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Partitioning of inorganic nitrogen assimilation between the roots and shoots of cerrado and forest trees of contrasting plant communities of South East Brasil

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Summary. Woody plants growing in cerrado and forest communities of south-east Brasil were found to have low levels of nitrate reductase activity in their leaves suggesting that nitrate ions are not an important nitrogen source in these communities. Only in the leaves of species growing in areas of disturbance, such as gaps and forest margins, were high levels of nitrate reductase present. When pot-grown plants were supplied with nitrate, leaves and roots of almost all species responded by inducing increased levels of nitrate reductase. Pioneer or colonizing species exhibited highest levels of nitrate reductase and high shoot: root nitrate reductase activities. Glutamine synthetase, glutamate synthase and glutamate dehydrogenase were present in leaves and roots of the species examined. ^{15}N-labelled nitrate and ammonium were used to compare the assimilatory characteristics of two species: *Enterolobium contortisiliquum,* with a high capacity to reduce nitrate, and *Calophyllum brasiliense,* of low capacity. The rate of nitrate assimilation in the former was five times that of the latter. Both species had similar rates of ammonium assimilation. Results for eight species of contrasting habitats showed that leaf nitrogen content increased in parallel with xylem sap nitrogen concentrations, suggesting that the ability of the root system to acquire, assimilate or export nitrate determines shoot nitrogen status. These results emphasise the importance of nitrogen transport and metabolism in roots as determinants of whole plant nitrogen status.

Key words: Cerrado – Rainforest – Root nitrate assimilation – Ammonia assimilation – Nitrate reductase

Much emphasis has been placed on the role of the shoot system, and in particular the chloroplast, in the nitrogen metabolism of higher plants (Wallsgrove et al. 1983; Oaks 1992). In the majority of species studied leaves are the main site of nitrate reduction (Pate and Layzell 1990), and most subsequent reactions of ammonium assimilation (Lea et al. 1990) and amino acid biosynthesis are located in chloroplasts (Bryan 1990). However almost all the plant species on which these generalisations are based are short-lived herbaceous species, mostly annual crop plants. Andrews (1986) has suggested that temperate perennial species are predominantly root nitrate assimilators whereas tropical perennial species are predominantly leaf assimilators. However in studies of inorganic nitrogen assimilation by Australian rainforest (Stewart et al. 1988) and open-forest plants (Stewart et al. 1990) it was found that while pioneer or colonizing tree species did exhibit a large capacity to assimilate nitrate ions in their leaves, leaves of under- and over storey species had low levels of nitrate reductase and showed little capacity to utilize nitrate even when nitrate ions were readily available. A comparative study of six rainforest species of *Piper* showed that while gap species had higher levels of and a greater capacity to induce nitrate reductase than those of shade, none of them had any marked capacity to reduce nitrate in their roots (Fredeen et al. 1991). Leaf nitrate reductase activity was however strongly correlated with average daily photosynthetically active photon flux rather than soil nitrate availability.

Differences are also reported between rainforest species with respect to the relative activities of chloroplastic and cytosolic isoforms of the main ammonium assimilatory enzyme, glutamine synthetase (Stewart et al. 1988). Typically pioneer species had a large part of total leaf glutamine synthetase present in their chloroplasts while in leaves of understorey and overstorey species the cytosolic isoform predominated.

Pioneer or colonising trees appear then to resemble annual crop plants with respect to the predominance of the shoot system in inorganic nitrogen assimilation, while climax species appear more reliant on their root system for inorganic nitrogen assimilation.

In this paper the localisation of nitrate reduction in woody plants from contrasting cerrado and forest communities in south-east Brasil is examined and the assimilation of nitrate and ammonium ions are compared in

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species whose roots have different capacities to reduce nitrate ions.

Materials and methods

Sampling sites

The samples in this study were collected from the following communities in Sao Paulo State, Brasil.

