

Variation in nitrogen use strategies and photosynthetic pathways among vascular epiphytes in the Brazilian Central Amazon¹

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ABSTRACT – (Variation in nitrogen use strategies and photosynthetic pathways among vascular epiphytes in the Brazilian Central Amazon). The variation in nitrogen use strategies and photosynthetic pathways among vascular epiphyte families was addressed in a white-sand vegetation in the Brazilian Central Amazon. Foliar nitrogen and carbon concentrations and their isotopic composition ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively) were measured in epiphytes (Araceae, Bromeliaceae and Orchidaceae) and their host trees. The host tree *Aldina heterophylla* had higher foliar N concentration and lower C:N ratio ($2.1 \pm 0.06\%$ and 23.6 ± 0.8) than its dwellers. Tree foliar $\delta^{15}\text{N}$ differed only from that of the orchids. Comparing the epiphyte families, the aroids had the highest foliar N concentration and lowest C:N ratios ($1.4 \pm 0.1\%$ and 34.9 ± 4.2 , respectively). The orchids had more negative foliar $\delta^{15}\text{N}$ values ($-3.5 \pm 0.2\%$) than the aroids ($-1.9 \pm 0.7\%$) and the bromeliads ($-1.1 \pm 0.6\%$). Within each family, aroid and orchid *taxa* differed in relation to foliar N concentrations and C:N ratios, whereas no internal variation was detected within bromeliads. The differences in foliar $\delta^{15}\text{N}$ observed herein seem to be related to the differential reliance on the available N sources for epiphytes, as well as to the microhabitat quality within the canopy. In relation to epiphyte foliar $\delta^{13}\text{C}$, the majority of epiphytes use the water-conserving CAM-pathway ($\delta^{13}\text{C}$ values around -17%), commonly associated with plants that live under limited and intermittent water supply. Only the aroids and one orchid *taxon* indicated the use of C_3 -pathway ($\delta^{13}\text{C}$ values around -30%).

Key words - $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, stable isotopes, white-sand vegetation

RESUMO – (Variação nas estratégias de uso do nitrogênio e nas vias fotossintéticas entre epífitas vasculares na região central da Amazônia, Brasil). A variação nas estratégias de uso do nitrogênio e das vias fotossintéticas de famílias de epífitas vasculares foi investigada em uma vegetação de areia branca na Amazônia Central. Foram medidas as concentrações e composições isotópicas de nitrogênio e carbono ($\delta^{15}\text{N}$ e $\delta^{13}\text{C}$, respectivamente) de folhas de epífitas (Araceae, Bromeliaceae e Orchidaceae), assim como de suas árvores hospedeiras. As folhas da árvore hospedeira *Aldine heterophylla* tiveram a maior concentração de nitrogênio foliar e menor razão C:N ($2,1 \pm 0,06\%$ e $23,6 \pm 0,8$) que de suas hóspedes. O valor de $\delta^{15}\text{N}$ foliar da árvore somente diferiu do valor das orquídeas. Ao comparar as famílias de epífitas, a maior concentração de nitrogênio foliar e menor razão C:N foi observada nas aráceas ($1,4 \pm 0,1\%$ e $34,9 \pm 4,2$, respectivamente). As orquídeas tiveram valores mais negativos de $\delta^{15}\text{N}$ foliar ($-3,5 \pm 0,2\%$) que aráceas ($-1,9 \pm 0,7\%$) e bromélias ($-1,1 \pm 0,6\%$). Ao comparar os táxons de cada família, observou-se que tanto os táxons de aráceas como os de orquídeas diferiram em relação ao nitrogênio foliar e razão C:N, enquanto que não foi detectada variação entre os táxons de bromélias. As diferenças nos valores de $\delta^{15}\text{N}$ foliar aqui observadas podem ser relacionadas à variação na dependência das fontes de nitrogênio disponíveis para as epífitas, assim como na variação da qualidade do microhabitat no dossel. Em relação aos valores de $\delta^{13}\text{C}$ foliar das epífitas analisadas, verificou-se que a maioria usa a via fotossintética CAM (valores em torno de -17%), comumente associada com plantas que vivem em condições de suprimento de água limitado ou intermitente. Apenas as aráceas e um *táxon* de orquídea mostraram usar a via C_3 (valores em torno de -30%).

