewhere, nor was it correlated with LL. Green-leaf and senesced-leaf nutrient concentrations were lower for species on poorer soils. A simple model was described in which the proportion of resorbed *vs* soil-derived nutrients deployed in new leaves is set by the relative cost of nutrients from the two sources. The model provides a prospective explanation for the observed differences between species from nutrient-rich and nutrient-poor habitats.

4. The results from this study provide support for the argument that selection to minimize nutrient losses has affected the residual nutrient concentration in senesced leaves, rather than proportional resorption *per se*. Further, variation among species in residual nutrient concentration was correlated with one of the key spectra of strategic variation between plant species, the leaf lifespan–LMA axis of variation.

Key-words: Leaf lifespan, leaf mass per area, leaf nutrients, nutrient resorption

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Introduction

A major spectrum of variation runs between species with traits that favour nutrient conservation and those with traits that allow rapid short-term growth. Species at the nutrient-conserving end of the spectrum typically have long leaf lifespan (LL), high leaf mass per area (LMA), low leaf nutrient concentrations, and low photosynthetic capacity (Reich, Walters & Ellsworth 1997); species at the other end of the spectrum typically have the opposite characteristics. Nutrient-poor habitats tend to be dominated by nutrient-conserving species, while fertile habitats tend to be dominated by species with higher short-term productivity per leaf

mass (Chapin 1980; Grime 1977). Still, within any given habitat, species with a range of leaf traits may coexist (Reich *et al.* 1999).

Nutrient resorption is the process in which nutrients are withdrawn from leaves prior to abscission and redeployed in developing tissues (such as leaves or reproductive structures such as seeds), or stored for later use. Resorption may occur throughout a leaf's life, particularly as leaves become progressively shaded (Ackerly & Bazzaz 1995; Hikosaka 1996), but a major pulse of resorption normally occurs shortly before leaf abscission. It is an integral part of the highly ordered process of leaf senescence and appears to occur in most species (Noodén 1988). On average, around 50% of leaf N and P is recycled via resorption (Aerts 1996). Still, the proportion of nutrients withdrawn from leaves (the resorption efficiency) varies widely between

species. For example, <5 to 80% of leaf N, and 0–95% of leaf P, may be resorbed (Aerts & Chapin 2000). Nutrient resorption allows leaf nutrients to be reused rather than lost with leaf fall, thus extending the mean residence time of nutrients in the plant. Long nutrient mean residence time is thought to be particularly advantageous in infertile habitats (Aerts & van der Peijl 1993); however, resorption efficiency does not seem to vary systematically between habitat types (Aerts 1996). Rather, nutrient residence times appear to be extended in nutrient-poor habitats via generally longer leaf lifespans (Eckstein, Karlsson & Weih 1999; Escudero *et al.* 1992).

The level to which nutrient concentrations are reduced in senesced leaves or litter (resorption proficiency) is a different (but complementary) index of nutrient conservation from the proportion of nutrients resorbed. Evergreens have lower litter P concentrations than deciduous species, while N₂-fixers have higher litter N concentrations than non-N₂-fixers (Killingbeck 1996). The inverse of litter nutrient concentration has been used as an index of nutrient-use efficiency (Vitousek 1982). Litter nutrient concentration also exerts strong control over litter decomposition rate within a given climate zone (Cornelissen & Thompson 1997; Perez-Harguindeguy *et al.* 2000).

In this study, live and senesced leaves were collected for 73 species over a 2.5-year period. The species were spread across four sites dominated by evergreen species in eastern Australia: nutrient-rich and nutrient-poor sites within each of two rainfall zones. Our aim was to quantify N and P resorption in these species, to assess whether shifts in species means of these traits occurred between site types, and also to assess the extent to which nutrient resorption (proportional resorption and senesced-leaf nutrient concentrations) was correlated with the leaf lifespan–leaf mass per area–leaf nutrient spectrum of variation between plant species.

Materials and methods

SITE AND SPECIES SELECTION

The four study sites and the species selection criteria were described in detail by Wright, Reich & Westoby (2001) and Wright, Westoby & Reich (2002). Briefly, all sites were located in National Park reserves and were dominated by evergreen, sclerophyllous trees and shrubs. In each of two rainfall zones (coastal New South Wales, 1220 mm annual rainfall; western NSW, 390 mm), two vegetation types were chosen: one on nutrient-rich soil, one on nutrient-poor soil. Total soil P was used as the main index of soil nutrient status, the nutrient-rich and nutrient-poor coastal sites having 442 (SD 232) and 94 (28) $\mu\text{g g}^{-1}$ total P, respectively, the drier sites 250 (34) and 132 (15) $\mu\text{g g}^{-1}$ total P. The pairs of nutrient-rich and nutrient-poor sites differed also in total soil N and cation-exchange capacity (Wright *et al.* 2001). As much as possible, sites were

matched for other attributes (seasonality of rainfall, mean annual temperature, slope). Fifteen to 22 taxa were studied at each site, chosen from among perennial, non-climbing plants. Six species occurred at both nutrient-rich and nutrient-poor drier sites; these were not combined in analyses as the aim was to compare traits of representative vegetation at each site. The 73 study species ('species' is used in the loose sense to include subspecies and, in two cases, currently unrecognized varieties) were taxonomically diverse, representing 22 families, and included trees, shrubs and subshrubs, N₂-fixers and non-N₂-fixers. With the exception of one conifer and one cycad, all study species were dicots.

