

NUTRIENTS IN SENESCED LEAVES: COMMENT

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Killingbeck (1996) introduced the metric of resorption proficiency, which he defined as the level to which species reduce nutrients in senescing leaves. If there are different controls over pre- and postsenescence nutrient concentrations, Killingbeck's isolation of the postsenescence nutrient concentrations may be an important step in resolving underlying patterns associated with nutrient resorption from the leaves of trees. Killingbeck compiled and analyzed previously published data on nitrogen and phosphorous concentrations in senesced leaves to "discover the limits of ultimate potential resorption" and "compare resorption in evergreen vs. deciduous species." From this analysis, Killingbeck concluded that "analysis of N and P in senesced leaves indicates that evergreens and deciduous woody perennials do not differ in their abilities to reduce N in senescing leaves, but differ substantially in their abilities to reduce P." Here, we show that the conclusions may be highly dependent on the choice of functional group classifications, potential covariates associated with the classifications, and the summary statistics used for comparison of ultimate potential resorption.

First, Killingbeck's evergreen classification is based on continual leaf presence, rather than leaf longevity. Reich et al. (1992) reported that some leaf traits, such as mass-based N concentration and specific leaf area, vary continuously with leaf longevity. Thus, an evergreen leaf with a shorter life-span might be more similar to a deciduous leaf than to an evergreen leaf with a longer life-span. To test this hypothesis, we recompiled data from the original sources and included leaf longevity where it was provided or easily inferred. Reported values for evergreen leaf longevity in this study ranged from <1 yr (Jonasson 1989, Escudero et al. 1992) to >5 yr (Tyrell and Boerner 1987, Escudero et al. 1992). Leaf longevity of the species studied by Scott et al. (1992) was often <1 yr (Richards 1996), but was not reported in the original study and not included in our analyses. We found that dividing the species based on leaf longevity (<1.5 yr vs. >1.5 yr) appears to split the evergreens into two proficiency groups, which appear

more distinct than the deciduous–evergreen classification (Fig. 1). Evergreen species with leaf longevity >1.5 yr had significantly lower tissue N and P concentrations at the time of senescence than the evergreen species with leaf longevity <1.5 yr: $1.13 \pm 0.08\%$ and $0.058 \pm 0.05\%$ N, mean ± 1 SE, respectively (Student's *t*, $P < 0.001$); $0.092 \pm 0.007\%$ and $0.034 \pm 0.004\%$ P, respectively (Student's *t*, $P < 0.001$) (SAS Institute 1996).

If resorption characteristics were a continuous function of leaf longevity, then dividing data sets around a criterion of continuous leaf presence for one year may be arbitrary; the categorization of continuous relationships may mask underlying relationships. In addition, the mean values for deciduous and evergreen trees in Killingbeck's study may be biased by the proportion of studies in the data set that measured leaves with shorter vs. longer leaf longevity.

Second, Killingbeck's analyses do not account for experimental covariates that may restrict nutrient resorption and may be associated with the two functional group classifications. These covariates could include site fertility and resultant plant nutrient status (Monk 1966, Escudero et al. 1992, Aerts 1995), or the distribution in time or space of factors that restrict resorption (Chapin and Molainen 1991). Killingbeck compares the means of his two functional group classifications to determine the differences between groups in the ability to reduce nutrient concentrations in senescing leaves. The existence of a given covariate that may tend to restrict resorption for one group more than for another would result in a shifting of a group's curve, or a change in the distribution of data points for a curve. For example, it is possible that all species have the same potential to resorb nutrients, and that variability in the data merely represents variability in the factors that restrict resorption. Without knowledge of the influence of the covariate, the potential ability to reduce nutrient concentrations could not be inferred from any statistical measure of the compiled data set, including the mean.

Taking the potential of covariation into account, Killingbeck's interpretation may miss simpler explanations. He found that nitrogen-fixers, for instance, realized lower proficiency in the resorption of nitrogen. He concluded that this represents an evolutionary trade-off between N fixation and resorption. Alternatively, plants with favorable status for a given nutrient may be less proficient in resorption of that nutrient. Simpler interpretations may also apply to the differences found between deciduous and evergreen species. Because increased leaf longevity is associated with lower site fertility (Monk 1966, Escudero et al. 1992, Reich et al. 1992, Aerts 1996), individuals in the evergreen classification would be more likely to occur on sites with

