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Nitrogen stable isotopic composition of leaves and soil: Tropical versus temperate forests

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Abstract. Several lines of evidence suggest that nitrogen in most tropical forests is relatively more available than N in most temperate forests, and even that it may function as an excess nutrient in many tropical forests. If this is correct, tropical forests should have more open N cycles than temperate forests, with both inputs and outputs of N large relative to N cycling within systems. Consequent differences in both the magnitude and the pathways of N loss imply that tropical forests should in general be more ¹⁵N enriched than are most temperate forests. In order to test this hypothesis, we compared the nitrogen stable isotopic composition of tree leaves and soils from a variety of tropical and temperate forests. Foliar $\delta^{15}\text{N}$ values from tropical forests averaged 6.5‰ higher than from temperate forests. Within the tropics, ecosystems with relatively low N availability (montane forests, forests on sandy soils) were significantly more depleted in ¹⁵N than other tropical forests. The average $\delta^{15}\text{N}$ values for tropical forest soils, either for surface or for depth samples, were almost 8‰ higher than temperate forest soils. These results provide another line of evidence that N is relatively abundant in many tropical forest ecosystems.

Introduction

A number of lines of evidence suggest that N in most tropical forests is relatively more available than is N in most temperate forests. On average, more N circulates annually through lowland tropical forests, and does so at higher concentrations, than through temperate forests (Proctor et al. 1983;

Vitousek 1984; Vitousek & Sanford 1986; Vogt et al. 1986). Emissions of N-containing trace gases are also higher, both absolutely and as a fraction of N circulating through forests (Keller et al. 1986, 1993; Matson & Vitousek 1987, 1990). Comparable data on rates of N mineralization and leaching losses are sparser, but they generally show greater rates of N cycling and loss in many lowland tropical forests (Vitousek & Denslow 1986; Lewis 1986; Matson et al. 1987; Neill et al. 1995). Overall, these observations suggest that N functions as an excess nutrient in most tropical forests, but not in the majority of temperate forests. The major exceptions to this generalization in the tropics are forests on white-sand soils and montane tropical forests; by the measures above, N is in relatively short supply in these ecosystems (Salati et al. 1982; Cuevas & Medina 1988; Tanner et al., in press). In the temperate zone, the major exceptions are forests dominated by symbiotic N fixing trees (usually monocultures), and forests that receive substantial anthropogenic N deposition (Binkley et al. 1992; Aber et al. 1995; Berendse et al. 1993).

If N functions as an excess nutrient in tropical forests, the N cycle in such systems should be more open than in temperate forests, with both inputs and outputs of N large relative to internal N cycling. Moreover, the pathways of N loss should differ: losses from low-N systems may be predominantly in the form of DON (Hedin et al. 1995), while leaching losses of nitrate and nitrification/denitrification driven trace gas fluxes should predominate where N is in excess (Matson et al., this volume). These differences in both the magnitude and the pathways of loss imply that tropical forests should in general contain N that is more enriched in ^{15}N than most temperate forests. This relative enrichment should occur because pathways of loss in N-rich systems are more likely to be fractionating, and because losses by fractionating pathways leave the N remaining within the system enriched (Hogberg 1997). In order to test this hypothesis, we compared the nitrogen stable isotopic composition of tree leaves and soils from a variety of tropical and temperate forests.

Methods

We surveyed N stable isotopic composition and N content of leaves from adult trees of non-leguminous species from temperate and tropical forests. Where available, the same data for soil organic matter also were evaluated. As there is significant variation with depth in both concentration and stable isotopic composition of nitrogen in soils, data were grouped according to depth. Surface samples were those collected from no more than 10 cm deep, and samples collected below this depth were called depth samples. The nitrogen stable isotopic composition was expressed as δ (‰) notation:

$$\delta^{15}\text{N} = (\text{R}_{\text{sample}}/\text{R}_{\text{std}} - 1) \cdot 1000,$$

where R is the ratio of $^{15}\text{N}/^{14}\text{N}$ of the sample and standard (std). The isotopic standard for nitrogen is atmospheric air. We predicted that tropical forests would have higher ^{15}N values in relation to temperate forests; statistical differences were tested with a *t*-test for unequal variance.

Results and discussion

Tropical vs temperate systems

The average $\delta^{15}\text{N}$ value for tropical foliage was $3.7 \pm 3.5\text{‰}$ ($n = 73$), which is significantly greater ($p < 0.01$) than the temperate forest value of $-2.8 \pm 2.0\text{‰}$ ($n = 90$) [Table 1, Figure 1]. This 6.5‰ difference occurred despite the fact that trees from low-N montane and white-sand tropical sites were included in the analysis. If these are excluded, the average $\delta^{15}\text{N}$ value for tropical trees increases to $4.7 \pm 2.1\text{‰}$ ($n = 65$). The average concentration of nitrogen in leaves from tropical forests was $1.9 \pm 0.8\text{‰}$ ($n = 78$), which was not significantly different from the $1.6 \pm 0.5\text{‰}$ ($n = 28$) average value found for temperate forests. When data are grouped by site, there is a significant positive correlation between ^{15}N and N concentration ($p < 0.007$); sites with higher nitrogen concentration in their leaves tend to have higher ^{15}N values (Figure 2).

Tropical forest soils were also much more ^{15}N -enriched than temperate forest soils (Table 2, Figure 3a), with tropical ^{15}N values averaging almost 8‰ higher, both at the surface and at depth. Variation with depth followed the classical pattern discussed by Nadelhoffer and Fry (1988); the average ^{15}N value for depth samples was approximately 2‰ higher than for surface samples in both tropical and temperate forests (Figure 3a).

The comparison of nitrogen concentration of soil organic matter between tropical and temperate forests was difficult to make due to the small number of samples from temperate forest soils. With the available data, the average N concentration was smaller in the tropical soils than in the temperate forests for both surface and depth samples (Figure 3b).

The results clearly showed that the ^{15}N values of tree leaves and soil organic matter were significantly higher in tropical forests than in temperate forests. Therefore, the initial working hypothesis was confirmed, in that the results are consistent with tropical forests having a more open nitrogen cycle, with greater losses via fractionating pathways, suggesting that N is in relative excess in many moist tropical forests.

Table 1. $\delta^{15}\text{N}$ (‰) values of plant species. %N is the nitrogen concentration (%).

