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Soil nutrient availability and reproductive effort drive patterns in nutrient resorption in *Pentaclethra macroloba*

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Abstract. The removal of nutrients from senescing tissues, nutrient resorption, is a key strategy for conserving nutrients in plants. However, our understanding of what drives patterns of nutrient resorption in tropical trees is limited. We examined the effects of nutrient sources (stand-level and tree-level soil fertility) and sinks (reproductive effort) on nitrogen (N) and phosphorus (P) resorption. We evaluated resorption efficiency (percentage of original nutrients removed during senescence) and resorption proficiency (indicated by senesced-leaf nutrient concentrations) in a symbiotic N-fixing tree species, *Pentaclethra macroloba*, common to tropical forests in Costa Rica. Although tree-level soil P alone did not drive patterns in nutrient resorption, P efficiency and proficiency declined with increasing tree-level soil P when reproductive status was also considered. Nutrient resorption declined with increasing tree-level soil P in trees that were actively fruiting or that experienced high seedfall the year prior to sampling. Trees with greater short- and long-term reproductive demands had lower senesced-leaf N and P concentrations than trees with smaller reproductive demands indicating that trees increase resorption proficiency in response to phenological demand. *P. macroloba* is the dominant tree species in this tropical ecosystem. Thus, source–sink relationships will feed back on nutrient cycling in these forests.

Key words: foliar nutrients; nitrogen; nutrient cycling; nutrient resorption; Pentaclethra macroloba; *phosphorus; reproductive effort; soil nutrients; wet tropical forest.*

Introduction

Nutrient resorption is the process by which plants reallocate nutrients from senescing structures to other living tissues (Chapin 1980, Killingbeck 1986). This process increases the residence time of nutrients within the plant and also reduces plant dependence on the soil nutrient pool, and thus is a key nutrient conserving mechanism (Killingbeck 1996). Variability in nutrient resorption also controls stand-level biogeochemical cycling via its effect on senesced-leaf nutrient concentrations, which in turn feed back on decomposition rates and soil nutrient availability (Aerts 1997). Therefore, nutrient resorption enables an organism to both remain separate from and influence its "local" available soil nutrient pool.

Variability in nutrient resorption can be driven by changes in both source (i.e., soil nutrient pool) and sink (i.e., nutrient demand) strength. However, the plasticity of nutrient resorption in tropical tree species is not well understood. In temperate forests, strong seasonal variation in temperature represents a very clear environmental control on plant phenology, resulting in a temporal separation of reproductive effort, leaf production, and leaf fall. In contrast, wet tropical forests have continual growing seasons, with warm temperatures and moist conditions throughout the year. As such, major phenological events can occur concomitantly. Further, leaf flushing, fruiting, and flowering can occur on both seasonal and supra-annual time scales (Frankie et al. 1974, Reich et al. 1991). The high diversity of tropical forests further confounds the ability to establish clear environmental triggers for phenological events in tropical trees.

Variation in reproductive effort is likely to directly affect the demand for some nutrients over others, yet the effect of reproductive costs on nutrient resorption is surprisingly understudied. Reproductive costs are typically defined in terms of losses in future reproductive success caused by the current investments in reproduction (Jönsson 2000). Therefore, it is important to examine both short- and long-term investments in reproductive effort. The production of fruits and seeds, which have high nitrogen (N) and phosphorus (P) concentrations compared to other structures (Abrahamson and Caswell 1982, Goldman 1986), may require significant reallocation of nutrients from leaves to

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reproductive tissues (Ashman 1994*a*, *b*). Thus, nutrient resorption may increase during the formation of reproductive structures (Chapin and Moilanen 1991) and decline following the removal of these structures (Pugnaire and Chapin 1993). Past studies in temperate regions indicate that leaf nutrients are depleted in reproductive individuals compared to vegetative individuals (Pakonen et al. 1988, Cipollini and Stiles 1991). Thus, reproductive status can exert strong controls over nutrient allocation, including resorption.

In addition to the influence of phenologically driven changes in nutrient demand, soil nutrient availability may also alter patterns of nutrient resorption. Within species, Kobe et al. (2005) found that nutrient resorption declines as soil nutrient availability increases. However, Aerts (1996) examined 24 species of evergreen trees and shrubs and found that only five species were capable of enhancing resorption in low nutrient conditions. These studies focused primarily on temperate species, and the controls on nutrient resorption in tropical species may differ. Tropical plants are thought to be P rather than N limited (Vitousek 1982), which may lead to higher P resorption and thus higher N:P ratios in senesced leaves than live leaves (McGroddy et al. 2004, Yuan and Chen 2009). Although several other factors may influence resorption such as water availability (Del Arco et al. 1991), timing of abscission (Escudero et al. 1992, Killingbeck 1996), and shade (Chapin and Moilanen 1991), this study will focus on the source–sink effects on nutrient resorption in *P. macroloba*.

Nitrogen-fixing trees have microbial associations in their root nodules that can convert atmospheric N to plant-available forms and are prevalent in tropical systems (Gentry 1988, Barron et al. 2011). However, biological N fixation is energetically expensive (Menge et al. 2009), and evidence from forests in Panama suggests that these trees are most likely facultative N-fixers with the capacity to down-regulate N fixation as N availability increases (Barron et al. 2011). It follows that these species may also reduce N resorption with increasing N availability as was shown in N-fixing *Lysilmona mucrophyllum* across an N gradient in Mexican tropical dry forests (Cardenas and Campo 2007).

