Ecophysiology

Nitrogen-15 natural abundance in a montane cloud forest canopy as an indicator of nitrogen cycling and epiphyte nutrition

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Abstract. Nutrients obtained by epiphytes may either be of atmospheric origin or from organic matter in the canopy, which decomposes to form canopy soil on large branches. We hypothesised that the N supply for epiphytes on small branches was lower, and a larger proportion provided by rainwater, than for epiphytes rooting in canopy soil. We tested this by measuring the N concentration and isotopic composition in terrestrial and canopy soil and in various canopy compartments of a Costa Rican cloud forest. In general, epiphytes on small branches without canopy soil had lower N foliar concentrations and $\delta^{15}N$ signals than plants rooted in canopy soil, suggesting that the former receive a higher proportion of N directly from the rain. Epiphytes on small branches also had less negative $\delta^{13}C$ values, indicating more frequent water stress. Epiphytes had lower $\delta^{15}N$ values (-3.92±2.26‰)

than ground-rooted trees (-1.01±1.55‰), and canopy soil had lower values (0.66±1.18‰) than terrestrial soil (3.75±0.72‰). Assuming that the isotopic effect of terrestrial and canopy soil organic

matter formation is similar, our findings support earlier results showing that canopy soil is derived mainly from epiphytes, with only minor inputs from host tree matter. Thus, the epiphyte N cycle appears to be largely detached from the tree-soil cycle. Epiphylls on leaves of understorey shrubs had higher $\delta^{15}N$ signals than cryptogams in the upper canopy, as a result of either ^{15}N accumulation in throughfall or increased N_2 fixation. The correlation between epiphyll and understorey host leaf $\delta^{15}N$ suggests some exchange of N between epiphylls and host leaves. Differences between epiphyte groups also appear to be related to uptake of N through mycorrhizas or N_2 fixation. Thus, the source and quantity of N supply is highly variable, depending on the systematic group and canopy position.

Keywords. Canopy soil - Epiphylls - Monteverde - Nutrient dynamics - Tropical montane forest

Introduction

Epiphytes lack access to nutrient sources available to ground-rooted plants. They obtain their N either from the atmosphere (via wet and dry deposition and N_2 fixation) or, indirectly, from their host (leaching or decomposition of host tissue). Some epiphytes have evolved adaptations that provide efficient access to nutrients, such as litter-trapping leaf arrangements, phytotelmata, absorbent trichomes, ant-inhabited cavities, and mycorrhiza (Benzing 1990).

Tropical montane cloud forests support a greater epiphyte biomass than any other ecosystem (Madison 1977). Thick mats of epiphytes cover large branches, and this or other organic matter partially decomposes within the canopy to form suspended soils (Jenik 1973) in which epiphytes and some host trees root (Nadkarni 1981). Epiphyte biomass can rival that of tree foliage (Nadkarni 1984; Hofstede et al. 1993), which suggests that epiphytes can play a major role in the nutrient cycles of cloud forests (Coxson and Nadkarni 1995).

These patterns have been described in long-term canopy and ecosystem studies in Monteverde, Costa Rica, using descriptive and experimental approaches (Nadkarni et al. 2000a, 2000b). Indicators that epiphytes and their accompanying canopy dead organic matter influence ecosystem nutrient cycles in the Monteverde forest include their high biomass (Nadkarni et al. 2000b), the high capacity of non-vascular epiphytes to absorb atmospheric NO_3^- and NH_4^+ (Clark et al. 1998), the contribution of epiphyte litterfall to total fine litterfall (Nadkarni and Matelson 1992), and the slow rates of death and decomposition of epiphytes that have fallen to the forest floor (Matelson et al. 1993).

Although these studies suggest that epiphytes affect N cycling in tropical cloud forests, the interactions between epiphyte and host tree nutrient cycles remain unclear. These descriptive studies have not satisfactorily identified the means by which different types of epiphytes secure and retain their nutrients. Experimental studies that differentiate the sources of nutrients are needed to address those questions.