LEAF COLLECTIONS

Leaves were collected over a 2.5-year period at the drier, nutrient-rich site (December 1997–June 2000) and for *c.* 2 years at all other sites (June 1998–August 2000). Two to four collections were made of green leaves per species over that time (average 3.0). One collection consisted of leaves used for photosynthesis measurements (Wright *et al.* 2001). For other collections, five leaves were collected from each of five individuals for each species. Only current-season, fully expanded, outer canopy leaves were included in each sample.

Senesced leaves are those in which an abscission layer has formed in the base of the petiole, preventing further nutrient withdrawal (Norby *et al.* 2000). These leaves are easily identified as they are generally a different colour from live leaves (often red or yellow), and can be removed by a gentle flicking of the branch or leaf; leaves without an abscission layer are not removed by this technique. Senesced leaves were collected directly off plants rather than from leaf litter, as we were concerned that decomposition of litter and leaching of leaf nutrients would lead to underestimates of nutrient concentrations in senesced leaves. At each collection time several leaves were collected from several individuals (generally three to five) and pooled for nutrient analysis. It was not possible to collect a standard number of leaves from a standard number of individuals (as for collections of green leaves), as the number of senesced leaves, where present, varied among species. However, by pooling across several individuals we hoped to obtain a fair estimate of nutrient concentrations at each sampling time, in a comparable manner to estimates made of green-leaf nutrient concentrations. On average, 2.7 collections of senesced leaves were made for each species.

CALCULATION OF LEAF TRAITS

Average leaf lifespan was previously published for this set of species by Wright *et al.* (2002). Leaf samples were dried for a minimum of 48 h at 70 °C. Leaf mass per area (LMA) was calculated from dry mass and

one-sided leaf area (flat-bed scanner; needle leaves assumed to have circular cross-section and leaf area adjusted by $\pi/2$). Live and senesced leaves from each sampling period were finely ground, and leaf N and P concentrations were determined in an autoanalyser from a solution obtained by Kjeldahl digestion (analyses undertaken at CSIRO Plant Industry, Canberra). Green-leaf N and P concentrations (hereafter N_{live} and P_{live}) were calculated as the mean across the several samples for each species. Similarly, the mean N and P concentration in senesced leaves was calculated across sampling times for each species and used in the calculation of proportional resorption (see below). The minimum nutrient concentration of senesced leaves is also of interest. Killingbeck (1996) noted that litter nutrient concentrations may differ over time, which he attributed to incomplete resorption at some sampling times (for example, due to reduced water availability, or the absence of sinks for resorbed nutrients elsewhere on a plant). Accordingly, the lowest recorded N and P concentration of (pooled) senesced leaves was used to estimate the lower limit to which nutrients are reduced prior to leaf fall for each species (N_{dead} and P_{dead} , hereafter). These minimum and mean senesced-leaf nutrient concentrations were tightly correlated among species ($r > 0.9$). Pooling leaves within sampling periods, and between collections (for green-leaves and mean senesced-leaf nutrient concentrations), prohibited detailed estimates of within-species variation in leaf nutrient concentrations. Still, variance components analysis could be run on the nutrient concentrations as an estimate of the variance explained by species *vs* sampling period within species. These analyses indicated that most variation was explained by the species term for each trait (percentage explained by species term in ANOVA model, type I sums of squares: N_{live} 88.6%, P_{live} 89.0%, mean senesced-leaf N 75.5%, mean senesced-leaf P 77.3%).

Estimates of proportional nutrient resorption made on a leaf area basis may be more accurate than estimates made on a leaf mass basis, as LMA may increase with leaf age (often with concomitant dilution of N_{live}), and then decrease during senescence (Chapin, Schulze & Mooney 1990). Accordingly, proportional resorption was calculated as the percentage reduction in leaf N (or P) per unit leaf area from green to senesced leaves. Green-leaf and senesced-leaf nutrient concentrations per unit leaf area were themselves calculated from mass concentrations and the LMA of green and senesced leaves. However, as it was not possible reliably to measure the LMA of senesced leaves for several species (leaves had curled or become otherwise deformed), only 60 of 73 species were able to be used in analyses concerning proportional resorption, whereas all species were used in other analyses. A note of caution is necessary regarding estimates of proportional resorption. In species where nutrients are progressively withdrawn from leaves as they age or become shaded, and in species where significant pools of nutrients are stored

in roots or stems (e.g. forbs, or deciduous trees), resorption estimates based on nutrient concentrations in green and senesced leaves may underestimate the contribution of remobilized nutrients to developing tissues. This can be overcome by using isotope tracers to track nutrient dynamics (Millard *et al.* 2001; Proe, Midwood & Craig 2000). By contrast, quantifying resorption in terms of the nutrient concentration in senesced leaves is not prone to this effect.