Palavras-chave - $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, isótopos estáveis, vegetações de areia branca

Introduction

A portion of the Amazon Basin not seasonally flooded, also known as *terra-firme*, is mainly covered

by lowland tropical forest (Braga 1979, Pires & Prance 1985). Although the Amazon forest and white-sand soils are not often associated, *terra-firme* forest is scattered with a substantial proportion of evergreen sclerophyllous vegetation, characterized by elevated endemism and low diversity (Braga 1979, Anderson 1981). This vegetation is known as “heath forest” and comprises stunted (*campina*) and taller (*campinarana*) formations (Proctor 1999, Luizão *et al.* 2007a, b). Compared with the *terra-firme* Amazonian forest, its canopy is less dense allowing more light to reach the lower understory. Epiphytes are abundant on its tree branches as well as on the ground (Takeuchi 1960, Guillamet 1987).

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Epiphytes are a conspicuous and characteristic life form in tropical forests (Richards 1996, Benavides *et al.* 2005), accounting for up to 35 percent of the vascular flora in some wet neotropical forests (Gentry & Dodson 1987). In some cloud forests, their biomass rivals that of tree foliage (Nadkarni 1984, Nadkarni *et al.* 2000, Stewart *et al.* 2002), while in some montane rainforests, their foliage may equal 50 percent of tree leaf biomass (Edwards & Grubb 1977, Nadkarni 1984, Ingram & Nadkarni 1993). As they produce a considerable amount of suspended biomass and retain water and debris (Nadkarni 1986), epiphytes and associated dead organic matter constitute a considerable portion of the above-ground biomass and nutrient pools in these systems (Nadkarni 1984), playing an important role in forest primary production and nutrient cycling (Nadkarni 1986, Zotz & Winter 1994).

The epiphytic habit implies some physiological constraints as the demand for water and nutrients is often not buffered by layers of soil as the plants are not rooted in ground soil (Nadkarni 1984, Nadkarni & Matelson 1991, Hietz *et al.* 2002).

Epiphytes may only access N sources derived from the atmosphere (via wet and/or dry deposition or N₂ fixation), canopy (organic forms derived from leaching or decomposition of trapped canopy litter, and also from inputs by animals) and epiphyte-microorganisms symbiosis (Stewart *et al.* 1995, Hietz *et al.* 2002, Inselsbacher *et al.* 2007). Furthermore, epiphytes are exposed to a higher insolation condition (Yoda 1974), greater extremes of temperature and relative humidity than forest understory vegetation (Ingram & Nadkarni 1993).

The variety of morphological and physiological strategies allowed plants to successfully inhabit more exposed sites and completely evolve independently of ground soil (Benzing 1990). Epiphytes have slower growth rates, accessory structures (*e.g.* trichomes and velamen), as well as association with insects and microorganisms (Nadkarni 1984, Stewart *et al.* 1995, Kauff *et al.* 2000, Hietz *et al.* 2002, Rains *et al.* 2003, Tsavkelova *et al.* 2003, Shefferson *et al.* 2005).

The epiphytic habitat is generally the driest niche within tropical forests and many species use the photosynthetic water-conserving CAM-pathway, including epiphytes from Bromeliaceae, Cactaceae and Orchidaceae (Medina *et al.* 1977, 1989, Fontoura & Reinert 2009). Moreover, morphological adaptations (water-storing phytotelmata, succulence, xeromorphic leaves, poikilohydry, deciduousness, and general reduction of the shoot) also allow many C₃-species to

live under these extreme conditions (Benzing 1990, Hietz *et al.* 1999).

The natural abundance of stable isotopes has been widely applied as a powerful tool in ecosystem and plant ecology research. While the natural abundance of ¹⁵N is a useful indicator of the sources and pathways of N (Högberg 1997), the $\delta^{13}\text{C}$ values of leaves is widely used to identify the photosynthetic pathway and to estimate plant water-use efficiency (WUE) (Dawson *et al.* 2002, Holtum & Winter 2005). Previous studies have pointed out differences in foliar $\delta^{15}\text{N}$ values of epiphytes and their host trees, where trees have more ¹⁵N-enriched values than their dwellers due to differences in life style and use of differentiated N sources (Stewart *et al.* 1995). Stewart *et al.* (1995) also compared within epiphytes and were able to group them according to ¹⁵N depletion and N content, attributing these results to the differential use of N sources (wet and dry atmospheric deposition, debris and N₂ fixation).