1. Serra do Japi, Jundiai, (23°11′ S, 46°52′ W, 1,200 m) an upland, semi-deciduous forest of thin, low (7–8 m) densely distributed trees, with a subtropical climate with a dry winter and wet summer. There is a dry season between May and September. The soil is shallow, of low pH (4.4-4.7), oligotrophic, with a thick layer of organic material (5% carbon). The floristic composition has been described by Rodriques et al. (1989).
2. Santa Genebra, Campinas, (22°49′ S, 47°06′, altitude 669 m) a semi-deciduous rain forest with a tropical climate with a dry winter and wet summer. There is a marked dry season from May to September. The soil is acid (pH 5–5.5), oligotrophic with a surface layer of organic matter (2% carbon) The trees are high (18–22 m), with thick trunks and a relatively open canopy.
3. Mata Atlantica, Ubatuba, (23°25′ S, 45°25′04′ W, 780 m) an atlantic evergreen forest with a wet tropical climate with rains distributed throughout the year. The soil is acid (pH 4–4.5), oligotrophic with a thick layer of organic matter on the top (6.7% carbon). The trees are high (22–28 m), and all trunks are covered in epiphytes. Light penetration is good. The floristic composition of this kind of forest is described by Silva and Leitao Filho (1982).
4. Brotas, (22°15′ S, 48°07′ W, 640 m) a gallery forest with a tropical climate with a wet summer and dry winter. Although there is a marked dry season (May-September) there is no strong water deficiency due to the high water table. The soil is acid (pH 4.5–5), oligotrophic with a thin layer of organic matter at the surface (1% carbon). The trees are high (18–22 m) and light penetration is good. The floristic composition of this type of forest is described by Gibbs and Leitao Filho (1978).
5. Fazenda Campininha, Mogi Guacu, (22°11–18′ S, 47°7–10′ W,), cerrado (dense scrub of shrub-trees) and campo cerrado (open scrub), with a pronounced dry season (July-August). The soils are acid (pH 4.5–5), oligotrophic and have a high aluminium content. A detailed account of these sites is given in Gibbs et al. (1983).

Sunlit, mature leafy branches were collected from species common in the margins and gaps and overstorey of the plant communities listed above; leaves of understorey species were collected from mature branches.

Nitrate reductase (EC 1.6.6.1) activity was estimated by *in vivo* assay (Stewart et al. 1986). All field sampling was carried out in February–March. Assays for leaf enzyme were performed in triplicate using 0.25–0.5 g fresh material of fully expanded leaves. Root assays used 0.5–1.0 g fresh material, each determination being based on three replicate assays per species. Wherever practical only the finer lateral roots were used. In pot experiments with saplings, plants were grown under glasshouse or screenhouse conditions, from seed in either forest soil or sand, the latter being watered at regular intervals with 1/10th strength Long Ashton medium.

Glutamine synthetase (EC 1.6.3.2) and glutamate synthase (EC 1.4.1.13) were extracted and assayed as described by Stewart et al. (1988) and Rhodes et al. (1975). Separation of the isoforms of glutamine synthetase by ion-exchange chromatography was as described in Stewart et al. (1986). Immunoprecipitation studies were performed as described by Hirel et al. (1984), using rabbit anti-GSIgG raised against purified barley cytosolic and tobacco chloroplastic glutamine synthetase.

Labelling studies

Saplings growing in sand culture were watered with nutrient solution containing 2.5 mM [^{15}N] $(NH_4)_2SO_4$ or 5 mM [^{15}N]KNO_3 (99% ^{15}N), harvested after 48 h and divided into roots and leaves of different ages. Free amino acids were extracted and analyzed as their N-heptafluorobutrylisobutyl esters and their ^{15}N abundance was determined by combined gas chromatography-mass spectrometry (Rhodes et al. 1981). Xylem sap was collected from decapitated shoot systems. Amino acids were determined as above and nitrate, as nitrite following reduction with cadmium. The data shown represent pooled results for a minimum of three individual plants.

Results

Occurrence of nitrate reduction in natural habitats

Nitrate reductase activities of species growing in mature, undisturbed forest were low at all sites examined (Fig. 1). In upland forest, gallery forest and evergreen rain forest sites 80–85% of species had activities less than 50 pkat g^{-1} fresh weight (fw). Activities in plants of cerrado were somewhat higher, but even in these sites over 40% of species sampled had activities lower than 50 pkat g^{-1}. No differences were found in levels of nitrate reductase present in leaves of overstorey and understorey species.