In the past two decades, stable isotope techniques have become important tools for ecophysiology and ecosystem research (Ehleringer et al. 1993; Högberg 1997; Griffiths 1998). However, apart from the use of ^{13}C discrimination to identify Crassulacean acid metabolism (CAM) and to estimate water-use efficiency of epiphytes, isotopes have only rarely been used in canopy research. Deuterium depletion (δD) was used to distinguish between different sources of water used by epiphytic and ground-rooting life-stages of *Didymopanax pittieri* (Feild and Dawson 1998). Much lower $\delta^{15}N$ signals were found in foliage of epiphytes compared to trees, which supports the hypothesis that ^{15}N-depleted rain is a major source of nutrients for epiphytes (Stewart et al. 1995). Differences in $\delta^{15}N$ values between systematic groups of epiphytes and growth forms have been documented, with lower $\delta^{15}N$ values in

bromeliads with phytotelmata than in other epiphytic families. Atmospheric bromeliads exhibit even lower values, as they rely almost exclusively on direct absorption of precipitation via trichomes (Hietz et al. *1999*).

Epiphytes that root in canopy soils almost certainly have a more stable water supply than those attached to bare bark, and should thus suffer less frequent drought stress. The effects of these soils on epiphyte nutrition, however, have not been studied. We used stable isotopes to study N sources of epiphytes in a lower montane cloud forest in Monteverde, Costa Rica to investigate four hypotheses. First, if N in rain is ^{15}N depleted relative to available soil N, the δ ^{15}N of epiphytes should be lower than in trees because of a stronger reliance on precipitation N. Second, because canopy soil builds from organic material in the canopy, its δ ^{15}N should reflect both that of epiphytes and host material from which it is derived. Third, epiphytes rooting in canopy soil should have δ ^{15}N signals that are more similar to their hosts than individuals living on branches without canopy soil. Finally, cryptogams, which absorb water through their surfaces, should be largely independent of their substrate, absorb N mostly from precipitation, and show correspondingly low δ ^{15}N signals.

Materials and methods

Study site

Fieldwork was conducted in February 2000 in the Monteverde Cloud Forest Preserve (MCFP), a lower montane moist forest along the Cordillera de Tilarán, Costa Rica (10°12' N, 84°42' W) (Lawton and Dryer *1980*; Nadkarni and Wheelwright *2000*). Epiphytes are extremely prominent in this forest, forming thick mats on large branches of mature trees, but also covering branches and stems of subcanopy trees and understorey vegetation. Epiphytic biomass (including canopy soil) is estimated at 33.1 t ha^{-1} (Nadkarni et al. *2000a, 2000b*). Bryophytes and scandent vascular epiphytes dominate on the outer branches; higher vascular plants and dead organic matter are more prominent on the inner portions of the branches (Nadkarni *1984*; Ingram and Nadkarni *1993*).

Sampling

Epiphytes, bark, tree leaves, and canopy soil were collected from nine non-leguminous canopy trees (25-30 m tall). Trees were rigged and ascended with single-rope techniques (Perry *1978*). Seven categories of epiphytes were sampled: *Pleurothallis* (Orchidaceae), Ericaceae (*Vaccinium, Satyria, Disterigma*), *Peperomia* (Piperaceae), *Elaphoglossum* (Lomariopsidaceae), *Polypodium* (Polypodiaceae), lichens, and bryophytes. From each tree, and for each epiphyte category except lichens, we collected one sample in each of two rooting substrates: (1) thick branches that supported mats of organic matter (hereafter, "thick branches"), and (2) thin branches that had scant to no dead organic matter ("thin branches"). Bryophytes on thick branches formed mats covering the canopy soil; those on thin branches were pendent. Not all categories were found on thick and thin branches or on each tree, but, except for lichens, five to nine of the samples could be paired within a tree, and all categories could be paired when all samples were pooled. All leaves were cleaned of epiphylls and debris with a wet cloth.