Species	Site	Region	Country	^{15}N	% N	Ref
<i>Metrosideros polymorpha</i>	Thurston	Hawaii	U.S.A.	-6.8	0.87	1
<i>Metrosideros polymorpha</i>	Olaa	Hawaii	U.S.A.	-4.9	1.12	1
<i>Metrosideros polymorpha</i>	Laupahoehoe	Hawaii	U.S.A.	+0.9	1.42	1
<i>Metrosideros polymorpha</i>	Kohala	Hawaii	U.S.A.	-2.2	1.14	1
<i>Metrosideros polymorpha</i>	Malokai	Hawaii	U.S.A.	-2.3	1.06	1
<i>Metrosideros polymorpha</i>	Kauai	Hawaii	U.S.A.	-0.5	0.86	1
<i>Cibotium glaucum</i>	Thurston	Hawaii	U.S.A.	-9.3	1.79	1
<i>Cibotium glaucum</i>	Olaa	Hawaii	U.S.A.	-6.0	1.53	1
<i>Cibotium glaucum</i>	Laupahoehoe	Hawaii	U.S.A.	+0.7	1.82	1
<i>Cibotium glaucum</i>	Kohala	Hawaii	U.S.A.	-3.7	1.79	1
<i>Cibotium glaucum</i>	Malokai	Hawaii	U.S.A.	-1.3	1.79	1
<i>Cibotium glaucum</i>	Kauai	Hawaii	U.S.A.	-1.3	1.47	1
<i>Amphirox latifolia</i>	Samuel	Rondônia	Brazil	+6.8	3.16	2
<i>Licania hispidula</i>	Samuel	Rondônia	Brazil	+5.7	1.15	2
<i>Maquira guianensis</i>	Samuel	Rondônia	Brazil	+6.4	1.06	2
<i>Naucleopsis sp</i>	Samuel	Rondônia	Brazil	+8.3	3.51	2
<i>Naucleopsis sp</i>	Samuel	Rondônia	Brazil	+6.5	0.85	2
<i>Neea sp</i>	Samuel	Rondônia	Brazil	+9.6	3.76	2
<i>Protium carnosum</i>	Samuel	Rondônia	Brazil	+5.7	0.98	2
<i>Protium sp</i>	Samuel	Rondônia	Brazil	+4.4	1.12	2
<i>Protium sp</i>	Samuel	Rondônia	Brazil	+5.7	1.10	2
<i>Tachigalia cavipes</i>	Samuel	Rondônia	Brazil	+7.4	3.02	2
Undetermined	Samuel	Rondônia	Brazil	+6.4	3.96	2
Undetermined	Samuel	Rondônia	Brazil	+6.3	1.04	2
Mixture	Faz. Nova Vida	Rondônia	Brazil	+8.0	1.43	2
<i>Rinorea racemosa</i>	Varzea	rio Amazonas	Brazil	+2.0	1.00	2
<i>Inga sp</i>	Varzea	rio Amazonas	Brazil	+1.2	2.22	2
<i>Oxandra polyantha</i>	Varzea	rio Amazonas	Brazil	+2.5	2.74	2
<i>Nectandra amazonum</i>	Varzea	rio Amazonas	Brazil	+3.7	2.76	2
<i>Leonia racemosa</i>	Varzea	rio Amazonas	Brazil	+4.7	2.80	2
Undetermined	Varzea	rio Amazonas	Brazil	+4.0	1.22	2
<i>Sacoglottis sp</i>	Varzea	rio Amazonas	Brazil	+1.8	1.22	2
<i>Ficus glabrata</i>	Varzea	rio Amazonas	Brazil	+1.3	1.77	2
<i>Tichila sp</i>	Varzea	rio Amazonas	Brazil	+1.2	0.29	2
<i>Laetia crynbulosa</i>	Varzea	rio Amazonas	Brazil	+2.4	2.76	2
Undetermined	Campina	Manaus	Brazil	-2.2	1.86	3
Undetermined	Campina	Manaus	Brazil	-0.2	2.49	3
Undetermined	Campina	Manaus	Brazil	+0.6	1.30	3
<i>G.thophilurum</i>	Campina	Manaus	Brazil	-7.0		4
Sapotaceae	Campina	Manaus	Brazil	-7.0		4
Lecitidaceae	R. Ducke	Manaus	Brazil	+5.8		4
<i>Virola surinasuensis</i>	R. Ducke	Manaus	Brazil	+5.9		4
<i>Carapa guianensis</i>	R. Ducke	Manaus	Brazil	+7.0		4
<i>Theobroma cacao</i>	R. Ducke	Manaus	Brazil	+6.2	1.32	5

Table 1. Continued.

Species	Site	Region	Country	^{15}N	% N	Ref
<i>Melastoma bellucia</i>	R. Ducke	Manaus	Brazil	+3.3	2.38	5
<i>Melastoma bellucia</i>	R. Ducke	Manaus	Brazil	+4.6	1.68	5
<i>Melastoma bellucia</i>	R. Ducke	Manaus	Brazil	+4.7	1.81	5
<i>Cecropia eucomona</i>	R. Ducke	Manaus	Brazil	+5.9	2.20	5
<i>Cecropia eucomona</i>	R. Ducke	Manaus	Brazil	+4.9	1.86	5
<i>Piper piperaceae</i>	R. Ducke	Manaus	Brazil	+4.6	2.58	5
<i>Aegiphula scandens</i>	R. Ducke	Manaus	Brazil	+5.6	3.09	5
<i>Rolinea exsucca</i>	R. Ducke	Manaus	Brazil	+2.0	1.48	5
<i>Verbenaceae</i>	R. Ducke	Manaus	Brazil	+6.0	2.12	5
<i>Alchornea schomburgkii</i>	R. Ducke	Manaus	Brazil	+1.7	2.10	5
Myrtaceae	Cerrado	Brasilia	Brazil	+1.8	0.94	6
Compositae	Cerrado	Brasilia	Brazil	+0.1	1.31	6
Rubiaceae	Cerrado	Brasilia	Brazil	-0.6	1.09	6
Melastomataceae	Cerrado	Brasilia	Brazil	+1.3	1.30	6
<i>Flacourtia rukam</i>	Toong-fax		Thailand	+4.5	1.70	5
<i>Anacardium occidentale</i>	Toong-fax		Thailand	+3.6	1.30	5
<i>Zizyplus mauritana</i>	Toong-fax		Thailand	+2.5	1.83	5
<i>Terminalia catappa</i>	Kwae		Thailand	+7.5	1.88	5
<i>Lansium domesticum</i>	Nakhon Pathom		Thailand	+6.0	2.18	5
<i>Ficus glaberrima</i>	Kwae		Thailand	+9.4	1.78	5
<i>Crataeva erythrocarpa</i>	Kwae		Thailand	+8.0	2.44	5
Kerangas scrub			Sarawak	-2.3		7
Kerangas scrub			Sarawak	-7.4		7
Kerangas forest			Sarawak	-2.4		7
Kerangas forest			Sarawak	-3.5		7
8 ECM species	Korup	Cameroon	Africa	+4.9	2.10	20
10 VAM species	Korup	Cameroon	Africa	+4.6	2.11	20
<i>Quercus kelloggii</i>	Mix Canyon	California	U.S.A.	+0.4		8
<i>Pinus sabiniana</i>	Mix Canyon	California	U.S.A.	+0.8		8
<i>Pinus contorta ssp.</i>	Grass Lake	California	U.S.A.	+0.2		8
<i>Pinus albicaulis</i>	Carson Pass-3	California	U.S.A.	-0.3		8
<i>Pinus contorta ssp.</i>	Carson Pass-4	California	U.S.A.	+0.4		8
<i>Tsuga mertensiana</i>	Carson Pass-5	California	U.S.A.	+1.0		8
<i>Abies concolor</i>	Rice canyon	California	U.S.A.	-0.8		8
<i>Pinus ponderosa</i>	Rice canyon	California	U.S.A.	-0.5		8
<i>Prunus emarginata</i>	Rice canyon	California	U.S.A.	-0.5		8
<i>Salix scouleriana</i>	Rice canyon	California	U.S.A.	-0.6		8
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.1	1.75	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.5	1.70	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.6	1.70	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.7	1.50	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.3	1.50	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.8	1.45	9

Table 1. Continued.

