Four sites with contrasting environmental stress in southeastern Brazil: relations of species, life form diversity, and geographic distribution to ecophysiological parameters

F. R. SCARANO FLS, H. M. DUARTE, K. T. RIBEIRO, P. J. F. P. RODRIGUES and
E. M. B. BARCELLOS

*Universidade Federal do Rio de Janeiro, CCS, IB, Depto. de Ecologia, caixa postal 68020,
cep 21941-970 Rio de Janeiro, RJ, Brazil*

A. C. FRANCO

Universidade de Brasília, Depto. de Botânica, caixa postal 04457, cep 70919-970 Brasília, DF, Brazil

J. BRULFERT and E. DELÉENS

*Institut de Biotechnologie des Plantes, UMR CNRS 8618, Université Paris-Sud, F-91405, Orsay,
France*

U. LÜTTGE*

*Darmstadt University of Technology, Institute of Botany, Schnittspahnstrasse 3-5, D-64287 Darmstadt,
Germany*

Some ecophysiological parameters related to plant performance and fitness (carbon and nitrogen isotope composition and total C and N concentrations; *in situ* chlorophyll fluorescence measurements) were determined for over 30 species in four habitats bordering the montane Atlantic rain forest of Brazil, along a gradient of altitude and rainfall: a dry coastal forest, two areas of sandy coastal plain vegetation (*restingas*), and a high altitude *campo*. There was a considerable diversity of ecophysiological behaviour within and between the functional groups we created based on plant life-forms. For instance, both crassulacean acid metabolism (CAM) and C_3 species were found in most life-forms sampled and throughout all habitats. Despite the variation in rainfall regimes, average overall water-use efficiency was similar between sites, particularly for C_3 species, while no clear pattern regarding nitrogen-use emerged in this respect. Acute and chronic photoinhibition were found in many species across this gradient, even in CAM plants. However, on average, chronic photoinhibition and lower energy dissipation capacity were more characteristic of plants from the restinga habitats. This suggests that, although plants colonizing these habitats have evolved features to deal with water shortage, adaptation to high light levels has not been fully achieved yet. The ecophysiological performance of some individual species in distinct habitats and in distinct microhabitats within habitats is also discussed. © 2001 The Linnean Society of London

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Corresponding author. E-mail: luettge@bio.tu-darmstadt.de

INTRODUCTION

The Atlantic rainforest complex in Brazil is famous for its dominant montane rainforest (Rizzini, 1979), which stands out as one of the world's main centres of biodiversity (World Conservation Monitoring Centre, 1992), with a high species diversity and a high level of endemism (Fonseca, 1985). The exuberance of this forest, however, often contrasts with its marginal vegetation types. Although part of the so-called Atlantic rainforest complex, these marginal habitats are not so rich in diversity and, at first sight, not so striking as a typical dense, tall and multi-layered rainforest. For instance, woody shrubs and succulent herbs, gathered in hemispheric clumps surrounded by white sand or granitic rock, dominate the landscape of sandy coastal plains (Lacerda, Araujo & Maciel, 1993) and rocky outcrops (Meirelles, Mattos & Silva, 1997) which separate the montane forest from the sea. Mono-dominant swamps (Scarano *et al.*, 1997; Scarano, Rios & Esteves, 1998) or seasonally, semi-deciduous dry-forests (Araujo, 1997) are found at the very feet of the mountain chains. A variety of small-sized life forms are found at high altitude fields (>2300 m a.s.l.), where temperatures in winter nights can be as low as $-10°C$ (Segadas-Vianna, 1965; Segadas-Vianna & Dau, 1965).

The plants growing in these habitats are exposed to a range of extreme conditions (heat, cold, freezing, flooding, drought, wind, salinity, lack of nutrients) and are either endemic or found also in montane forest or other marginal habitats.

Ecophysiological studies traditionally are autecological in that they are devoted to the behaviour of single species or to the comparative study of a small group of plant species. In this study, however, we measured some ecophysiological parameters related to plant performance and fitness for over 30 species in four habitats bordering the montane Atlantic rainforest: two areas of sandy coastal plain vegetation (*restingas*) with different annual rainfall, a dry coastal forest and a high altitude *campo*. For such an assessment of a large number of species and habitats, it was necessary to use ecophysiological screening methods readily applicable in the field. Analysis of ^{13}C and ^{15}N stable isotope composition have been used to assess differences in carbon metabolism, water use and the magnitude of different N sources available for plants at the ecosystem level or along geographical gradients of rainfall (Sprent *et al.*, 1996; Pate *et al.*, 1998; Schulze *et al.*, 1998). Thus, we used collections of dried leaf samples for ^{13}C, ^{15}N analyses giving indications on long-term behaviour of the plants in C and N acquisition and water-use efficiency, and a small portable pulse amplitude modulation fluorometer for rapid determination of instantaneous parameters of photosynthetic electron flow on site. We selected species with different life forms and with different geographic ranges of distribution in order to assess how these different strategies related to their ecophysiological behaviour. Moreover, we were also able to compare the ecophysiological performance of some species in distinct habitats and in different microhabitats within habitats. This is a first approach in a long term endeavour to proceed from autecological ecophysiology to developing a synecological ecophysiology integrating plant geographical, phytosociological, morphological and ecophysiological evidence.
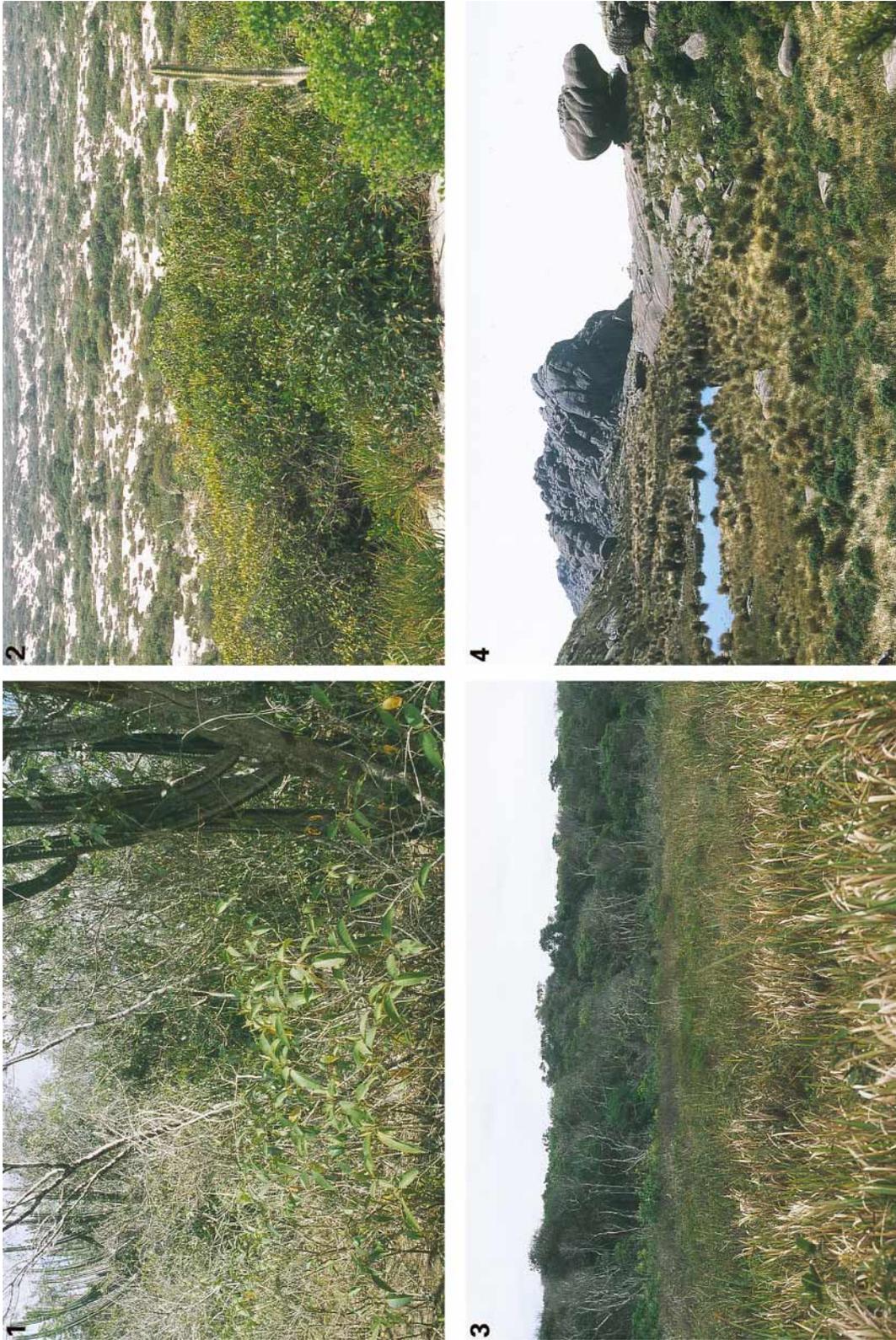
STUDY SITES

The four sites studied are marginal habitats of the Atlantic rainforest complex and are described below.

SEASONALLY DRY FOREST (DF)

This site (Fig. 1) is located at the Búzios Bauen Club Resort, municipality of Armação de Búzios (22°49′S, 41°59′W), state of Rio de Janeiro. Together with the dry restinga (see below), this is the most arid of all sites, since mean annual rainfall here is around only 800 mm, with a monthly average of less than 80 mm. The rainy season lasts from the end of spring (November) to summer (January); the dry season runs from June to August, when monthly rainfall is around 40 mm (FEEMA, 1988). The vegetation is the last remnant in the state of a typical semi-deciduous forest. This forest has several endemic species and other species with patchy disjunct geographic distribution, only to be found otherwise in the semi-arid Brazilian northeast (Araujo, 1997). Pau-brasil (*Caesalpinia echinata* Lam.), the leguminous tree which has given its name to the country, is the best known inhabitant of these forests and is now reduced to a few threatened populations (Cunha & Lima, 1992). This site is protected by a beach resort, Búzios Bauen Club, which specializes in ecotourism.

'DRY' RESTINGA (DR)

This site (Fig. 2) is located at the Area for Environmental Protection (APA) of Massambaba, municipality of Arraial do Cabo (22°56′S, 42°13′W), state of Rio de Janeiro. The Massambaba restinga spreads between the ocean and the Araruama lagoon, Brazil's second largest salt lake. It is composed of two parallel beach ridges of different ages, separated by a low area, where Holocene lagoons showing different sedimentation stages are situated (Muehe, 1994). On its east side, where plants were selected for this study, the Pleistocene, innermost beach ridge (Martin & Suguio, 1989) was covered by a dune system *c.* 2000 years BP (FEEMA, 1988). Here, the distance between the ocean and the Araruama lagoon is *c.* 1.5 km. Mean annual

Figures 1–4. The study sites. Fig. 1. Seasonally dry forest (DF) in the Búzios Bauen Club. Fig. 2. 'Dry' restinga (DR) in the APA (Area for Environmental Protection) – Massambaba. Fig. 3. 'Wet' restinga (WR) in the Jacarepiá State Ecological Reserve. Fig. 4. High altitude vegetation in the Itatiaia National Park.

rainfall is *c.* 800 mm and during the whole year the monthly precipitation tends to be less than 100 mm, with a minimum of approximately 40 mm during the winter months (Barbiére, 1984). The result is a soil water deficit throughout the year (Araujo, 1997). Mean annual temperature is 25°C and daily temperatures may range from 12° to 36°C (Araujo, 1997).

'WET' RESTINGA (WR)

This site (Fig. 3) is located at the State Ecological Reserve of Jacarepiá (22°47′S–22°57′S, 42°20′W–42°43′W), municipality of Saquarema, state of Rio de Janeiro. Between the ocean and the Jacarepiá lagoon, some of the most representative vegetation forms of the Brazilian restingas occur, including one of the last remnants of dry, dune forest in the state. Sá (1992) provides a detailed description of this site, which has been exposed to some damage from man-made fires in the recent past (Cirne & Scarano, 1996). Mean annual rainfall is 1000 mm and mean annual temperature ranges from 24–26°C.