Leaves with a dense epiphyll cover were sampled from ten different understorey shrubs or small trees, 1-2 m above ground from an area of approximately 15 × 15 m, and separated into leaves and

epiphylls. Epiphylls comprised predominantly bryophytes, though some lichens, algae, and fungi were present. Ten samples of terrestrial soil (hereafter, "soil", in contrast to "canopy soil") from 5-10 cm

below the soil surface were also taken from the area beneath the sampled trees.

Laboratory analysis

Samples were dried and ground to a fine powder in a ball mill (Retsch MM2, Vienna, Austria) and analysed by continuous-flow gas isotope ratio mass spectrometry. The elemental analyser (EA 1110, CE Instruments, Italy) was interfaced via a ConFlo II device (Finnigan MAT, Bremen) to the gas isotope ratio mass spectrometer (Delta^{PLUS}, Finnigan MAT). High-purity CO_2 and N_2 reference gases were run with each analysis. Reference gases were calibrated to V-PDB and atmospheric N international standards using IAEA-CH-6, IAEA-CH-7 for $\delta^{13}C$, and IAEA-N-1, IAEA-N-2 and IAEA-NO-3 for $\delta^{15}N$. The SD of repeated measurements of a working standard was 0.10‰ and

0.15‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Statistical analysis

For those groups collected from thin and thick branches, the effects of category and branch size on $\delta^{15}N$, N concentration, and $\delta^{13}C$ were tested by a fixed-effect two-way ANOVA. Differences in $\delta^{15}N$ between individual groups on thin branches were tested with the least significant difference (LSD) post-hoc test. Because epiphytes and epiphylls may receive part of their N from host tree sources and the crown architecture may affect their nutrient acquisition or ecophysiology, samples collected from one tree were not considered independent and the effect of species or branch position was compared by paired t-tests. Results were almost identical to those of a normal two-sided t-test.

Results

Soil-rooting shrubs and trees had higher N concentrations [average 2.4±0.8% dry weight (±SD)] than vascular epiphytes (1.1±0.4%, $P<0.001$). The N concentration in canopy soil was slightly, but not significantly, higher than in soil (Fig. 1). $\delta^{15}N$ signals were much higher in soil than in canopy soil, higher in ground-rooted plants than in epiphytes, and higher in soils than in epiphytes and ground-rooted plants (Fig. 1). Canopy soil $\delta^{15}N$ (0.66±1.18‰) was significantly higher than that of

any material in the canopy, including bryophytes (-4.42±1.96%), vascular epiphytes (-3.79±2.31%), bark (-1.64±0.93%) and tree leaves (-1.01±1.55%). Although the variability of $\delta^{15}N$ and of N concentration was generally low within one type of samples (at least when the different branch types were accounted for, see below), epiphytic lichen variability was extremely high and lichens had either among the highest or the lowest $\delta^{15}N$ values and N concentrations found in plants (Fig. 1).

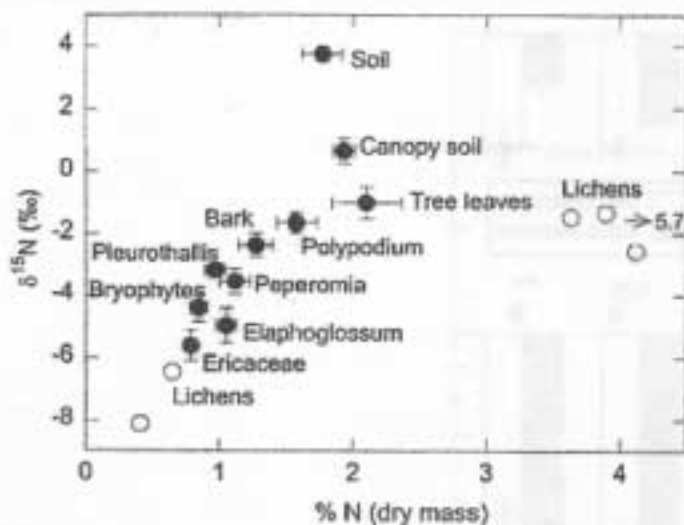**Fig. 1.** Mean ($\pm$SE) N concentrations and δ^{15}N signals of vascular epiphyte and host tree leaves, bryophytes, and canopy and terrestrial soil from a tropical cloud forest in Monteverde, Costa Rica. ? Represent individual lichen samples, one of which had a N concentration of 5.7%