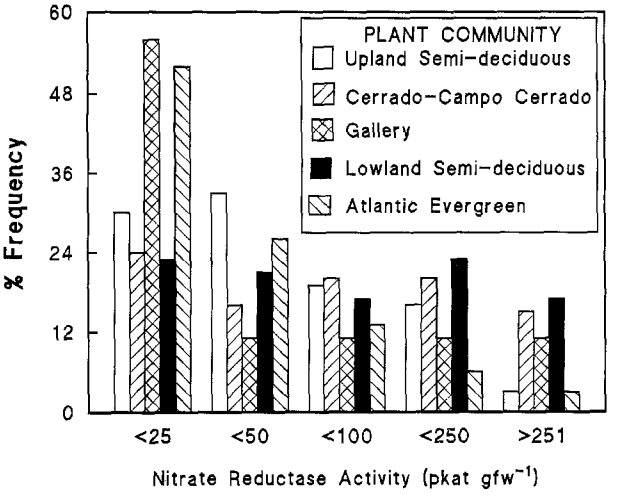

Fig. 1. Frequency distribution of nitrate reductase activity in the leaves of cerrado and forest plants

Table 1. Leaf nitrate reductase activity of species in gaps, margins and undisturbed cerrado and forest communities of south-east Brasil ($n > 20$, ± SD)

Nitrate reductase (pkat g^{-1}fw)		
Plant community	Undisturbed	Gaps and Margins
Upland semi-deciduous forest	39 ± 9	76 ± 11
Lowland semi-deciduous forest	74 ± 14	236 ± 46
Cerrado	99 ± 28	137 ± 17
Gallery forest	29 ± 4	202 ± 26
Evergreen forest	33 ± 5	96 ± 29

Table 2. Localisation of nitrate reductase activity in the leaves and roots of cerrado and forest trees

	Habitat	NITRATE REDUCTASE (pkat gfw^{-1})			
		Control		Induced	
		Leaf	Root	Leaf	Root
Acosmium subelegans (Mohl.) Yakovlev	C			286	22
Anadenanthus peregrina (Benth.) Speg.	SD	222	101	372	106
Astronium lecointe Ducke	SD, G	372	40	707	38
Aspidosperma australe Muell. Arg.	SD	222	6	722	211
Bauhinia holophylla (Bong.) Steudel	C			295	75
Calophyllum brasiliense Camb.	G	10	28	50	38
Casearia sylvestris Swartz	C, U	78	46	616	184
Cecropia glaziovi Snethlage	E	500	200	983	302
Cedrela fissilis Vell.	G, U	50	30	838	67
Centrolobium tomentosum Guillemin ex Benth	SD, G	48	13	139	142
Chorisia speciosa St. Hil.	SD	261	28	746	50
Copaifera langsdorffii Desf.	SD, G, C, U	46	18	540	47
Cordia ecalyculata Vell.	E, U	135	42	187	54
Cordia superba Cham.	SD	85	16	205	56
Dalbergia brasiliense Vog.	U	56	154	200	197
Dimorphandra mollis Benth.	C			27	125
Enterolobium contortisiliquum (Vell.) Morong	SD, G			578	73
Genipa americana L.	G	211	42	533	54
Hymenea coubaril L.	G	48	30	616	180
Inga flagelliformis (Vell.) Mart. ex Benth.	E	390	43	1164	68
Jacaranda micrantha Cham.	U	100	80	327	97
Kielmyera coriacea (Spreng.) Mart.	C			13	133
Magonia pubescens St. Hil.	C			339	75
Nectandra rigida (H.B.K.) Nees	U	63	37	466	52
Peltophorum dubium (Spreng.) Taubert	SD			297	97
Pithecelobium pedicellare Benth.	E	87	206	348	547
Platypodium elegans Vog.	SD, U	126	120	522	111
Prunus sellowii Koehne	U	23	17	35	19
Pseudobombax grandiflora (Cav.) A. Robyns	G	157	62	768	124
Pseudobombax marginatum (St. Hil., Jusst. Camb) A. Robyns	C			868	268
Pterocarpus violaceus Vog	E	222	96	435	100
Rapanea ferruginea (Ruiz et Pav.) Mez	C, U	46	56	117	63
Schinus terebinthifolius Raddi	C, U	59	41	318	158
Styphnodendron adstringens (Mart.) Coville	C			603	56
Styphnodendron obovatum Benth.	C			400	122
Styrax pohlii A.DC	U	44	118	94	226
Tabebuia chrsyotrichia (Mart. ex DC) Standley	SD, U	344	76	546	98