Differences in foliar $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of epiphytes may also be related to epiphytic group and environmental conditions. When comparing taxonomic and ecological groups of epiphytes along an altitudinal gradient, Hietz *et al.* (1999) pointed out that variation in epiphytic life form, physiology, as well as position of individuals within the canopy is capable of affecting N nutrition and foliar $\delta^{15}\text{N}$ values. A survey of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of N sources and epiphyte leaves sampled from different canopy strata provided evidence for a $\delta^{15}\text{N}$ -gradient which varied with height: more positive values in the lower canopy zones to more negative values in the upper canopy zones (Wania *et al.* 2002). This variation was not only attributed to differences in N-source use by epiphytes of different strata, but also to differences in isotope discrimination during N acquisition and internal variation. An inverse trend was observed for foliar $\delta^{13}\text{C}$ values, as ¹³C abundance increased from lower to upper zones. This reduction in ¹³C discrimination was related to the lower water availability and/or light incidence experienced by epiphytes of higher strata.

In this paper, the foliar content of N and the relative abundances of foliar ¹³C and ¹⁵N ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of different taxonomic groups of vascular epiphytes (Araceae, Bromeliaceae and Orchidaceae) of a white-sand vegetation in Central Brazilian Amazon were measured in order to test whether epiphytes from different families had distinct strategies related to N use and photosynthetic pathways. Variations within families, as well as differences in the nutritional status between epiphytes and host tree species were also searched.

Material and methods

Study site – The study was carried out at the Biological Reserve of Campina, administered by the Instituto Nacional de Pesquisas da Amazônia – Inpa. The reserve is situated 60 km north of the city of Manaus, AM, Brazil (02°35' S, 60°02' W), and covers an area of 900 ha. Climate in this region is tropical, with mean annual temperature of 26 °C and air humidity ranging from 85-88%. The annual precipitation in the region averages 2200-2400 mm, with 2-3 months with less than 100 mm of rainfall (Sombroek 2001).

The Reserve is formed by *campina* (dense sclerophyllous shrub, 4-10 m high, generally forming a sparse cover over bare sand), *campinarana* (dense sclerophyllous forest, with trees 10-20 m high) and dense *terra-firme* forest (lowland tropical forest). The *campina* is usually surrounded by *campinarana* vegetation, and may show a gradual succession to the *campinarana*, the climax in white-sands (Braga 1979, Pires & Prance 1985, Luizão *et al.* 2007a).

Campina and *campinarana* vegetations grow in this area on highly weathered sandy soils, composed primarily of quartz (Hydromorphic Spodosols) (table 1). White-sand soils are very similar to spodosols of temperate zones (Proctor 1999, Horbe *et al.* 2004), and are characterized by fast drainage, high acidity, and accumulation of a layer of mor humus of varying thickness over soil surface under woody vegetation patches (Anderson 1981, Horbe *et al.* 2004, Luizão *et al.* 2007a). The topography of the area is essentially flat with a mean altitude of 44 m above sea level (Luizão *et al.* 2007b).

Plant sampling – Plant material was sampled during the rainy season (April 2006). Four 200 m long to 10 m wide transects were established, ranging from open *campina* to *campinarana* vegetation.

In each transect, we sampled individuals of the seven most frequent tree species occurring in both *campina* and *campinarana* vegetations: *Aldina heterophylla* Spruce ex Benth. (Leguminosae; sub-family Papilionoidae),

Clusia nemorosa G. Mey (Clusiaceae), *Matayba opaca* Radlk. (Sapindaceae), *Ouratea spruceana* (Mart.) Engl. (Ochnaceae), *Pagamea duckei* Standley (Rubiaceae), *Pradosia schomburkiana* (A. DC.) Cronq. subsp. *schomburkiana* (Sapotaceae), and *Protium heptaphyllum* March. (Burseraceae), summing up 52 trees sampled (table 1). The full description of these trees and their nutrient status can be found in Mardegan *et al.* (2009). Only sampled trees where epiphytes were present were sampled.

From the branches of each sampled tree, the epiphytes from Araceae, Bromeliaceae and Orchidaceae families were sampled, summing up a total of 66 individuals (table 1). Although no height measurements of the trunk were made, epiphytes occurred in diverse canopy strata; some of them were sampled close to the ground, while other species could only be sampled after climbing the host tree.

Epiphytic *taxa* were identified to the genus level, as no fertile material was found. Two aroids – *Anthurium* sp. and *Stenospermatium* sp., three bromeliads – *Aechmea* sp., *Guzmania* sp. and *Streptocalyx* sp., and four orchids – *Encyclia* sp., *Octomeria* sp., *Maxillaria* sp.1 and sp.2 were identified.

For determining N and C concentration and their isotope ratios, four to five leaves of each epiphyte and around 10 leaves from their host tree were sampled. All samples were healthy fully expanded leaves.