Average δ^{13}C values of soil (-28.0$\pm$0.72‰) and canopy soil (-28.4$\pm$0.52‰) were very similar, as

were those of the foliage of trees (-31.1$\pm$2.3‰) and vascular epiphytes (-31.4$\pm$1.7‰).

Of the six epiphyte categories regularly found on thin branches and also on thick branches, those on thin branches had in four cases (*Elaphoglossum*, Ericaceae, bryophytes, and *Polypodium*) significantly lower δ^{15}N signals and in three cases (*Elaphoglossum*, *Pleurothallis*, and *Polypodium*) lower leaf N concentration (Fig. 2A, B). Differences in δ^{15}N between groups were higher on thin than on thick branches. On thin branches, δ^{15}N values were significantly lower in *Elaphoglossum*, Ericaceae, and pendant mosses than in *Peperomia*, *Pleurothallis* and *Polypodium* (ANOVA $F_{5,44}$=9.02, P<0.001, LSD P<0.05). Values of δ^{13}C were 0.8-1.4‰ lower in vascular epiphytes growing on thick

branches (Fig. 2C). Although there were no significant differences within any single category, the effects of both category ($F_{5,92}$=27.48, P<0.001) and branch size ($F_{1,92}$=9.27, P<0.01) were highly significant. Only one sample of *Pleurothallis* had a δ^{13}C signature that indicated low CAM activity (-22.8‰). This specimen was excluded from the analysis described above.
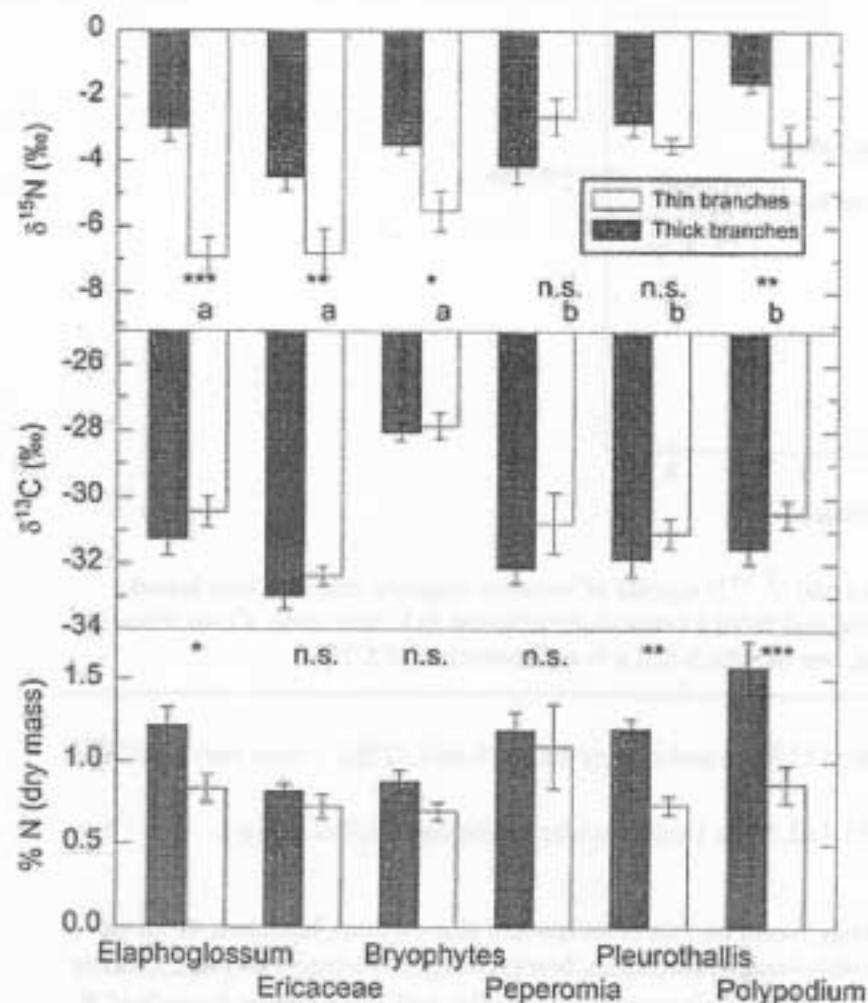
Fig. 2. Isotope signatures ($\delta^{15}N$, $\delta^{13}C$) and N concentration of epiphytes from six systematic groups sampled from thin and thick branches on nine trees. Error bars indicate±1SE. Groups from small branches with the *same letters* are not significantly different in $\delta^{15}N$ values ($P<0.05$, least significant difference test). No significant differences of $\delta^{13}C$ were found within individual groups, but a two-way ANOVA resulted in a highly significant effect of branch size. *$P<0.05$, **$P<0.01$, ***$P<0.001$ (paired t-test between an epiphyte group colonising thin or thick branches)