HIGH ALTITUDE VEGETATION (HA)

The Itatiaia massif (20°25′S, 44°50′W) is located at the municipality of Itamonte, state of Minas Gerais. Its peak, the *Agulhas Negras* (= black needles), reaches 2740 m. The study site (Fig. 4) was at 2400 m of altitude and is locally called *Prateleiras* (shelves). This plateau is composed of a large boggy plain, crossed in all directions by rocky hills and covered by scattered boulders. Grassland and bamboo clumps are the most common vegetation cover, but small shrubs and tree-lets also grow between boulders, and a high diversity of plant species and life-forms are found on the rocky surfaces (Camerik & Werger, 1981). A list for the whole plateau gives 415 plant species (Martinelli, Bandeira & Bragança, 1989). Mean annual rainfall is about 2273 mm and there is no marked dry season. Seasonality is more apparent in regard to solar irradiation, evaporation and day/night temperature regimes: winter months (May–August) are less cloudy than the rest of the year. Registered extreme temperature values range from a daytime maximum of 23°C in the summer (November–February), to a nocturnal minimum of -10°C in the winter, when temperatures below 0°C are common. In the winter, after low night temperatures, plants are exposed to rapid warming and high insolation during the day (Segadas-Vianna & Dau, 1965). This site, plus the adjacent montane Atlantic forest, is protected by the Itatiaia National Park which is the oldest National Park in the country.

MATERIAL AND METHODS

STUDIED SPECIES

The criteria for selection of plant species for this study were that they should:

(1)   represent different life-forms (woody plants, climbers, hemiparasites, graminoids, rosette plants, cacti and geophytes; Figs 5–8);
(2)   represent different patterns of geographic distribution (widely neotropical, regional, endemic);
(3)   have distinct habitat preferences (generalists or specialized);
(4)   occur in more than one of the sites studied.

Table 1 shows a list of the 32 species studied, the habitat where they were sampled, their geographic distribution, habitat preference and life form. Information on geographic distribution and habitat preference was collected in the literature and, when literature was not available, on labels of exsicates in the Herbarium of the Botanic Gardens of Rio de Janeiro (RB). The following references were used: *Allagoptera arenaria* (Fernandes, 1994; Morais, 1996), *Bougainvillea spectabilis* (Schmidt, 1872; Reitz, 1970), bromeliads (Smith & Downs, 1977, 1979; Martinelli & Vaz, 1988; Fontoura, Costa & Wendt, 1991; Leme & Marigo, 1993; Van Sluys & Stotz 1995), cacti and orchids (Britton & Rose, 1937; Rambo, 1961; Scheinvar, 1985; Freitas, 1993), *Hippeastrum* cf. *psittacinum* (J. Dutilh, pers. comm.), legumes (Hoehne, 1941; Mattos, 1979), *Mollugo verticillata* (Reitz, 1984), *Myrsine* spp (Pipoly, 1996; Otegui, 1998), *Paepalanthus polyanthus* (Giulietti & Hensold, 1990), *Panicum trinii* (Renvoize & Zuloaga, 1984; Sarahyba, 1993), *Philodendron corcovadense* (Mayo, 1991), *Pleurostima gounnelleana* (Smith & Ayensu, 1976), *Psittacanthus dichroos* (Moreira & Rizzini, 1997), *Rheedia brasiliensis* (Vieira, 1997), *Roupala impressiuscula* (Sleumer, 1954).

Of the four sites, the seasonally dry forest (DF) is the least known floristically. Thus, the three taxa we were unable to determine to the species level (*Croton* sp., *Myrsine* sp. and indetermined graminoid) were sampled there. *Croton* sp. and *Myrsine* sp. were used for interspecific comparisons, but the graminoid was not, since not even the family was determined (see Table 2). However, the graminoid data were used in site and life-form comparisons. Without complete identification, we could provide no information on geographic distribution and habitat preferences of these species, and therefore their data were not included in the calculations of Table 7.

FIELD AND LABORATORY MEASUREMENTS

In situ fluorescence measurements were conducted in all study sites 8–17 October 1997 on selected fully

Figures 5–8. Some of the plant species and life-forms studied. Fig. 5. Juvenile plant of the arboreal cactus *Opuntia brasiliensis* in the understory of the dry forest. Fig. 6. Geophyte palm *Allagoptera arenaria* commonly found in both 'dry' and 'wet' restingas. Fig. 7. Shrub *Croton* sp. at midday, in a light-exposed patch of the dry forest; despite the wilted appearance of the leaves, no photoinhibition was shown by these plants throughout the whole day. Fig. 8. Neighbouring rosettes of *Paepalanthus polyanthus* (left-hand side) and *Eryngium eurycephalum* (right-hand side): a strong morphological convergence for shoot shape and marked differences in nitrogen use (see also Table 6).

Table 1. List of species studied on each site, their life-forms, patterns of geographic distribution and habitat preferences. HA = high altitude, WR = wet restinga, DR = dry restinga, DF = dry forest, ntrop. = neotropical, reg. = regional, local = endemic, S = specialized (one habitat only), G = generalist (more than one habitat of occurrence). *Schlumbergera obtusangula* (K. Schum.) D.R. Hunt is now *Schlumbergera microsphaerica* (K. Schum.) Hoevel. **Hippeastrum psittacinum* Herb. is a species complex; the species studied is *Hippeastrum morelianum* Lem.

Species and life-forms	Family	Site	Geographic distribution			Habitat	
			ntrop.	reg.	local	G	S
WOODY PLANTS							
Andira legalis (Vell.) Toledo	Leg-Faboideae	DR, WR		...X.....		X	
Clusia fluminensis Planch. & Triana	Clusiaceae	DR, WR		...X.....		X	
Croton spec.	Euphorbiaceae	DF	—	—	—	—	—
Machaerium obovatum Kuhlm. & Hoehne	Leg-Faboideae	DF			...X....		X
Myrsine parvifolia A.DC.	Myrsinaceae	DR, WR	.....X.....			X	
Myrsine spec.	Myrsinaceae	DF	—	—	—	—	—
Myrsine gardneriana A.DC.	Myrsinaceae	HA		...X.....			....X.
Rheedia brasiliensis (Mart.) Planch. & Triana	Clusiaceae	DR	.....X.....			X	
Roupala impressiuscula Mez ex Taub.	Proteaceae	HA			...X....		X
CLIMBERS							
Bougainvillea spectabilis Willd.	Nyctaginaceae	DF	.....X.....			X	
Philodendron corcovadense Kunth	Araceae	DR		...X.....			X
Vanilla chamissonis Klotzsch	Orchidaceae	DF		...X.....		X	
HEMIPARASITES							
Psittacanthus dichroos (Mart.) Mart.	Loranthaceae	DR	.....X.....			X	
GRAMINOIDS							
Cladium ensifolium Benth. & Hook .f.	Cyperaceae	HA		...X.....			..X...
Undetermined graminoid	Undetermined	DF	—	—	—	—	—
Panicum trinii Kunth	Poaceae	DR		...X.....		X	
ROSETTES							
Billbergia amoena (Lodd.) Lindl.	Bromeliaceae	DF	.....X.....			X	
Fernseea itatiaiae (Wawra) Backer	Bromeliaceae	HA			...X....		X
Neoregelia cruenta (Grah) L. B. Smith	Bromeliaceae	WR		...X.....			X
Nidularium itatiaiae L. B. Smith	Bromeliaceae	HA			...X....		X
Streptocalyx floribundus (Mart. ex Schult.f.) Mez	Bromeliaceae	DF		...X.....		X	
Vriesea neoglutinosa (Mart. ex Schult.f.) Mez	Bromeliaceae	DR		...X.....		X	
Vriesea itatiaiae Wawra	Bromeliaceae	HA		...X.....			X
Paepalanthus polyanthus Kunth	Eriocaulaceae	HA		...X.....		X	
Eryngium eurycephalum Malme	Umbelliferae	HA		...X.....			X
Pleurostima gounnelleana (Beauv.) N. L. de Menezes	Velloziaceae	HA			...X....		X
CACTI							
Opuntia brasiliensis (Willd.) Haw.	Cactaceae	DF	.....X.....			X	
Pereskia aculeata Mill.	Cactaceae	DF	.....X.....			X	
Schlumbergera obtusangula (K. Schum.)* D. R. Hunt	Cactaceae	HA		...X.....			..X.....
GEOPHYTES							
Allagoptera arenaria (Gomes) Kuntze	Arecaceae	DR, WR		...X.....		....X.	
Hippeastrum psittacinum Herb.**	Amaryllidaceae	HA		...X.....			X
Mollugo verticillata L.	Molluginaceae	DR	.....X.....			X	

Table 2. Carbon and nitrogen isotope composition ($\delta^{13}C$, $\delta^{15}N$), carbon isotope discrimination ($\Delta^{13}C$), C/N ratio and some chlorophyll *a* fluorescence parameters measured from leaves of various species occurring in habitats marginal to the Atlantic rain forest, in southeastern Brazil (HA = high altitude, WR = wet restinga, DR = dry restinga, DF = dry forest). HP = host to a hemiparasite. dark t (h:m) = dark-adaptation time (hours:minutes)