We investigated drivers of nutrient resorption in *Pentaclethra macroloba*, a N-fixing tree dominant in mature and secondary wet tropical forest in Latin America (Gentry 1988). It is an evergreen species that flushes leaves and produces flowers and fruits throughout the year (Frankie et al. 1974). We were interested in understanding (1) how N and P resorption in *P. macroloba* vary along a natural soil P fertility gradient (source effect), (2) whether reproductive status affects N and P resorption (sink effect), (3) whether reproductive status modifies the relationship between resorption and soil N and P fertility, and (4) the patterns in the ratio of N to P in live and senesced leaves (stoichiometry) in relation to nutrient sources and sinks. We expected nutrient resorption would increase with a decline in soil P. We expected both N and P resorption would be higher in reproductive individuals compared to non-reproductive individuals. However, in contrast to findings from temperate forests, we expected P resorption would be more tightly linked to reproductive status than N resorption due to the N-fixing capabilities of the focal species. Further, as P is the primary limiting nutrient in the tropics, we expected a general trend toward greater P resorption relative to N resorption (Vitousek and Sanford 1986).

Materials and Methods

Study site

This research was conducted in the mature wet tropical forest of La Selva Biological Station in Costa Rica (10°26′ N, 84°00′ W; elevation 37–150 m above sea level; Holdridge 1947). The stands are located on highly weathered, volcanic soils (Oxisols) that are predominantly clayey with low bulk density, high organic matter content, and high porosity (Sollins et al. 1994). Mean annual rainfall is 4200 mm and mean annual temperature is 28.5°C. The study was conducted near three of the 18 0.5-ha forest stands that are part of the Carbono Project's landscape-scale study of carbon storage (Clark et al. 1998, Clark and Clark 2000). The three sites spanned three levels of total soil P to 10 cm depth—high (1650 mg P/kg), medium (1080 mg P/kg), and low (580 mg P/kg)—and available soil P followed the same trend (Espeleta and Clark [2007]; see Appendix A for stand-level available P). Our definition of high, medium, and low fertility reflects within site variability of soil P concentrations. The concentrations of total P in the soils of La Selva Biological Station are on the high end of what is reported for lowland tropical forests (median of 245 mg P/kg from 0 to 10 cm; Cleveland et al. 2011). We examined resorption in *Pentaclethra macroloba* (Willd.) Kuntze, a shade-tolerant, canopy-dominant, leguminous species in the family Fabaceae (see Plate 1). At La Selva, *P. macroloba* is the dominant tree species, comprising 34% of the total basal area in the mature forests (Clark et al. 1998), and 22% in secondary forests (Chazdon et al. 2005, Wood et al. 2011). Therefore this species plays a particularly crucial role in the functioning of mature and regenerating forests in the region.

Soils and leaf collection and analysis

We collected live and senesced leaves from 14–16 trees in each of the three stands (44 individuals total). From 10 to 14 July 2008, we collected at least five live full-sun leaves from each individual using a 12-gauge shotgun. Eight soil cores (to 15 cm depth) were collected within 1 m of the base of each of the 44 trees at the same time live leaves were harvested. Soils from each tree were homogenized and passed through a 2-mm sieve. After live leaf collection, six 1-m^2 mesh traps were placed around the base of each of the 44 *P. macroloba* trees.

Leaf litter was collected from the traps six days after installation, air-dried, and sorted to obtain senesced *P. macroloba* leaflets (hereafter "leaves"). We only selected trees with well-defined canopies to avoid the collection of leaves that did not belong to the target trees. Traps were also strategically placed with respect to the canopy to avoid "cross-fall" by near-by *P. macroloba* trees. Furthermore, when several *P. macroloba* trees were in close proximity with overlapping canopies, we averaged the data on tissue, soil nutrients, and seed count among the trees to avoid error associated with leaves falling in traps that did not belong to the target tree. *Pentaclethra macroloba* leaves are biparipinnate, with numerous leaflets and a central stem. For our analysis, only leaflets were analyzed. Live and senesced leaves and soil samples were oven dried to a constant mass ($<65°C$). Leaves were ground in a 20-mesh Wiley mill (Thomas Scientific, Swedesboro, New Jersey, USA). Soils and ground leaves were digested using a modified Kjeldhal protocol (18 mol/L sulfuric acid plus salicylic acid and 30% hydrogen peroxide). Resulting solutions were analyzed for total P on an Alpkem Flow Solution IV Autoanalyzer (OI Analytical, College Station, Texas, USA). Total N and C were measured in leaf tissues and soils by dry combustion on an elemental analyzer with acetanilide as the standard (Model NA 2500; Carlo Erba, Milan, Italy).

Nutrient resorption calculations

Nutrient resorption is measured in two ways: resorption efficiency and resorption proficiency. Resorption efficiency is the proportion of nutrients resorbed prior to leaf abscission and is measured as a function of the relationship between the senesced-leaf nutrient concentration ($[\text{nutrient}]_{\text{sen}}$) and the live-leaf concentration ($[\text{nutrient}]_{\text{live}}$; Killingbeck 1996: Eq. 1):

$$\text{resorption efficiency} = \frac{[\text{nutrient}]_{\text{live}} - [\text{nutrient}]_{\text{sen}}}{[\text{nutrient}]_{\text{live}}} \times 100. \tag{1}$$