Species	Site	Region	Country	^{15}N	% N	Ref
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.8	1.50	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-4.0	1.45	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.9	1.40	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.9	1.40	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.9	1.20	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.4	1.48	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.8	1.52	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-3.9	1.54	9
<i>Picea abies</i>	Fichtelgebirge	Bavaria	Germany	-4.0	1.48	9
<i>Salix purpurea</i>	Col d'Ornon	Northern Alps	France	-3.8		10
<i>Betula verrucosa</i>	Col d'Ornon	Northern Alps	France	-6.0		10
<i>Salix purpurea</i>	Col d'Ornon	Northern Alps	France	-3.4		10
<i>Acer pseudoplatanus</i>	Col d'Ornon	Northern Alps	France	-4.3		10
<i>Acer pseudoplatanus</i>	Col d'Ornon	Northern Alps	France	-3.6		10
<i>Corylus avellana</i>	Col d'Ornon	Northern Alps	France	-4.4		10
<i>Fraxinus excelsior</i>	Col d'Ornon	Northern Alps	France	-3.8		10
<i>Abies alba</i>	Col d'Ornon	Northern Alps	France	-3.6		10
<i>Rubus sp</i>	Col d'Ornon	Northern Alps	France	-4.3		10
Spruce-fir	Great Smoky Mt.	Tennessee	U.S.A.	-2.2		11
Beech	Great Smoky Mt.	Tennessee	U.S.A.	-0.8		11
Cove hardwood	Great Smoky Mt.	Tennessee	U.S.A.	-1.9		11
Mixed hardwood	Great Smoky Mt.	Tennessee	U.S.A.	-1.9		11
Floodplain poplar	Great Smoky Mt.	Tennessee	U.S.A.	-2.4		11
Yellow poplar	Great Smoky Mt.	Tennessee	U.S.A.	-3.5		11
Pine	Great Smoky Mt.	Tennessee	U.S.A.	-1.7		11
Xeric oak	Great Smoky Mt.	Tennessee	U.S.A.	-1.8		11
<i>Picea glauca</i>	Dalton Highway	Alaska	U.S.A.	-6.2	0.97	12
<i>Picea mariana</i>	Dalton Highway	Alaska	U.S.A.	-10.1	0.91	12
<i>Acer rubrum</i>	Walker Branch	Tennessee	U.S.A.	-3.5		13
<i>Cornus florida</i>	Walker Branch	Tennessee	U.S.A.	-3.9		13
<i>Liliodendron tulipifera</i>	Walker Branch	Tennessee	U.S.A.	-3.4		13
<i>Acer rubrum</i>	Walker Branch	Tennessee	U.S.A.	-1.7		13
<i>Cornus florida</i>	Walker Branch	Tennessee	U.S.A.	-1.0		13
<i>Liliodendron tulipifera</i>	Walker Branch	Tennessee	U.S.A.	-2.4		13
<i>Fagus grandifolia</i>	Bear Brook	Maine	U.S.A.	-0.7	2.30	14
<i>Acer spp.</i>	Bear Brook	Maine	U.S.A.	-1.7	2.30	14
<i>Betula alleghaniensis</i>	Bear Brook	Maine	U.S.A.	-1.1	2.20	14
<i>Picea rubens</i>	Bear Brook	Maine	U.S.A.	-0.6	1.10	14
<i>Picea abis</i>	Southern Sweden	Sweden	Sweden	-2.2	1.30	15
<i>Juniperus communis</i>	Subsite 1&2	Scotland	Scotland	0.6	1.70	16
<i>Juniperus communis</i>	Subsite 3 (boggy)	Scotland	Scotland	-5.3	1.00	16
<i>Betula nana</i>		Northern Sweden	Sweden	-7.4	1.90	17
<i>Betula nana</i>		Northern Sweden	Sweden	-3.9	3.30	17
<i>Pinus sylvestris</i>		Northern Sweden	Sweden	-3.9		17

Table 1. Continued.

Species	Site	Region	Country	^{15}N	% N	Ref
<i>Picea abies</i>		Central Sweden	Sweden	-1.3		18
<i>Pseudotsuga menziesii</i>	Andrews	Oregon	U.S.A.	-3.2		19
<i>Acer rubrum</i>	Harvard Forest	Massachusetts	U.S.A.	-3.6		19
<i>Quercus rubra</i>	Harvard Forest	Massachusetts	U.S.A.	-2.7		19
<i>Tsuga canadensis</i>	Harvard Forest	New Hampshire	U.S.A.	-3.7		19
<i>Acer rubrum</i>	Harvard Forest	New Hampshire	U.S.A.	-5.9		19
<i>Pinus strobus</i>	Harvard Forest	New Hampshire	U.S.A.	-1.4		19
<i>Betula papyrifera</i>	Harvard Forest	New Hampshire	U.S.A.	-0.6		19
<i>Fagus grandifolia</i>	Harvard Forest	New Hampshire	U.S.A.	-1.2		19
<i>Prunus pensylvanica</i>	Harvard Forest	New Hampshire	U.S.A.	-0.4		19
<i>Betula lutea</i>	Harvard Forest	New Hampshire	U.S.A.	-2.7		19
<i>Pinus spp</i>	North Inlet	South Carolina	U.S.A.	-0.9		19
<i>Pinus resinosa</i>	North Lakes	Wisconsin	U.S.A.	-2.0		19
<i>Quercus rubra</i>	North Lakes	Wisconsin	U.S.A.	-3.0		19
<i>Betula papyrifera</i>	North Lakes	Wisconsin	U.S.A.	-2.5		19
<i>Picea glauca</i>	Bonanza creek	Alaska	U.S.A.	-3.3		19
<i>Populus tremuloides</i>	Bonanza creek	Alaska	U.S.A.	-1.4		19
<i>Fraxinus spp</i>	Cedar Creek	Minnesota	U.S.A.	-4.2		19
<i>Betula papyrifera</i>	Cedar Creek	Minnesota	U.S.A.	-4.0		19
<i>Acer rubrum</i>	Cedar Creek	Minnesota	U.S.A.	-5.2		19
<i>Quercus macrocarpa</i>	Cedar Creek	Minnesota	U.S.A.	-4.5		19
<i>Quercus rubra</i>	Cedar Creek	Minnesota	U.S.A.	-3.3		19
<i>Cornus florida</i>	Coweeta	North Carolina	U.S.A.	-1.8		19
<i>Acer rubrum</i>	Coweeta	North Carolina	U.S.A.	-5.2		19
<i>Liliodendron tulipifera</i>	Coweeta	North Carolina	U.S.A.	-5.3		19