Species and life-forms	Site	$\delta^{13}C$	$\Delta^{13}C$	carbon fixation mode	$\delta^{15}N$	C/N ratio	Fv/Fm predawn (n)	darkened (n)	dark t (h:m)	ETR max	PPFD at ETRmax	Yield at ½ETRmax	NPQ at ½ETRmax	rel. ex PPFD at ½ETRmax
WOODY PLANTS														
Andira legalis	DR	−27.0	19.6	C3	−2.8	29	0.78±0.01 (05)	0.77±0.02 (09)	0:30	98	800	0.55	0.8	0.19
Andira legalis	WR	−26.2	19.3	C3	−1.4	31	—	0.76±0.10 (03)	6:00	82	580	0.58	—	0.23
Clusia fluminensis—adult	DR	−16.1	8.2	CAM	−2.5	58	0.78±0.01 (05)	0.77±0.01 (10)	0:30	110	540	0.48	2.7	0.39
C. fluminensis—seedling exposed	DR	—	—	—	—	—	0.78±0.01 (05)	0.76±0.06 (10)	0:30	146	830	0.34	3.3	0.57
C. fluminensis—seedling shaded	DR	—	—	—	—	—	0.78±0.02 (05)	0.77±0.04 (08)	0:30	42	142	0.65	0.8	0.17
C. fluminensis—adult	WR	−16.2	8.4	CAM	−1.1	55	—	0.82±0.01 (03)	0:36	104	485	0.56	—	0.32
Croton sp.	DF	—	—	C3	—	—	0.84±0.02 (10)	0.82±0.02 (19)	6:00	118	1160	0.41	2.1	0.52
Machaerium obovatum	DF	−27.1	19.6	C3	2.3	22	0.81±0.01 (10)	0.78±0.04 (19)	6:00	54	350	0.62	0.0	0.24
Myrsine parvifolia	DR	−27.2	19.8	C3	−1.9	41	0.78±0.01 (05)	0.76±0.01 (04)	0:30	53	380	0.65	0.3	0.16
Myrsine parvifolia	WR	−27.7	20.2	C3	−0.2	44	—	0.79±0.01 (03)	6:00	71	410	0.59	—	0.26
Myrsine sp.	DF	−28.1	20.7	C3	3.1	37	0.74±0.03 (10)	0.66±0.05 (22)	6:00	42	500	0.36	4.2	0.50
Myrsine gardneriana	HA	−27.5	20.0	C3	−0.7	31	0.80±0.02 (05)	0.78±0.02 (05)	0:30	87	820	0.46	1.1	0.43
Rheedia brasiliensis	DR	−27.5	20.1	C3	1.3	50	0.71±0.02 (05)	0.73±0.04 (13)	0:30	88	600	0.48	1.0	0.32
Rheedia brasiliensis (HP)	DR	—	—	—	—	—	0.75±0.02 (05)	0.75±0.03 (09)	0:30	37	210	0.62	0.9	0.17
Roupala impressuscula	HA	−27.2	19.7	C3	2.2	38	0.80±0.04 (05)	0.77±0.02 (04)	0:30	102	820	0.52	0.1	0.35
CLIMBERS														
Bougainvillea spectabilis	DF	−28.9	21.4	C3	5.9	12	0.80±0.02 (10)	0.78±0.03 (19)	6:00	54	425	0.57	0.7	0.28
Philodendron corcovadense	DR	−26.3	18.8	C3	−4.9	29	0.78±0.01 (05)	0.80±0.01 (10)	0:30	70	548	0.62	1.0	0.22
Vanilla chamissonis	DF	−14.1	6.2	CAM	3.8	22	0.73±0.05 (10)	0.72±0.06 (14)	6:00	54	260	0.44	1.6	0.39
HEMIPARASITES														
Psittacanthus dichroos	DR	−31.2	23.9	C3	−1.9	105	0.72±0.02 (05)	0.72±0.05 (09)	0:30	19	160	0.56	0.9	0.22
GRAMINOIDS														
Cladium ensifolium	HA	−20.1	18.6	C3	1.3	37	0.81±0.01 (10)	0.80±0.01 (10)	0:30	80	560	0.61	1.1	0.24
Panicum trinii	DR	−24.1	16.5	C3	−2.3	50	0.78±0.02 (05)	0.76±0.05 (09)	0:30	66	990	0.31	2.3	0.60
ROSETTES														
Billbergia amoena	DF	−15.0	7.2	CAM	1.0	39	0.76±0.01 (10)	0.69±0.07 (18)	6:00	18	135	0.40	0.0	0.49
Fernseea itatiaiae	HA	−25.3	17.8	C3	−0.8	55	—	0.71±0.06 (07)	0:30	46	970	0.51	—	0.37
Neoregelia cruenta	WR	−14.0	6.1	CAM	−0.8	79	—	0.73±0.00 (03)	0:36	40	375	0.39	1.0	0.60
Nidularium itatiaiae	HA	−15.2	7.4	CAM	2.9	52	—	—	—	—	—	—	—	—
Streptocalyx floribundus (exposed)	DF	−14.9	7.0	CAM	1.9	68	0.77±0.03 (10)	0.70±0.09 (18)	6:00	66	580	0.52	1.9	0.33
S. floribundus (shaded)	DF	−14.3	6.4	CAM	2.2	40	0.80±0.02 (10)	0.80±0.02 (15)	6:00	80	422	0.52	1.3	0.36
Vriesea itatiaiae	HA	−24.5	16.9	C3	−2.2	79	—	0.69±0.09 (08)	0:30	34	540	0.39	—	0.43
Vriesea neoglutinosa (exposed)	DR	−24.8	17.2	C3	−2.1	58	0.73±0.03 (05)	0.73±0.04 (10)	0:36	44	510	0.48	1.6	0.34
V. neoglutinosa (shaded)	DR	—	—	C3	—	—	0.79±0.01 (05)	0.79±0.02 (09)	0:36	57	460	0.64	0.6	0.18
Paepalanthus polyanthus	HA	−25.2	17.7	C3	2.9	51	0.81±0.01 (05)	0.82±0.01 (05)	0:30	100	1100	0.50	—	0.39
Eryngium eurycephalum	HA	−25.1	17.5	C3	−5.9	63	0.79±0.04 (05)	0.73±0.02 (04)	0:30	80	780	0.52	0.9	0.34
Pleurostima gounnelleana	HA	−24.2	16.6	C3	−2.3	19	—	0.81±0.02 (04)	0:30	146	1100	0.59	—	0.26
CACTI														
Opuntia brasiliensis (exposed)	DF	−13.1	5.1	CAM	3.51	49	0.82±0.01 (10)	0.78±0.05 (19)	6:00	110	1011	0.45	3.2	0.48
O. brasiliensis (shaded)	DF	−12.4	4.4	CAM	5.0	47	0.82±0.02 (10)	0.82±0.02 (14)	6:00	60	225	0.70	0.8	0.14
Pereskia aculeata (leaves)	DF	−23.5	15.8	C3	5.8	10	—	—	—	—	—	—	—	—
P. aculeata (stem)	DF	−25.9	18.4	C3	1.5	34	—	—	—	—	—	—	—	—
Schlumbergera obtusangula	HA	−18.7	10.8	CAM	−0.7	12	—	—	—	—	—	—	—	—
GEOPHYTES														
Allagoptera arenaria	DR	−24.7	17.1	C3	−1.9	41	0.75±0.02 (05)	0.75±0.01 (08)	0:30	80	580	0.60	0.9	0.20
A. arenaria	WR	−26.6	19.1	C3	1.1	46	—	0.79±0.02 (03)	0:36	88	525	0.58	0.8	0.30
Hippeastrum psittacinum	HA	−22.3	14.6	C3	0.2	11	—	0.80±0.02 (04)	0:30	95	990	0.46	—	0.43
Mollugo verticillata	DR	−27.3	19.8	C3	5.5	22	—	—	—	—	—	—	—	—

expanded leaves of the species listed in Table 1. The chlorophyll *a* fluorescence measurements were performed using a miniaturized pulse-amplitude modulation fluorometer, Mini-PAM (H. Walz, Effeltrich, Germany). The fibre optics was kept at a constant distance (*c.* 1 cm) and angle (60°) to the leaf by the leaf clip that comes with the instrument. Measurements of photosynthetic photon flux density (PPFD, $\lambda = 400–700$ nm) close to the leaf surface were taken by the micro-quantum sensor of the leaf clip calibrated against a LI-COR 190 quantum sensor (Lincoln, Nebraska, USA). For the measurements of the parameters in the light adapted state under conditions of ambient irradiance, care was taken not to shade the leaves by the fibre optics and the leaf clip.

The pre-dawn measurements of maximum fluorescence (F_m) and minimal fluorescence (F_0) were used to obtain the ratio between variable fluorescence ($F_v = F_m - F_0$) to maximum fluorescence (F_v/F_m) giving the potential quantum yield of photosystem II (PSII). To assess acute and chronic photoinhibition, in addition to the pre-dawn measurements of F_v/F_m, measurements were made after 30–40 min and in some cases also after 6 h of darkening of the light-adapted leaves. Darkening in all cases was done by placing clips on selected leaves, at the peak of irradiance around midday.

Values of F_v/F_m <0.83 indicate photoinhibition (Björkman & Demmig, 1987) given by non-photochemical quenching of chlorophyll *a* fluorescence. Fast components of non-photochemical quenching are due to a build-up of a trans-thylakoid-membrane electrochemical proton gradient and thermal energy dissipation, which are reversible within several tens of minutes, and slow components of non-photochemical quenching are due to photosystem damage especially at the level of D1 and D2 proteins, and they are reversible only within many hours (Thiele, Krause & Winter, 1998). Thus, we call photoinhibition given by F_v/F_m <0.83 after 30–40 min of dark adaptation acute photoinhibition, and given by F_v/F_m <0.83 at the end of the night (pre-dawn measurements) chronic photoinhibition, not recovering during the entire dark period. In some cases logistics did not allow us to reach sites before dawn. In these cases, measurements were taken after 6 h of darkening to obtain potential quantum yield of PSII.

Light-adapted state fluorescence measurements were taken at regular intervals along daily courses. The effective quantum yield of PSII ($\Delta F/F'_m$) was calculated as ($F'_m - F$)/F'_m (Genty, Briantais & Baker, 1989), where F is the steady-state fluorescence in the light and F'_m is the maximum fluorescence in the light when a saturating light pulse of 600 ms duration is superimposed to the prevailing environmental irradiance levels (Schreiber & Bilger, 1993). Apparent electron transport rates (ETR) were obtained as $0.5 \times \Delta F/F'_m \times PPFD$, where the factor 0.5 considers that both PSII and PSI are excited by PPFD, and excitation is equally distributed between the two photosystems.

The Stern-Volmer non-photochemical quenching (NPQ) of chlorophyll *a* fluorescence was obtained as $NPQ = (F_m - F'_m)/F'_m$ (Genty *et al.*, 1989; Bilger & Björkman, 1990), where we used F_m from the pre-dawn measurements or, if these were not available, F_m after 6 h of darkening when F_v/F_m was close to 0.8. Relative excessive PPFD (rel. exPPFD) was calculated as ($F_v/F_m - \Delta F/F'_m$)/F_v/F_m (Bilger, Schreiber & Bock, 1995) again using pre-dawn measurements or measurements after 6 h dark-adaptation for F_v/F_m.

The daily course values for all parameters above were plotted against PPFD, for each species. This indicated the light response characteristics which were obtained by applying polynomial curve fitting of Sigma Plot. In order to compare the high number of species objectively, which sometimes were under different light regimes, we selected from the curves the following descriptive parameters: maximal apparent electron transport rate (ETR_{max}), the effective quantum yield of PSII at $\frac{1}{2}$ ETR_{max} ($\Delta F/F'_m$ at $\frac{1}{2}$ ETR_{max}), non-photochemical quenching at $\frac{1}{2}$ ETR_{max} (NPQ at $\frac{1}{2}$ ETR_{max}) and relative excessive photosynthetic photon flux density at $\frac{1}{2}$ ETR_{max} (rel. exPPFD at $\frac{1}{2}$ ETR_{max}).

Determination of C- and N- contents of dried powdered samples and analyses of stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) were performed at the Institut de Biotechnologie des Plantes, Université de Paris Sud, France, with an elemental analyser (Carlo Erba, NA 1500, Courtaboef, France), where a complete combustion of the matter occurs and which is coupled to an isotope mass spectrometer (Optima, Micromass, Villeurbane, France) (Deléens *et al.*, 1997). Standards for carbon isotope composition, $\delta^{13}C$, were Pee Dee belemnite. Nitrogen isotope composition, $\delta^{15}N$, in each sample was calculated by comparison with the $^{15}N/^{14}N$ ratio of atmospheric N. ^{15}N in the atmospheric N is 0.366%.

From the measurements of carbon isotope ratio ($\delta^{13}C$), ^{13}C discrimination ($\Delta^{13}C$) was calculated as follows:

$$\Delta = \frac{\delta_a - \delta_p}{1000 + \delta_p} \times 1000 \; (\text{‰}) \qquad (1)$$

where δa and δp (in ‰) are carbon isotope composition of the ambient air (assumed here to be -8‰) and dried plant material, respectively (Farquhar, Ehleringer & Hubick, 1989; Farquhar *et al.*, 1989; Broadmeadow *et al.*, 1992). For C_3-plants this parameter is related to the overall ratio of internal to external CO_2-partial pressure (c_i/c_a) during photosynthesis, averaged over the life of the plant material analysed as follows:

$$c_i/c_a = \frac{\Delta - a}{b - a} = \frac{\Delta - 4.4}{22.6} \qquad (2)$$

where a (4.4‰) is ^{13}C discrimination due to CO_2 diffusion in air and b (27‰) is net fractionation caused by carboxylation itself (Farquhar *et al.*, 1989a, b; Broadmeadow *et al.*, 1992). Hence, for comparisons among C_3 plants, $\Delta^{13}C$ and c_i/c_a are correlated to long-term average stomatal opening and, in this way, are an indirect indicator of integrated plant's water-use efficiency.

STATISTICS

Averages are given with standard deviations (SD) and number of replicates (n) where possible and appropriate. Assessments of pairwise significant differences were made using *t*-test. For multiple sample comparison, we used one-way analysis of variance followed by Tukey test (Zar, 1996).

RESULTS AND DISCUSSION

MODE OF PHOTOSYNTHESIS

Table 2 shows that there is a considerable diversity of ecophysiological behaviour within and between the functional groups we created based on plant life-forms. For instance, both crassulacean acid metabolism (CAM) and C_3 species, as assessed by $\delta^{13}C$ measurements where values down to *c.* -16‰ were taken to indicate CAM and values below -22‰ to correspond to C_3 photosynthesis (Lüttge, 1997: p. 31, fig. 2.12), can be found with most life-form categories sampled and throughout all habitats.

The high altitude site (HA) showed some surprising results regarding species' mode of photosynthesis. *Schlumbergera obtusangula* (Cactaceae) showed a high C_3 contribution to photosynthesis, as evidenced by its intermediate $\delta^{13}C$ (-18.6‰) value between the typical C_3 Cactaceae *Pereskia aculeata* (-25.9 to -23.5‰) and the typical CAM *Opuntia brasiliensis* (*c.* -13‰), both from the dry forest (DF). It is not clear if *S. obtusangula* might belong to the C_3/CAM intermediate plants which can switch between the two modes of photosynthesis. However, even obligate CAM plants (such as most Cactaceae outside the Pereskioideae and some leafy Opuntioideae; Nobel & Hartsock, 1987) may use day-time phases (phases II and IV, *sensu* Osmond, 1978) for direct CO_2 acquisition with open stomata via ribulose bisphosphate carboxylase/oxygenase (Rubisco) with its very high ^{13}C discrimination, as compared to phosphoenolpyruvate carboxylase (PEPc) operating in dark CO_2 fixation during phase I of CAM.