DATA CONSIDERATIONS

For each measured trait, the distribution of species means within each site was tested for non-normality (Shapiro–Wilk test, $\alpha = 0.05$). N and P resorption were deemed normal and left untransformed in all subsequent analyses. All other traits showed approximately log-normal distributions and were deemed normal following log transformation. Site means for the traits were compared with *t*-tests: nutrient-rich and nutrient-poor sites were compared within each rainfall zone, and wetter and drier sites were compared at each level of soil nutrients. Trait relationships were explored with Pearson correlation analyses and by fitting standardized major axis (SMA) slopes. SMA slope-fitting techniques are appropriate for describing bivariate relationships where *X* as well as *Y* variables have variation associated with them due to measurement error and species sampling, hence when it is inappropriate to minimize sums of squares in the *Y* dimension only (Sokal & Rohlf 1995). SMAs were fitted for each site individually. Tests for homogeneity of slopes and calculation of common slopes followed Warton & Weber (2002). Where a common slope could be fitted (test for homogeneity, $P > 0.05$), differences in elevation (intercept) of slopes were tested by *t*-test of group mean Y' , where Y' is *Y*-transformed as $Y - bX$ for each group, and *b* is the common slope (i.e. slopes transformed so slope = 0 and group means compared). That is, these analyses used an SMA analogue of standard ANCOVA. All statistical tests were significance tested at $\alpha = 0.05$.

Results

COMPARISON OF SITE MEANS

Mean N and P concentrations (%) of green leaves were generally higher at the nutrient-rich site within each rainfall zone (*t*-tests, N_{live} : high rain $P = 0.010$, low rain $P = 0.077$; P_{live} : high rain $P < 0.0001$, low rain $P = 0.003$), and higher at the drier of the two sites within each soil nutrient class (all $P < 0.007$; Fig. 1a,b). Similarly, mean nutrient concentrations in senesced leaves (N_{dead} and P_{dead}) were higher at the nutrient-rich site within either rainfall zone (N_{dead} : high rain $P = 0.019$, but low rain $P = 0.103$; P_{dead} : high rain $P < 0.0001$, low rain $P = 0.001$), and higher at the drier site within each soil nutrient class (all $P < 0.003$; Fig. 1c,d). By Killingbeck's

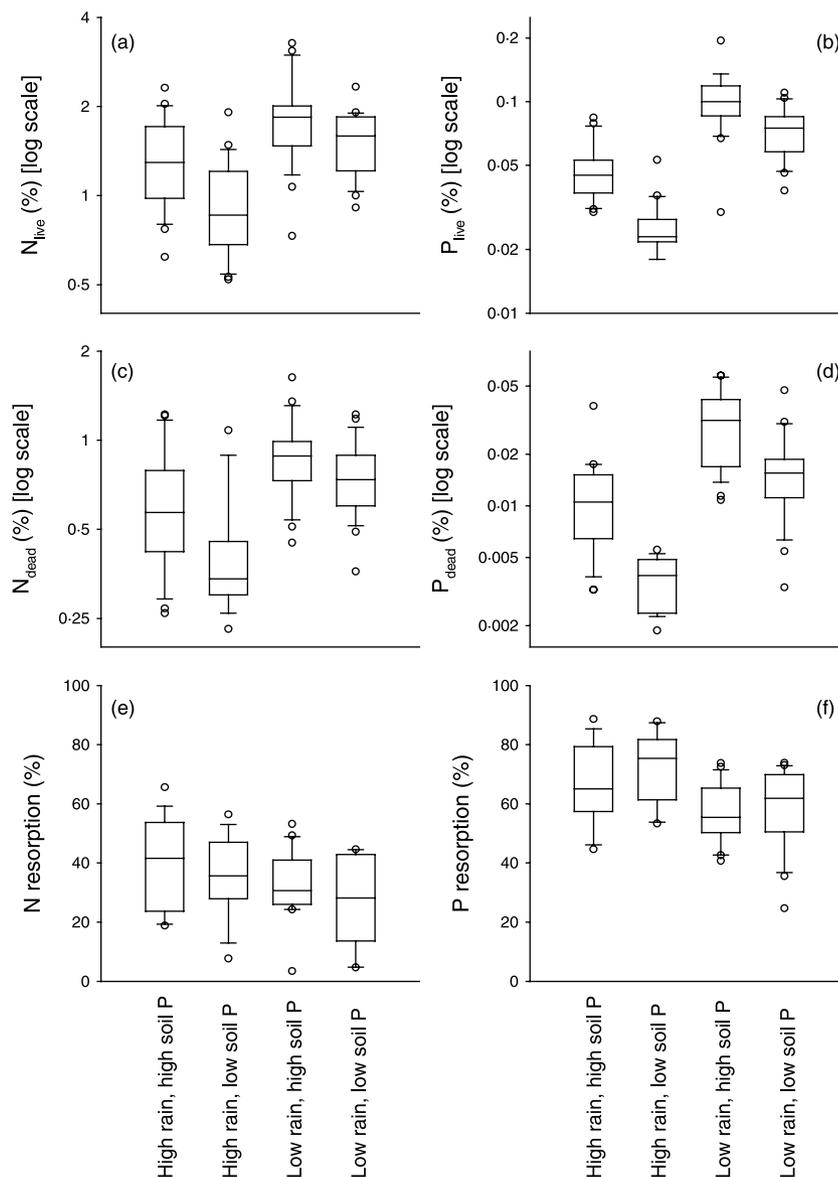


Fig. 1. Box plots of leaf N and P concentration and proportional resorption for species at the four sites. Each box represents the interquartile range, with median indicated. Whiskers represent the 10th and 90th quartiles, circles indicate species outside this range. (a,b) Nutrient concentrations in green leaves; (c,d) nutrient concentrations in senesced leaves; (e,f) proportional resorption of leaf N and P.