1 – Vitousek PM (nonpublished data); 2 – Almeida S (1995); 3 – McClain M (nonpublished data); 4 – Salati et al. (1982) 5 – Yoneyama et al (1993); 6 – Sprent et al. (1996); 7 – Treseder K (nonpublished data); 8 – Virginia and Delwiche (1982); 9 – Gebauer and Schulze (1991); 10 – Domenach et al. (1989); 11 – Garten Jr and Miegroet (1994); 12 – Schulze et al. (1994); 13 – Garten Jr (1993); 14 – Adelhoffer et al. (1995); 15 – Nasholm et al. (1997); 16 – Hill et al. (1996); 17 – Michelsen et al. (1996); 18 – Hogberg et al. (1996); 19 – Fry (1991); 20 – Hogberg and Alexander (1995)

Nutrient rich vs nutrient poor systems in the tropics

Forests on white-sand soils in the tropics are considered to be nitrogen-poor systems (Vitousek & Sanford 1986; Cuevas & Medina 1988). Table 3 summarizes the elemental composition of leaves in contrasting vegetation types in the Amazon. Higher N concentrations were found in Varzea forest, followed by Terra-firme forests in Samuel and Manaus. The same trend was also found by Furch and Klinge (1989). As expected, the lowest concentrations were in the Campina forests. Following our initial hypothesis,

Table 2. ^{15}N values (‰) for soil samples. Z is the soil depth (cm), %N is the nitrogen concentration (%) and Re stands for references.

Country	Region	Soil type	z	^{15}N	%N	Re
Brazil	Pará	Yellow latosol (Hapludox)	0-5	+9.8	0.26	1
Brazil	Pará	Yellow latosol (Hapludox)	5-10	+10.8	0.17	1
Brazil	Pará	Yellow latosol (Hapludox)	10-20	+12.0	0.11	1
Brazil	Pará	Yellow latosol (Hapludox)	20-30	+12.5	0.09	1
Brazil	Pará	Yellow latosol (Hapludox)	30-40	+12.6	0.07	1
Brazil	Pará	Yellow latosol (Hapludox)	40-50	+13.2	0.05	1
Brazil	Pará	Yellow latosol (Hapludox)	50-60	+12.8	0.04	1
Brazil	Pará	Yellow latosol (Hapludox)	60-70	+12.9	0.03	1
Brazil	Pará	Yellow latosol (Hapludox)	100-110	+12.4	0.02	1
Brazil	Pará	Yellow latosol (Hapludox)	140-150	+11.9	0.01	1
Brazil	Pará	Yellow latosol (Hapludox)	0-5	+8.4	0.13	1
Brazil	Pará	Yellow latosol (Hapludox)	5-10	+9.2	0.05	1
Brazil	Pará	Yellow latosol (Hapludox)	10-20	+9.4	0.04	1
Brazil	Pará	Yellow latosol (Hapludox)	20-30	+9.9	0.02	1
Brazil	Pará	Yellow latosol (Hapludox)	30-40	+9.8	0.01	1
Brazil	Pará	Yellow latosol (Hapludox)	40-50	+9.3	0.01	1
Brazil	Pará	Yellow latosol (Hapludox)	50-60	+9.3	0.00	1
Brazil	Pará	Yellow latosol (Hapludox)	60-70	+8.5	0.01	1
Brazil	Pará	Yellow latosol (Hapludox)	80-90	+9.8	0.00	1
Brazil	Pará	Yellow latosol (Hapludox)	120-130	+8.6	0.00	1
Brazil	Amazonas	Yellow latosol (Hapludox)	0-3	+7.7	0.38	1
Brazil	Amazonas	Yellow latosol (Hapludox)	3-12	+9.8	0.19	1
Brazil	Amazonas	Yellow latosol (Hapludox)	12-36	+11.9	0.09	1
Brazil	Amazonas	Yellow latosol (Hapludox)	36-51	+14.9	0.02	1
Brazil	Amazonas	Yellow latosol (Hapludox)	51-80	+15.6	0.01	1
Brazil	Amazonas	Yellow latosol (Hapludox)	80-140	+20.0	0.00	1
Brazil	Amazonas	Yellow latosol (Hapludox)	140	+21.7	0.00	1
Brazil	Rondônia	Red-yellow latosol (Hapludox)	0-5	+9.8	0.24	1
Brazil	Rondônia	Red-yellow latosol (Hapludox)	5-10	+10.1	0.22	1
Brazil	Rondônia	Red-yellow latosol (Hapludox)	10-20	+10.5	0.16	1
Brazil	Rondônia	Red-yellow latosol (Hapludox)	20-30	+10.8	0.13	1
Brazil	Rondônia	Red-yellow podzolic latosol (Kandiudult)	0-5	+8.6	0.18	1
Brazil	Rondônia	Red-yellow podzolic latosol (Kandiudult)	5-10	+9.2	0.14	1
Brazil	Rondônia	Red-yellow podzolic latosol (Kandiudult)	10-20	+9.9	0.08	1
Brazil	Rondônia	Red-yellow podzolic latosol (Kandiudult)	20-30	+10.3	0.08	1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	0-5	+10.7	0.21	1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	5-10	+11.4	0.14	1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	10-20	+11.9	0.11	1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	20-30	+11.9	0.09	1
Brazil	Rondônia	Yellow latosol (Hapludox)	0-5	+9.3	0.28	1
Brazil	Rondônia	Yellow latosol (Hapludox)	5-10	+9.8	0.19	1
Brazil	Rondônia	Yellow latosol (Hapludox)	10-20	+11.3	0.12	1

Table 2. Continued.