Fernseea itatiaiae (Bromeliaceae), another HA species, showed $\delta^{13}C$ values in the range of typical C_3 plants (*c.* -25‰), although it belongs to a sub-family (Bromelioideae) where all species have been reported to be CAM (Medina *et al.*, 1977; Martin, 1994; but see Scarano *et al.*, 1999). In the genus *Clusia* CAM has been found to be limited to altitudes ≤ 1500 m a.s.l. (Díaz *et al.*, 1996). However CAM, notwithstanding cold night temperatures, is performed by e.g. *Echeveria columbiana* (Medina & Delgado, 1976) and cacti (Keeley & Keeley, 1989) in the Andes at elevations up to 4700 m a.s.l. At the high altitude site studied here typical CAM $\delta^{13}C$ values (*c.* -15‰) were found for the bromeliad *Nidularium itatiaiae*, whose occurrence is apparently restricted to creeks in between boulders, where these plants are probably protected from high amplitude variations in temperature and relative humidity (Table 2).

COMPARISON OF PLANTS GROUPED ACCORDING TO RAINFALL REGIMES, LIFE FORMS AND GEOGRAPHIC DISTRIBUTION PATTERNS

In an attempt to work out possible synecological ecophysiological patterns, comparisons were made grouping the plants according to rainfall regimes, life forms and types of geographical distribution.

Instantaneous parameters of photosynthesis derived from chlorophyll fluorescence measurements did not differentiate these groups. For the various groups maximal apparent electron transport rate (ETR_{max}), and the effective quantum yield of PSII ($\Delta F/F'_m$), non-photochemical quenching (NPQ) and relative excessive photosynthetic photon flux density (rel. exPPFD) measured at $\frac{1}{2} ETR_{max}$ did not show significant differences. Likewise potential quantum yield of PSII (F_v/F_m) after darkening for short periods (30–40 min) or longer periods (6 h to overnight) did not significantly distinguish these groups. Average values at pre-dawn were mostly close to optimal. Thus, criteria of sites in general, of geographic distribution pattern and of life form characteristics were not decisive in this respect (data analyses for these comparisons derived from Table 2 are not shown). Conversely, long-term carbon and nitrogen isotope composition and possible nutritional relations might be more susceptible and are detailed below.

Plants grouped according to rainfall regimes (sites)

As pointed out above, high values of $\Delta^{13}C$ (and c_i/c_a) in C_3-plants indicate higher overall long-term stomatal opening and in CAM plants increased use of phases II and IV with daytime stomatal opening. Hence, in both C_3- and CAM plants higher values of $\Delta^{13}C$ may suggest reduced water-use efficiency. Carbon contents, $\Delta^{13}C$ and c_i/c_a values did not vary significantly between C_3 plants grouped according to sites (Table 3). This suggests that the different rainfall regimes between

Table 3. Carbon isotope discrimination ($\Delta^{13}C$) (and for C_3-plants also derived c_i/c_a ratios), nitrogen isotope composition ($\delta^{15}N$), C and N contents and C/N ratios measured from leaves of different C_3 and CAM plants occurring in habitats marginal to the Atlantic rain forest, along a rainfall gradient in southeastern Brazil (HA = high altitude, WR = wet restinga, DR = dry restinga, DF = dry forest). See text for statistical comparisons

	Sites and mean annual rainfall			
	HA 2273 mm	WR 1000 mm	DR 800 mm	DF 800 mm
C_3-plants				
$\Delta^{13}C$ (‰)	17.7 ± 1.6 (9)	19.7 ± 0.6 (3)	18.6 ± 1.4 (8)	19.6 ± 2.2 (6)
c_i/c_a	0.59	0.67	0.63	0.67
$\delta^{15}N$ (‰)	−0.5 ± 2.5 (9)	−0.2 ± 1.2 (3)	−1.1 ± 3.2 (8)	3.5 ± 1.9 (6)
C(%)	49.1 ± 3.0 (9)	53.6 ± 1.7 (3)	49.0 ± 9.3 (8)	44.7 ± 3.4 (6)
N(%)	1.6 ± 1.1 (9)	1.4 ± 0.3 (3)	1.3 ± 0.4 (8)	2.6 ± 1.3 (6)
C/N	43 ± 22 (9)	40 ± 8 (3)	40 ± 12 (8)	22 ± 11 (6)
CAM-plants				
$\Delta^{13}C$ (‰)	9.1 ± 2.4 (2)	7.2 ± 1.6 (2)	8.2 (1)	6.0 ± 1.1 (6)
$\delta^{15}N$ (‰)	1.1 ± 2.5 (2)	−1.0 ± 0.2 (2)	−2.5 (1)	2.9 ± 1.4 (6)
C(%)	43.4 ± 2.3 (2)	46.3 ± 1.4 (2)	48.3 (1)	42.8 ± 5.3 (6)
N(%)	2.2 ± 1.9 (2)	0.7 ± 0.2 (2)	0.8 (1)	1.1 ± 0.5 (6)
C/N	32 ± 28 (2)	67 ± 17 (2)	58 (1)	44 ± 15 (6)

the sites studied did not imply differences in water-use efficiency between the various C_3 plants studied. This is in agreement with similar studies made by Schulze *et al.* (1991, 1996, 1998) along rainfall gradients in Namibia, Patagonia and Australia. In the Australian study, they proposed that this pattern is possibly due to a sequence of species replacements acting towards maintaining performance at low nutrient and water availability in the arid region (although this did not remain uncontroversial: Austin & Sala, 1999; Schulze *et al.*, 1999). Evidence for this pattern can be seen in our results, regarding overall water use efficiency, observing genera which are represented by different species along the gradient studied. Values for c_i/c_a obtained from $\Delta^{13}C$ in Table 2 suggest that *Vriesea itatiaiae* in HA (*c.* 2200 mm rainfall year) showed a very similar performance (c_i/c_a = 0.56) to *Vriesea neoglutinosa* (0.57) in DR (*c.* 800 mm rainfall year). The three woody Myrsinaceae studied followed a similar pattern: *Myrsine gardneriana* (c_i/c_a = 0.69 at HA, 2200 mm), *Myrsine parvifolia* (0.70 at WR, 1000 mm; 0.68 at DR, 800 mm) and *Myrsine* sp. (0.72 at DF, 800 mm) showed similar c_i/c_a values suggesting similar long-term average water use efficiency.

CAM plants also occurred at all four sites and hence are not restricted to the drier sites (Table 3). Despite the small number of species sampled in each site, there appeared to be a trend—although not statistically significant—for higher $\Delta^{13}C$ values in the rainiest site (HA; *c.* $\Delta^{13}C$ = 9‰) against lower values of one of the driest sites (DF; $\Delta^{13}C$ = *c.* 6‰). For the CAM plants higher values of $\Delta^{13}C$ indicate that plants make more use of direct CO_2 acquisition with primary C_3-type

fixation via Rubisco with its higher ^{13}C discrimination during day-time phases of stomatal opening (phases II and especially IV). The tendency for lower $\Delta^{13}C$ values at the driest site implies that the CAM plants made less use of the option of day-time stomatal opening than plants from the rainiest site, which also results in an overall higher water use efficiency. However, the rainiest site here corresponds to the highest altitude and, therefore, to the lower average temperatures. Thus, the pattern found for CAM plants could also have been affected by climatic factors other than water availability.

$\delta^{15}N$ values contain information on the supply, partitioning, and use of nitrogen within a plant as well as within an ecosystem (Gebauer & Schulze, 1991), and may assist in interpretations of plant N-source use within ecosystems, although it cannot be used directly in comparisons between ecosystems (Högberg, 1997; Pate *et al.*, 1998). Högberg lists six items upon which $\delta^{15}N$ abundance of plants depends and which, in turn, make ecosystem comparisons difficult: (i) the source of plant N (e.g. soil, precipitation, gaseous N compounds, N_2-fixation); (ii) the soil depth from which nitrogen is taken up; (iii) the form of N used (e.g. NH_4^+, NO_3^-, organic N sources); (iv) the influence of mycorrhizal symbiosis and fractionations during and after N uptake by plants; (v) plant phenology; (vi) interactions between all these factors.

Thus, we interpreted N-assimilation results by combining $\delta^{15}N$ and N-content values. Table 3 shows a general trend of ^{15}N enrichment (more positive $\delta^{15}N$) for DF in comparison with the other habitats, among both C_3 (with a range from 3.7–4.7‰) and CAM plants

Table 4. Carbon isotope discrimination ($\Delta^{13}C$) (and for C_3-plants also derived c_i/c_a ratios), nitrogen isotope composition ($\delta^{15}N$), C and N contents and C/N ratios measured from leaves of different C_3 and CAM plant life-forms occurring in habitats marginal to the Atlantic rain forest, in southeastern Brazil. See text for statistical comparisons

| | Life-forms | | | | | |
	woody plants	climbers	graminoids	rosettes	cacti	geophytes
C_3-plants						
$\Delta^{13}C$ (‰)	19.9 ± 0.4 (9)	20.1 ± 1.8 (2)	18.9 ± 2.6 (3)	17.3 ± 0.5 (6)	17.1 ± 1.8 (2)	17.7 ± 2.3 (4)
c_i/c_a	0.69	0.70	0.64	0.57	0.56	0.59
$\delta^{15}N$ (‰)	0.2 ± 2.1 (9)	0.5 ± 7.6 (2)	0.5 ± 2.5 (3)	-1.6 ± 2.6 (6)	3.7 ± 3.0 (2)	1.2 ± 3.1 (4)
C(%)	51.9 ± 2.4 (9)	47.6 ± 7.2 (2)	46.5 ± 5.3 (3)	48.6 ± 2.1 (6)	44.4 ± 2.8 (2)	45.1 ± 13.4 (4)
N(%)	1.5 ± 0.4 (9)	2.7 ± 1.3 (2)	1.6 ± 0.8 (3)	1.1 ± 0.7 (6)	2.9 ± 2.2 (2)	2.0 ± 1.4 (4)
C/N	36 ± 9 (9)	21 ± 12 (2)	34 ± 17 (3)	54 ± 20 (6)	22 ± 17 (2)	30 ± 16 (4)
CAM-plants						
$\Delta^{13}C$ (‰)	8.3 ± 0.1 (2)	6.2 (1)	—	6.8 ± 0.5 (5)	6.8 ± 3.5 (3)	—
$\delta^{15}N$ (‰)	-1.8 ± 1.0 (2)	3.8 (1)	—	1.4 ± 1.4 (5)	2.6 ± 2.9 (3)	—
C(%)	46.8 ± 2.1 (2)	44 (1)	—	46.4 ± 1.1 (5)	38.1 ± 3.8 (3)	—
N(%)	0.8 ± 0.0 (2)	2 (1)	—	0.9 ± 0.3 (5)	1.7 ± 1.6 (3)	—
C/N	57 ± 2 (2)	22 (1)	—	56 ± 18 (5)	36 ± 21 (3)	—

(average 1.8–5.4‰). For the C_3 plants, $\delta^{15}N$ is significantly higher at DF than at HA ($P<0.01$), WR ($P<0.02$) and DR ($P<0.01$), while for the CAM plants significance was only given for DF compared with WR ($P<0.01$). This could be due to the fact that ^{15}N abundance in forest soils is often low (Gebauer & Schulze, 1991). N-content in C_3 plants at DF was on average two-fold higher than in the other sites (although differences were not statistically significant). This does not match the pattern detected in a global comparison by Körner (1989), where nitrogen concentrations in plants increase with higher elevations. No patterns could be seen among CAM plants due to low n. Although plants are integrators of $\delta^{15}N$ of available N sources, $\delta^{15}N$ in foliage might be affected by the signature of N stored in the plants in addition to the signature of recent soil-derived N (Högberg, 1997). Since leaves were sampled at the end of the dry season, it is possible that $\delta^{15}N$ reflects the general N status of the plant, while the N-content indicates a recent, seasonal N assimilation from the soil.

Plants grouped according to life forms
One-way ANOVA followed by Tukey test (Zar, 1996) in Table 4, has detected only one significant difference, which was for $\Delta^{13}C$ values of leaves of C_3 woody plants vs C_3 rosettes ($P<0.05$), favoured by their higher number of species sampled, compared to the other life-forms. Rosette morphology, adapted to water conservation, may allow C_3 rosette plants to afford a lower water-use efficiency than woody plants. For CAM plants (Table 4) differences were not significant; however, $\Delta^{13}C$ appeared to be slightly higher for woody

plants, namely *Clusia fluminensis* in two sites (DR and WR; *c.* 8‰), as compared to the other life-forms (climbers, rosettes and cacti; *c.* 6‰). The high standard deviation of the cacti was due to the high $\Delta^{13}C$ of *S. obtusangula* (*c.* 10.8‰) as compared to the other cacti (*c.* 4–5‰). C-contents showed little variation among the CAM life-forms. It would appear that between different habitats, woody CAM plants and the high altitude cactus make more use of direct C_3-type carbon acquisition, and hence afford lower overall water-use efficiency than the other CAM species studied. The woody CAM plants are species of *Clusia* where CAM-phase flexibility and C_3/CAM intermediate plasticity is generally very large, which also includes *C. fluminensis* (see Lüttge, 1999).