Resorption efficiency is a ratio, and thus indicates the amount of nutrients recycled by vegetation, and may range from 0% to 90% (Chapin and Kedrowski 1983, Aerts 1996), but it may be driven by changes either in live or senesced leaves. Therefore, we also examined "realized" resorption proficiency, which is measured by the final element concentration in the senesced leaves. "Potential" resorption proficiency indicates the physiological limit to the amount of nutrients that can be resorbed from a senescing leaf. For *P. macroloba*, the lowest possible concentration of nutrients in senesced leaf tissue ($[\text{nutrient}]_{\text{sen}}$) is considered the physical limit on resorption. Values that approach this terminal value indicate complete nutrient resorption, with higher values indicating incomplete resorption (Killingbeck 1996). In general, lower relative concentrations, suggestive of greater absolute resorption, indicate a higher degree of proficiency. Higher relative values, suggestive of lower resorption, indicate a lower degree of proficiency. Therefore, in this paper, we define higher proficiency to mean lower observed values for senesced-leaf nutrient concentrations. Finally, we calculated the relative change in N:P in tissues by taking the absolute value of the difference between live and senesced-leaf N:P and dividing by live-leaf N:P as follows:

$$\text{relative change in tissue N:P} = \left| \frac{[\text{N:P}]_{\text{live}} - [\text{N:P}]_{\text{sen}}}{[\text{N:P}]_{\text{live}}} \right| \times 100. \tag{2}$$

We analyzed nutrient resorption on a mass basis (mg nutrient per unit mass) as well as an area basis (mg nutrient per unit area) based on average leaf mass area (LMA) from a nearby secondary forest (Wood et al. 2011). Mass-based resorption calculations do not account for mass loss during senescence (Aerts 1996, Killingbeck 1996). Mass loss may be 0–10% during senescence (Chapin et al. 1990, Van Heerwaarden et al. 2003). Wood et al. (2011) reported no significant difference in LMA between live and senesced leaves (0.004 g/cm^2 on average for both live and senesced leaves). Therefore we report nutrient resorption proficiency in both $[\text{nutrients}]_{\text{mass}}$ and $[\text{nutrient}]_{\text{area}}$. However, we report N:P in live and senesced leaves and resorption efficiency on a mass basis.

Measuring reproductive effort

In May of 2007, we selected 87 *P. macroloba* trees across the three sites and established three (0.5 × 5 m) sampling plots around the base of each tree at 120° from one another (7.5 m^2 per tree total). Each month from July 2007 to August 2008, we counted the number of seeds that fell within the sampling areas. *P. macroloba* has dehiscent pods. When only the pod was present, we counted the number of seeds held by the pod. We otherwise counted the seeds themselves. Annual seed count (continuous variable) was calculated as the sum of monthly seed count between July 2007 and June 2008. Trees were ranked by total annual seed count; the lower half was classified as low annual seedfall trees and the upper half as high annual seedfall trees (categorical variable). The active nutrient sink was calculated as the sum of seed count between July and August 2008 (resorption was measured July 2008), as there is a lag time between fruit formation and seedfall. This is a conservative estimate of the sink strength, as fruits that fell in September were likely affecting nutrient demand in July. Seed count in July and August 2008 were converted into a binary series: recently seeding vs. not recently seeding. In July 2008, we used binoculars to note the presence or absence of fruits in the canopy (i.e., actively fruiting vs. not actively fruiting). When the canopy could not be distinguished from other canopies then data on tissue, soil nutrients, and seed count were averaged among the trees. If the view was obscured due

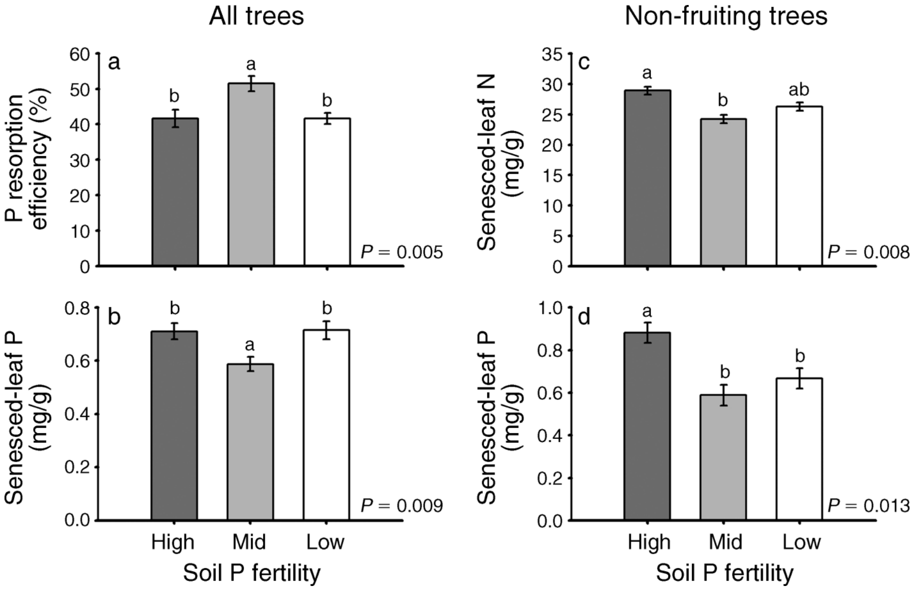

FIG. 1. Mean (a) P resorption efficiency and (b) senesced-leaf P concentrations in all *Pentaclethra macroloba*, and mean (c) senesced-leaf N and (d) senesced-leaf P in non-fruiting *P. macroloba* by stand-level soil P stocks in La Selva, Costa Rica. Reported P values originate from ANOVA with stand as main effect. Error bars indicate ±SE. Values significantly different at $P < 0.05$ are indicated by different letters above bars.

to poor light conditions, the observation was left blank and these trees were not included in the corresponding analysis.