Country	Region	Soil type	z	¹⁵ N	%N	Re
Brazil	Rondônia	Yellow latosol (Hapludox)	20–30	+11.7	0.08	1
Brazil	Rondônia	Yellow latosol (Hapludox)	0–5	+6.4	0.09	1
Brazil	Rondônia	Yellow latosol (Hapludox)	5–10	+7.6	0.07	1
Brazil	Rondônia	Yellow latosol (Hapludox)	10–20	+9.2	0.05	1
Brazil	Rondônia	Yellow latosol (Hapludox)	20–30	+10.6	0.04	1
Brazil	Rondônia	Red yellow podzolic latosol (Kandiudult)	0–5	+11.2	0.12	1
Brazil	Rondônia	Red yellow podzolic latosol (Kandiudult)	5–10	+12.2	0.10	1
Brazil	Rondônia	Red yellow podzolic latosol (Kandiudult)	10–20	+13.3	0.06	1
Brazil	Rondônia	Red yellow podzolic latosol (Kandiudult)	20–30	+13.6	0.04	1
Brazil	Rondônia	Red yellow podzolic latosol (Kandiudult)	30–40	+13.1	0.04	1
Brazil	Rondônia	Red yellow podzolic latosol (Kandiudult)	40–50	+12.9	0.04	1
Brazil	Rondônia	Red yellow podzolic latosol (Kandiudult)	80–90	+12.4	0.06	1
Brazil	Rondônia	Red yellow podzolic latosol (Kandiudult)	120–130	+12.7	0.04	1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	0–10	+10.5	0.07	1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	10–20	+11.7	0.04	1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	20–30	+11.9	0.02	1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	30–40	+12.1	0.02	1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	40–50	+12.2	0.01	1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	70–80	+11.4		1
Brazil	Rondônia	Red-yellow podzolic (Paleudult)	90–100	+9.8		1
Brazil	Pará	Xanthic Ferralsols		+10.3		2
Brazil	Amazonas	Xanthic Ferralsols		+7.4		2
Brazil	Paraná	Rhodic Ferralsols	0–10	+10.9		2
U.S.A.	Hawaii	Volcanic tephra	Surface	-2.2		3
U.S.A.	Hawaii	Volcanic tephra	Surface	-2.0		3
U.S.A.	Hawaii	Volcanic tephra	Surface	+1.4		3
U.S.A.	Hawaii	Volcanic tephra	Surface	-1.0		3
U.S.A.	Hawaii	Volcanic tephra	Surface	-0.8		3
U.S.A.	Hawaii	Volcanic tephra	Surface	+0.2		3
U.S.A.	Hawaii	Volcanic tephra	30–40	+1.4		3
U.S.A.	Hawaii	Volcanic tephra	30–40	-0.4		3
U.S.A.	Hawaii	Volcanic tephra	30–40	+6.2		3
U.S.A.	Hawaii	Volcanic tephra	30–40	+4.7		3
U.S.A.	Hawaii	Volcanic tephra	30–40	+4.6		3
U.S.A.	Hawaii	Volcanic tephra	30–40	+5.1		3
Thailand	Chachoengsao	Gray podzolic	0–15	+7.7	0.02	4
Thailand	Chantaburi	Red yellow podzolic	0–30	+7.1	0.03	4
Thailand	Rayong	Red yellow podzolic	0–10	+8.4	0.06	4
Thailand	Chantaburi	Regosols		+3.7	0.04	4
Thailand	Chainat	Gray lowland	0–10	+9.5	0.08	4
U.S.A.	Wisconsin	Typic Hapludalfs	0–10	+2.6	0.25	5
U.S.A.	Wisconsin	Typic Hapludalfs	10–20	+5.3	0.08	5
U.S.A.	Maine	Caribou	0–11.4	+4.9		6
U.S.A.	Maine	Caribou	11.4–12.7	+8.5		6

Table 2. Continued.

Country	Region	Soil type	z	¹⁵ N	%N	Re
U.S.A.	Maine	Caribou	12.7–20.3	+8.3		6
U.S.A.	Maine	Caribou	20.3–33.0	+8.0		6
U.S.A.	Maine	Caribou	33.0–43.2	+5.7		6
U.S.A.	Maine	Caribou	43.2–55.9	+3.7		6
U.S.A.	Maine	Caribou	55.9–101	+3.0		6
U.S.A.	New Hampshire			+9.6		7
U.S.A.	Central Illinois	Drummer silty clay loam		+10.4		7
U.S.A.	Oregon		0–60	+2.1		8
U.S.A.	Oregon		0–60	+2.5		8
Japan	Tokyo	Podzol	0–90	+5.0		9
Japan	Nagano	Brown Forest	0–90	+5.0		9
Belgium	Ardennes	Acid Brown	0–1	–3.9		10
Belgium	Ardennes	Acid Brown	1–4	–0.7		10
Belgium	Ardennes	Acid Brown	4–22	+0.7		10
Belgium	Ardennes	Acid Brown	22–43	+2.1		10
Belgium	Ardennes	Acid Brown	43–70	+2.6		10
Belgium	Ardennes	Acid Brown	70–100	+1.0		10
Belgium	Ardennes	Acid Brown	0–1.5	–5.1		10
Belgium	Ardennes	Acid Brown	1.5–10.5	–0.3		10
Belgium	Ardennes	Acid Brown	10–25	–0.1		10
Belgium	Ardennes	Acid Brown	25–51	+1.3		10
Belgium	Ardennes	Acid Brown	51–80	+3.6		10
Belgium	Ardennes	Acid Brown	80–110	+1.0		10
France	Northern Alps	Ochreous podzolic	0–1	–4.0	1.57	11
France	Northern Alps	Ochreous podzolic	2–6	–2.8	1.39	11
France	Northern Alps	Ochreous podzolic	6–11	+0.3	1.21	11
France	Northern Alps	Ochreous podzolic	11–12	+2.8	0.84	11
France	Northern Alps	Ochreous podzolic	12–14	+4.7	0.20	11
France	Northern Alps	Ochreous podzolic	14–35	+5.1	0.17	11
France	Northern Alps	Ochreous podzolic	80	+5.0	0.21	11
U.S.A.	Tennessee			+3.6		12
U.S.A.	Tennessee			+5.4		12
U.S.A.	Tennessee			+3.9		12
U.S.A.	Tennessee			+4.8		12
U.S.A.	Tennessee			+5.1		12
U.S.A.	Tennessee			+4.3		12
U.S.A.	Tennessee			+5.5		12
U.S.A.	Tennessee			+5.3		12
U.S.A.	Tennessee			–2.4		13
U.S.A.	Tennessee			–1.0		13
U.S.A.	Maine			+2.3		14
Germany	Bavaria		Olf	–3.5		15
Germany	Bavaria		Oh	+0.1		15
Germany	Bavaria		A0-5	+2.9		15

Table 2. Continued.