Plants were grown from seed in forest soil under screenhouse conditions (University of Campinas Botanic Garden). Induced samples were watered with 5 m*M* nitrate 24 h prior to sampling. All values are the average of three deteminations
C–Cerrado; SD–semideciduous forest; G–gallery forest; U–upland semidecious forest; E–evergreen forest

However nitrate reductase activities of species growing at forest margins or in gaps were generally higher than those of species growing in undisturbed forest. This is particularly evident for species of lowland semi-deciduous forest and gallery forest (Table 1), where nitrate reductase activities of plants growing in gaps or at forest margins were 3 and 6 times greater than those found in plants of closed forest. Many species with the highest activities are colonizing or early successional species such as *Solanum prianthum, Chorisia speciosa* and *Cecropia glaziovii* and activities in such species are comparable with those found in pioneer species of Nigerian

(Stewart and Orebamjo 1983), Australian (Stewart et al. 1988, 1990) and Mexican forests (Fredeen et al. 1991). Low levels of nitrate reductase found in leaves of most species examined could reflect a low level of induction resulting from restricted soil nitrate availability or light-limited nitrate reduction, or it could be that many of these species are active in root nitrate assimilation.

Occurrence of nitrate reduction in leaves and roots

Nitrate reduction was detected in roots and shoots of almost all species grown in pots of forest soil (Table 2) and when nitrate was applied both root and leaf nitrate reductase activities increased. Exceptions to this were *Calophyllum brasiliense* and *Prunus sellowii* which were unresponsive to the addition of nitrate and had very low initial nitrate reductase activities. When nitrate reductase activities of roots and leaves are compared some species (about 15% of those examined) appear to preferentially assimilate nitrate ions in their roots, the ratio of leaf to root nitrate reductase being less than 1. Among such species are *Centrolobium tomentosum, Dalbergia brasiliense, Dimorphandra mollis, Kielmeyra coriacea, Pithecelobium pedicellare* and *Styrax pohlii.* In contrast there is another group of species (about 30%) where the ratio of leaf to root nitrate reductase activity is greater than 5:1. Among species which show this preference for leaf nitrate assimilation are *Acosmium subelegans, Astronium lecointe, Chorisia speciosa, Enterolobium contortisiliquum, Inga flagelliformis, Styphnodendron adstringens* and *Tabebuia chrysotricha.* In the remaining 55% of species the ratio of leaf to root nitrate reductase activity was greater than 1 but less than 5. The localisation of nitrate assimilation on a whole-plant basis will be determined by enzyme activities and the relative allocation of biomass between roots and leaves and by the potential of other plant parts to contribute to nitrate reduction. At the seedling or sapling stage of development shoot: root biomass was generally in excess of 1, so that biomass allocation is unlikely to alter the categorisation of these species into root and shoot assimilators.

Enzymes of ammonium assimilation

All species examined exhibited activity of glutamine synthetase, glutamate synthase and glutamate dehydrogenase (Table 3). Shoot activities of glutamine synthetase exceeded those of roots in the five species studied. Activities of glutamate dehydrogenase always exceeded those of glutamate synthase and in roots of *Pseudobombax* and *Calophyllum* glutamate dehydrogenase activities were considerably greater than those of glutamine synthetase. These three enzymes were not measurable in lignotubers of *Kielmeyera coriacea* and *Pseudobombax marginatum.*

Ion exchange chromatography of leaf extracts indicated the presence of two peaks of glutamine synthetase in leaves of *Enterolobium* and *Calophyllum.* Immunological characteristics of the peaks indicated that they correspond to cytosolic and chloroplastic isoforms. In *Enterolobium* leaves the chloroplastic isoform accounted for over 80% of total activity while in *Calophyllum* leaves it made up less than 15%. Similar differences in relative proportions of glutamine synthetase isoforms have been reported in other woody plants (Stewart et al. 1987, 1988), with the chloroplastic isoform predominating in leaves of early colonizing species while in those of late successional species the cytosolic isoform predominates.