(1996) benchmarks of ‘complete’ N or P resorption for evergreen species (N_{dead} reduced to $<0.7\%$ N, P_{dead} to $<0.04\%$ P), most species had complete P resorption (66/73) and about 50% had complete N resorption (38/73).

Proportional resorption of N, calculated on a leaf area basis, varied from 4 to 66% (mean 34%), P resorption from 25 to 89% (mean 63%). No differences in mean N or P resorption were found between nutrient-rich and nutrient-poor sites within either rainfall zone (all $P > 0.195$; Fig. 1e,f). N resorption did not differ with site rainfall within either soil nutrient class (both $P > 0.13$) although, with all species pooled, less N was resorbed at low rainfall (30.0 vs 37.8%, $P = 0.041$). P resorption was lower at drier sites, comparing both nutrient-rich and nutrient-poor sites, or comparing all species (all $P < 0.02$).

TRAIT CORRELATIONS

Green-leaf N and P concentrations were generally correlated across species within each site and across all species considered together (Table 1), but especially so when N_2 -fixing species were excluded from analyses, as they tended to have high leaf N but varied widely in P concentration. Similarly, N_{dead} and P_{dead} were correlated, at least when N_2 -fixers were excluded.

Considering all data, species with long-lived leaves had high LMA (Table 1) and low nutrient concentrations in both green and senesced leaves (Fig. 2). This was also generally true within individual sites, although the LL relationships involving N_{live} or N_{dead} were stronger with N_2 -fixers excluded from analyses (Table 1). Slopes describing LL–leaf nutrient concentrations (in green

Table 1. Pearson correlations between leaf traits at the four study sites (r and P values; sample sizes in parentheses)

Traits	High rain, high soil P	High rain, low soil P	Low rain, high soil P	Low rain, low soil P	All species
$N_{\text{live}}, P_{\text{live}}^*$	0.42, 0.087 (18)	0.32, 0.214 (17)	0.71, <0.001 (23)	0.62, 0.004 (19)	0.73, <0.001 (77)
$N_{\text{live}}, P_{\text{live}}^\dagger$	0.73, 0.004 (13)	0.76, 0.001 (14)	0.78, <0.001 (19)	0.89, <0.001 (14)	0.87, <0.001 (60)
$N_{\text{dead}}, P_{\text{dead}}^*$	0.24, 0.345 (18)	0.22, 0.430 (15)	0.57, 0.006 (22)	0.42, 0.080 (18)	0.66, <0.001 (73)
$N_{\text{dead}}, P_{\text{dead}}^\dagger$	0.73, 0.005 (13)	0.75, 0.003 (13)	0.64, 0.004 (18)	0.89, <0.001 (14)	0.89, <0.001 (58)
LL, LMA	0.71, 0.001 (17)	0.58, 0.014 (17)	0.86, <0.001 (23)	0.77, <0.001 (18)	0.67, <0.001 (75)
LL, N_{live}^*	-0.63, 0.006 (17)	-0.36, 0.156 (17)	-0.83, <0.001 (23)	-0.55, 0.017 (18)	-0.60, <0.001 (75)
LL, N_{live}^\dagger	-0.84, <0.001 (13)	-0.67, 0.009 (14)	-0.88, <0.001 (19)	-0.67, 0.009 (14)	-0.72, <0.001 (60)
LL, P_{live}^*	-0.57, 0.016 (17)	-0.62, 0.008 (17)	-0.66, 0.001 (23)	-0.80, <0.001 (18)	-0.50, <0.001 (75)
LL, P_{live}^\dagger	-0.48, 0.053 (17)	-0.14, 0.619 (15)	-0.49, 0.021 (22)	-0.22, 0.387 (17)	-0.40, 0.001 (71)
LL, N_{dead}^\dagger	-0.83, <0.001 (13)	-0.62, 0.025 (13)	-0.49, 0.040 (18)	-0.52, 0.066 (13)	-0.56, <0.001 (57)
LL, P_{dead}	-0.25, 0.329 (17)	-0.66, 0.007 (15)	-0.52, 0.013 (22)	-0.45, 0.070 (17)	-0.43, <0.001 (71)

$N_{\text{live}}, P_{\text{live}}, N_{\text{dead}}, P_{\text{dead}}$: nutrient concentrations (%) in green and senesced leaves, respectively; LL: leaf lifespan.

*Including N_2 -fixers; †excluding N_2 -fixers.

All traits were log-transformed prior to analysis.