Statistical approach

Initially, we considered only the effect of soil fertility, and at two scales: the stand level and the tree level. We used one-way analysis of variance (ANOVA) to evaluate the effect of stand-level soil P (high, mid, and low) on resorption efficiency and proficiency, and we used a univariate regression to determine the effect of tree-level soil P on resorption (both efficiency and proficiency). We used analysis of covariance (ANCOVA) to examine the effect of reproductive effort (i.e., current fruiting and seeding status, annual seedfall) on resorption, with tree-level soil P concentration included as a covariate. We also used two-way ANOVA to determine the effects of stand-level soil P fertility (i.e., high, mid, and low) and the measures of reproductive effort on resorption. We examined the response of the *number* of seeds that fell (i.e., seed count vs. seedfall) in July–August and annually to tree-level soil P (using univariate regression) and stand-level soil P (using one-way ANOVA). We used univariate regression to determine if short or long-term seedfall could predict patterns in resorption.

We performed correlations among N and P concentrations in live leaves, N and P resorption proficiency and efficiency, and senesced-leaf N:P and live N:P. To examine which nutrient was preferentially resorbed at the tree level, we performed a matched pairs analysis between senesced-leaf N and senesced-leaf P. We also used matched pairs analysis between live N:P and senesced-leaf N:P to examine patterns in tree-level tissue stoichiometry. All statistical analyses were performed in JMP 9.0 for Macintosh (SAS Institute, Cary, North Carolina, USA).

RESULTS

Examined without reference to reproductive status, P resorption efficiency and proficiency were not significantly related to tree-level soil P concentrations. However, when grouped by stand, both P resorption efficiency and proficiency were significantly greater in the mid-fertility stand compared to the high- and low-fertility stands ($P = 0.005$ and $P = 0.009$, respectively; Fig. 1 and Appendix B for area-based values). Nitrogen resorption efficiency and proficiency did not respond to tree-level or stand-level soil P (or N) status.

Both senesced and live-leaf P concentrations increased significantly with tree-level soil P when we considered the effect of fruiting status (i.e., we distinguished fruiting from non-fruiting trees in the model; $P = 0.005$ and $P = 0.041$, respectively; Fig. 2a, d; Appendix C for area-based values). Accordingly, senesced-leaf N:P and P resorption efficiency declined with increasing tree-level soil P ($P = 0.006$ and $P = 0.05$, respectively; Fig. 2c, e). Across the soil P gradient, where total P increased threefold, resorption proficiency declined twofold. Although not significant, senesced-leaf N concentrations also tended to increase with tree-level soil P ($P = 0.09$; Fig. 2b; Appendix C for area-based values). The relative change in the ratio of N to P (N:P) from live to senesced leaves (Eq. 2) significantly decreased as tree-level soil P increased ($P = 0.005$; Fig. 2f).