Table 3. Ammonia-assimilating enzymes in leaves and roots of cerrado and forest trees

Species	nkat gfw^{-1}		
	Glutamine synthetase	Glutamate synthase	Glutamate dehydrogenase
Calophyllum brasiliense			
Roots	1.2	0.2	5.7
Leaves	4.0	0.9	5.5
Enterolobium contortisiliquum			
Roots	3.4	1.8	5.1
Leaves	25.1	8.3	15.5
Kielmeyera coriacea			
Roots	3.2	0.3	4.7
Leaves	4.9	0.4	9.3
Peltophorum dubium			
Roots	1.9	1.0	1.8
Leaves	6.4	0.4	10.8
Pseudobombax marginatum			
Roots	2.2	0.8	16.9
Leaves	6.5	2.7	9.1

Values given are the average of at least three determinations. Plants were raised from seed, grown in sand and watered with nutrient solution containing 0.5 m*M* nitrate

Relationship between leaf nitrate reduction and xylem nitrate concentration

Species differences in relative activities of root and shoot nitrate reduction were reflected in xylem sap nitrogen composition. It is evident from the results in Fig. 2 that activity of leaf nitrate reductase was positively correlated with nitrate concentration in xylem sap. Almost no nitrate was present in xylem sap of *Calophyllum brasiliense* and little nitrate reductase was measurable in its leaves. In contrast *Enterolobium contortisiliquum* had large leaf nitrate reductase activities and a high xylem nitrate concentration. It is also apparent from these results that as xylem nitrate concentration decreased the concentration of amino nitrogen increased suggesting that species with a high proportion of xylem nitrogen in an organic form are active in root nitrate reduction.

There was also a clear relationship between xylem sap nitrogen concentration, that is the sum of nitrate-N and amino-N, and leaf nitrogen concentration (Fig. 3). This suggests the capacity of the root system to acquire, export and/or to metabolise nitrate determines leaf nitrogen status. Thus the root system of *Enterolobium*

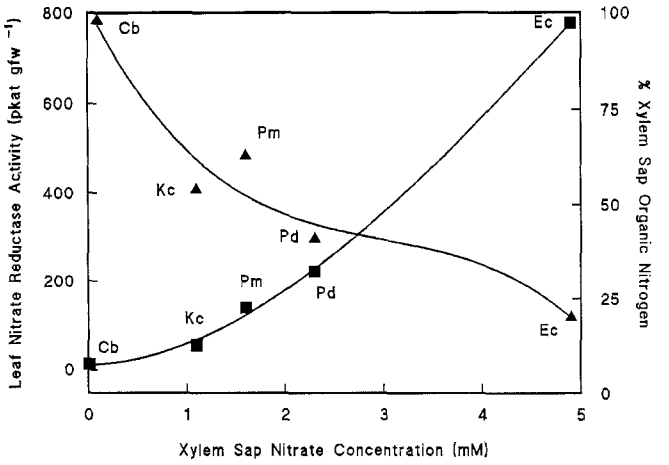

Fig. 2. Relationship between xylem sap nitrate concentration, leaf nitrate reductase activity and xylem organic nitrogen content. *Cb*, Calophyllum brasiliense; *Ec*, Enterolbium contortisiliquum; *Kc*, Kielmyera coriacea; *Pd*, Peltophorum dubium; *Pm*, Pseudobombax marginatum ■ Nitratereductase; ▲ Xylem organic nitrogen

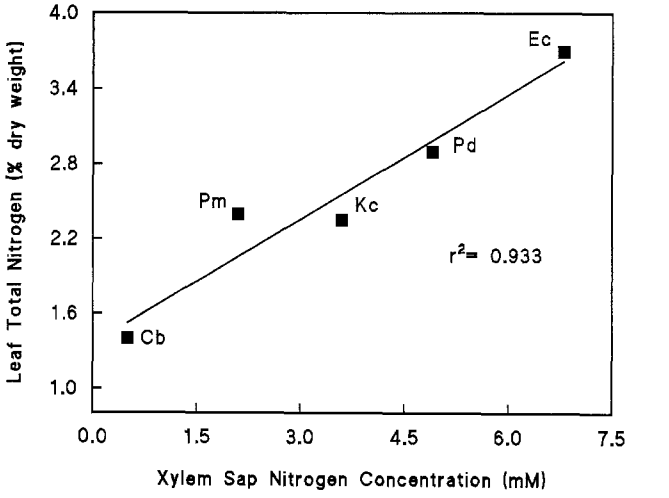

Fig. 3. Relationship between xylem nitrogen concentration and leaf nitrogen content. *Cb*, Calophyllum brasiliense; *Ec*, Enterolobium contortisiliquum; *Kc*, Kielmyera coriacea; *Pd*, Peltophorum dubium; *Pm*, Pseudobombax marginatum

contortisiliquum had a greater capacity to acquire and export nitrate ions than that of *Calophyllum brasiliense*.