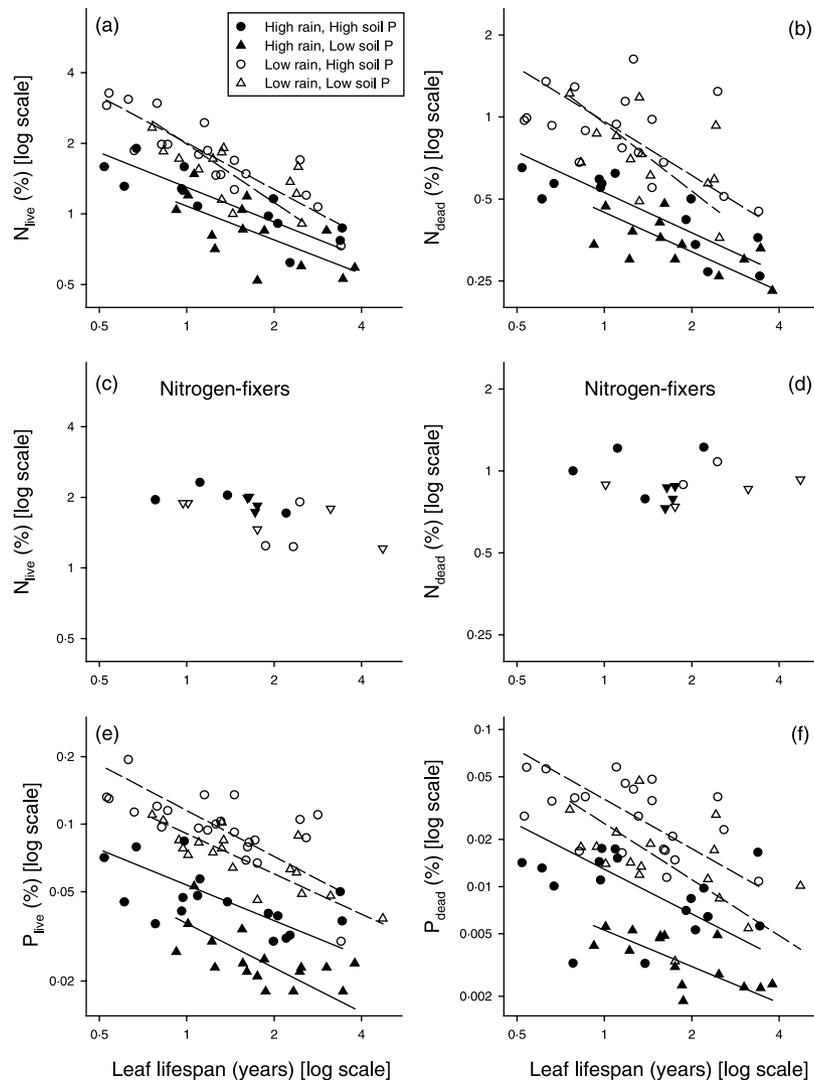


Fig. 2. Relationships between leaf lifespan (LL) and leaf nutrient concentrations of green and senesced leaves. Correlation statistics are given in Table 1. (a) N_{live} on LL (excluding N_2 -fixers). Common fitted slope, $\beta = -0.65$ (test for slope heterogeneity, $P = 0.413$). (b) N_{dead} on LL (excluding N_2 -fixers). Common fitted slope, $\beta = -0.57$ ($P = 0.310$). (c) N_{live} on LL (N_2 -fixers only). (d) N_{dead} on LL (N_2 -fixers only). (e) P_{live} on LL (all species). Common fitted slope, $\beta = -0.62$ ($P = 0.836$). (f) P_{dead} on LL (all species). Common fitted slope, $\beta = -1.02$ ($P = 0.710$).

Table 2. Pearson correlations between leaf traits (r and P values; sample sizes in parentheses)

Traits	High rain, high soil P	High rain, low soil P	Low rain, high soil P	Low rain, low soil P	All species
LMA, N_{live}^*	-0.63, 0.007 (17)	-0.45, 0.069 (17)	-0.85, <0.001 (23)	-0.81, <0.001 (18)	-0.39, 0.001 (75)
LMA, N_{live}^\dagger	-0.73, 0.005 (13)	-0.69, 0.007 (14)	-0.92, <0.001 (19)	-0.89, <0.001 (13)	-0.47, <0.001 (59)
LMA, P_{live}	-0.37, 0.150 (17)	-0.51, 0.036 (17)	-0.70, <0.001 (23)	-0.73, 0.001 (18)	-0.12, 0.328 (75)
LMA, N_{dead}^*	-0.57, 0.018 (17)	-0.15, 0.593 (15)	-0.39, 0.077 (22)	-0.53, 0.030 (17)	-0.17, 0.158 (71)
LMA, N_{dead}^\dagger	-0.75, 0.003 (13)	-0.36, 0.222 (13)	-0.39, 0.110 (18)	-0.71, 0.007 (13)	-0.23, 0.080 (57)
LMA, P_{dead}	-0.20, 0.433 (17)	-0.14, 0.614 (15)	-0.52, 0.013 (22)	-0.51, 0.035 (17)	-0.13, 0.287 (71)
LL, N_{resorp}	-0.07, 0.819 (15)	0.07, 0.824 (14)	-0.38, 0.151 (16)	-0.56, 0.029 (15)	-0.21, 0.112 (60)
LL, P_{resorp}	0.02, 0.954 (15)	0.47, 0.095 (15)	0.39, 0.126 (17)	-0.26, 0.337 (16)	0.17, 0.174 (63)
LMA, N_{resorp}	-0.06, 0.837 (15)	-0.20, 0.500 (14)	-0.42, 0.104 (16)	-0.38, 0.17 (15)	-0.37, 0.004 (60)
LMA, P_{resorp}	0.03, 0.907 (15)	0.37, 0.174 (15)	0.32, 0.213 (17)	-0.25, 0.348 (16)	-0.02, 0.888 (63)
$N_{\text{resorp}}, P_{\text{resorp}}$	0.59, 0.021 (15)	0.46, 0.100 (14)	0.16, 0.546 (16)	0.75, 0.001 (15)	0.53, <0.001 (60)