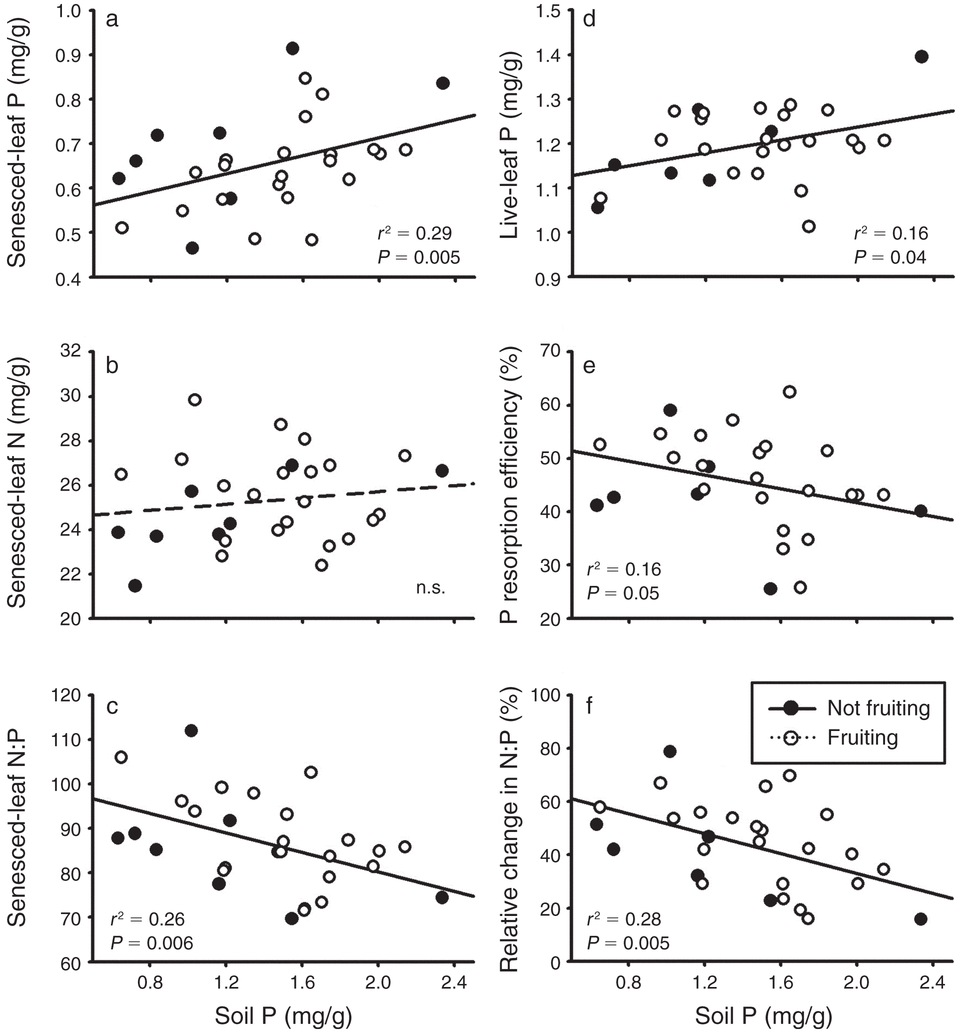

FIG. 2. (a) Senesced-leaf P, (b) senesced-leaf N, (c) senesced-leaf N:P (molar ratio), (d) live-leaf P, (e) P resorption efficiency, and (f) the relative change in N:P in *P. macroloba* in fruiting (open circles) and non-fruiting (solid circles) trees as a function of tree-level soil P in La Selva, Costa Rica. Solid lines of best-fit are presented for all trees combined; regression statistics are for full model with fruiting status included.

In most cases, the response of nutrient resorption to tree-level soil P depended on reproductive effort. For example, the relationships between tree-level soil P and both senesced-leaf P and the relative change in tissue N:P were driven by actively fruiting trees ($P = 0.04$, $r^2 = 0.21$ and $P = 0.04$, $r^2 = 0.20$, respectively; Fig. 3a). These relationships were not found among non-fruiting trees. On the other hand, live-leaf N and P concentrations increased significantly with increasing tree-level soil P in non-fruiting trees ($P = 0.04$, $r^2 = 0.52$ and $P = 0.01$, $r^2 = 0.76$, respectively; Fig. 3b, c), whereas in actively fruiting trees, live-leaf N and P were relatively constant across the soil fertility gradient. Further, senesced-leaf N and P were significantly higher in the high-fertility stand compared to the mid- and low-fertility stands in non-fruiting individuals ($P = 0.008$ and $P = 0.013$, respectively; Fig. 1c, d). Overall, trees actively fruiting during sampling were more proficient at both N and P resorption. Senesced-leaf N and P concentrations were significantly lower in fruiting trees (24.8 mg N/g and 0.64 mg P/g) compared to non-fruiting trees (26.5 mg N/g and 0.71 mg P/g; $P = 0.03$ for leaf N and $P = 0.04$ for P).

Overall, neither annual nor recent seed count (number of seeds) was a significant predictor of nutrient resorption proficiency or efficiency. Tree-level soil P could not predict recent (July–August) or annual seed count. However, both annual and recent seed count were significantly higher in high P fertility stands compared to low P fertility stands, with seed count intermediate in mid fertility stands ($P = 0.04$ and $P = 0.02$, respectively.)

Among trees with high annual seedfall, P resorption efficiency, senesced-leaf N:P, and the relative change in tissue N:P decreased with increasing tree-level soil P ($P = 0.05$, $r^2 = 0.22$; $P = 0.05$, $r^2 = 0.21$, $P = 0.035$, $r^2 = 0.25$, respectively). These patterns were not found among trees with low seedfall. Further, the pattern of higher nutrient resorption in mid fertility stands was driven by an effect of nutrient stress on trees recently seeding and/or with high annual seedfall; non-seeding and low-seedfall trees showed no mid-fertility stand-level effect. Senesced and live-leaf N (but not P) concentrations were significantly higher in trees with low annual seedfall compared to those with high annual seedfall ($P = 0.03$ and $P = 0.01$, respectively; Fig. 4).

As expected, P resorption efficiency was significantly higher than N resorption efficiency across all individuals (45% vs. 23%, respectively; matched pairs analysis $P < 0.0001$). Live-leaf and senesced-leaf N were significantly positively correlated ($r = 0.43$, $P = 0.006$) as were live-leaf and senesced-leaf P ($r = 0.43$, $P = 0.008$). In addition, N and P resorption efficiencies were significantly positively correlated to one another ($r = 0.63$, $P < 0.0001$, Fig. 5a), as were N and P in senesced tissues ($r = 0.77$, $P < 0.0001$, Fig. 5b) and N and P in live tissues ($r = 0.74$, $P < 0.0001$, Fig. 5c). We found no significant correlation between N:P in live and senesced leaves when evaluated across individuals; however, senesced-leaf N:P was significantly higher than live-leaf N:P (matched pairs analysis $P < 0.0001$).

Discussion

Source effects: Soil nutrients and patterns of nutrient resorption

Overall, soil nutrients alone did not adequately predict patterns in nutrient resorption. Rather, the response of *P. macroloba* to source effects (soil nutrients) was regulated by sink strength (reproductive effort). In contrast to our original expectations, P resorption efficiency and proficiency peaked in the mid-fertility stand. We expected *P. macroloba* would maximize P resorption when P is scarce (thus showing the highest efficiency in the lowest fertility site). Such a result would have agreed with the findings of Wood et al. (2006), which showed a significant positive relationship between community-level leaf-litter P and soil P across the soil P gradient of this forest. Many other studies have also shown the importance of soil P influences on leaf litter P (e.g., community-wide resorption proficiency; Vitousek and Sanford 1986, Crews et al. 1995, Vitousek 1998, Aerts and Chapin 2000). However, our study examined the response of nutrient resorption to sources and sinks in a particular species within the community, and tracked the response of individual trees to local resource availability and specific reproductive demands. Thus, it is not surprising that our findings at the stand-level diverge from overall community patterns. Nevertheless, our finding (that resorption is maximized in the mid-fertility stand), does diverge from the common theory that nutrient resorption is maximized in low fertility soils. At the scale of the individual tree, however, resorption responded to soil P as predicted by theory and previous empirical study.