Differences in root nitrate reductase activities and xylem sap composition were accompanied by differences in the pattern of incorporation of ^{15}N-labelled nitrate and ammonium (Table 4). There was a high level of enrichment of amino acids in leaves and roots of *Enterolobium* supplied with ^{15}N-nitrate and ^{15}N-ammonium. Labelled ammonium was incorporated into amino acids of leaves and roots of *Calophyllum* but when labelled nitrate was supplied enrichment of leaf amino acids was low and that of root amino acids was considerably lower than when labelled ammonium was supplied. A plant of *Calophyllum* assimilated 180 nmol day^{-1} g^{-1} fw of nitrate, while a plant of *Enterolobium* assimilated 780 nmol. When ammonium ions were the nitrogen source differences in assimilation between the two species

Table 4. Incorporation of ^{15}N-labelled nitrate and ammonium into the leaves and roots of *Enterolobium contortisiliquum* and *Calophyllum brasiliense*

Amino acid	^{15}N% abundance							
	Enterolobium contortisiliquum				*Calophyllum brasiliense*			
	Nitrate		Ammonium		Nitrate		Ammonium	
	Leaves	Roots	Leaves	Roots	Leaves	Roots	Leaves	Roots
Alanine	13	30	14	69	0	14	8	60
Serine	11	10	14	14	0	3	11	0
Aspartate	14	22	18	38	5	7	8	35
Aspara-gine	13	35	16	47	0	6	2	3
Gluta-mate	18	21	20	45	6	13	8	53
Gluta-mine	12	22	14	58	4	11	27	25

Plants were grown from seed in sand and watered with nutrient solution containing 0.5 m*M* ammonium or nitrate

Table 5. Assimilation of ^{15}N-labelled nitrate and ammonium and assimilatory potential

	Calophyllum brasiliense		*Enterolobium contortisiliquum*	
	Nitrate	Ammonium	Nitrate	Ammonium
Total ^{15}N incorporation (nmol d^{-1} gfw^{-1} of plant)	180	580	780	696
^{15}N incorporation (nmol h^{-1} gfw−1 of root)	14.2	64.9	67	59
Nitrate Reductase (nmol h^{-1} gfw^{-1} of root)	100		260	
Glutamine synthetase (nmol h^{-1} gfw^{-1} of root)	4320	13860	12120	19800
Glutamate synthase (nmol h^{-1} gfw^{-1} of root)	720	960	2880	3020

(Details as for Table 4)

were much less, *Calophyllum* assimilated 580 nmol and *Enterolobium* 696 nmol (Table 5). Growing on nitrate as nitrogen source *Enterolobium* appeared to have nearly a five times greater capacity for assimilation than *Calophyllum*. When assimilation was calculated on a root rather than a whole-plant basis these differences were still apparent, with the roots of *Enterolobium* being at least five times more active than those of *Calophyllum* in assimilating nitrate. The measured activites of nitrate reductase were well in excess of the measured rates of assimilation, seven-fold for *Calophyllum* and four-fold for *Enterolobium*. Similarly the activities of glutamine synthetase and glutamate synthase appeared to be well in excess of those required to meet the demand for ammonium assim-

ilation, derived from either nitrate reduction or direct root absorption. All the enzyme assays employed here were highly standardised with respect to optimization of substrate concentrations and pH and as a consequence probably overestimate the potential *in vivo* rates.