Data analyses – Tree and vascular epiphyte leaf samples (100-200 g) were oven-dried at 65 °C until a constant weight and ground to a fine powder. Sub samples of 1-2 mg of organic ground material were sealed in tin capsules and combusted in a Carlo Erba elemental analyzer (Milan, Italy) to determine N and C concentrations. The gas generated from the combustion was purified in a gas chromatography column and passed directly to the inlet of a gas isotope ratio mass spectrometer (IRMS Delta Plus; Finnigan Mat, San Jose, California, USA). Internal standard (atropine) was included in each run. From these analyses, both the N and C isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively) and elemental concentrations (%N and %C) were obtained.

Stable isotope ratios are expressed in a parts-per-thousand basis (‰) in “delta” notation: $\delta^{15}\text{N}$ or $\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$; where R_{sample} and R_{standard} are the ratios of heavy isotope to light isotope of the samples and the respective standard. The international standards for N and C were the atmospheric air and Pee Dee Belemnite limestone, respectively.

Statistical analysis – First the epiphytes of the three families in relation to foliar C and N contents, C:N ratios, and their N and C isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were compared. *Taxa* of each epiphyte family were also compared in order to determine variations within each family sampled. We also compared individuals of *Aldina heterophylla*, the tree species with the highest number of individuals, from which the majority of epiphytes were sampled (including the aroids, which were absent from other tree canopies), and their

Table 1. Number of host trees and respective epiphytes sampled in an area of white-sand vegetation in the Central Brazilian Amazon.

Tree species	n	Epiphytes sampled		
		Aroids	Bromeliads	Orchids
<i>Aldina heterophylla</i>	25	13	7	20
<i>Clusia nemorosa</i>	9	–	1	8
<i>Matayba opaca</i>	3	–	1	2
<i>Miconia argyrophylla</i>	3	–	2	1
<i>Ouratea spruceana</i>	3	–	1	3
<i>Pagamea duckei</i>	5	–	1	5
<i>Protium heptaphyllum</i>	1	–	–	1
Total	49	13	13	40

dwellers. Correlations were made between foliar C and N concentration and the isotopic signatures of ^{13}C and ^{15}N , as well as between C:N ratios.

Data distribution was tested using the Kolmogorov-Smirnov one-sample test. Because some data did not follow normal distribution, the analyses were performed using non-parametric tests. Differences among each epiphyte family were tested using a Kruskal-Wallis test to determine statistically significant differences among the three groups compared. This test was also used to determine significant differences among the *taxa* of the families Bromeliaceae and Orchidaceae. As Araceae had only two *taxa* sampled, the Mann-Whitney U test was used to determine statistical differences.

All statistical analyses were performed using the software STATISTICA, version 6.1 for Windows (StatSoft Inc. 2004). A probability level of 0.05 was used as a critical level of significance in all tests.

Results

Comparisons among vascular epiphyte families – Araceae species had the highest foliar N concentration and the lowest C:N ratio ($P < 0.05$), while those from Bromeliaceae and Orchidaceae had similar average foliar

N concentration and C:N ratio (table 2). The orchids had the most depleted foliar $\delta^{15}\text{N}$ values compared to the aroids and the bromeliads ($P < 0.05$). The aroids had more negative foliar $\delta^{13}\text{C}$ values than bromeliads and orchids, ($P < 0.05$), while the latter had similar foliar $\delta^{13}\text{C}$ values (table 2).

Comparisons within epiphyte families – Comparisons within each epiphyte family revealed that within the aroids, the two *taxa* sampled (*Anthurium* sp. and *Stenospermatum* sp.) significantly differed in relation to foliar N concentration and C:N ratio ($P < 0.05$). *Anthurium* sp. had higher N concentration and lower C:N ratio than *Stenospermatum* sp. ($P < 0.05$). Foliar $\delta^{15}\text{N}$ values were highly variable, ranging from -6.7 to +3.8‰, while average foliar $\delta^{13}\text{C}$ values were around -30‰ (figure 1A, table 3).

No variation within the three bromeliad species (*Aechmea* sp., *Guzmania* sp., and *Streptocalyx* sp.) was detected in relation to N and C concentrations and their isotopic composition. Only *Streptocalyx* sp. had a more ^{15}N -enriched signature than the other two *taxa* (table 2). Foliar $\delta^{13}\text{C}$ values did not vary significantly, and a

Table 2. Mean values (\pm SE) for foliar N and C concentration, C:N ratio, and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of epiphytes sampled in an area of white-sand vegetation in the Central Brazilian Amazon ($n = 66$).