When distinct functional groups were compared regarding $\delta^{15}N$, although standard deviations were very high and statistical differences were not significant, it is worth mentioning the high discrimination of the woody CAM plants as compared to the other life forms, including the C_3 woody plants, but not the C_3 rosettes (Table 4). This is surprising since ^{15}N abundance in trees is known to be below average (Virginia & Delwiche, 1982).

Plants grouped according to geographic distribution pattern
Table 5 shows that no differences were found with respect to $\Delta^{13}C$ and %C between distinct groups of C_3 plants, according to their distinct geographical distribution patterns. In the case of the CAM plants, neotropically-distributed, habitat generalists tended to make less use of day-time CO_2 fixation than regionally

Table 5. Carbon isotope discrimination ($\Delta^{13}C$) and derived c_i/c_a ratios (for C_3 plants), nitrogen isotope composition ($\delta^{15}N$), C and N contents, C/N ratios of C_3 and CAM plants grouped according to four geographic distribution/habitat occurrence patterns: neotropical/generalists (NG); regional/generalists (RG); regional/specialist (RS); and endemic/specialists (ES). For CAM plants, RS and ES had one species each and, therefore, are not displayed on this Table. See text for statistical comparisons

	NG C_3	NG CAM	RG C_3	RG CAM	RS C_3	ES C_3
$\Delta^{13}C$ (‰)	19.4 ± 1.8 (7)	5.6 ± 1.4 (3)	19.1 ± 1.9 (7)	7.2 ± 1.0 (5)	17.4 ± 1.9 (6)	18.4 ± 1.5 (4)
c_i/c_a	0.66	—	0.65	—	0.58	0.62
$\delta^{15}N$ (‰)	2.6 ± 3.2 (7)	3.2 ± 2.0 (3)	-0.9 ± 2.4 (7)	0.8 ± 2.6 (5)	-2.6 ± 2.4 (6)	0.4 ± 2.3 (4)
C(%)	45.2 ± 9.6 (7)	39.8 ± 6.4 (3)	51.5 ± 3.3 (7)	46.1 ± 1.6 (5)	49.6 ± 3.3 (6)	49.5 ± 2.4 (4)
N(%)	2.0 ± 1.0 (7)	0.9 ± 0.3 (3)	1.2 ± 1.3 (7)	1.1 ± 0.5 (5)	1.7 ± 1.3 (6)	1.8 ± 0.7 (4)
C/N	30.4 ± 15.9 (7)	45.0 ± 5.3 (3)	51.6 ± 24.9 (7)	48.6 ± 17.9 (5)	43.8 ± 24.9 (6)	38.3 ± 16.5 (4)

distributed, habitat generalist plants. Although this difference of $\Delta^{13}C$ values is not statistically significant, it may indicate that a higher flexibility of using C_3 options and CAM phases does not necessarily allow the colonization of a broader geographical area. Paradoxically, a specialized mechanism, such as night-time CO_2 fixation, may have allowed some species to colonize a broader geographical range.

Conversely, $\delta^{15}N$ was 2–5‰ higher in C_3 plants with wide neotropical distribution than in those with regional distribution (Tukey; $P<0.05$ vs regional generalists; $P<0.01$ vs regional specialists). Endemic plants did not differ significantly from the others, nor did groups of CAM plants, possibly due to the small number of species in these groups. No significant differences were found for N-content between groups. These apparent differences in nitrogen metabolism for plants with distinct geographical distribution patterns suggest that such patterns may be added to the list of factors potentially affecting ^{15}N composition in plants, such as several abiotic and biotic factors, plus plant characteristics such as age or life-form (Stewart *et al.*, 1995; Schulze *et al.*, 1999).

SPECIFIC COMPARISONS

In addition to the attempts at working out synecological ecophysiological relations presented above, the data collected also lend themselves to some inter- and intraspecific and, in one case, also intra-individual comparisons which will be presented below.

Interspecific differences

General considerations can be made on the basis of Table 2. The highest values of ETR_{max} ($\geq 100 \, \mu mol \, m^{-2} s^{-1}$) were reached by some high altitude C_3 plants (*Pleurostima gounnelleana*, *Paepalanthus polyanthus* and *Roupala impressiuscula*) and also by some CAM arboreal plants (see below). The only exception to this trend was *Croton* sp. in the

dry forest, which reached a high ETR_{max} of $118 \, \mu mol \, m^{-2} s^{-1}$, despite a rather wilted appearance, particularly at midday (Fig. 7). $\Delta F/F'_m$ at $\frac{1}{2} ETR_{max}$ was often higher (>0.60) for DR species. Out of nine species with values in this range, six were DR species, however, two of those were shaded.

Among C_3 plants high values of NPQ at $\frac{1}{2} ETR_{max}$ (2–4) were found in species of the drier sites (DR, DF) such as *Panicum trinii* at DR, *Myrsine* sp. and *Croton* sp. at DF. This is further confirmed by the highest rel. ex PPFD values for the same C_3 plants (>0.50). Comparing with the ETR_{max} results, an inverse relation emerges: C_3 plants with high ETR_{max} were found mostly in the rainiest site (HA), whereas high values of NPQ at $\frac{1}{2} ETR_{max}$ were found in the driest coastal sites (DR, DF). This can possibly be explained by a higher restriction to immediate water loss in the driest sites, resulting in lower photosynthesis and electron transport rates. Additionally, in the rainiest site where most of the highest ETR_{max} for C_3 species are found, overall light intensity is also possibly lower than in the coastal sites, due to frequent cloudiness (Segadas-Vianna & Dau, 1965).

With respect to photoinhibition among C_3 plants, *Cladium ensifolium* (graminoid, HA), *Paepalanthus polyanthus* (rosette, HA) and *Croton* sp. (woody plant, DF) showed the highest F_v/F_m values (all above 0.8, i.e. no photoinhibition) both after a daytime dark adaptation interval (30 min for the HA plants and 6 h for the latter) and at pre-dawn. *Croton* sp. offers a very interesting case. Although its leaves gave a rather wilted appearance at midday (Fig. 7) it showed particularly high rates of ETR_{max} (see above) combined with high NPQ at $\frac{1}{2} ETR_{max}$ and protection from chronic photoinhibition and appears to be well adapted to its dry forest habitat, which calls for more detailed autecological study. Acute, but not chronic photoinhibition, was found in *Machaerium obovatum* (a woody plant with paraheliotropic leaflet movements, DF; see Caldas *et al.*, 1997), *Myrsine gardneriana*,

Table 6. Carbon isotope discrimination ($\Delta^{13}C$) and derived c_i/c_a ratios, nitrogen isotope composition ($\delta^{15}N$), C and N contents, C/N ratios and some chlorophyll *a* fluorescence parameters measured from leaves of high altitude rosette plants with a strong morphological convergence: *Paepalanthus polyanthus* and *Eryngium eurycephalum*

	Paepalanthus polyanthus	*Eryngium eurycephalum*
$\Delta^{13}C$ (‰)	17.7	17.5
c_i/c_a	0.59	0.58
$\delta^{15}N$ (‰)	2.9	−5.0
C(%)	45.2	47.2
N(%)	0.9	0.8
C/N	50	59
F_v/F_m (pre-dawn)	0.81 ± 0.01 (5)	0.79 ± 0.04 (5)
F_v/F_m (0.5 h dark)	0.82 ± 0.01 (5)	0.73 ± 0.02 (4)
ETR_{max}	100	80
PPFD at ETR_{max}	1100	780
Yield at $\frac{1}{2} ETR_{max}$	0.50	0.52
NPQ	0.8	0.9
rel. ex PPFD	0.39	0.34

Roupala impressiuscula (woody plants, HA), *Bougainvillea spectabilis* (climber, DF) and *Eryngium eurycephalum* (rosette, HA). Chronic photoinhibition (pre-dawn values below 0.75) was detected especially in *Allagoptera arenaria* at DR, *Psittacanthus dichroos* and *Rheedia brasiliensis* at DR, exposed *Vriesea neoglutinosa* at DR, and *Myrsine* sp. at DF (Table 2).

As seen by the high standard deviations among the plant categories we created, both when grouped according to rainfall regimes (Table 3) or according to life-forms (Table 4), there was a high interspecific variation regarding $\delta^{15}N$, even within habitats. In DR alone (Table 2), we found both the lowest (−4.89‰, *Philodendron corcovadense*, a climbing Araceae) and one of the three highest $\delta^{15}N$ values (+5.51‰, *Mollugo verticillata*, a geophyte). Interspecific variation of up to 10‰ within sites have been previously reported only for high latitude systems (for review see Högberg, 1997). On the other hand, these two species with the largest difference on $\delta^{15}N$ had very similar $\delta^{13}C$ values (−26.35‰ and −27.33‰ respectively) (Table 2).

Specific comparisons are made in Tables 6 to 10. Table 6 shows the example of two sympatric C_3 rosette species. In general, C_3 rosettes showed similar $\Delta^{13}C$ (and consequently c_i/c_a), including cases with strong morphological convergence, such as *Paepalanthus polyanthus* and *Eryngium eurycephalum* occurring sympatrically in HA (Table 6). Together with their strong morphological convergence, these two rosette species also showed little interspecific variation regarding the photosynthetic parameters measured. However, while no photoinhibition was detected in

Paepalanthus polyanthus, *Eryngium eurycephalum* showed acute photoinhibition which was however reverted after the night period (Table 6). Moreover, there has been a great deal of variation regarding nitrogen use. Although the two rosette species shown in Table 6 are often found growing side by side (Fig. 8), they showed very different $\delta^{15}N$ values (+2.9‰ and −5.0‰ respectively). These results are most likely due to differences in the soil zone explored by the species' root systems. We observed *in situ* that both species have deep root systems, however with different architectures: *P. polyanthus* has numerous, thin fasciculated roots, which are likely to explore a wider subterranean gradient, while *E. eurycephalum* has few, axial roots, more likely to explore deeper zones. $\delta^{15}N$ of soil surfaces in many ecosystems is lower than further down in the soil (Högberg, 1997), as the rocky layer is approached. However, in this site, the surface is rocky, while peat lies below boulders and in creeks (see Fig. 4). Thus, axial roots as in *E. eurycephalum* may pass the boulders and reach the peat, which may account for its more negative $\delta^{15}N$ values.

Among the rosette species, the bromeliads also showed an interesting pattern in regard to $\delta^{15}N$ values. Although we sampled only terrestrial individuals, all species samples were facultative epiphytes (Smith & Downs, 1979). Stewart *et al.* (1995) compared epiphyte foliar $\delta^{15}N$ for different forests of the world and found that in Brazilian epiphytic bromeliads mean values ranged from −4.9 to −5.2‰, which is at least twice more negative than the highest value found for our terrestrial bromeliads (*Vriesea itatiaiae*; −2.2‰; Table 2). They suggested that epiphytes may utilize ^{15}N-depleted nitrogen from atmospheric deposition and N_2 fixation, while our results seem to indicate that the terrestrial forms of facultative epiphyte species may resort also to the soil as a nitrogen source, and thus be more enriched in ^{15}N.