Epiphylls had higher $\delta^{15}N$ (-2.32±0.77 ‰) and N concentrations (1.42±0.15%) than vascular and

bryophytic epiphytes. Understorey leaves had significantly ($P<0.001$) higher values of $\delta^{15}N$ (-1.03±1.03 ‰) and N concentrations (2.69±0.76%) than the epiphylls growing on them. We found a

significant correlation (Pearson, $P<0.05$) between epiphyll and host $\delta^{15}N$ and between epiphyll and host $\delta^{13}C$ (Fig. 3). No correlation was found for N concentration.
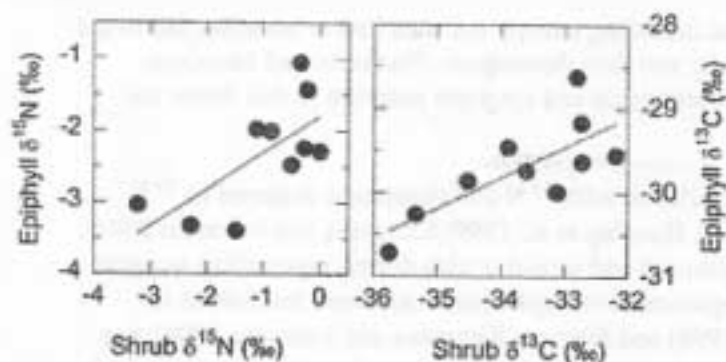
Fig. 3. Correlations of δ ^{15}N and δ ^{13}C between epiphylls and leaves of understorey shrubs they grew on in the Monteverde Cloud Forest Preserve, Costa Rica

Discussion

N occurs in organic and inorganic forms and circulates via complex processes among many different compartments in forest ecosystems. Because many of these processes exhibit an isotope effect (i.e. discrimination against ^{14}N or ^{15}N) N isotope ratios may be used to study ecosystem N cycling. However, this complexity also makes interpreting δ ^{15}N signals difficult. Fortunately, the isotopic effects of many processes have been studied (Handley and Raven 1992; Högberg 1997). For a recent review of the possibilities and limitations of using natural ^{15}N abundance see Robinson (2001).