Epiphyte Family	N (%)	C:N	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
Araceae	1.4 ± 0.1^a	34.9 ± 4.2^a	-1.9 ± 0.7^a	-30.9 ± 1.0^a
Bromeliaceae	0.9 ± 0.1^b	55.6 ± 4.9^b	-1.1 ± 0.6^a	-17.3 ± 0.2^b
Orchidaceae	0.8 ± 0.01^b	56.3 ± 1.7^b	-3.5 ± 0.2^b	-21.9 ± 1.0^b

Different letters indicate significant statistical differences among epiphyte families ($P < 0.05$).

Table 3. Mean values (\pm SE) for foliar N and C concentration, C:N ratio, and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the *taxa* of each epiphyte family sampled in an area of white-sand vegetation in the Central Brazilian Amazon ($n = 66$).

Family	Taxa	<i>n</i>	N (%)	C:N	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
Araceae	<i>Anthurium</i> sp.	7	1.6 ± 0.1^a	26.9 ± 1.5^a	-1.4 ± 1.1^a	-31.7 ± 0.3^a
	<i>Stenospermatum</i> sp.	6	1.1 ± 0.1^b	44.3 ± 7.5^b	-2.4 ± 1.0^a	-30.1 ± 2.2^a
Bromeliaceae	<i>Aechmea</i> sp.	3	0.7 ± 0.08^a	57.8 ± 6.5^a	-2.1 ± 0.9^a	-17.4 ± 0.5^a
	<i>Guzmania</i> sp.	4	1.0 ± 0.2^a	50.3 ± 9.2^a	-2.0 ± 0.8^a	-17.5 ± 0.2^a
	<i>Streptocalyx</i> sp.	6	0.8 ± 0.1^a	57.2 ± 8.9^a	-0.02 ± 1.0^a	-17.2 ± 0.4^a
Orchidaceae	<i>Encyclia</i> sp.	12	1.0 ± 0.03^a	47.9 ± 1.6^a	-3.9 ± 0.3^a	-32.2 ± 0.2^a
	<i>Maxillaria</i> sp.1	12	0.7 ± 0.02^b	66.3 ± 3.2^a	-3.5 ± 0.4^a	-17.4 ± 0.1^b
	<i>Maxillaria</i> sp.2	12	0.9 ± 0.02^{ab}	53.1 ± 1.8^{ab}	-2.8 ± 0.3^a	-17.8 ± 0.2^b
	<i>Octomeria</i> sp.	4	0.7 ± 0.07^b	60.7 ± 7.3^{ab}	-4.2 ± 0.7^a	-17.3 ± 0.1^b

Different letters indicate significant statistical differences among species within each epiphyte family ($P < 0.05$).

mean value of $-17.3 \pm 0.2\text{‰}$ was observed (figure 1B, table 3).

Within the orchids, *Encyclia* sp. and *Maxillaria* sp.2 had similar foliar N concentration, as well as *Maxillaria* sp.1 and *Octomeria* sp. ($P < 0.05$). The foliar C:N ratio of the four *taxa* was highly variable. The foliar $\delta^{15}\text{N}$ values were negative and highly variable for the four species, with mean values ranging from -6.2 to -1.1‰ . *Encyclia* sp. had significantly more depleted foliar $\delta^{13}\text{C}$ signature values compared to the other three *taxa* ($P < 0.05$) (figure 1C, table 3).