A host-hemiparasite (mistletoe) comparison is made in Table 7. *Psittacanthus dichroos* showed the highest $\Delta^{13}C$ (23.95‰; $c_i/c_a = 0.87$) of all species studied (Table 2), that means, it was operating overall at the highest c_i/c_a-ratios and had the lowest efficiency of water-use. Since it is a hemiparasite, this was to be expected. In order to suck sap out of the host xylem, these often amphistomatic plants, tend to have high transpiration rates (Schulze, Turner & Glatzel, 1984). The host plant, *Rheedia brasiliensis*, had a $\Delta^{13}C$ value of 20.1‰ ($c_i/c_a = 0.69$; Table 7). Table 7 shows that there was little difference between the photosynthetic parameters measured for parasite (*Psittacanthus dichroos*) and host (*Rheedia brasiliensis*), although they showed a marked difference in water-use efficiency as also found for many other Brazilian host-mistletoe pairs (Lüttge *et al.*, 1998). A non-infected *R. brasiliensis* showed higher ETR_{max} and lower $\Delta F/F'_m$ than an infected one,

Table 7. Carbon isotope discrimination ($\Delta^{13}C$) and derived c_i/c_a ratios (for C_3 plants), nitrogen isotope ratios ($\delta^{15}N$), C and N contents, C/N ratios and some chlorophyll *a* fluorescence parameters measured from leaves of the woody plant *Rheedia brasiliensis* and its hemiparasite (HP) *Psittacanthus dichroos* at a dry restinga in southeastern Brazil

	Rheedia brasiliensis non-parasitized	*Rheedia brasiliensis* host	*Psittacanthus dichroos* HP
$\Delta^{13}C$ (‰)	20.1	—	23.9
c_i/c_a	0.69	—	0.87
$\delta^{15}N$ (‰)	1.3	—	-1.9
C(%)	54.2	—	50.6
N(%)	1.1	—	0.5
C/N	49	—	101
F_v/F_m (pre-dawn)	0.71 ± 0.02 (5)	0.75 ± 0.02 (5)	0.72 ± 0.02 (5)
F_v/F_m (0.5–0.6 h dark)	0.73 ± 0.04 (13)	0.75 ± 0.03 (9)	0.72 ± 0.05 (5)
ETR_{max}	88	37	19
PPFD at ETR_{max}	600	210	160
Yield at $\frac{1}{2} ETR_{max}$	0.48	0.62	0.56
NPQ	1.0	0.8	0.9
rel. ex PPFD	0.32	0.17	0.22

which could be due to differences in light regime rather than caused by infection. Fernandes *et al.* (1998) showed that ETR and $\Delta F/F'_m$ did not vary between control and host *Mimosa naguirei,* infected by the holoparasite *Pilostyles ingae.* Both the hemiparasite *Psittacanthus dichroos* and its host, *Rheedia brasiliensis,* were chronically photoinhibited. Neither 30 min of dark adaptation nor overnight adaptation brought F_v/F_m values to the optimal range. Curiously, a non-parasitized *R. brasiliensis* showed even lower values (Table 2, *P*<0.02 for predawn values). Therefore, photoinhibition in *R. brasiliensis* apparently did not result from *P. dichroos* parasitism. Hibberd *et al.* (1996) have found evidence for photoinhibition of grasses, but not of cowpeas, parasitized by the hemiparasite *Striga hermonthica.* These results also seem to indicate that despite an apparently guaranteed source of water, the hemiparasite *P. dichroos* is still sensitive to high light levels.

Woody leguminous plants are often among the dominant ones in various Atlantic forest sites (Leitão Filho, 1982), and Leguminosae are among the six dominant families in the restingas of five Brazilian states, when all life-forms of this family and all plant communities of the restingas are considered (Pereira & Araujo, 2000). In marked contrast, woody Leguminosae are very rarely found in the clumped formations of the restingas, such as the ones studied here (e.g. Ribas, 1992; Montezuma, 1997; Zaluar, 1997). The seasonal dry forest (DF) studied here (Araujo *et al.,* 1998; Farág, 1999) and the dune forest neighbouring the open formation studied in WR (Sá & Araujo, unpubl. data) also showed woody Leguminosae among the two most dominant groups. Among the two leguminous trees investigated, *Andira legalis* (DR and WR) is one of

Table 8. Nitrogen isotope composition ($\delta^{15}N$) and N-contents of potentially nitrogen-fixing C_3 woody legumes compared with average results for C_3 non-legume species (number of species) in three sites in southeastern Brazil: WR = wet restinga, DR = dry restinga, DF = dry forest

Site	Species	$\delta^{15}N$ (‰)	N(%)
WR	*Andira legalis*	-1.4	1.7
	non-legumes (2)	$+0.4 \pm 0.9$	1.2 ± 0.0
DR	*Andira legalis*	-2.8	1.8
	non-legumes (7)	$+0.9 \pm 3.3$	1.2 ± 0.3
DF	*Machaerium obovatum*	$+2.3$	2.2
	non-legumes (5)	$+3.8 \pm 2.0$	2.7 ± 0.9

the few woody Leguminosae found in open restinga formations, and *Machaerium obovatum* (DF) is typically a dry forest species. We compared $\delta^{15}N$ and N-content between these species and non-leguminous C_3 plants in their field sites to assess their potential as N_2-fixing plants (Table 8). *M. obovatum* and non-Leguminosae at DF did not differ. The results for *A. legalis* did not differ from the non-Leguminosae either, given the high standard deviation of the latter group. However, the trend shown indicates a tendency for nitrogen fixation in *A. legalis* in both sites. Faria *et al.* (1984, 1989) showed that this species nodulates and fixes nitrogen, particularly in restinga soils, whereas in forest soils this does not occur when soil nitrogen is available. Together with the remarkable phenotypic plasticity and clonal growth capacity of *Andira legalis* (Cirne & Scarano, 1996), nitrogen metabolism could help explain its colonization success in open restinga

formations, unlike most leguminous woody species originating from the Atlantic forest.

As explained above, the lowest $\Delta^{13}C$ are expected to occur among the CAM plants since this is a characteristic of this mode of photosynthesis. *Opuntia brasiliensis*, the arboreal cactus, both when shaded and exposed had the lowest $\Delta^{13}C$ values found in this study (4.43‰ and 5.14‰ respectively; Table 2). This strong limitation of direct C_3-type CO_2-acquisition was in marked contrast with that found for the other CAM cactus, *Schlumbergera obtusangula* (10.82‰; see Table 7), and also with the other CAM arboreal plants of *Clusia fluminensis* (8.21‰; Table 2). Some of the highest values of ETR_{max} (>100 $\mu mol\ m^{-2}s^{-1}$) were reached by the CAM arboreal plants at PPFD ranging from 540 (*Clusia fluminensis*) to 1011 $\mu mol\ m^{-2}s^{-1}$ (*Opuntia brasiliensis*) (Tables 2 and 9). Also the CAM arboreal plants were amongst plants with the highest values of NPQ at $\frac{1}{2}$ ETR_{max} (>3). *Opuntia brasiliensis*, the only cactus in which we measured fluorescence, was the only CAM plant to show no chronic photoinhibition when fully exposed. The CAM orchid *Vanilla chamissonis*, three CAM bromeliads, and *Clusia fluminensis* showed pre-dawn values of F_v/F_m, after a sunny day, ranging from 0.73 to 0.78 (Table 2) indicating some photoinhibition even in the CAM plants (see also below for intraspecific comparisons).

Among the CAM plants, the higher values for photosynthetic parameters which were found in arboreal forms compared with rosette plants or climbers seem to indicate that several cases of shade-adapted CAM plants can be found in the latter life-forms which may need to compromise between conditions of sun and shade. Indeed, *Vanilla chamissonis* is typically a tree climber in the forest understory, while the CAM rosette plants studied have been reported to be facultative epiphytes (Smith & Downs, 1979).

Intraspecific differences

Among the species investigated, four were sampled in each of two sites (WR and DR), namely the woody species *Andira legalis*, *Clusia fluminensis* and *Myrsine parvifolia* and the geophyte *Allagoptera arenaria*. The CAM plants *Opuntia brasiliensis* and *Streptocalyx floribundus* (DF) and *Clusia fluminensis* (DR), and the C_3 plant *Vriesea neoglutinosa* had different individuals studied at a given site.

The four species measured in the two different sites showed similar values of ETR_{max}, PPFD at ETR_{max} and $\Delta F/F'_m$ at $\frac{1}{2}$ ETR_{max} in both sites (Table 2), except for *Myrsine parvifolia* which had a slightly higher ETR_{max} in WR (71 $\mu mol\ m^{-2}s^{-1}$) than in DR (53 $\mu mol\ m^{-2}s^{-1}$). As seen for the carbon isotope discrimination data, there appears to be a maintenance of performance for these species even in the DR site. The woody species *Andira*

legalis, *Clusia fluminensis* and *Myrsine parvifolia* showed similar values of $\Delta^{13}C$, and differences in average $\Delta^{13}C$ between sites were only marked for *Allagoptera arenaria*, where the WR plants also showed lower chronic photoinhibition (see below). In this context it is also of interest, that in WR, in the dry season, NPQ values were often higher, suggesting a higher necessity for energy dissipation for these species in the rainiest site during the dry season. Regarding photoinhibition for the given species sampled in the two sites, F_v/F_m was closer to optimal values after only 6 h of darkness (following the peak of radiation at midday) in WR than after the whole night at pre-dawn in DR for *Allagoptera arenaria*, *Clusia fluminensis* and *Myrsine parvifolia*. *Andira legalis* did not show significant differences between the two sites. However, averages were never below 0.75 in any of the cases.

Four species were measured under both exposed and shaded conditions. Table 2 shows that exposed plants of the CAM species *Opuntia brasiliensis* (DF; see also Table 9) and seedlings of *Clusia fluminensis* (DR) showed higher ETR_{max}, $\Delta F/F'_m$ at $\frac{1}{2}$ ETR_{max}, NPQ at $\frac{1}{2}$ ETR_{max} and rel. ex PPFD at $\frac{1}{2}$ ETR_{max} than their shaded counterparts, indicating acclimation to high light levels. Conversely, for the CAM bromeliad *Streptocalyx floribundus* in different individuals at the same site (DF), ETR_{max} was higher in shaded plants than in exposed ones (Table 10). This suggests that this facultative epiphyte, here growing terrestrially, is a shade-adapted CAM Bromelioideae, similar to *Nidularium procerum* previously studied by Scarano *et al.* (1999). *Vriesea neoglutinosa* (DR), a C_3 bromeliad, also showed higher ETR_{max} and $\Delta F/F'_m$ at $\frac{1}{2}ETR_{max}$ in shaded than in exposed plants.

In the case of *Clusia fluminensis*, it is relevant that in DR, leaves of exposed adults, exposed seedlings and shaded seedlings showed statistically similar F_v/F_m results ranging from 0.76 to 0.78, both after 30 min darkness at midday and at pre-dawn. Photosynthetic parameters also showed similar values for exposed adults and seedlings. Franco *et al.* (1996) had already shown that the CAM tree *C. hilariana*, the ecological counterpart of *C. fluminensis*, also has seedlings tolerant of high irradiation, which favours successful establishment and phytosociological dominance in restingas, further north along the coast of Rio de Janeiro State.

Exposed cladodes of *Opuntia brasiliensis* in DF could not resume optimal F_v/F_m values even after 6 h of darkness, following the peak of irradiance at midday (*c.* 0.78), contrasting with a better recovery of shaded cladodes (*c.* 0.82). Photoinhibition was not chronic, however, as seen by the pre-dawn values (*c.* 0.82). On the other hand, exposed leaves of the CAM bromeliad *Streptocalyx floribundus* in DF showed chronic photoinhibition, since after 6 h of darkness F_v/F_m values remained very low (*c.*

Table 9. Carbon isotope discrimination ($\Delta^{13}C$), nitrogen isotope composition ($\delta^{15}N$), C and N contents, C/N ratios and some chlorophyll α fluorescence parameters measured from distinct organs of three cacti species: cladodes of exposed and shaded plants of the CAM tree *Opuntia brasiliensis* and leaves and stem of the C_3 plant *Pereskia aculeata*, in a dry forest; and cladodes of *Schlumbergera obtusangula*, in a high altitude vegetation in southeastern Brazil

| | Dry forest | | | | High altitude |
| | *Opuntia brasiliensis* | | *Pereskia aculeata* | | *Schlumbergera obtusangula* |
	exposed	shaded	leaves	stem	
$\Delta^{13}C$ (‰)	5.1	4.4	15.8	18.4	10.8
$\delta^{15}N$ (‰)	3.5	5.0	5.8	1.5	−0.7
C(%)	38.3	34.3	42.4	46.4	41.8
N(%)	0.8	0.7	4.5	1.4	3.5
C/N	48	49	9	33	12
F_v/F_m (pre-dawn)	0.82±0.01 (10)	0.82±0.02 (10)	—	—	—
F_v/F_m (6 h dark)	0.78±0.05 (19)	0.82±0.02 (14)	—	—	—
ETR_{max}	110	60	—	—	—
PPFD at ETR_{max}	1011	225	—	—	—
Yield at $\frac{1}{2}ETR_{max}$	0.45	0.70	—	—	—
NPQ	3.2	0.8	—	—	—
rel. ex PPFD	0.48	0.14	—	—	—

Table 10. Carbon isotope discrimination ($\Delta^{13}C$), nitrogen isotope composition ($\delta^{15}N$), C and N contents, C/N ratios and some chlorophyll α fluorescence parameters measured from leaves of exposed and shaded plants of the CAM bromeliad *Streptocalyx floribundus* in a dry forest in southeastern Brazil

	S. floribundus – exposed	*S. floribundus* – shaded
$\Delta^{13}C$ (‰)	7.00	6.4
$\delta^{15}N$ (‰)	1.9	2.2
C(%)	47.4	45.8
N(%)	0.7	1.1
C/N	68	42
F_v/F_m (pre-dawn)	0.768±0.030 (10)	0.802±0.019 (10)
F_v/F_m (6 h dark)	0.697±0.091 (18)	0.803±0.016 (15)
ETR_{max}	66	80
PPFD at ETR_{max}	580	422
Yield at $\frac{1}{2}ETR_{max}$	0.52	0.52
NPQ	1.9	1.3
rel. ex PPFD	0.33	0.36

0.70), and overnight it was not capable of full recovery, as pre-dawn values reached an average of *c.* 0.77. Exposed leaves of the C_3 bromeliad *Vriesea neoglutinosa* in DR were also chronically photoinhibited. In contrast, shaded leaves of both bromeliads did not show photoinhibition.