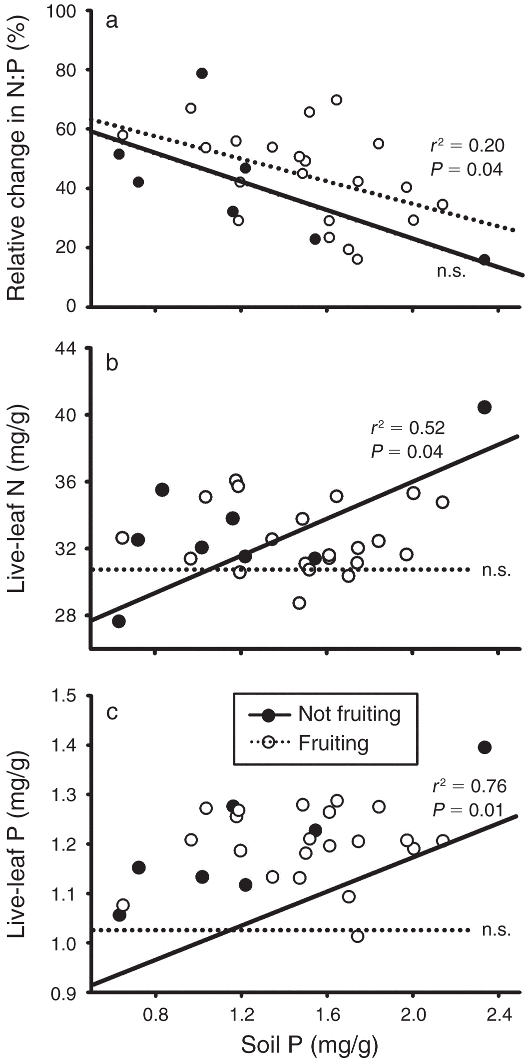

Fig. 3. (a) The relative change in tissue N:P from live to senesced *Pentaclethra macroloba* leaves and (b, c) live-leaf (b) N and (c) P in *P. macroloba*, by tree reproductive status, as a function of tree-level soil P in La Selva, Costa Rica. The abbreviation n.s. stands for not significant.

Resorption may be limited by physiology and therefore not always track variability in nutrient sources. For example, total soil P stocks were 43–80% higher in the mature forest stands compared to a secondary forest nearby (0.4 Mg P/ha; D. Lawrence and C. Logan, *unpublished data*). Yet, the lowest recorded senesced-leaf P concentration (for *P. macroloba*) in mature forests (0.41 mg P/g) was very similar to that found in the nearby secondary forest (0.47 mg P/g; T. E. Wood, *unpublished data*). The similarity, despite soil differences, suggests a physiological limit on the amount P that can be removed from senescing leaves by

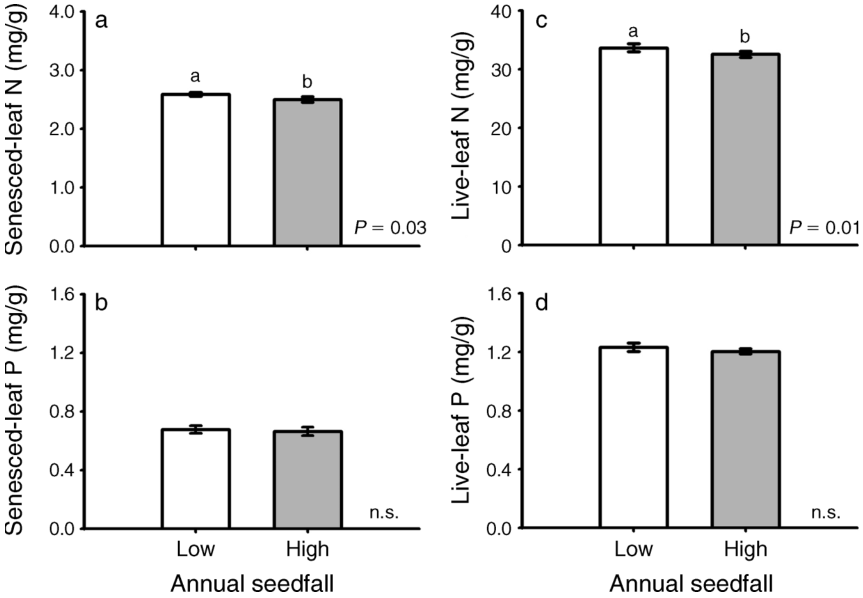

FIG. 4. Senesced-leaf (a) N and (b) P concentrations and live-leaf (c) N and (d) P concentrations in *Pentaclethra macroloba* with low and high annual seedfall in La Selva, Costa Rica. Values are means ± SE. Values significantly different at $P < 0.05$ are indicated by different letters above bars.