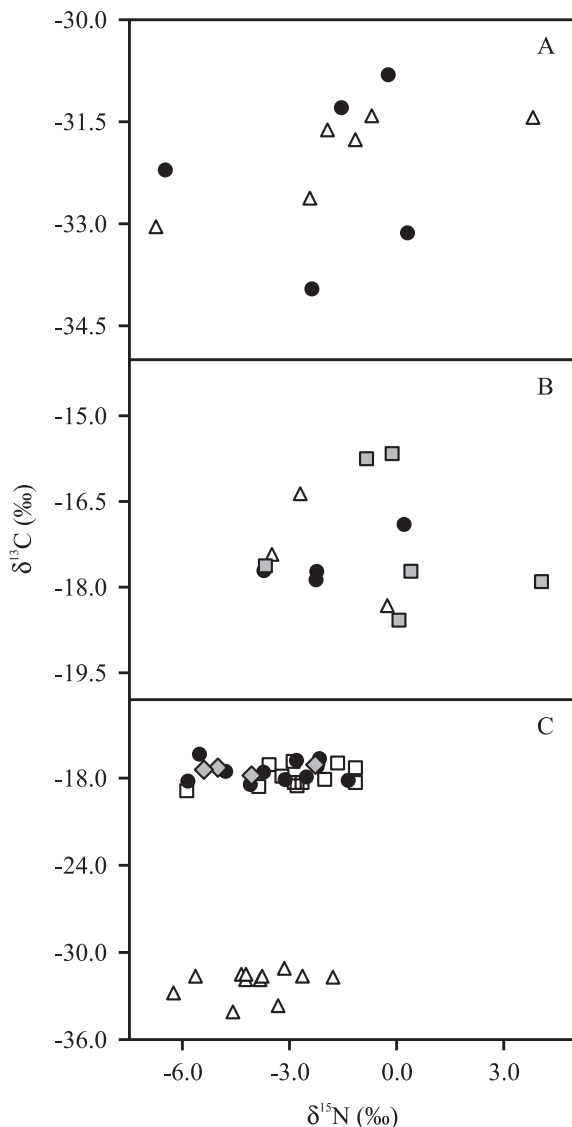


Figure 1. Foliar $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of the *taxa* of the families Araceae (A) – *Anthurium* sp. (Δ) and *Stenospermatum* sp. (\bullet); Bromeliaceae (B) – *Aechmea* sp. (Δ), *Guzmania* sp. (\bullet) and *Streptocalyx* sp. (\square); and Orchidaceae (C) – *Encyclia* sp. (Δ), *Maxillaria* sp.1 (\bullet), *Maxillaria* sp.2 (\square) and *Octomeria* sp. (\diamond) sampled in an area of white-sand vegetation in the Central Brazilian Amazon.

Comparisons between host trees and epiphytes – The tree *A. heterophylla* had a higher foliar N concentration ($P < 0.05$) than the aroids, bromeliads, and orchids (table 4). Consequently, the host tree had a significantly lower C:N ratio ($P < 0.05$) than its dwellers (table 4). *A. heterophylla*, had similar foliar $\delta^{15}\text{N}$ values to the aroid and the bromeliad dwellers, whereas the orchid dwellers had significantly more depleted signatures ($P < 0.05$) than their host (figure 2, table 4). Regarding foliar $\delta^{13}\text{C}$ values, the tree and its aroid dwellers had similar signatures, while the bromeliad and the orchid dwellers had less depleted values ($P < 0.05$) than their hosts (figure 2, table 4).

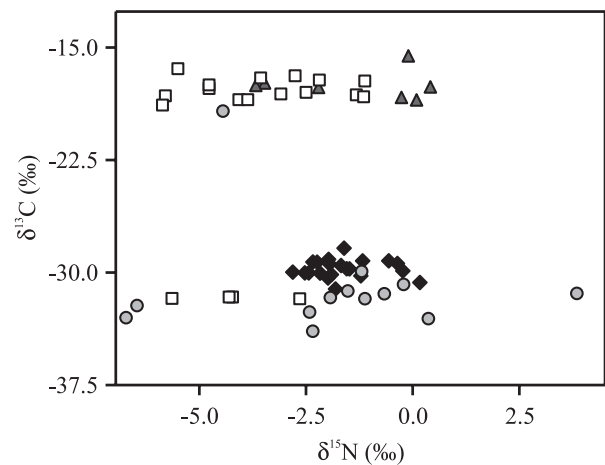


Figure 2. Foliar N and C isotopic signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of *A. heterophylla* trees (\blacklozenge) and their dwellers – aroids (\circ), bromeliads (Δ) and orchids (\square) sampled in an area of white-sand vegetation in the Central Brazilian Amazon.

Discussion

Potential sources of N to epiphytes using stable N isotopic composition – The divergence on foliar $\delta^{15}\text{N}$ values of epiphytes and their host trees is typically related to variation in life forms and N sources available for these plant groups. While forest trees are rooted in the soil, deriving the majority of nutrients from it, epiphytes derive at least a portion of their nutrients from atmospheric sources (atmospheric wet and dry deposition or biological N fixation), which are known to be more ^{15}N -depleted than soil (Nadkarni & Matelson 1992, Stewart *et al.* 1995, Högberg 1997, Hietz *et al.* 2002). However, differing from previous studies comparing foliar $\delta^{15}\text{N}$ values of host trees and their epiphytes (Stewart *et al.* 1995, Hietz *et al.* 2002), in the present study, only orchids had a more negative foliar $\delta^{15}\text{N}$

Table 4. Mean values (\pm SE) for foliar N and C concentration, C:N ratio, and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the tree *A. heterophylla* ($n = 25$) and their epiphytes ($n = 13$ aroids, 7 bromeliads and 20 orchids) sampled in an area of white-sand vegetation in the Central Brazilian Amazon.