Values of δ ^{15}N in precipitation cover a wide range (reviewed in Kendall 1998). The δ ^{15}N signatures of NH_4 $^+$, NO_3 $^-$ and dissolved organic N are often negative, particularly in non-polluted areas (Wada et al. 1981; Heaton 1987; Cornell et al. 1995). Although data on the δ ^{15}N of rain is not available from our study site, this pattern should apply to Monteverde, which is not affected by substantial anthropogenic emissions (Clark et al. 1998). Previous studies (Stewart et al. 1995; Hietz et al. 1999) found consistently low δ ^{15}N values in epiphytes. The authors argued that the contribution of ^{15}N-depleted N from precipitation to an epiphyte's nutrition would produce plant tissue lower in ^{15}N than a terrestrial plant's tissue, which would be derived from less ^{15}N-depleted soil. However, in all of the forests previously studied, canopy soils were absent or only very poorly developed.

The δ ^{15}N values of epiphytes from the MCFP were within the range previously reported for epiphytes. However, the ^{15}N depletion of epiphytes relative to canopy soil (ranging from 2.1 ‰ to 6.2 ‰ for the six categories with an average of 4.6 ‰ for epiphytes excluding lichens) was not stronger than that of tree or shrub leaves relative to soil (average 4.8 ‰). If canopy soil N is derived from host leaves or bark which are already depleted in ^{15}N, the low δ ^{15}N of epiphytes could be explained by a twofold fractionation during uptake of soil N, i.e. first through trees, and then through epiphytes.

Several observations contradict this argument. A study on litter dynamics within the canopy of the MCFP revealed that nearly all host leaves intercepted by branches were quickly blown off the branches within a very short period of time (Nadkarni and Matelson 1991). The amount remaining (<2 g m^{-2} year^{-1}) was only a very small fraction of annual epiphyte production. In contrast, a high proportion of epiphytic organic matter remains and decomposes in place and falls to the forest floor as

large, distinct pieces. Often, intact epiphyte mats including canopy soil attached to branches fall to the ground and rest on the terrestrial soil to slowly die and then decompose (Nadkarni and Matelson 1992). These results suggest that the canopy nutrient cycle and epiphyte nutrition in this forest are largely decoupled from tree litterfall.

In many forests, soil organic matter is strongly enriched with ^{15}N and vegetation depleted in ^{15}N (Högberg et al. 1996, 1999; Martinelli et al. 1999; Handley et al. 1999; Kitayama and Iwamoto 2001), which is a result of fractionation during mineralisation and probably also during mycorrhiza-assisted uptake (Högberg et al. 1996). Soil-to-foliage depletion in several tropical montane rainforests in Hawaii (Vitousek et al. 1989; Martinelli et al. 1999) and Borneo (Kitayama and Iwamoto 2001) was similar to that reported here. Given the similar temperature and humidity conditions within a tropical cloud forest (relative to forests in other zones), the similar microbial biomass and activity of soil and canopy soil (Vance and Nadkarni 1990) and the almost identical $\delta^{13}C$ values of soil and canopy soil and of tree and epiphyte foliage, a similar soil-to-foliage ^{15}N depletion and isotope effect during soil formation appears likely, with canopy organic matter therefore being derived from epiphytes. The pattern of ^{15}N therefore provides additional, time-integrated evidence of an N cycle of epiphytes and canopy soil being largely independent of host tree N.

A comparison with an age series of Hawaiian forests offers an alternative, but not contradictory explanation. The $\delta^{15}N$ in volcanic soil that is 67,000 years old is about 5‰ higher than in