LMA: leaf mass per area.

*Including N_2 -fixers; †excluding N_2 -fixers.

All traits except resorption efficiencies ($N_{\text{resorp}}, P_{\text{resorp}}$) were log-transformed prior to analysis.

or senesced leaves) did not differ between sites (all $P > 0.3$), facilitating tests for differences in slope elevations. Species at low-rainfall sites had significantly higher $N_{\text{live}}, P_{\text{live}}, N_{\text{dead}}$ and P_{dead} at a given LL than species at wetter sites (comparisons made between nutrient-rich and nutrient-poor sites separately, all $P < 0.001$). Species at nutrient-rich sites had higher P_{live} and P_{dead} at a given LL than species at nutrient-poor sites (comparisons made within each rainfall zone, all $P < 0.03$), while no accompanying trend in N_{live} or N_{dead} was observed.

Green-leaf N and P concentrations were generally negatively correlated with LMA, just as they were with LL (Table 2). LMA was negatively associated with N_{dead} and P_{dead} within individual sites, although these relationships were significant ($P < 0.05$) at nutrient-rich sites only for N_{dead} , and low-rainfall sites only for P_{dead} .

Leaf lifespan and LMA were not correlated with either N or P resorption, either within individual sites or across all species, save for a negative relationship between LL and N resorption at the dry, nutrient-poor site, and a negative relationship between LMA and N resorption across all species (Table 2). Thus, while the N and P concentrations of green and senesced leaves were tightly associated with the spectrum of LL–LMA variation between species, the efficiency of nutrient resorption was not.

TAXONOMIC PATTERNING IN NUTRIENT CONCENTRATION AND RESORPTION

There was considerable taxonomic patterning in leaf nutrient concentrations and resorption, with some cross-correlation with distribution. Species in the Asteraceae, Myoporaceae and Sapindaceae tended to have high N and P concentrations in green and senesced leaves. These families occurred almost exclusively at drier sites. Proteaceae, occurring almost exclusively at wetter sites, generally had low green-leaf and litter N and P concentrations. On average, nutrient resorption was lower in Myoporaceae than in other families,

particularly N resorption (mean 14%). Mimosaceae, represented by six N_2 -fixing *Acacia* species and found in all regions, had high N concentrations in green and senesced leaves, but low average N resorption (19%). The seven N_2 -fixing Fabaceae species also had high N concentration in live and senesced leaves, although resorption could be calculated only for two of the seven, averaging 42% (similar to the mean across all species).

Discussion

We were able to consider aspects of N and P resorption of 73 species in terms of site means, but also in conjunction with key traits involved in the carbon gain/nutrient-use strategy of species: leaf lifespan, LMA and leaf nutrient content. Together, the results indicated that proportional resorption was not a strong correlate of these traits, nor did it differ on average between species inhabiting nutrient-rich and nutrient-poor sites. However, the nutrient concentration in senesced leaves (resorption ‘proficiency’ in the terminology of Killingbeck 1996) did clearly differ with site nutrient status, being lower in species occurring on nutrient-poor soils. Across all species and/or within individual sites, senesced-leaf N and P concentrations tended to be negatively correlated with LL and LMA, particularly if N_2 -fixers were excluded. Thus, this aspect of nutrient conservation appears to be part of the coordinated set of leaf traits that comprises a major spectrum of variation between plant species.

