

Ecophysiology of six selected shrub species in different plant communities at the periphery of the Atlantic Forest of SE-Brazil

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Abstract

The Atlantic rain forest of Brazil is one of the 25 biodiversity hotspots of the world. It is surrounded by distinct marginal plant communities which are floristically related to the rain forest. We performed an in situ ecophysiological study of six shrub and tree species which are abundant in one or more of these marginal ecosystems. They formed three pairs of taxonomically related species, which, however, differed in geographic distribution and/or habitat preference. We aimed to answer the following questions: (1) Do habitat generalists and specialists differ in ecophysiological behaviour? (2) Are there general trends responsive to site characteristics, irrespective of taxonomic affiliation? (3) In which variables between-site intraspecific variation is more often detected? Plants chosen were the Clusiaceae *Calophyllum brasiliense* Cambess (swamp forest specialist) and *Rheedia brasiliensis* (Mart.) Planch & Triana (a generalist plant, occurring in swamp forests and dry, sandy coastal vegetation); the Myrsinaceae *Myrsine parvifolia* A.DC. (widespread in sandy plains) and *Myrsine gardneriana* A.DC. (widespread in high-altitude habitats); and the Euphorbiaceae *Stylingia dichotoma* Muell. Arg. (a coastal inselberg specialist) and *Croton compressus* Lam. (a generalist found in coastal inselbergs and dry forests). We compared measurements of photosynthesis (chlorophyll fluorescence parameters), stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and metabolic carbon and nitrogen compounds. Generalists and specialists did not always differ in ecophysiological behaviour: for instance, while widespread generalists such as *M. parvifolia* and *C. compressus* were ecophysiological versatile, *R. brasiliense* appeared to perform below optimum in all sampled habitats. Light and water were abiotic factors which apparently explained most of the variation found. Overall, ecophysiological responses were often more clearly related to individual species rather than to taxonomic affinities in higher hierarchies (family, genus) or habitat. These results are discussed as a further indication of high biodiversity even in habitats marginal to the rain forest hotspot.

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Introduction

The Atlantic rain forest of Brazil is one of the 25 biodiversity hotspots in the world for its high species diversity, high level of endemism and a tragically high level of habitat destruction (Morellato and Haddad, 2000; Myers et al., 2000). In the southeastern State of Rio de Janeiro, this rain forest is surrounded by various marginal plant communities, which differ in the type of stress they are seasonally or occasionally subjected to (Scarano, 2002). Scarano et al. (2005a) separated these communities into two types according to their origins: (a) those standing on geologically recent, Quaternary terrains between the rain forest and the sea, such as the restingas on the sandy coastal plains and the swamp forests (see Martin et al., 1993; Scarano et al., 1997); and (b) those that are relicts of drier (coastal semideciduous dry forest and coastal inselbergs) or cooler (high-altitude fields and montane *Araucaria* forests) geological times (see Araujo, 1997; Behling, 1998; Brade, 1956; Franco et al., 2005; Ledru et al., 1998).

These two types of marginal plant communities bear contrasting floristic and phytogeographic relations with the rain forest at the core of this vegetation complex. While the vegetation on Quaternary terrains (restingas, swamps) have their origins mostly associated to the rain forest and hardly have any endemic plant species (Araujo, 2000; Rizzini, 1979), the vegetation on older geological ground (dry forests, inselbergs, high-altitude zones) presents a number of endemic species and disjoint distribution patterns. For instance, the semideciduous dry forest has several species only to be found again in the semiarid region of the Brazilian northeast (Araujo, 1997), while high-altitude plants are often found again in similarly cooler regions such as the Andes or subtropical, southern-most Brazil (Brade, 1956; Segadas-Vianna, 1965). Nevertheless, even these vegetation types have many floristic links with the rain forest. Thus, while many rain forest plants were capable at some stage to migrate from the mesic rain forest and colonise more extreme habitats, other plants remained isolated in relict islands that represent past climatic conditions (Scarano, 2002). These two types of plants are of intrinsic ecophysiological interest for the apparently paradoxical nature of their distribution patterns, which may result from plasticity at one extreme to specialisation at the other (Scarano et al., 2005a).