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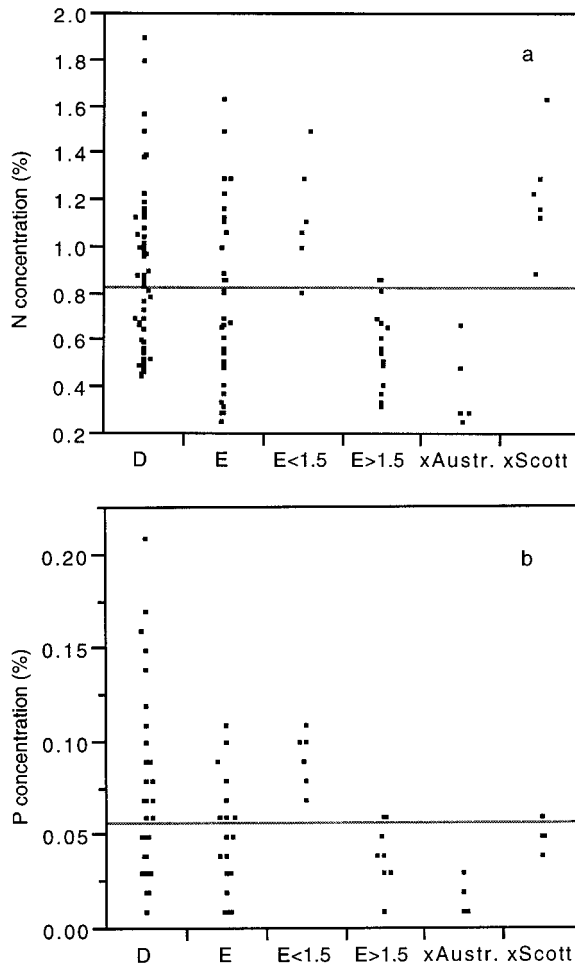


FIG. 1. Concentrations of (a) nitrogen and (b) phosphorus for senesced leaves of deciduous (D) and evergreen (E) species. Evergreen species are also plotted based on reported leaf longevity ($E < 1.5$ yr and $E > 1.5$ yr), and on studies that did not report values for evergreen leaf longevity (O'Connell et al. 1978, 1982, Polglase and Attiwill 1992 [xAustr.], and Scott et al. 1992 [xScott]). The horizontal line represents the mean for the entire data set.

lower nutrient availability. Killingbeck did not distinguish between the confounding variables of site fertility and continual leaf presence. Differences between the functional groups may reflect site nutrient availability, rather than an inherent potential to resorb the nutrient.

Aerts (1996) also analyzed a comprehensive data set on nutrient resorption and concluded that evergreen trees and shrubs reduced concentrations of both N and P to lower levels than did deciduous trees and shrubs. However, this was due to lower initial concentrations, rather than higher resorption efficiency. He also found that both functional groups tended to respond to increased nutrient availability in a manner that left increased nutrient con-

centrations in senesced leaves, although the efficiencies of resorption did not change. Aerts showed that nutrient proficiency is decreased with increased nutrient availability. We conclude that inferences regarding potential nutrient proficiency must include potential covariates, most importantly, plant nutrient status.

Lastly, Killingbeck used the mean N or P concentrations of the two functional groups to determine relative abilities to reduce nutrients. Comparing the means of two groups may not be the appropriate method for comparing the lower bounds, especially if the data are not normally or similarly distributed. Our reexamination of the data set using lower quartiles as the summary statistic indicates that the potential for resorption may be opposite that concluded by Killingbeck. Some evergreens reduced N concentrations in their leaves to levels lower than in any deciduous species (Fig. 1). The lower quartile mean N concentration for evergreens was significantly lower than that of deciduous trees ($0.35 \pm 0.02\%$ and $0.52 \pm 0.02\%$ N, respectively; Wilcoxon z , $P < 0.001$). In contrast, Killingbeck's analysis of means led him to conclude that there was no difference between the two groups. For P resorption, analysis of lower quartiles reveals that evergreens had significantly lower P concentrations than did deciduous trees ($0.014 \pm 0.008\%$ and $0.047 \pm 0.013\%$ P, respectively; Wilcoxon z , $P < 0.01$), yet some species in both groups reduced phosphorous concentrations in leaves to the minimum concentration observed, 0.01%. Without controlled studies or more careful analysis of potential covariates, it is difficult to comment on whether this represents the potential of the group or a difference in factors that affect the realization of this potential.

Killingbeck's isolation of postsenescence nutrient concentrations may prove an important approach to determining sources of variation in patterns of nutrient resorption proficiency. It would be interesting to know if there are differences between species or functional groups in the ability to draw down nutrient concentrations in senescing leaves, as well as the mechanisms determining these differences. We think that further progress toward this goal could be made by combining analyses of proficiency with information about potential covariates, including site fertility and presenescence nutrient concentrations. Killingbeck's work also raises many questions about ultimate potential resorption and biochemical optima: these questions may be better resolved with explicit measurements of postsenescence, phloem-labile nutrient concentrations.

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to potential resorption (Killingbeck 1996). Although none of their concerns challenges the efficacy of using resorption proficiency and potential resorption to enhance our understanding of nutrient conservation strategies, these concerns are interesting in their own right and merit a response.