Plant group	%N	CN ratio	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<i>Aldina heterophylla</i>	2.1 ± 0.06^a	23.6 ± 0.8^a	-1.5 ± 0.2^a	-29.4 ± 0.1^a
Aroids	1.5 ± 0.1^b	34.9 ± 4.2^{ab}	-1.9 ± 0.7^a	-30.9 ± 1.0^a
Bromeliads	0.9 ± 0.09^b	50.0 ± 5.0^b	-1.3 ± 0.6^a	-17.5 ± 0.3^b
Orchids	0.1 ± 0.03^b	58.5 ± 2.6^b	-3.6 ± 0.3^b	-20.4 ± 1.2^b

Different letters indicate significant statistical differences among plant group ($P < 0.05$).

compared to the host tree *A. heterophylla*. This lack of difference may be related to the N dynamics in white-sand vegetations. While most of the tropical forests are N-rich ecosystems (Cuevas & Medina 1986, Matson & Vitousek 1987, Martinelli *et al.* 1999, Nardoto *et al.* 2008), white-sand vegetations are known to be N-poor ecosystems (Mardegan *et al.* 2009). They are known to efficiently use the available N sources (Medina & Cuevas 2000) and to have significantly depleted foliar $\delta^{15}\text{N}$ signatures when compared to dense *terra-firme* forests (Nardoto *et al.* 2008, Mardegan *et al.* 2009).

The differences in foliar $\delta^{15}\text{N}$ values observed among aroid, bromeliad, and orchid dwellers, as well as within their *taxa* might be influenced by available N-sources (Stewart *et al.* 1995). As some of these sources have a limited supply, it is possible that epiphytes from distinct groups may access N from a similar and/or more than a single source (Gebauer & Meyer 2003). In addition, epiphyte foliar $\delta^{15}\text{N}$ may also be influenced by the microhabitat within the canopy (Hietz & Hietz-Seifert 1995, Hietz *et al.* 1999).

Canopy soil is the source with higher N concentrations in epiphytic habitats (Inselsbacher *et al.* 2007) and is mainly composed of organic matter; inorganic compounds when present are derived from the decomposition of organic debris (Wania *et al.* 2002). Canopy organic matter mostly accumulates over thicker branches and a decreasing gradient of nutrient supply from thicker to thinner branches may be expected (Wania *et al.* 2002). Thus, it is expected that epiphytes rooted in soil canopy over thicker branches improve their N supply by accessing N sources from decomposing canopy litter (soil canopy) compared to those over thinner branches (Hietz *et al.* 2002).

Despite that the aroids had a higher N foliar concentration and lower C:N ratios, their isotopic signature was similar to the bromeliads. Aroid and bromeliad dwellers have distinct life forms. While the former are rooted in canopy soil, bromeliads obtain

nutrients from water and debris accumulated within their impounding shoots (Benzing & Renfrow 1974, Endres & Mercier 2001, Scarano *et al.* 2002, Lüttge 2008). The initial discrimination against ^{15}N -enriched N compounds during microbial decomposition of accumulated canopy litter could lead to ^{15}N -enrichment of N sources within the tank water (Hietz & Wanek 2003). In contrast, N compounds derived from rainwater usually have negative foliar $\delta^{15}\text{N}$ values (Clark & Nadkarni 1990, Fukuzaki & Hayasaka 2009). Based on our results, we were unable to quantify the contribution of these sources to the bromeliad N nutrition. According to the literature, it is likely that bromeliads may rely on the mineralization of canopy litter within tank shoots as a major source of N (Clark & Benzing 1990, Reinert *et al.* 1997, Benzing 2000, Inselsbacher *et al.* 2007).

On the other hand, orchids had the most depleted foliar $\delta^{15}\text{N}$ values. They grow over thinner and bare branches and lack access to high quantities of canopy soil, such as the aroids, and do not have a reservoir structure for storing water and nutrients, such as bromeliads. As a consequence, they only have access to nutrients in the water running over their surface (Hietz *et al.* 1999) and from atmospheric deposition, sources that are proportionally more ^{15}N -depleted ($< -3\text{‰}$) (Benzing 2000, Fukuzaki & Hayasaka 2009). Moreover, lowland rainforest-orchids are commonly associated with mycorrhiza (Lesica & Antibus 1990). This association enables a more efficient water and nutrient assimilation (Wania *et al.* 2002, Gebauer & Meyer 2003, Midgley *et al.* 2005), although symbionts deliver isotopically depleted N compounds (Högberg 1997). Thus, the isotopic signatures found in orchids (up to 2‰ more depleted) may reflect a high reliance on N sources derived from atmospheric deposition and symbiotic association.