197-year-old soil, and the $\delta^{15}N$ content of Meterosideros polymorpha foliage is about 4‰ lower

than in the soil of both sites (Vitousek et al. 1989). The negative $\delta^{15}N$ of young sites was interpreted as representing accumulated N input from precipitation, and higher values in older soils as an effect of slow losses of ^{14}N during soil development (Vitousek et al. 1989). This mechanism could also apply to the formation of canopy soil and the difference between terrestrial and canopy plants (Fig. 4). Canopy soils are young (younger than the age of the tree on which they accumulate), and if they are derived from epiphytic rather than host tree material, their N will represent the accumulated input from precipitation, which is retained by epiphytes and decomposes on the branches, minus some N losses through leaching, gaseous losses, and herbivory.
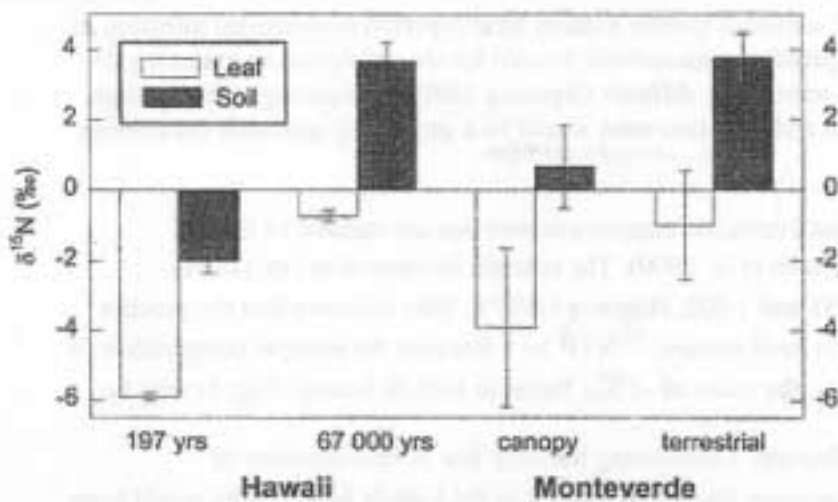
Fig. 4. $\delta^{15}N$ signals of soil and *Meterosideros* leaves on young and old volcanic substrate in Hawaii (Vitousek et al. 1989) compared with canopy and terrestrial soils and plants in Monteverde. The value for *terrestrial plants* is the average of tree leaves, for *epiphytic plants* the average of vascular epiphytic leaves and bryophytes (Fig. 1). *Error bars* are ±1 SE. *yrs* Years

The hypothesis that epiphytes rooting in canopy soil will absorb N dissolved therein, and those rooting on bare branches should rely more on nutrients obtained directly from the rain is supported by our results. Individuals from all six groups rooting on thin branches with little or no canopy soil had lower $\delta^{15}N$ signals than those on thick branches, and four groups significantly so (Fig. 2). Epiphytes on thick branches had higher N concentrations than those on thin branches, which suggests that canopy soil improved their nutrient supply.

While epiphytes on thin branches without canopy soil rely on water stored internally and on adhesive water held on plant and branch surfaces, epiphytes on thick branches will have additional access to water stored in several centimetres of canopy soil. Although differences in $\delta^{13}C$ values were small, plants on thick branches had consistently lower values than plants on thin branches (Fig. 2). This is indicative of drought stress (Farquhar et al. *1989*) and suggests more frequent water limitation on thin branches even in this humid cloud forest.

If a relatively N-rich substrate is not available, differences in nutrient uptake mechanisms may become more apparent. This is supported by the greater variability in $\delta^{15}N$ of epiphytes on thin branches relative to those on thick branches (Fig. 2).

Mycorrhizas are important in nutrient acquisition of plants in nutrient-poor habitats and may also be important for epiphytes. Fruiting bodies of mycorrhizal fungi have been documented as highly enriched in ^{15}N relative to plant foliage, which is thought to reflect the importance of mycorrhiza-assisted N uptake, as ^{15}N was retained in the fungus and plants were ^{15}N-depleted (Taylor et al. *1997*; Hobbie et al. *1999*). Infection rates were high in epiphytic *Elaphoglossum* and Ericaceae (Bermudes and Benzing *1989*; Gemma and Koske *1995*), but low in *Peperomia* (Bermudes and Benzing *1989*; Maffia et al. *1993*), which is consistent with the differences in $\delta^{15}N$ between these two groups reported here. High infection rates were also found in epiphytic orchids (Bermudes and Benzing *1989*), but a specific feature of orchid mycorrhiza is that N may be transferred by lysis of hyphae within the plant cells, which results in much lower ^{15}N fractionation between plants and fungi (Högberg *1997*). It thus appears likely that the influence of mycorrhiza on epiphyte $\delta^{15}N$ can explain