The P concentrations in senesced leaves were lower than most values previously reported (Killingbeck 1996), while senesced-leaf N concentrations were comparable with those reported elsewhere for evergreen species. Thus it appears that P conservation (via low P_{dead}) is highly developed in this set of species, even from those occurring on richer soils. This is in accord with the widely accepted view that soil P is the key limiting nutrient in many Australian ecosystems (Beadle 1966; Webb 1968). Koerselman & Meuleman (1996)

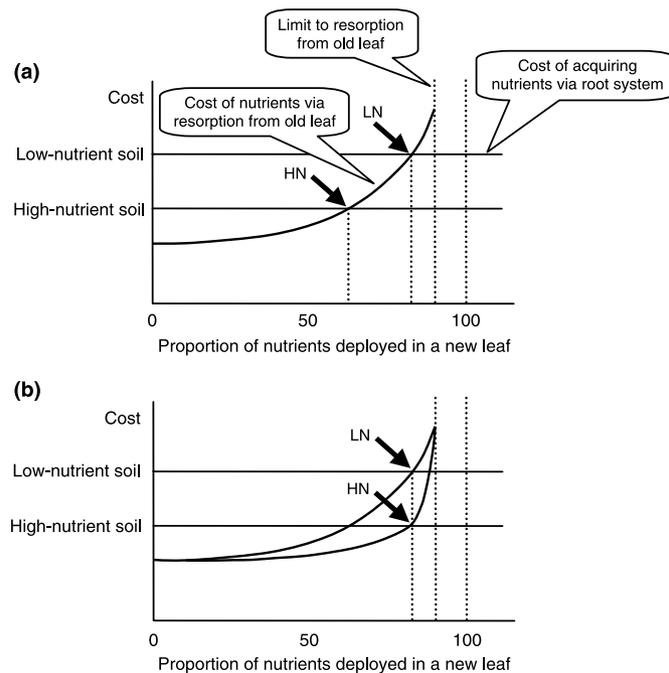


Fig. 3. A simple model in which the proportion of resorbed *vs* soil-derived nutrients deployed in new leaves is set by the relative cost of nutrients from the two sources. The crossover point (arrow) is where, in a given habitat, soil nutrients become less expensive to acquire than those from resorption, thus setting the level to which nutrients should be extracted from senescing leaves (see text). (a) Resorption-nutrient cost function has the same shape in both low (LN) and high (HN) nutrient habitats. (b) Resorption-nutrient cost function has shallower initial slope in high-nutrient habitat such that crossover points occur at the same proportional resorption.

argued that site-mean leaf N/P ratios >16 indicate that community biomass production is P-limited. Here, site-mean leaf N/P ratios varied from 18 to 37, and were all significantly >16 (one-tailed *t*-tests, all $P < 0.025$). Still, there was 30-fold variation in P_{dead} across the entire data set, and three- to 14-fold variation between sets of coexisting species. Comparative data for N_{dead} were sevenfold variation across all species and three- to fivefold variation between species at a given site. Why is there not convergence towards minimum possible nutrient concentrations in senesced leaves of all species, or at least between coexisting species?

MODELLING THE COSTS OF SOIL NUTRIENTS *VS* RESORBED NUTRIENTS

Nutrients deployed in new leaves come from two sources: from the soil, and via resorption from older leaves (sometimes with an intervening storage stage). At least some soil nutrient uptake is required to replace nutrients which are inevitably lost in litter. The unit cost of acquiring soil nutrients may be set largely by site characteristics such as nutrient availability (Bloom, Chapin & Mooney 1985). This cost may be more-or-less constant, or might vary throughout the year. Nutrients obtained via resorption also have a cost. Energy is required for the hydrolysis of organic compounds, for phloem loading of the resulting export molecules, and for maintaining osmotic gradients between sources and sinks (Chapin & Kedrowski 1983;

Hawkins & Polglase 2000; Norby *et al.* 2000). Stress-related genes may also be expressed during senescence, their products protecting the increasingly fragile cell during nutrient salvage (Bleecker 1998), a process that might also require energy expenditure. Storage of resorbed nutrients for later use may incur additional costs from chemical conversion to storage compounds, and from construction of special storage cells or tissues (Lambers, Chapin & Pons 1998). Presumably, the cost of resorbed nutrients varies between the particular class of compound from which they are derived. For example, P is exported in inorganic form, hence accumulated inorganic P would be cheaper to export than organic forms that must first be hydrolysed (e.g. phospholipids and nucleic acids). The majority of N exported may be in the form of amino acids (Chapin & Kedrowski 1983); again, the unit cost for mobilization of some N-containing compounds may be cheap, while others may require significantly more energy expenditure to access.

In Fig. 3, a model is proposed in which the relative cost of soil nutrients and resorbed nutrients determines what balance of nutrients from the two sources ends up in new leaves. In this model, the unit cost of soil-derived nutrients is independent of the amount taken up, with the unit cost set by the environment: soil nutrients are more expensive in a low-nutrient habitat. The unit cost of nutrients derived from resorption increases as less accessible nutrient pools are mobilized. This is depicted as a smooth increasing curve, but could equally be a step function, with successive

steps representing the increasing unit cost as less accessible nutrient pools are mobilized. The balance of soil-derived and resorption nutrients deployed in new leaves is set where soil nutrients become less expensive to acquire than those from resorption (at the crossover point, indicated by an arrow). Two possible scenarios are outlined in Fig. 3. In Fig. 3(a), the resorption-nutrient cost function has the same shape in low- and high-nutrient habitats. The crossover point occurs at a higher proportional resorption in the low-nutrient habitat, where soil nutrients are more expensive. Assuming that green-leaf nutrient concentration was lower (or similar) for a species in the low-nutrient habitat (as is commonly observed), the senesced-leaf nutrient concentration would then be lower for that species. In Fig. 3(b), the resorption-nutrient cost function has a shallower initial slope in the high-nutrient habitat such that the two crossover points occur at the same proportional resorption. Assuming that green-leaf nutrient concentration is lower for a species in the low-nutrient habitat, the senesced-leaf nutrient concentration will also be lower for that species. If the green-leaf nutrient concentrations were the same for the two species, senesced-leaf nutrient concentrations would also be equal. How do these two scenarios fit with the observed patterns in resorption and litter nutrient concentrations?