Country	Region	Soil type	z	^{15}N	%N	Re
Germany	Bavaria		A5-15	+4.0		15
Sweden	Southern Sweden		Oh	-1.1		16
Sweden	Northern Sweden			-0.7		17
Sweden	Northern Sweden			+0.5		17
Sweden	Northern Sweden		Oi	-2.0		18
Sweden	Northern Sweden		Oa	-0.4		18
Sweden	Northern Sweden		Oe	+1.1		18
Sweden	Northern Sweden		A0-5	+5.0		18
U.S.A.	Massachusetts		F	+0.4		19
U.S.A.	Massachusetts		H	+4.0		19
U.S.A.	Massachusetts		10-15	+6.3		19
U.S.A.	Minnesota		Oa/A	-1.3		19
U.S.A.	Minnesota		20-25	+5.3		19

1 – Piccolo et al. (1996); 2 – Yoneyama et al. (1993) 3 – Vitousek et al. (1989); Vitousek PM (nonpublished data); 4 – Yoneyama et al. (1990); 5 – Nadelhoffer KJ and Fry B (1988); 6 – Shearer et al. (1978); 7 – Shearer et al. (1974); 8 – Binkley et al. (1992); 9 – Wada et al. (1984); 10 – Riga et al. (1971); 11 – Mariotti et al. (1980); 12 – Garten Jr & Miagroet (1994); 13 – Garten Jr CT (1993); 14 – Nadelhoffer et al. (1995); 15 – Gebauer and Schulze (1991); 16 – Nasholm et al. (1997); 17 – Michelsen et al. (1996); 18 – Hogberg et al. (1996); 19 – Fry (1991).

we expected that in forests on white sand soils, such as the Campina site, $\delta^{15}\text{N}$ values would be lower than those from the relatively N-rich Terra-firme and Varzea forests. Indeed, the only negative $\delta^{15}\text{N}$ values among all lowland tropical forests occurred in the two white sand sites: the Brazilian Campina and the Kerangas site in Sarawak. The average value of these sites was significantly lower ($P < 0.001$) than for any of the other tropical forests types we surveyed.

Within the Terra-firme forests, the site which had higher elemental concentrations in leaves (Samuel) also showed an average $\delta^{15}\text{N}$ value significantly higher ($P < 0.001$) than the Terra-firme forest at Reserva Ducke in Manaus (Table 3). In contrast, the Varzea forest had the highest elemental concentration in leaves, but a significantly lower $\delta^{15}\text{N}$ in relation to the two Terra-firme forests. Isotopic values for surface soil samples (0–10 cm) were also significantly lower in Varzea ($^{15}\text{N} = +4.1 \pm 0.5\%$, $n = 17$) than in Terra-firme ($\delta^{15}\text{N} = +9.21.5\%$, $n = 10$) sites. One possible cause for the lower $\delta^{15}\text{N}$ values in the Varzea is the very high rate of nitrogen fixation by legumes (and probably by Paspalum grasses) that occurs in this system (Martinelli et al. 1992); fixed N has a $\delta^{15}\text{N}$ value close to zero. In addition, Varzea soils are formed and renewed each year by sediments brought by the white-water rivers

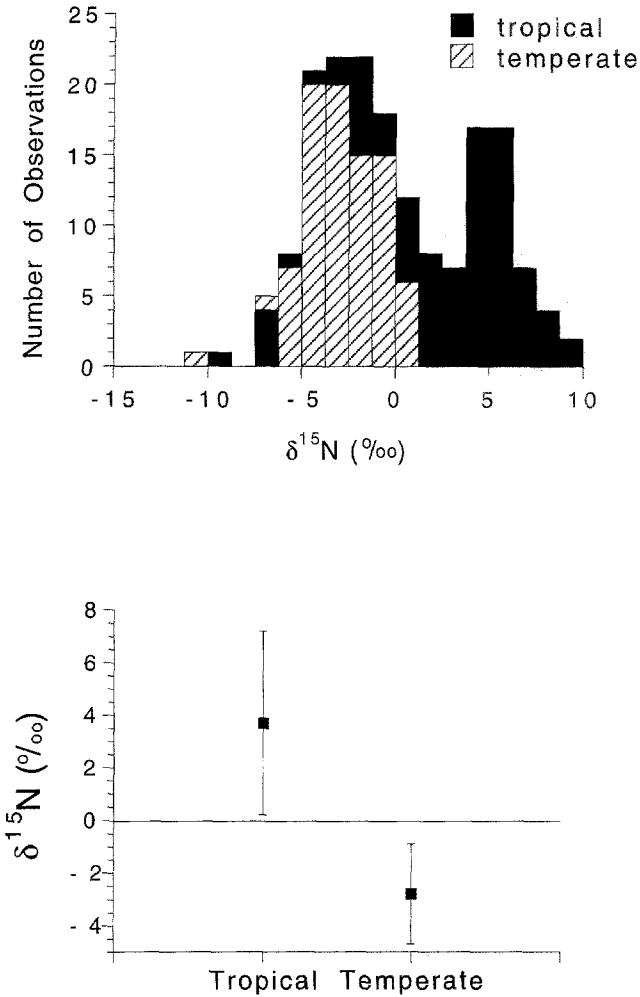


Figure 1. Histogram of $\delta^{15}\text{N}$ (‰) for tree leaves collected in tropical and temperate forests. Solid bars are tropical sites and hatched bars are temperate sites. (b) Plot of $\delta^{15}\text{N}$ (‰) for tree leaves collected in tropical and temperate forests. Error bars represent one standard-deviation.

of the Amazon, and therefore substrate age differences between Varzea and Terra-firme sites may also contribute to the differences in ^{15}N . It is possible that the Varzea site has not been in place long enough for ^{15}N enrichment to occur to the same extent as in Terra-firme. This age effect is discussed in the next section.

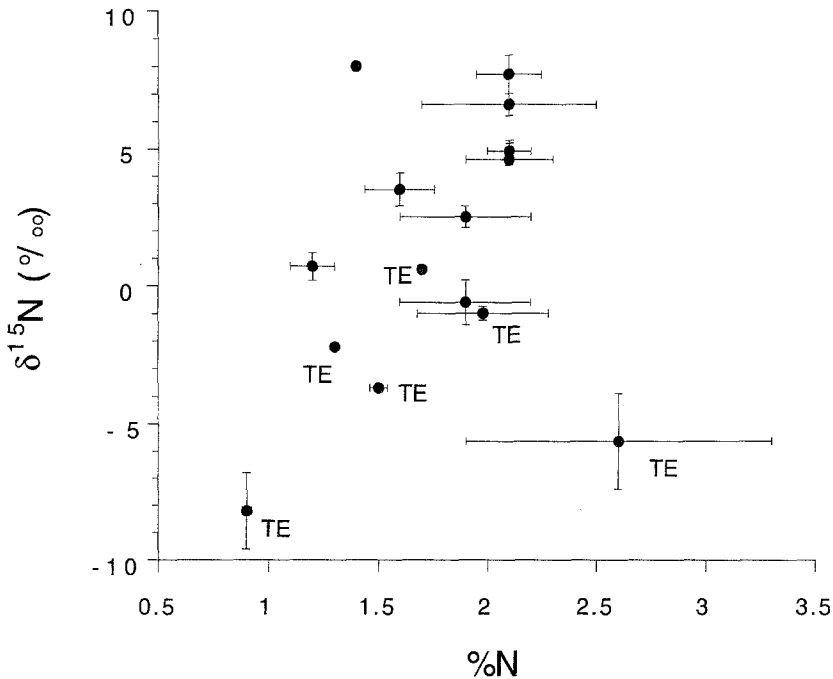


Figure 2. Relationship between average $\delta^{15}\text{N}$ values (‰) and average nitrogen concentration (%) of foliar samples. Temperate sites are labeled “TE”, the unlabeled points are tropical sites. Bars are standard errors.