differences between groups. However, although several authors have reported mycorrhizal infection of epiphytes, the presence of fungi is no proof of a mutualistic benefit for the epiphytes, so assessing the importance of mycorrhiza in epiphyte nutrition is difficult (Benzing 1990). Comparing stable isotope abundance with the type of mycorrhiza and infection rates would be a promising approach (Michelsen et al. 1998; Hobbie et al. 1999).

Many tropical lichens are known to host symbiotic microorganisms that are capable of fixing atmospheric N_2 (Forman et al. 1975; Budel et al. 2000). The isotopic fractionation (α) of N_2 fixation is small [ranging between 0.998 and 1.002; Högberg (1997)]. This indicates that the process discriminates slightly against ^{14}N or, in most studies, ^{15}N (δ >1). Because the isotopic composition of atmospheric N_2 is, by definition, 0‰, the value of -2‰ found in high-N lichens (Fig. 1) may be

expected if all N originated from N_2 fixation. Considering the very low N concentration of non-N_2-fixing and rain-fed lichens, it appears likely that most N of the high-N lichens must result from N_2 fixation. In our study, the number of lichen samples was very low. However, the very distinct N concentration and $\delta^{15}N$ signals of lichens strongly suggest that N_2 fixation significantly contributes to N nutrition of the samples with high N concentrations.

The high $\delta^{15}N$ signals of epiphylls in the understorey compared to mat-forming or pendent bryophytes in the canopy could result from an accumulation of ^{15}N in throughfall due to exchange processes in the canopy or from N_2 fixation of epiphylls. Bergstrom and Tweedie (1998) found that δ ^{15}N values of two epiphytes were 4-6‰ lower 30 m above ground in the upper crown than at 15 m,

presumably because throughfall lower in the canopy was ^{15}N enriched compared to precipitation. However, the correlation between host leaf and epiphyll $\delta^{15}N$ also suggests some exchange of N between epiphylls and host leaves. Epiphylls include symbiotic or free-living N_2-fixing micro-organisms and may be important contributors to host plant N, particularly in the humid understorey of tropical forests (Freiberg 1998). Using acetylene reduction and ^{15}N labelling, Bentley and Carpenter (1984) estimated that 10-25% of leaf N in an understorey palm (*Welfia georgii*) was supplied by N_2-fixing epiphylls. The correlation between epiphyll and host leaf $\delta^{13}C$ could either be caused by a substantial transfer of organic compounds, or to small-scale variations in ambient δ $^{13}CO_2$ or microclimatic conditions affecting $^{13}CO_2$ discrimination during uptake.

Conclusions

Our study demonstrates that the natural abundance of stable N isotopes in various compartments in combination with known isotope effects of transformation processes is a useful tool with which to study canopy nutrient cycles and epiphyte nutrition. Results of this and previous studies from Monteverde suggest that the N cycle of epiphytes and canopy soil is largely independent from that of their host trees and terrestrial soil. The patterns of $\delta^{15}N$ of canopy and terrestrial soils and plants we reported in this study are consistent with conclusions from other terrestrial studies that indicated that δ ^{15}N is related to residence time of whole ecosystem (or canopy) N.

This study also provides quantitative evidence of different "nutritional microsites" within single trees. Our comparison within systematic groups showed that epiphytes on thin branches with little substrate rely more strongly on rainfall relative to epiphytes rooted in canopy soil. N uptake via mycorrhizas or N_2-fixing epiphylls appears to be of importance for the N nutrition of some groups. Future studies should quantify the colonisation of the rhizosphere and phyllosphere by symbionts.

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