P. macroloba (potential resorption proficiency; Killingbeck 1996), and perhaps that limit is near 0.4 mg P/g.

Unlike soil P, which varied almost threefold across the mature forest stands we sampled, soil N status was quite similar among stands (5.1–6.1 mg N/g; Appendix A), which may partly explain why we did not observe a relationship between N resorption and soil N at the scale of the tree or the stand. However, in the nearby secondary forest, where soil N concentration was 35–46% lower (D. Lawrence and C. Logan, *unpublished data*), N resorption proficiency was correspondingly higher (senesced-leaf N is lower at 8.1 mg N/g; T. E. Wood, *unpublished data*) compared to that in mature forests of this study (25.4 mg N/g). Thus, it is possible for *P. macroloba* to resorb more N from senescing leaves as soil N becomes scarce. In this study, soil N concentrations were not low (or varied) enough in the mature forest stands to observe such a response. It is possible that there exists a specific response window (soil nutrients are not too low and not too high) within which a relationship between soil nutrient status and nutrient resorption can be observed. Finally, the variability in N and P resorption cannot be entirely explained by differences in soil nutrients. Our study shows that other factors do modify this relationship, specifically, reproductive effort.

Sink effects: Reproductive effort and patterns of nutrient resorption

In general, trees with higher reproductive demands resorbed more nutrients than trees with lower reproductive demands. Senesced-leaf N and P concentrations were lower in trees that were fruiting at the time of leaf collection compared to non-fruiting trees, and senesced- and live-leaf N were significantly lower in trees with high annual seedfall compared to trees with low annual seedfall (Fig. 4). Further, the coefficient of variation in resorption was smaller in fruiting trees compared to non-fruiting trees (N, 6% vs. 9% and P, 15% vs. 21%), providing further evidence that there is a physiological limit to the amount of N and P that *P. macroloba* can resorb from senescing leaves. These findings support our hypothesis that the high nutrient demand associated with reproductive effort leads to increased nutrient resorption.

In addition, reproductive effort altered the resorption response to tree-level soil nutrients. Phosphorus resorption efficiency and proficiency decreased with increasing soil P when we considered the effect of fruiting status. The relative change in tissue N:P from live to senesced leaves declined with increasing soil P because with greater P available from the soil, trees could afford to be less conservative with P already in their leaf tissues. However, it is also important to consider the timing and magnitude of phenological nutrient demands. Accordingly, when examined more closely, the declines in measures of nutrient resorption with increasing soil P were only found in trees that (1) were actively fruiting (short-term nutrient demand; Fig. 2) or (2) had high annual seedfall (long-term nutrient demand). Finally, higher resorption in mid fertility stands (compared to low and high fertility stands) was only found in those trees with recent seedfall (i.e., seeding in July and August) or had high annual seedfall. Together, these patterns show that nutrient resorption is not determined by soil nutrients alone, and that the response of *P. macroloba* to source effects (soil nutrients) was regulated by sink strength (reproductive effort). Thus, careful examination of both is necessary to tease out the complex response of nutrient resorption to either factor. Indeed, future research should examine the interactions between nutrient sources and sinks, as it is possible for these factors to confound one another.

Non-fruiting trees showed their own response to soil nutrient availability, one predicted well by ecological theory: that both live-leaf N and P increased with tree-level soil P. This suggests that the ratio of N:P in live leaves can remain relatively constant even as soil P increases (because both nutrients increase with soil P). It further supports the idea that the relative change in tissue N:P is driven by the decline in senesced-leaf P as soil P resources become scarce and trees must be more conservative.

If we now return to the seemingly surprising result that measures of nutrient resorption were higher in the mid-fertility stand, it becomes clear that this pattern can be understood in the context of reproductive demand. Seed count (both annual and recent) was 20 times higher in the high P fertility stand compared to the low P fertility stand. Seed count in the mid fertility stand was on par with the high fertility stand; it was 16 and 20 times higher than in the low fertility stand for annual and recent timescales, respectively. In the low-fertility stand, reproductive demand was low, constrained by the overall level of available P. With low reproductive demand, trees were less conservative with nutrients relative to trees with higher demand; thus P resorption was less efficient. In the high-fertility stand, P resorption was also less efficient, because soil P resources were adequately meeting the high reproductive demand for P. Nutrient resorption efficiency and proficiency were highest in the mid-fertility stand because the trees were producing reproductive material (and presumably roots and new leaves) in similar quantities as trees in the high-fertility soils, and yet they were doing so in soils with one-third less soil P. Nutrient-conserving mechanisms like resorption likely provided for some of the demand unmet by soil P resources.

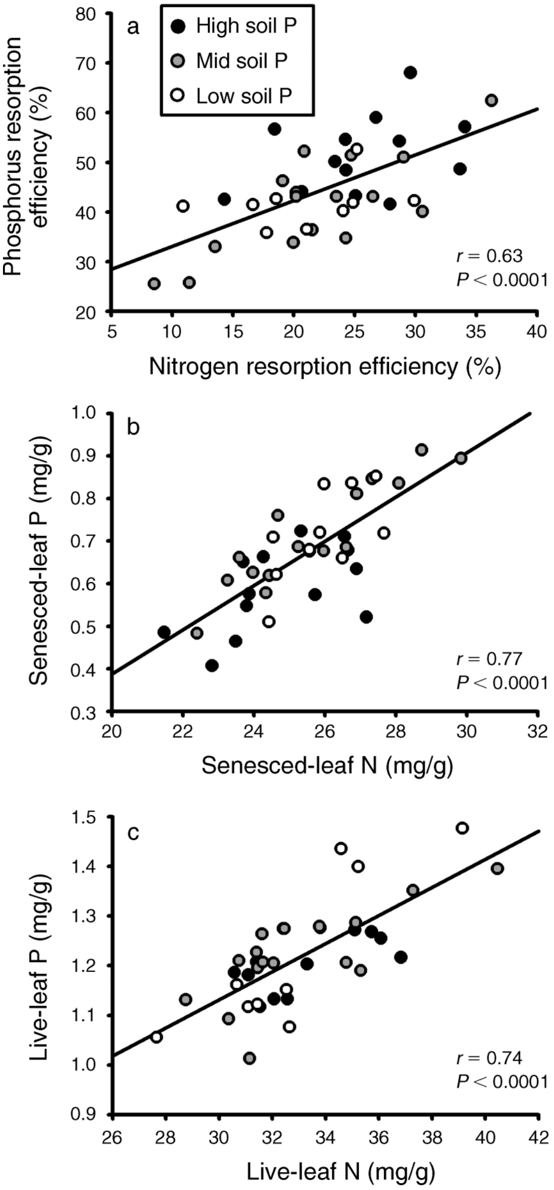

FIG. 5. Correlations between (a) N and P resorption efficiency, (b) N and P concentrations in senesced leaves, and (c) N and P concentration in live leaves. Solid lines of best-fit are presented.