The Hawaii substrate age gradient and $\delta^{15}\text{N}$ of plants and soils

We used a developmental sequence of montane forests in the Hawaiian Islands to evaluate how losses of N by fractionating pathways could shape

Table 3. Average $\delta^{15}\text{N}$ value (‰) and average elemental composition of leaves (%) from distinct forest types in the Amazon Basin and averaged $\delta^{15}\text{N}$ (‰) of Kerangas site in Sarawak.

Vegetation	$\delta^{15}\text{N}$	N	P	K	Ca	Mg
Varzea ¹	+2.5	2.19	0.19	1.23	1.34	0.36
Terra-Firme ²	+6.7	1.90	0.08	0.77	0.77	0.33
Terra-Firme ³	+4.5	1.84	0.05	0.43	0.43	0.29
Campina ⁴	-3.2	1.11	0.05	0.37	0.37	0.26

¹ Inundation forest – Senna (1996); ² Terra-firme forest at Samuel, Rondônia – Almeida (1995); ³ Terra-firme forest at Manaus – Klinge et al. (1984); ⁴ White-sand soil forest (campina) near Manaus – Klinge et al. (1984).

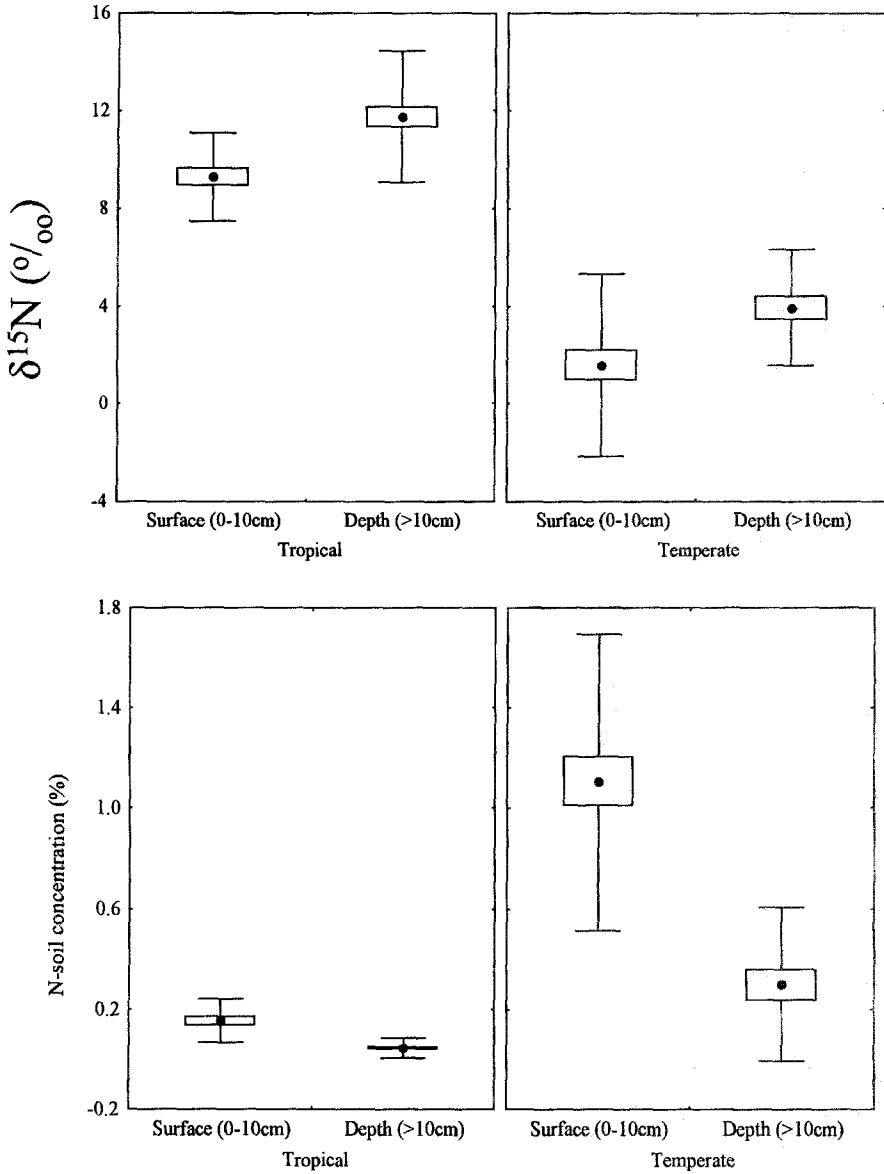


Figure 3. Box-whisker plot of (a) $\delta^{15}\text{N}$ (‰) and (b) nitrogen concentration (systems). The circles are average values, boxes are standard-errors, and bars represent one standard-deviation.

^{15}N values in forest ecosystems over time. The Hawaiian Islands result from the movement of the Pacific tectonic plate over a stationary convective plume or “hot-spot” in Earth’s mantle. The hot-spot is now located under the active volcanoes at the southeast edge of the Hawaiian chain; the age of the islands increases progressively to the northwest.

Six sites with substrate ages of 300, 2100, 20,000, 150,000, 1.4 million, and 4.1 million years, located across the Islands, have been used in several soil and biogeochemical studies (Crews et al. 1995; Vitousek et al. 1997). All of the sites have basaltic parent material, are on constructional shield volcanic surfaces, at 1200 m elevation, and with 2500 mm annual precipitation. All are dominated by the native myrtaceous tree *Metrosideros polymorpha*; none have been cleared by humans. No symbiotic N fixers are important components of any site. Fertilization studies show that productivity in the youngest sites is profoundly limited by low levels of N availability (Vitousek et al. 1993); N concentrations in plant tissues, inorganic N pools, rates of soil N transformations, and gaseous losses of N are also low in these sites (Riley & Vitousek 1995; Vitousek et al. 1995). By 20,000 years, more N has accumulated and N alone no longer limits production (Vitousek & Farrington 1997). Nitrogen concentration, transformations, and trace gas losses are all much greater than in the younger sites (Vitousek et al. 1995; Crews et al. 1995). Finally, plant production in the oldest site is limited by P (Herbert & Fownes 1995), while rates of N transformations and gaseous losses remain high (Riley & Vitousek 1995). We anticipated that if losses of N by fractionating pathways drive ^{15}N enrichment, then the youngest sites should have the lowest $\delta^{15}\text{N}$; they should be accumulating N from the atmosphere, with little N loss. As nitrification and losses of nitrate through leaching and/or denitrification increase through soil and ecosystem development, $\delta^{15}\text{N}$ in the systems as a whole should become enriched.