Physiological ecology is often considered as autoecology, addressed to the performance of individual species. In a previous study in ecosystems at the periphery of the Atlantic forest (Scarano et al., 2001), we have attempted to extend this to ecophysiological synecology (for the rationale see Lüttge and Scarano, 2004) comparing, throughout habitats, a large number of plants of a variety of life forms. Our main goal was then to describe and assess ecophysiological diversity

throughout such habitats. Here, we follow the same approach but, this time, we have chosen to restrict ourselves to shrubs and trees that are abundant in one or more of these marginal ecosystems. We performed in situ ecophysiological measurements of six shrub and tree species that form three pairs of taxonomically related species, which however differed in geographic distribution and/or habitat preference. Thus, we could now increase the number of physiological traits examined in Scarano et al. (2001), i.e., chlorophyll fluorescence and stable isotope analyses, by measuring contents of soluble carbohydrates and non-protein nitrogen compounds to assess basic metabolism, to the extent this is possible in a large range field study. This approach was adopted so as to try to answer the following questions: (1) Do habitat generalists and specialists differ in ecophysiological behaviour? (2) Are there general trends responsive to site characteristics, irrespective of taxonomic affiliation? (3) In which variables between-site intraspecific variation is more often detected? Therefore, four different ecosystems at the periphery of the Atlantic forest were chosen, namely a restinga complex, a high-mountain *Araucaria* forest, an inselberg and a semideciduous dry forest. Six shrub and tree species were studied: *Calophyllum brasiliense* Cambess (Clusiaceae; swamp forest specialist), *Rheedia brasiliensis* (Mart.) Planch & Triana (Clusiaceae; generalist in swamp forests and dry, sandy coastal vegetation), *Myrsine parvifolia* A.DC. (Myrsinaceae; widespread in sandy plains), *Myrsine gardneriana* A.DC. (Myrsinaceae; widespread in high-altitude habitats), *Stylingia dichotoma* Muell. Arg. (Euphorbiaceae; coastal inselberg specialist) and *Croton compressus* Lam. (Euphorbiaceae; generalist in coastal inselbergs and dry forests).

Materials and methods

Study sites and study species

Restingas: two Clusiaceae and *Myrsine parvifolia*

The Brazilian sandy coastal plains stretch between the ocean and the hills where the Atlantic rain forest is located. They have a Quaternary origin and consist of marine sandy deposits and dunes. Along the coastline of Rio de Janeiro, the sandy plains date mostly from the Holocene, having been established and re-established from 5000 to 3000 yr BP. However, further north in the region under the influence of the Paraíba do Sul river, in some areas sandy marine deposits dating from the Pleistocene (120,000 yr BP) remained, acquiring their final shape after a series of invasions and regressions of the sea during the Holocene (Martin et al., 1993). A mosaic of plant communities collectively called restingas, which range from open, patchy formations to

forests, covers these sandy plains (Lacerda et al., 1993). The flora of the restingas of Rio de Janeiro almost completely lacks endemisms and is mostly composed of plant species originating from the neighbouring Atlantic rain forest (Araujo, 2000; Rizzini, 1979). Scarano (2002) argues that migration from the Atlantic rain forest to the restingas was successful for ecologically plastic species, which were able to adjust to the more extreme and seasonal conditions imposed by the restinga habitats. The very diverse plant communities found in the restingas are subjected to conditions as extreme as seasonal drought and oligotrophy on the one hand, and permanent flooding on the other (Henriques et al., 1986). This leads to the fact that the flora of a given restinga plant community often is very different from the flora of closely adjacent communities (Araujo et al., 1998).

Studies were performed in a restinga complex with locations at two conservation units. First, the Restinga de Jurubatiba National Park (22°23'S, 41°45'W) covers an area of 14,860 ha and is located at approximately 200 km NE of the city of Rio de Janeiro, Brazil. This Park is also site 5 of the Brazilian Long-Term Ecological Research Project. With respect to moisture, this is an intermediate restinga in comparison to other restingas (see Scarano et al., 2005b), with an annual rainfall of 1164 mm and a ground water table at 2–3 m. Here, we have established a transect inland from the sea. Fig. 1 shows the first ridge behind the beach, where hemispherical vegetation islands can be seen. The transect started here, went through the first green stripe and reached the second ridge, where again vegetation islands can be seen. The two open formations are dominated by