The recurrence of illegal man-made fires in WR over the 1990s (Cirne & Scarano, 1996), may account for the intraspecific differences in $\delta^{15}N$ found for species common to this site as compared to DR. $\delta^{15}N$ can reflect the different ecological factors a given species has been experiencing. Högberg (1997) states that fire consumes the upper $\delta^{15}N$-depleted surface layer of soil, which drives plants to find N in lower horizons and leads to an increase in $\delta^{15}N$ of plants. Indeed, the three woody species studied in WR showed $\delta^{15}N$ values of *c.* 1–1.5‰ higher than individuals of the same species in DR. *Allagoptera arenaria*, a geophyte palm with even deeper root systems, showed $\delta^{15}N$ values of *c.* 3‰ higher in WR than in DR (Table 2).

Intraspecific variation of $\delta^{15}N$ within a single site was more marked for *Fernseea itatiaiae* (Table 2). Four individuals sampled showed values ranging from −2.52 to +1.81‰ (4.3‰ variation), which again might be related to root system functioning. This plant establishes itself on bryophyte mats, which vary in depth, before reaching bare rock. This range of variation was higher than the small differences found for shaded vs exposed individuals of *Opuntia brasiliensis* (Table 9) and *Streptocalyx floribundus* (a giant CAM bromeliad, which is a facultative epiphyte, here occurring mostly as a terrestrial plant (Table 10) in DR.

Intra-individual differences

Pereskia aculeata, a leafy C_3 cactus, photosynthesizes both in stems and leaves. Table 9 shows that there were marked differences in both $\Delta^{13}C$ and $\delta^{15}N$ values for these different organs. The overall water-use efficiency in the leaves ($c_i/c_a = 0.51$) was higher than in the stems

($c_i/c_a = 0.62$), and ^{15}N was more discriminated in the stems (1.53‰) than in the leaves (5.84‰).

CONCLUSIONS

It is to be expected that the Atlantic rainforest complex, one of the world's most outstanding centres of bio-diversity (Myers *et al.*, 2000), possesses among its plant species a plurality of ecophysiological mech-anisms enhancing fitness and survival. This has never been shown for the Atlantic forest *sensu stricto*, but from the present results it can certainly be said that ecophysiological diversity is a feature of the habitats which are marginal to the Atlantic forest. C_3 physio-logical forms and CAM are not prerogatives of one morphological form or another and, moreover, are equally subjected to stress, and are often astonishingly resistant, as seen by our photoinhibition and photo-synthesis results.

It is quite intriguing that both specialists and gen-eralists have on average the same overall water-use efficiency, particularly among C_3 plants. This result indicates a very high genetic potential for acclimation to a broad spectrum of environmental conditions, which in some cases seem to have resulted in speciation (as for the genera *Myrsine* and *Vriesea*, with more than one species, each of them in specific habitats along the gradient), but in others could be the result of genetically mediated (see Schlichting & Pigliucci, 1998) phenotypic plasticity (e.g. *Andira legalis, Allagoptera arenaria*, etc.; for studies in the Atlantic forest see Rôças, Barros & Scarano, 1997). On the other hand, adaptation to the high light levels in the restinga habitats does not seem to have been fully achieved yet, as indicated by the commonness of chronic photo-inhibition and lower energy dissipation capacity when compared to average values of plants in the dry forest and the high altitude vegetation.

The interpretation of the results obtained with the modern techniques used here to investigate plant nitro-gen-use still requires much further research, as in-dicated by a recent review of the subject (Högberg, 1997). However, the diversity of responses found within and between habitats and within and between life forms, points to ecophysiological richness also in this respect, and deserves future attention.

The importance of plant traits related to fitness, such as those measured here, in understanding interspecific interaction and species roles in ecosystems has already been highlighted by Wardle *et al.* (1998), and is an obvious application to be expected from our current results, in future studies.

On the one hand, it is stimulating to see in this first approach that there lies a wealth of strategies to deal with stress and environmental change in these apparently fragile vegetations. On the other, there is reason for much worry that this wealth may not be capable to cope with the (not so) novel sources of stress: land speculation and predatory tourism.

REFERENCES

Araujo DSD. 1997. Cabo Frio region, south-eastern Brazil. In: Davis SD, Heywood VH, Herrera-Macbryde O, Villa-Lobos J, Hamilton AC, eds. *Centres of plant diversity: a guide and strategy for their conservation 3. The Americas.* Washington: WWF/IUCN, 373–375.

Araujo DSD, Lima HC, Farág PRC, Lobão AQ, Sá CFC, Kurtz BC. 1998. O Centro de Diversidade Vegetal de Cabo Frio: levantamento preliminar da flora. Anais do IV Simpósio de Ecosistemas Brasileiras, Águas de Lindóia, SP. *Academia de Ciências do Estado de São Paulo* **3:** 147–157 (Publicações ACIESP no. 104-III).

Austin AT, Sala OE. 1999. Foliar $\delta^{15}N$ is negatively cor-related with rainfall along the IGBP transect in Australia. *Australian Journal of Plant Physiology* **26:** 293–295.

Barbiére EB. 1984. Cabo Frio e Iguaba Grande, dois microclimas distintos a um curto intervalo espacial. In: Lacerda LD, Araújo DSD, Cerqueira R, Turcq B, eds. *Restingas: origem, estrutura, processos*, Niterói: CEUFF, 413–423.

Bilger W, Björkman O. 1990. Role of the xanthophyll cycle in photoprotection elucidated by measurements of light-induced absorbance changes, fluorescence and photo-synthesis in leaves of *Hedera canariensis. Photosynthesis Research* **25:** 173–185.

Bilger W, Schreiber U, Bock M. 1995. Determination of quantum efficiency of photosystem II and of non-photo-chemical quenching of chlorophyll fluorescence in the field. *Oecologia* **102:** 425–432.

Björkman O, Demmig B. 1987. Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77K among vascular plants of diverse origins. *Planta* **170:** 489–504.

Britton NL, Rose JN. 1937. *The Cactaceae* vol. I. Wash-ington: The Carnegie Institution.

Broadmeadow MSJ, Griffiths H, Maxwell C, Borland A. 1992. The carbon isotope ratio of plant organic material reflects temporal and spatial variations in CO_2 within tropical forest formation in Trinidad. *Oecologia* **89:** 435–441.

Caldas LS, Lüttge U, Franco AC, Haridasan M. 1997. Leaf heliotropism in *Pterodon pubescens,* a woody legume from the Brazilian cerrado. *Revista Brasileira de Fisiologia Vegetal* **9**(1)**:** 1–7.

Camerik AM, Werger MJA. 1981. Leaf characteristics of the flora of the High Plateau of Itatiaia, Brazil. *Biotropica* **13**(1)**:** 39–48.

Cirne P, Scarano FR. 1996. Rebrotamento após o fogo de *Andira legalis* (Leguminosae) em restinga fluminense. In: Miranda HS, Saito CH, Dias BFS, eds. *Impactos de queimadas em áreas de Cerrado e Restinga: Anais do Simpósio Impacto das Queimadas sobre os Ecosistemas e Mudanças Globais.* Brasília: UnB/ECL, 128–136.

Cunha MW, Lima HC. 1992. *Viagem à terra do Pau-Brasil.* Rio de Janeiro: Agência Brasileira de Cultura.

Deléens E, Morot-Gaudry JF, Martin F, Thoreux A, Gojon A. 1997. Méthodologie ^{15}N. In: Morot-Gaudry JF, ed. *Assimilation de l'azote chez les plantes: aspects physiologiques, biochimiques et moléculaires.* Paris: INRA Éditions, 265–280.

Díaz M, Haag-Kerwer A, Wingfield R, Ball E, Olivares E, Grams TEE, Ziegler H, Lüttge U. 1996. Relationships between carbon and hydrogen isotope ratios and nitrogen levels of *Clusia* species and two other Clusiaceae genera at various sites and different altitudes in Venezuela. *Trees Structure and Function* **10:** 351–358.

Farág PRC. 1999. Estrutura do estrato arbóreo da mata litorânea semicaducifólia sobre solo arenoso no Município de Búzios, RJ. Unpublished M.Sc. Dissertation. Rio de Janeiro: Botânica, Museu Nacional/Universidade Federal do Rio de Janeiro.

Faria SM, Franco AA de, Jesus RM, Menandro MS de, Baitello JB, Mucci ESF, Dobereiner J, Sprent JI. 1984. New nodulating legume trees from South-East Brazil. *New Phytologist* **98:** 317–328.

Faria SM, Lewis GP, Sprent JI, Sutherland JM. 1989. Occurrence of nodulation in the Leguminosae. *New Phytologist* **111:** 607–619.

Farquhar GD, Ehleringer JR, Hubick KT. 1989a. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology* **40:** 503–537.

Farquhar GD, Hubick KT, Coudon AG, Richards RA. 1989b. Carbon isotope fractionation and plant water-use efficiency. In: Rundel PW, Ehleringer JR, Nagy KA, eds. *Stable istopes in ecological research.* New York: Springer, 21–40.

FEEMA. 1988. *Importância da biota da região de Cabo Frio.* Rio de Janeiro: Fundação Estadual do Meio Ambiente.

Fernandes GW, Mattos EA, Franco AC, Lüttge U, Ziegler H. 1998. Influence of the parasite *Pilostyles ingae* (Rafflesiaceae) on some physiological parameters of the host plant, *Mimosa naguirei* (Mimosaceae). *Botanica Acta* **111:** 51–54.

Fernandes H de QB. 1994. Native palms of Espírito Santo state. *Acta Horticulturae* **360:** 95–111.

Fonseca GAB. 1985. The vanishing Brazilian Atlantic forest. *Biological Conservation* **34:** 17–43.

Fontoura T, Costa A, Wendt T. 1991. Preliminary checklist of the Bromeliaceae of Rio de Janeiro State, Brazil. *Selbyana* **12:** 5–45.

Franco AC, Haag-Kerwer A, Herzog B, Grams TEE, Ball E, Mattos EA, Scarano FR, Barreto SMB, Garcia MA, Mantovani A, Lüttge U. 1996. The effect of light levels on daily patterns of chlorophyll fluorescence and organic acid accumulation in the tropical CAM tree *Clusia hilariana. Trees Structure and Function* **10:** 359–365.

Freitas MF. 1993. Cactaceae da área de proteção ambiental da Massambaba, Rio de Janeiro, Brasil. Unpublished M.Sc. Dissertation. Rio de Janeiro: Botânica, Museu Nacional/ Universidade Federal do Rio de Janeiro.

Gebauer G, Schulze E-D. 1991. Carbon and nitrogen isotope ratios in different compartments of a healthy and a declining *Picea abies* forest in the Fichtelgebirge, NE Bavaria. *Oecologia* **87:** 198–207.

Genty B, Briantais JM, Baker NR. 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica et Biophysica Acta* **990:** 87–92.

Giulietti AM, Hensold N. 1990. Padrões de distribuição geográfica dos gêneros de Eriocaulaceae. *Acta Botanica Brasilica* **4**(1)**:** 133–158.

Hibberd JM, Quick WP, Press MC, Scholes JD. 1996. The influence of the parasitic angiosperm *Striga gesnerioides* on the growth and photosynthesis of its host, *Vigna unguiculata. Journal of Experimental Botany* **47:** 507–512.

Hoehne FC. 1941. Leguminosas Papilionadas: gêneros *Machaerium* e *Paramachaerium. Flora Brasilica* **25**(3)**:** 1–99.