Discussion

The generally low activities of nitrate reductase observed in leaves of trees growing in different plant communities sampled in the present investigation suggest that nitrate ions are unlikely to be a major source of nitrogen for growth in these soils. The lack of nitrate reduction could imply that the soils in these sites may be ammonifying rather than nitrifying. Alternatively it might be that nitrate reduction in some of these species is light limited (Fredeen et al. 1991). Whilst this might apply to some of the understorey species growing in evergreen and semi-deciduous forest it is unlikely that nitrate reduction in the leaves of overstorey species in these forests or cerrado species is light limited. Within each sampling site the species with the greatest nitrate reductase activities are mostly found in areas of disturbance where it might be expected that rates of nitrification would be higher. In addition to these species of gaps or forest margins, there are some species within the mature community which exhibit nitrate reductase activities markedly greater than those of most of the vegetation. In Campo Cerrado, *Hancornia speciosa* and *Solanum auriculatum* had activities of 827 and 838, compared with an average of 80 pkat g^{-1} fw for the other species. In Cerrado, *Solanum grandiflorum* and *Miconia lanuginosa* had activities of 500 and 644 compared with 106 pkat g^{-1} fw for the remaining species. Some of these high-activity species may be early colonisers persisting in areas of nitrate enrichment. Alternatively they might be species that are restricted to microsites of persistent high nitrification. Generally pioneer-type species display high nitrate reductase activities and are found to be shoot nitrate assimilators, confirming previous observations (Stewart and Orebamjo 1983; Stewart et al. 1988, 1990; Fredeen et al. 1991). Similar differences have also been reported for herbaceous species, with pioneer species exhibiting high levels of leaf nitrate reductase (Lee and Stewart 1978; Smith and Rice 1983; Stewart and Orebamjo 1983).

Although many of the species growing in the field exhibit little capacity for leaf nitrate reduction, almost all of those grown with a high availability of nitrate responded by marked increases in leaf and root nitrate reductase activity. A small number of species appeared, on the basis of nitrate reductase activities and xylem sap composition, to be root assimilators. The present results do not provide any evidence of a relationship between site of nitrate assimilation and habitat. Within one habitat there are species typical of both root-dominant and shoot-dominant nitrate reduction.

Analyses of nitrogenous composition of xylem sap shows that there is a close correlation between xylem sap nitrate concentrations and leaf nitrate reductase levels. Those species which show low leaf nitrate reductase appear to be active in root assimilation and have a high proportion of their xylem nitrogen in the form of reduced nitrogen. *Calophyllum brasiliense,* a species with low nitrate reductase activity and a low capacity to induce the enzyme was shown to be able to metabolise ^{15}N-labelled nitrate although at very much slower rates than *Enterolobium contortisiliquum,* a species with large nitrate reductase activity. *Calophyllum* is typical of areas where the soil is almost permanently waterlogged and where ammonium might be expected to be the available nitrogen source. Rates of ammonium assimilation were similar for these two species. The roots of all species examined displayed substantial activities of glutamate dehydrogenase, a characteristic of many roots (Oaks et al. 1980; Lea et al. 1990). This has been interpreted as indicating an assimilatory role for the enzyme (Oaks and Hirel 1985). Recently however it has been shown that the enzyme has a catabolic function (Robinson et al. 1990) and that it is controlled by carbohydrate status (Robinson et al. 1992). In terms of this model our results imply considerable differences in carbohydrate status of the roots of the species examined here , with glutamate dehydrogenase activity ranging from 1.8 nkat g^{-1} fw in *Peltophorum* to 16.9 in *Pseudobombax*. This would be consistent with the notion that carbohydrate status of roots regulates the reactions of nitrogen assimilation (Aslam and Huffaker 1984; Rufty et al. 1989). Differences between species in the magnitutude of root nitrate assimilation may then be related to root carbohydrate status.

Various studies have indicated a close correspondance between leaf nitrogen content and photosynthetic capacity (Sharkey 1985; Ferrar and Osmond 1986; Field and Mooney 1986; Tuohy et al. 1991). Wallsgrove et al. (1983) have argued that the reactions of nitrogen metabolism are photosynthetic, taking place in the chloroplast, and Oaks (1992) has reiterated this view that "leaves are the really important sites for nitrate reduction". However the present results suggest that the ability of a root system to acquire, export or metabolize nitrate determines shoot nitrogen status, and as a consequence potential productivity. Furthermore we would argue that for some species the role of leaves in nitrogen metabolism may be considerably less than that of the root. Shade species in particular, which have a low potential for leaf nitrate reduction and exhibit low levels of chloroplastic glutamine synthetase, may carry out many of the reactions of nitrogen metabolism in their roots, particularly if they assimilate ammonium rather than nitrate. Assimilation of ammonium, compared with nitrate could in theory effect a four-fold energy saving for nitrogen assimilation (Pate 1986) which may be of considerable advantage to shade species (Smirnoff and Stewart 1985). Our results highlight the importance of the transport and especially the metabolic activities of root systems in determining the characteristics of inorganic nitrogen metabolism at the whole-plant level.

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