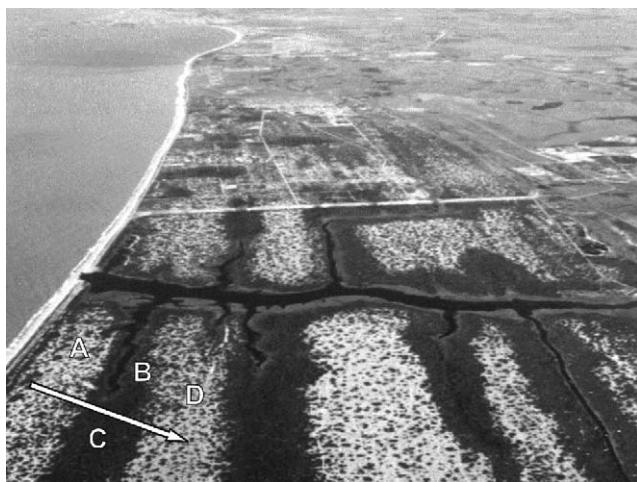


Fig. 1. Aerial picture (by Rômulo Campos) of the Restinga de Jurubatiba National Park in the area by the Cabiúnas lagoon. Arrow indicates the transect along which the sampling was done. (A) first beach ridge, *Clusia* scrub; (B) swamp forest; (C) dry forest; (D) second beach ridge, *Clusia* scrub.

Clusia hilariana Schlecht. and form the so-called “*Clusia* scrub” (Araujo et al., 1998; Henriques et al., 1986; Scarano et al., 2005b). The green stripe is a swale between the two *Clusia* scrubs, where at the lower topography there is a swamp forest. After the flooded zone at the bottom of the swale, climbing the second ridge, one finds a narrow dry forest, where tree specimens of some of the open vegetation shrubs are found. We sampled the Clusiaceae *R. brasiliensis* in the first beach ridge and in the swamp, *C. brasiliense* only in the swamp, and the Myrsinaceae *M. parvifolia* in the first and in the second beach ridges.

Second, the inner beach ridge in the Environmental Protection Area of Massambaba in the municipality of Arraial do Cabo (22°56'S, 42°13'W) is a dry restinga. Climate in the Cabo Frio region is drier due to a cold oceanic upwelling (Araujo, 1997). Mean annual rainfall is ca. 800 mm and monthly precipitation tends to be less than 100 mm, with a minimum of approximately 40 mm during the winter months, from May to August (Barbière, 1984). Mean annual temperature is 25 °C and daily temperatures may range from 12 to 36 °C (Araujo, 1997). The Massambaba restinga spreads between the ocean and the Araruama lagoon, which is Brazil's second largest salt lake and the largest hypersaline lake in the world. It is composed of two parallel beach ridges of different ages, separated by a low area, where holocenic lagoons showing different sedimentation stages are situated (Muehe, 1994). On its east side, where plants were selected for this study, the pleistocenic, innermost beach ridge (Martin and Suguio, 1989) was covered by a dune system ca. 2000 yr BP (FEEMA, 1988). Here, the distance between the ocean and the Araruama lagoon is ca. 1.5 km. The result is a soil water deficit throughout the year. Water table in this study site is at a depth of 1–2 m. The restinga vegetation here is patchy, consisting of small vegetation islands surrounded by white sand (Scarano et al., 2001). Here we also sampled *R. brasiliense* and *M. parvifolia*.

C. brasiliense Cambess is restricted to the swamp forests that are formed on the swales between beach ridges. This is a typical flood-tolerant plant (Scarano et al., 1997), a specialist in flood-prone habitats, which occurs in several flooded plant communities throughout the neotropics (Oliveira-Filho and Ratter, 1995) and is one of the dominant trees in these swamps (Araujo et al., 1998). The co-occurring *R. brasiliensis* is not restricted to this type of environment. This generalist occurs both as a 3–5 m tall shrub in the open, patchy vegetation occupying the beach ridges, and as a 10–15 m tall tree in the restinga swamps. However, in neither of these vegetation types is it highly abundant. This tree is also found in the montane Atlantic rain forest (Vieira, 1997). In addition, in the restinga complex we used *M. parvifolia* A. DC. (Myrsinaceae), another generalist and

geographically widely distributed plant (Otegui, 1998; Pipoly, 1996) and one of the dominant woody species on the beach ridges (Araujo et al., 1998; Pimentel, 2002). We also used it as a comparison to the mountainous *M. gardneriana* described next.

High-altitude *Araucaria* forest: *Myrsine gardneriana*

In the high mountains of the Itatiaia massif, the peak *Agulhas Negras* (or *black needles*) reaches 2740 m. The study site was in an *Araucaria* forest at 2000 m a.s.l., where *A. angustifolia* reaches its most northern distribution on the South American continent (see also Franco et al., 2005). This is located in the Itatiaia National Park (20°25'S, 44°50'W) in the municipality of Itamonte, state of Minas Gerais. Records indicate mean annual temperatures of 14 °C and there are often more than 60 days per year with night temperatures below 0 °C and the lowest temperatures can reach –10 °C (Scarano et al., 2001). Although mean annual rainfall is 2273 mm, the winter months are relatively dry (Hueck, 1972) and plants are exposed to cold nights and rapid warming and high isolation during the day (Segadas-Vianna and Dau, 1965). *M. gardneriana* A.DC., studied here, is a shrub restricted to montane habitats of southeastern Brazil (Otegui, 1998; Pipoly, 1996). It is also one of the few woody plants to cross the upper forest line and establish itself in the high-altitude grasslands and rocky outcrops (Scarano et al., 2001).