We measured $\delta^{15}\text{N}$ in the foliage of the dominant tree *Metrosideros polymorpha*, in the subcanopy tree fern *Cibotium glaucum*, and in surface and subsurface soils across the developmental sequence. In plants, we found the expected pattern of strongly depleted ^{15}N (to levels comparable to those in many temperate forests) in the youngest sites. Foliar $\delta^{15}\text{N}$ was enriched by 8–10‰ by the 20,000 year-old site, where foliar N concentrations and several other measures of N transformation and loss peaked. Thereafter, $\delta^{15}\text{N}$ became 1–3‰ more depleted, never approaching the very low levels observed in the youngest sites (Figure 4). $\delta^{15}\text{N}$ values in soils yielded a similar pattern, although variation in soils across the sequence was less than that in plants. All soils were enriched relative to plants, and enriched at depth relative to the surface (Figure 4).

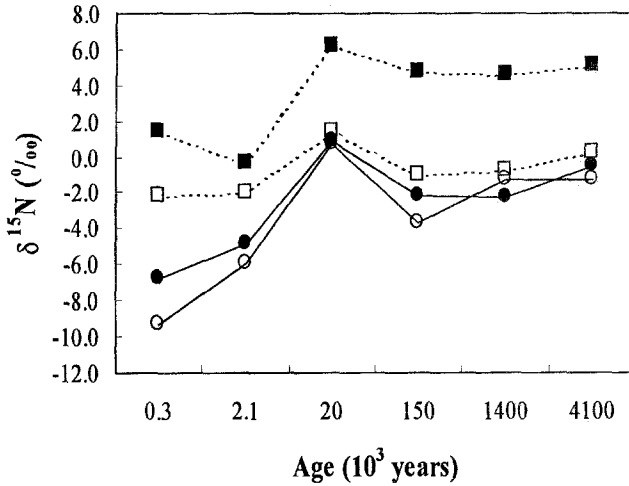


Figure 4. $\delta^{15}\text{N}$ (‰) variation for surface (open squares) and deeper (filled squares) soil samples, and for leaves of *Metrosideros polymorpha* (open circles) and *Cibotium glaucum* (filled circles) along a gradient of substrate age in Hawaii.

Overall, the observed pattern is consistent with the hypothesis that N losses by fractionating pathways cause plant and soil $\delta^{15}\text{N}$ to become relatively enriched in sites where N supply is less- or nonlimiting to biological processes. In contrast, plant and soil ^{15}N is relatively depleted in N-limited areas.

^{15}N enrichment with soil depth

A common feature in soil profiles is ^{15}N enrichment with soil depth. In order to compare different soil profiles, we defined the value $\Delta^{15}\text{N}$ as the difference between the $\delta^{15}\text{N}$ values of a soil depth and the $\delta^{15}\text{N}$ values of the soil surface. Table 4 summarizes the largest $\Delta^{15}\text{N}$ values found for soil profiles in tropical and temperate regions. In the tropical region, with the notable exception of the Manaus site, the $\Delta^{15}\text{N}$ values varied from 1.1 to 4.2‰, averaging 2.2 ± 1.0 ‰ ($n = 9$). When the $\Delta^{15}\text{N}$ value of the Manaus site is included (14‰), the average enrichment increases to 3.3 ± 3.9 ‰ ($n = 10$). In the temperate sites, $\Delta^{15}\text{N}$ values varied from 2.7 to 9.1‰ with an average of 6.4 ± 2.4 ‰ ($n = 7$). These differ significantly at the 0.2‰ level, if the Manaus site is excluded. With the Manaus value included, the $\Delta^{15}\text{N}$ is still marginally higher in the temperate zone ($p = 0.06$). The causes for ^{15}N enrichment with depth are relatively well known (Wada et al. 1984; Nadelhoffer & Fry 1988; Piccolo et al. 1994; Piccolo et al. 1996). More intriguing is the different behavior for soil profiles in the tropics versus temperate zones. Even among tropical soils,

Table 4. Isotopic enrichment with soil depth ($\Delta^{15}\text{N}$) for tropical and temperate regions. Depth of largest $\Delta^{15}\text{N}$ is the soil depth where the maximum isotopic enrichment occurred and Maximum depth is the deepest soil layer sampled.

Region	Site	Depth of largest $\Delta^{15}\text{N}$ (cm)	Maximum depth (cm)	$\Delta^{15}\text{N}^*$ (‰)
Tropical	Agua Parada	40–50	150	3.4
	Piqui	20–30	130	1.5
	Manaus	140	140	14.0
	Porto Velho	20–30	30	1.1
	Jamari	20–30	30	1.8
	Cacaulandia	20–30	30	1.2
	Vilhena-1	20–30	30	2.5
	Vilhena-2	20–30	30	4.2
	Nova Vida	20–30	130	2.4
	Benjamin	30–40	100	1.6
Temperate	Presque Isle	11–12	100	3.6
	Saint-Hubert	43–70	100	6.6
	Willerzie	51–80	110	8.6
	Chablais	14–35	80	9.1
	Bavaria	Horizon A (5–15 cm)	Horizon Oh	7.5
	Northern Sweden	Horizon A (0–5 cm)	Horizon A	7.0
	Madison	10–20	20	2.7

* $\Delta^{15}\text{N}$ is defined as $\delta^{15}\text{N}$ of depth i – $\delta^{15}\text{N}$ of surface .

the reason for the large $\Delta^{15}\text{N}$ value found in the Manaus profile is unclear; Piccolo et al. (1996) suggested that the very short dry season in the Manaus region makes losses of N higher in relation to other sites in the Amazon, where the dry season is more prolonged. However, the same explanation is unlikely when comparing tropical and temperate soils, since losses of nitrogen appear to be higher in tropical sites (Matson & Vitousek 1990; Keller et al. 1993; Neill et al. 1995). An alternative explanation could be based upon the effects of a higher cation exchange capacity and longer residence time of nitrogen in temperate soils. Higher exchange cation capacity would enhance the capability of the exchange complex to discriminate against ^{14}N , which would be preferentially lost from the profile, though the few measurements that exist suggest that ion exchange isotope effects may be minimal (B. Fry, pers. comm.). Finally, the observed differences between temperate and tropical soil profiles may be partly a function of soil age.

Conclusions

The $\delta^{15}\text{N}$ values of plants and soils are readily measured, but not always readily interpreted. We hypothesized that if N functions as an excess nutrient in many lowland tropical forests, then losses of N by fractionating pathways would cause $\delta^{15}\text{N}$ to become enriched in those forests. The results of our survey confirm this prediction: tropical forests in general are ^{15}N -enriched compared to temperate forests, and tropical forests in which N is abundant are ^{15}N -enriched compared to tropical forests in which N appears to be limiting. These ^{15}N results do not establish unequivocally that N is in excess in tropical forests; mechanisms other than N loss by fractionating pathways could cause part of the observed signal. For example, if N fixation is relatively more important than atmospheric deposition in tropical forests, that could account for part – although not all – of the observed difference. However, the pattern of ^{15}N enrichment in tropical forests does provide an additional, time integrated line of evidence supporting the conclusion that many tropical forests are N-rich and have open N cycles in comparison to most temperate forests.

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