Photosynthetic types among epiphytes using stable C isotopic composition – Except for the aroids and one

orchid genus (*Encyclia*), the majority of epiphytes sampled exhibited a CAM-photosynthetic pathway. Water availability is one of the main environmental factors limiting epiphyte growth and maintenance (Lüttge 2008). As a consequence, a large number of vascular epiphytes use the water-conserving CAM-pathway of photosynthesis, typically associated with plants that inhabit areas where water supply is limited or intermittent, such as observed in epiphyte tropical habitats (Medina 1996, Cushman 2001). The CO₂-concentrating strategy of the CAM photosynthetic pathway (Hietz *et al.* 1999) results in lower transpiration rates and higher water use efficiency (WUE) than C₃- and C₄-plants under comparable conditions (Zotz & Winter 1994, Cushman 2001), allowing these plants to be very plastic and successfully irradiate throughout diverse environments (Medina 1987).

CAM expression greatly varies within epiphyte groups (Pierce *et al.* 2002), and internal variations are related to variation of environmental conditions (*i.e.*, air humidity, light exposure) (Hietz *et al.* 1999). An evidence of such plasticity is the intrinsic ability that some species, known as facultative CAM, present to vary their photosynthetic strategy between C₃- and CAM- pathway in response to the environment (Pierce *et al.* 2002, Lüttge 2008, Reinert & Blankenship 2010). For example, when CAM-plants face a condition of higher water availability, they may maximize their productivity using the C₃-pathway, which has a lower energetic demand than the CAM-pathway. When water availability progressively reduces, plants return to merge this strategy with the CAM-pathway, reducing water loss and maintaining their photosynthetic integrity (Winter *et al.* 1978, Maxwell *et al.* 1995, Zotz & Ziegler 1997). Additionally, constitutive CAM-species may vary the relative contribution of phase IV of CAM-pathway (stomata open during the day and carbon fixation via Rubisco) in relation to phase I (nighttime CO₂ fixation) (Griffiths *et al.* 1986, Reinert *et al.* 1997). Such variation is also related to environmental conditions. However, the ability to merge different photosynthetic pathways, leads CAM-plants to have intermediate $\delta^{13}\text{C}$ values. Differently from C₃- and C₄-plants, which have well-defined and fixed values (-24 to -38‰, and -11 to -15‰, respectively), CAM-plants may have intermediate ones (Griffiths *et al.* 1986), accordingly to the level of reliance on the C₃-pathway. As pointed by Winter and Holtum (2002), epiphytic species with typical $\delta^{13}\text{C}$ values of C₃-plants may obtain a great part from their carbon through CAM-pathway. Thus, additional leaf analysis, such as those related to gas-exchange patterns and titrable acidity, may be useful

to quantify the magnitude of carbon gain through this pathway (Pierce *et al.* 2002).

A vertical gradient in foliar $\delta^{13}\text{C}$ can be observed in forests (Wania *et al.* 2002), with plants from lower strata typically having more negative $\delta^{13}\text{C}$ values than those from the upper canopy (Ometto *et al.* 2006). This differentiation is normally related to the reduction in light intensity and in vapor pressure deficits associated with more sheltered canopy layers (Holtum & Winter 2005), as well as to the origin of the assimilated CO₂ (Martinelli *et al.* 2009). Medina (1987) showed a variation of 2 to 5‰ between epiphytic bromeliads from shaded and sunny areas, observing that the plants exposed to sunlight had a more ¹³C-enriched signature, indicative of a higher water use efficiency. However, foliar $\delta^{13}\text{C}$ values were either typical of the C₃- or the CAM-pathway, suggesting, independently on canopy position, low impact of WUE variation throughout the year on the $\delta^{13}\text{C}$ signature of the dry mass.

The values of foliar $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ observed herein indicate that epiphytes develop numerous strategies to cope with the limiting conditions of their environment. Epiphyte foliar $\delta^{15}\text{N}$ values showed variation within families in relation to N resource used by these plants, being that source is related to habitat quality and epiphyte life form. Orchid foliar $\delta^{15}\text{N}$ indicates the use of depleted N sources from precipitation, as well as the use of sources derived from symbiotic associations. The foliar $\delta^{15}\text{N}$ values of aroid and bromeliad dwellers indicate that, despite having distinct life forms, these groups may access similar N sources. The N derived from the decomposition of organic matter in canopy soil, as well as within tanks seems to be the major source for these two epiphytic groups. Regarding the photosynthetic pathway, foliar $\delta^{13}\text{C}$ showed that both CAM and C₃-pathways are present among these epiphytes.

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