Nitrogen and phosphorus stoichiometry

Phosphorus appears to be the primary limiting nutrient for this forest (Wood et al. 2006, 2009). As such, we expected leaf litter P would be cycled more conservatively than litter N. Further, recent studies have shown tropical legumes have enhanced P acquisition compared to non-fixing species (Lee et al. 2006, Houlton et al. 2008). Higher extracellular phosphatase activities have been observed in soils under N-fixers in both temperate and tropical regions (Khanna 1998). Senesced-leaf N:P was high (molar ratio of 69–124 in *P. macroloba*) compared to the tropical mean (63; McGroddy et al. 2004). Further, Inagaki et al. (2011) showed that N:P ratios in litterfall were significantly higher in N-fixers compared to non-N-fixers. Unlike C : nutrient ratios where one element (C) remains relatively constant, changes in N:P can be difficult to assess as both elements are dynamic. In this study, however, changes in senesced-leaf N:P were likely driven by variation in P rather than N (CV of 18% vs. 7%). The relatively high senesced-leaf N:P therefore indicated that more P was resorbed compared to N. Higher P compared to N resorption efficiencies (45% vs. 23%) is also in keeping with this hypothesis. In contrast, Wood

PLATE 1. (Left) Six litter traps (1 m^2) were placed around the base of each *Pentaclethra macroloba* tree to collect senesced leaves. (Right) Mature tropical forest stand in La Selva Biological Station, Costa Rica. Photo credits: K. L. Tully.

et al. (2011) reported higher N compared to P resorption efficiency in *P. macroloba* in the neighboring secondary forest (40% for P vs. 53% for N). This relationship supports the theory that secondary tropical forests can be limited by N and transition to P limitation as they age (Davidson et al. 2004, 2007).

As previously discussed, soil N was similar among the three mature forest stands, but substantially lower in secondary forests, which may explain why mature forests did not efficiently resorb N, but secondary forests did: because more economic N cycling was required. On the other hand, similar P resorption efficiencies in the mature and secondary forests sites support the hypothesis that there exists a physiological limit to resorption in *P. macroloba*, which prevents increased resorption even when resources become scarce. Thus, despite lower soil P in the secondary forest, trees were already sufficiently P limited that no difference in nutrient resorption was observed between mature and secondary forests because nutrient savings due to resorption had already reached a physiological maximum.

We expected P resorption to be more tightly linked to reproductive effort than N resorption because of *P. macroloba*'s ability to fix atmospheric N. However, we found both N and P resorption tracked variation in reproductive effort. Further, we observed a strong correlation between P and N efficiencies (Fig. 5a), which suggests that either (1) one nutrient is driving a response in the other or (2) N and P are both sensitive to the same driver and are thus responding in sync. Our results contrast with studies that show N and P resorption efficiencies act independently of one another (Shaver and Melillo 1984). Until recently, most research has focused on temperate species, where ecosystems tend to be N limited. Patterns of nutrient resorption may differ in the tropics not only because these systems tend to be P rather than N limited, but also because tropical trees are often fruiting and flushing concomitantly, leading to strong, consistent demands for N and P. Indeed, recent studies on resorption in tropical species often have conflicting results on the drivers of resorption, indicating the complexity of these systems (Austin and Vitousek 1998, Cordell et al. 2001, Harrington et al. 2001, Lal et al. 2001, Rentería et al. 2005). Nevertheless, our research indicates the important role that the source–sink relationship plays in driving patterns of nutrient resorption in a tropical tree species that dominates rainforests of Costa Rica.

CONCLUSIONS

Both nutrient sources (soil) and sinks (reproduction) affect N and P resorption in *P. macroloba*, and soil P alone does not explain variation in nutrient resorption unless reproductive status is also considered. Further, it is the reproductive individuals that drive the patterns observed (i.e., declines in resorption as soil P increases). *Pentaclethra macroloba* plays a crucial role due to its local dominance. Thus, these findings have clear implications for understanding the processes regulating nutrient cycling of wet tropical forests throughout the region.

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SUPPLEMENTAL MATERIAL

Appendix A

Table showing soil characteristics (0–15 cm) surrounding target trees within the three stands in La Selva, Costa Rica (*Ecological Archives* E094-079-A1).

Appendix B

Table showing mass-based and leaf-area-based N and P concentrations in live and senesced *Pentaclethra macroloba* leaves (proficiency) by soil P fertility in La Selva, Costa Rica (*Ecological Archives* E094-079-A2).

Appendix C

Figure showing leaf-area-based senesced-leaf P and N and live-leaf P and N in *P. macroloba* in fruiting and non-fruiting trees as a function of tree-level soil P in La Selva, Costa Rica (*Ecological Archives* E094-079-A3).