Inselberg and dry forest: two Euphorbiaceae

Granitic outcrops or inselbergs are very old in geological origin (10–50 × 10⁶ yr) as they were formed during the late Proterozoic (Safford and Martinelli, 2000). In coastal areas, due to changes in sea level over the Quaternary, some outcrops were surrounded by ocean in the past. Currently, we can consider granitic outcrops as islands, surrounded by very different types of vegetation, i.e., rain forest, dry forest, cerrado, restinga, and there is a high number of endemic taxa amongst the flora of these inselbergs (Barthlott et al., 1993; Burke, 2003; Lüttge, 1977; Meirelles et al., 1999; Porembski and Barthlott, 2000). The composition of the vegetation of granitic outcrops is affected by the inclination of the substrate and the soil depth. In the south-eastern region of Brazil, granitic outcrops are common landmarks (Mattos et al., 1997; Meirelles et al., 1999; Safford and Martinelli, 2000; Scarano, 2002). They occur inland and in coastal areas and are surrounded by rain forests and restinga vegetation. In spite of occurring in a wet climate, the vegetation of granitic outcrops in southeastern Brazil is frequently subjected to low water availability due to run-off of precipitation from the rocks and soil scarcity and reduced depth. Vegetation islands often occur where inclination is smaller and conditions are more favour-

able for soil accumulation. At the top and at the base of the outcrops it is possible to encounter transitional forest formations. Very small vegetation islands, from 2.5 to 16 × 10⁻³ m², are generally dominated by desiccation-tolerant plants from the Velloziaceae, Cyperaceae or Selaginellaceae (Meirelles et al., 1997, 1999). Shrubs occur predominantly in larger vegetation islands and, in southeastern Brazil, species of *Clusia* (see Scarano et al., 2005b) and of woody Euphorbiaceae are commonly found, such as *St. dichotoma* and *C. compressus*, which were studied here. These species are 1–1.5 m tall shrubs and co-occur in the same hemispherical clumps of different sizes. The inselberg chosen for the present study was the Sugar Loaf rocky outcrop (22°57'S, 43°59'W) in the municipality of Rio de Janeiro. Annual rainfall in the city of Rio de Janeiro is about 1500 mm yr⁻¹ and mean temperature is 24 °C (Nimer, 1979).

C. compressus has a broad geographic distribution. It is also found in abundance in the dry forests at the region of Cabo Frio-Búzios, at the Lake District of the state of Rio de Janeiro, where one finds the last remnant in the state of a typical semideciduous forest (see Scarano et al., 2001). This forest grows on Tertiary ground and has several endemic species and other species with patchy disjoint geographic distribution, only to be found otherwise in the semiarid Brazilian northeast (Araujo, 1997; Oliveira-Filho and Fontes, 2000). The study site where *C. compressus* was sampled is located at the Búzios EcoResort (former Búzios Bauen Club), which specialises in ecotourism, at the municipality of Armação de Búzios (22°49'S, 41°59'W). Together with the dry restinga above, this is the most arid of all sites. Although rainfall and temperature in the seasonally dry forest of Búzios are similar to that of the open, sun-exposed restinga of Arraial do Cabo, the dry forest is less exposed to direct sunlight, wind and salt spray (both from the sea and from the hypersaline Araruama lake).

Collection and analysis of soil samples

Logistic constraints did not allow us to collect soils in all sites. Soil samples were then collected only in the restinga sites, in the rooting zone of 3–6 individuals of each species, in a soil depth of 0–5 cm. Total N contents of bulk soil material were determined in the dried soil samples using an elemental analyser (NA 2500; CE Instruments, Milan, Italy).

Collection of phloem exudates

Phloem exudates were collected by the EDTA technique described by Rennenberg et al. (1996) and Schneider et al. (1996). Small pieces of bark

(ca. 150 mg FW) were removed from twigs with a diameter of about 10 mm and from the stem and washed with double-demineralised water. Subsequently, the bark pieces were placed in 6 ml vials with 2 ml of 10 mM EDTA and 0.015 mM chloramphenicol at pH 7.0 for 5 h. Collecting the exudates from fresh bark pieces implies that the unit of reference is the fresh weight of bark and not the volume of exudates. Phloem exudates were frozen in liquid N₂ and stored at –80 °C until analysis. Previous studies (Geßler et al., 1998; Schneider et al., 1996) showed for different species that contamination of phloem exudates with cellular constituents could be neglected under the experimental conditions applied.