Högberg P. 1997. ^{15}N natural abundance in soil-plant systems. *New Phytologist* **137:** 179–203.

Keeley JE, Keeley SC. 1989. Crassulacean acid metabolism (CAM) in high elevation tropical cactus. *Plant Cell and Environment* **12:** 331–336.

Körner Ch. 1989. The nutritional status of plants from high altitudes: a worldwide comparison. *Oecologia* **81:** 379–391.

Lacerda LD, Araújo DSD, Maciel NC. 1993. Dry coastal ecosystems of the tropical Brazilian coast. In: van der Maarel E, ed. *Dry coastal ecosystems: Africa, America, Asia and Oceania.* Amsterdam: Elsevier, 477–493.

Leitão Filho HF. 1982. Aspectos taxonômicos das florestas do Estado de São Paulo. *Silvicultura em São Paulo* **16a**(1)**:** 197–206.

Leme E, Marigo LC. 1993. *Bromélias na natureza.* Rio de Janeiro: Marigo Comunicação Visual.

Lüttge U. 1997. *Physiological ecology of tropical plants.* New York: Springer.

Lüttge U. 1999. One morphotype, three physiotypes: sympatric species of *Clusia* with obligate C_3 photosynthesis, obligate CAM and C_3-CAM intermediate behaviour. *Plant Biology* **1:** 138–148.

Lüttge U, Haridasan M, Fernandes GW, Mattos EA, Trimborn P, Franco AC, Caldas LS, Ziegler H. 1998. Photosynthesis of mistletoes in relation to their hosts at various sites in tropical Brazil. *Trees Structure and Function* **12:** 167–174.

Martin CE. 1994. Physiological ecology of the Bromeliaceae. *Botanical Review* **60:** 1–82.

Martin L, Suguio K. 1989. Excursion route along the Brazilian coast between Santos (state of São Paulo) and Campos (northern state of Rio de Janeiro). *International Symposium on Global Changes in South America during the Quaternary: past, present and future.* São Paulo: Special publication no. 2.

Martinelli G, Vaz AMSF. 1986–88. Padrões fitogeográficos em Bromeliaceae dos campos de altitude da floresta pluvial tropical costeira do Brasil. *Rodriguesia* **64–66**(38–40)**:** 3–10.

Martinelli G, Bandeira J, Bragança JO. 1989. *Campos de Altitude.* Rio de Janeiro: Editora Index.

Mattos NF. 1979. O gênero *Andira* Lam. (Leguminosae Papilionoideae) no Brasil. *Acta Amazonica* **9:** 241–266.

Mayo S. 1991. A revision of *Philodendron* subgenus *Meconostigma* (Araceae). *Kew Bulletin* **46**(4)**:** 601–681.

Medina E, Delgado M. 1976. Photosynthesis and night CO_2 fixation in *Echeveria columbiana* Poellnitz. *Photosynthetica* **10:** 155–163.

Medina E, Delgado M, Troughton JH, Medina JD. 1977. Physiological ecology of CO_2 fixation in Bromeliaceae. *Flora* **166:** 137–152.

Meirelles ST, Mattos EA, Silva AC. 1997. Potential desiccation tolerant vascular plants from southeastern Brazil. *Polish Journal of Environmental Studies* **6**(4)**:** 17–21.

Montezuma RCM. 1997. Estruturação da vegetação de uma restinga de Ericaceae no Município de Carapebus, RJ. Unpublished M.Sc. Dissertation. Rio de Janeiro: Ecologia, Universidade Federal do Rio de Janeiro.

Morais M. 1996. *Allagoptera* (Palmae). *Flora Neotropica Monographs* **73:** 1–34.

Moreira BA, Rizzini CM. 1997. Loranthaceae e Viscaceae da APA de Maricá, Rio de Janeiro – Brasil. *Acta Botanica Brasilica* **11**(2)**:** 1–9.

Muehe D. 1994. Lagoa de Araruama: geomorfologia e sedimentação. *Cadernos de Geografia do IBGE* **10:** 53–62.

Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403:** 853–858.

Nobel PS, Harstsock TL. 1987. Drought-induced shifts in daily CO_2 uptake patterns for leafy cacti. *Physiologia Plantarum* **70:** 114–118.

Osmond CB. 1978. Crassulacean acid metabolism: a curiosity in context. *Annual Review of Plant Physiology* **29:** 379–414.

Otegui M. 1998. Sinopsis del género *Myrsine* L. (Myrsinaceae) en el Cono Sur de América del Sur. *Candollea* **53**(1)**:** 133–157.

Pate JS, Unkovich MJ, Erskine PD, Stewart GR. 1998. Australian mulga ecosystems – ^{13}C and ^{15}N natural abundances of biota components and their ecophysiological significance. *Plant, Cell and Environment* **21:** 1231–1242.

Pereira OJ, Araujo DSD. 2000. Análise florística das restingas dos estados do Espírito Santo e Rio de Janeiro. In: Esteves FA, Lacerda LD, eds. *Ecologia de Restingas e Lagoas Costeiras do Brasil.* Rio de Janeiro: NUPEM-UFRJ, 25–63.

Pipoly JJ. 1996. Contributions toward a new flora of the Philipines: I. A synopsis of the genus *Myrsine* (Myrsinaceae). *Sida* **17:** 155–162.

Rambo SJB. 1961. Migration routes of the south Brazilian rainforest. *Iheringia Série Botânica* **5**(12)**:** 1–54.

Reitz R. 1970. Nictagináceas. *Flora Ilustrada Catarinense* **1:** 1–52.

Reitz R. 1984. Mollugináceas. *Flora Ilustrada Catarinense* **1:** 16.

Renvoize SA, Zuloaga F. 1984. The genus *Panicum* group Lorea (Gramineae). *Kew Bulletin* **39:** 185–202.

Ribas LA. 1992. Análise da estrutura e composição específica das comunidades vegetais de moitas de restinga, em Maricá – RJ. Unpublished M.Sc. Dissertation. Brasília: Ecologia, Universidade de Brasília.

Rizzini CT. 1979. *Tratado de Fitogeografia do Brasil.* vol. 2. São Paulo: Edusp.

Rôças G, Barros CF, Scarano FR. 1997. Leaf anatomy plasticity of *Alchornea triplinervia* (Euphorbiaceae) under distinct light regimes in a Brazilian montane Atlantic rain forest. *Trees Structure and Function* **11:** 469–473.

Sá CFC. 1992. A vegetação da restinga de Ipitangas, Reserva Ecológica Estadual de Jacarepiá, Saquarema (RJ); fisionomia e listagem das angiospermas. *Arquivos do Jardim Botânico do Rio de Janeiro* **31:** 87–102.

Sarahyba LSP. 1993. Gramineae (Poaceae) da Area de Proteção Ambiental da Massambaba, Rio de Janeiro, Brasil. Unpublished M.Sc. Dissertation. Rio de Janeiro: Botânica, Museu Nacional/Universidade Federal do Rio de Janeiro.

Scarano FR, Ribeiro KT, Moraes LFD, Lima HC. 1997. Plant establishment on flooded and unflooded patches of a freshwater swamp forest in southeastern Brazil. *Journal of Tropical Ecology* **14:** 793–803.

Scarano FR, Rios RI, Esteves FA. 1998. Tree species richness, diversity and flooding regime: case studies of recuperation after anthropic impact in Brazilian floodprone forests. *International Journal of Ecology and Environmental Sciences* **24:** 223–235.

Scarano FR, Mattos EA, Franco AC, Herzog B, Ball E, Grams TEE, Mantovani A, Barreto S, Haag-Kerwer A, Lüttge U. 1999. Habitat segregation of C_3 and CAM *Nidularium* (Bromeliaceae) in response to different light regimes in the understory of a swamp forest in southeastern Brazil. *Flora* **194:** 281–288.

Scheinvar L. 1985. Cactáceas. *Flora Ilustrada Catarinense* **1:** 1–384.

Schlichting CD, Pigliucci M. 1998. *Phenotypic evolution: a reaction norm perspective.* Sunderland: Sinauer Associates.

Schmidt JA. 1872. Nyctagineae. In: Martius CFP, Eicher AG, eds. *Flora Brasiliensis,* vol.14, part 2. München, Leipzig, 345–376.

Schreiber U, Bilger W. 1993. Progress in chlorophyll fluorescence research: major developments during the last years in retrospect. *Progress in Botany* **54:** 151–173.

Schulze E-D, Turner NC, Glatzel G. 1984. Carbon, water and nutrient relations of two mistletoes and their hosts: a hypothesis. *Plant Cell and Environment* **7:** 293–299.

Schulze E-D, Gebauer G, Ziegler H, Lange OL. 1991. Estimates of nitrogen fixation by trees on an aridity gradient in Namibia. *Oecologia* **88:** 451–455.

Schulze E-D, Mooney HA, Sala OE, Jobbagy E, Buchmann N, Bauer G, Canadell J, Jackson RB, Loreti J, Oesterheld M, Ehleringer JR. 1996. Water availability, rooting depth, and vegetation zones along an aridity gradient in Patagonia. *Oecologia* **108:** 503–512.

Schulze E-D, Williams RJ, Farquhar GD, Schulze W, Langridge J, Miller JM, Walker BH. 1998. Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Australian Journal of Plant Physiology* **25:** 413–425.

Schulze E-D, Farquhar GD, Miller JM, Schulze W, Walker BH, Williams RJ. 1999. Interpretation of increased foliar $\delta^{15}N$ in woody species along a rainfall gradient in northern Australia. *Australian Journal of Plant Physiology* **26:** 296–298.

Segadas-Vianna F. 1965. Ecology of the Itatiaia range, southeastern Brazil. I – altitudinal zonation of the vegetation. *Arquivos do Museu Nacional* **53:** 7–30.

Segadas-Vianna F, Dau L. 1965. Ecology of the Itatiaia range, southeastern Brazil. II – climates. *Arquivos do Museu Nacional* **53:** 31–53.

Sleumer H. 1954. Proteaceae americanae. *Botanischer Jahrbücher* **76:** 139–211.

Smith LB, Ayensu ES. 1976. A revision of American Velloziaceae. *Smithsonian Contributions of Botany* **30:** 1–172.

Smith LB, Downs RJ. 1977. Tillandsioideae (Bromeliaceae). *Flora Neotropica Monograph* **14**(2)**:** 663–1492.

Smith LB, Downs RJ. 1979. Bromelioideae (Bromeliaceae). *Flora Neotropica Monograph* **14**(3)**:** 1493–2142.

Sprent JI, Geoghegan IE, Whitty PW, James EK. 1996. Natural abundance of ^{15}N and ^{13}C in nodulated legumes and other plants in the cerrado and neighbouring regions of Brasil. *Oecologia* **105:** 440–446.

Stewart GR, Schmidt S, Handley LL, Turnbull MH, Erskine PD, Joly CA. 1995. ^{15}N natural abundance of vascular rainforest epiphytes: implications for nitrogen source and acquisition. *Plant, Cell and Environment* **18:** 85–90.

Thiele A, Krause GH, Winter K. 1998. *In situ* study of photoinhibition of photosynthesis and xanthophyll cycle activity in plants growing in natural gaps of the tropical forest. *Australian Journal of Plant Physiology* **25:** 189–195.

van Sluys M, Stotz D. 1995. Padrões de visitação a *Vriesea neoglutinosa* por beija-flores no Espírito Santo, sudeste do Brasil. *Bromélia* **2**(3)**:** 27–35.

Vieira CM. 1997. Clusiaceae Lindley. In: Marques MCM, ed. *Flórula da APA Cairuçu, Parati, RJ: espécies vasculares*. Série Estudos e Contribuições no. 14. Rio de Janeiro: IPJBRJ-IBAMA.

Virginia RA, Delwiche CC. 1982. Natural ^{15}N abundance of presumed N_2-fixing and non-N_2-fixing plants from selected ecosystems. *Oecologia* **54:** 317–325.

Wardle DA, Barker GM, Bonner KI, Nicholson KS. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *Journal of Ecology* **86:** 405–420.

World Conservation Monitoring Centre. 1992. *Global biodiversity: status of the Earth's living resources.* London: Chapman & Hall.

Zaluar HLT. 1997. Espécies focais e a formação de moitas na restinga aberta de Clusia, Carapebus, RJ. Unpublished M.Sc. Dissertation. Rio de Janeiro: Ecologia, Universidade Federal do Rio de Janeiro.

Zar JH. 1996. *Biostatistical analysis.* New Jersey: Prentice Hall.