First, Craine and Mack (1998) question the legitimacy of asking whether resorption of nitrogen and phosphorus differ between deciduous and evergreen species. In addressing this question, my objective was simply to examine an often discussed ecological conundrum with a new measure of resorption, resorption proficiency. Papers by Monk (1966) and others that caught the imagination of ecologists by grappling with the notion that deciduous and evergreen species were ecologically different precipitated a spate of papers that considered whether resorption efficiency differed between deciduous and evergreen species (Gray 1983, Tyrell and Boerner 1987, del Arco et al. 1991, Pugnaire and Chapin 1993). These latter papers prompted the question that guided my analysis: how do previously published conclusions based on resorption efficiency data compare with conclusions drawn from resorption proficiency data? Craine and Mack note the advantages of making comparisons using functional classes that are more finely diced than “deciduous vs. evergreen.” Although I concur that such comparisons surely are valuable, to suggest that it was inappropriate to make a direct comparison between deciduous and evergreen species is to miss the primary point of the comparison.

Second, Craine and Mack disagree with my decision to ignore “experimental covariates that may restrict nutrient resorption.” Although I would be the first to applaud an effort to consider the impacts of all covariates known, or suspected, to have a significant impact on nutrient resorption in the 89 species on which I reported, an unequivocal analysis of this type is not presently possible. To meet the demands implicit in the Craine and Mack argument, one would need to consider all relevant parameters. However, site-specific data sets on even a few important covariates for these species are not available.

Nevertheless, data are available on green-leaf nutrient content, and we are in total agreement regarding the need for an exploration of the relationship between this measure of plant nutrient status and resorption proficiency. Yet, to suggest that the lack of such an analysis minimizes conclusions in the Concepts paper seems extreme, given the abundance of data indicating that nutrient resorption efficiency is not significantly related to plant nutrient status or site fertility (Staaft 1982, Birk and Vitousek 1986, Chapin and Moilanen 1991). Although the long-term effects of site fertility and plant nutrient status probably do play a role in

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NUTRIENTS IN SENESCED LEAVES: REPLY

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In the accompanying comment, Craine and Mack (1998) raise questions about three aspects of a recent Concepts paper, in which I introduced both the concept of resorption proficiency and models depicting the completeness of realized resorption in comparison

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the evolution of the resorption process in general (Killingbeck 1993), the most comprehensive analysis of resorption efficiency to date concluded that the relationships “between leaf nutrient status and leaf nutrient resorption were absent or very weak” (Aerts 1996:597). Further, Aerts (1996) did not show conclusively that “nutrient proficiency is decreased with increased nutrient availability,” as intimated by Craine and Mack (1998). Therefore, to imply that plant nutrient status is likely to have an important impact on nutrient resorption is presently unjustified.

Third, Craine and Mack (1998:1819) also draw attention to my use of statistical means: “comparing the means of two groups may not be the appropriate manner to compare the lower bounds.” A supplemental analysis of the extremes would have added to the breadth of my arguments, but to confine the analysis to the lower quartiles of the data, as suggested, strikes me as being unnecessarily arbitrary. This tack would work well if, for example, there was evidence indicating that all data in the upper quartiles represented incomplete resorption. There is no such evidence, but there does appear to be an alternative approach to considering the “lower bounds” of the proficiency data that is both simple and ecologically meaningful.

The key to the importance of the Craine and Mack suggestion is the need to focus on the portion of the data set that probably represents complete resorption. Utilizing the model of resorption proficiency in my Concepts paper that defined the limits of complete and incomplete resorption (Killingbeck 1996: Fig. 3), I identified all proficiency values in my original data set that represented complete resorption. Comparing just these data, neither N or P resorption proficiency (mean \pm 1 SE) differed between deciduous ($0.55 \pm 0.017\%$ proficiency for N, $n = 18$; $0.023 \pm 0.002\%$ proficiency for P, $n = 16$) and evergreen ($0.48 \pm 0.034\%$ for N, $n = 17$; $0.019 \pm 0.003\%$ for P, $n = 12$) species ($P > 0.05$, Student's t test, N data normally distributed [$P > 0.05$, Lilliefors' test]; $P > 0.05$, Mann-Whitney U test, P data not normally distributed [$P < 0.001$, Lilliefors' test]). Even though there were separate P resorption thresholds for deciduous and evergreen species in the model, I used $<0.04\%$ resorption of P as the cutoff for both sets of species to avoid bias in the comparison. This suggests that maximum potential resorption may be more similar in deciduous and evergreen species than previously thought. Regardless of the conclusions reached, the recommendation by Craine and Mack to more closely scrutinize the “lower bounds” of the data was an important one and resulted in yet another approach to comparing resorption, by focusing exclusively on data that represent complete resorption.

In the final analysis, I welcome the constructive criticism and insightful observations made by Craine and Mack (1998), but must also suggest that those observations are tangential to the thrust of my Concepts paper. The focus of that paper was on other issues: introducing the concept of resorption proficiency, discovering the limits of potential resorption, and establishing quantitative benchmarks that define the continuum between incomplete realized resorption and maximum potential resorption. The most significant controversies and challenges that surround my Concepts paper are not about the differences between oaks and pines. Rather, they are about the opportunities and hazards of probing the complexities of the resorption process with the concepts of resorption proficiency and potential resorption.

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