In nutrient-poor habitats, N_{dead} and P_{dead} were reduced to lower levels than in nutrient-rich habitats, whereas proportional resorption did not differ between low- and high-nutrient soils (Fig. 1). This is consistent with Fig. 3(b), where soil nutrients are more expensive to acquire where they are scarce, but the resorption-nutrient cost function is initially shallower for the species from the high-nutrient habitat. An initially shallower cost function for species at nutrient-rich sites implies that their high N and P leaves (Fig. 1a,b) have proportionally larger pools of cheap-to-resorb nutrients, which could be possible if, for example, they accumulated greater pools of inorganic P, or if their higher N concentration was due to a larger proportion of photosynthesis-related proteins which were relatively cheap to hydrolyse and export.

In a meta-analysis of within-species trends in nutrient resorption, Aerts (1996) found that there was no difference in proportional N or P resorption with enhanced nutrient availability in around 60% of studies, and lower proportional resorption approximately one-third of the time. It was concluded that nutrient availability exerts only weak control over nutrient resorption. However, both green-leaf and senesced-leaf nutrient concentrations tended to be higher under enhanced nutrient availability (as also reported by Chapin & Moilanen 1991; Pugnaire & Chapin 1993). Considering these results in terms of the balance between use of soil nutrients and resorbed nutrients in new leaves (Fig. 3), a different interpretation emerges: that nutrient availability in fact exerted *strong* control over nutrient resorption. Under enhanced nutrient

supply (cheaper soil nutrients), the residual N and P concentrations in senesced leaves were higher, as predicted in Fig. 3. Cases where no difference in proportional resorption was found are consistent with Fig. 3(b); cases where proportional resorption was lower at enhanced nutrient supply are consistent with Fig. 3(a).

HIGH GREEN-LEAF AND SENESCED-LEAF NUTRIENT CONCENTRATIONS IN DRY-SITE SPECIES

On average, the species from drier sites had higher green-leaf and senesced-leaf N and P than species from wetter sites. Their high green-leaf nutrient concentrations have been interpreted as part of a water-conservation strategy, facilitating reduced transpiration at a given photosynthetic capacity, but with greater costs reflected in higher dark respiration rates, increased need for nutrient acquisition, and higher leaf construction costs per leaf area for a given leaf lifespan (Wright & Westoby 2002; Wright *et al.* 2001). However, it is not clear why high senesced-leaf N and P, and low proportional P resorption (more so than N), should be associated with this suite of traits. These patterns are consistent with Fig. 3(a), suggesting similar resorption-nutrient cost functions at high and low rainfall, but also that soil nutrients were relatively cheaper than resorbed nutrients at the drier sites.

Total soil N and P did not differ systematically with site rainfall, and it seems unlikely that nutrients in the soil solution are typically more available (cheaper) at sites experiencing low annual rainfall. One possibility is that soil N is cheaper relative to resorbed N at drier sites, simply because fewer plants per m^2 ground compete for them, or because there is less total leaf area per unit ground area. Another possibility is that leaves tend to be shed before resorption is complete under dry conditions (del Arco, Escudero & Garrido 1991; Killingbeck 1996), and thus the residual nutrient concentrations in dry-site species do not accurately reflect a difference in relative cost between alternative sources of nutrients for new leaves.

CONCLUDING REMARKS

While the model outlined in Fig. 3 provides plausible explanations for observed trends in nutrient resorption and litter nutrient concentrations between different habitat types, it should be emphasized that other types of control over nutrient resorption have been identified, in particular the presence of active nutrient sinks on a plant (Gray 1983; Negi & Singh 1993). For example, removal of the shoot apex or reproductive sinks may reverse senescence in lower leaves (Noodén 1988), or affect the extent to which nutrients are withdrawn (Chapin & Moilanen 1991). Still, these observations are not necessarily inconsistent with the model; indeed, the presence of active sinks could be thought of as decreasing the unit cost of nutrient resorption.

Either way, the results from this study serve to confirm some previously reported trends in a new, multispecies dataset and provide a solid link between the leaf lifespan and nutrient resorption literatures. Considered across several dozen evergreen perennial species, proportional resorption did not differ according to site nutrient status, in agreement with the survey of Aerts (1996). Senesced-leaf nutrient concentrations were lower at the nutrient-poor site within each rainfall zone, providing support for the argument that it is the residual nutrient concentration in senesced leaves (rather than proportional resorption *per se*) that selection has acted on to minimize nutrient loss (Killingbeck 1996). Finally, these residual nutrient concentrations were generally correlated with the strategically important (Westoby *et al.* 2002) leaf lifespan–LMA axis of variation between plant species.

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