Analysis of soluble N compounds and sugars

Amino compounds and ammonium were extracted from leaves, wood and fine roots by the modification of the method of Winter et al. (1992) described in Schneider et al. (1996). Plant material frozen in liquid N₂ was ground with mortar and pestle. Aliquots of 0.3 g of the frozen powder were homogenised in 0.4 ml buffer containing 20 mM Hepes (pH 7.0), 5 mM EGTA, 10 mM NaF and 2.5 ml chloroform:methanol (1.5/3.5, v/v). The homogenate was incubated for 30 min at 4 °C. Subsequently, water-soluble metabolites were extracted twice with 3 ml double-demineralised water. The aqueous phases were combined and freeze-dried (Alpha 2–4, Christ, Osterode, Germany). The dried material was dissolved in 1 ml lithium citrate buffer (0.2 M, pH 2.2) for amino acid and ammonium analysis. Aliquots of 35–70 µl of the extracts and of phloem exudates samples were injected into an automated amino acid analyser (Biochrom, Pharmacia LKB, Freiburg, Germany). Amino compounds and ammonium were separated on a PEEK column (Ultrapac 8 Resin, Lithium 250 × 4.6 mm, Biochrom, Pharmacia, Freiburg, Germany) using a system of five lithium citrate buffers giving a pH gradient from 2.80 to 3.55. The separated amino components and ammonium were subjected to postcolumn derivatisation with ninhydrin. The absorption of the aminoninhydrin derivatives was measured at 440 and 570 nm. Peaks were identified and quantified by means of a standard solution (Sigma Chemie, Deisenhofen, Germany) containing 39 amino compounds and ammonium. Nitrate was extracted from homogenised leaves and roots for 60 min at 5 °C in 1 ml demineralised water plus 100 mg PVPP. Aliquots of 1 ml of phloem exudates were shaken for 2 h with 50 mg PVPP at 5 °C to remove phenolic compounds. Subsequently, all leaf, wood and root extracts and phloem exudates were heated to 95 °C for 5 min, shortly incubated on ice for recovery to room temperature and centrifuged for 10 min at 16,000g and 4 °C. Aliquots (0.5 ml) of the

clear supernatants were injected into an ion exchange chromatography system (DX 100; Dionex, Idstein, Germany). Anions were separated on an IonPac[®] column (AS9-Sc 250 × 4 mm; Dionex, Idstein, Germany) and eluted with a solution containing 1.8 mM Na₂CO₃ plus 1.7 mM NaHCO₃ at a flow rate of 1.0 ml min^{–1}. Nitrate in leaf, wood and root extracts was detected with a conductivity detector module (CDM, Dionex, Idstein, Germany) with a detection limit of <0.3 nmol ml^{–1}. In phloem exudates, determination of nitrate contents was performed with a UV–VIS detector (SDP-6AV; Shimadzu, Duisburg, Germany) with a comparable detection limit.

For the determination of soluble carbohydrates, the same extraction methods were applied as for nitrate determination. Aliquots (1–100 µl) of the root and shoot extracts and of phloem exudates were injected into a HPLC system (Dionex DX 500; Dionex, Idstein, Germany). Separation was achieved on a CarboPac 1 separation column (250 × 4.1 mm; Dionex, Idstein, Germany) with 36 mM NaOH as an eluent at a flow rate of 1 ml min^{–1}. Carbohydrates were measured by means of a pulsed amperometric detector equipped with an Au working electrode (Dionex DX 500, Idstein, Germany). Individual carbohydrates that eluted 8–16 min after injection were identified and quantified by internal and external standards.

Determination of total C and N and of carbon and nitrogen-isotope composition

Determinations of C and N contents and analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope composition of dried homogenised samples were carried out with an elemental analyser (NA 2500; CE Instruments, Milan, Italy) coupled by a ConFlo II interfaced (Finnigan MAT GmbH, Bremen, Germany) to an isotope ratio mass spectrometer (Delta Plus; Finnigan MAT GmbH, Bremen, Germany). The δ values were defined as: δ (‰) = $[(R_{\text{sample}}/R_{\text{ST}}) - 1] \times 1000$, where R_{sample} and R_{ST} are the $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ ratios of the sample and standard (PDB for $\delta^{13}\text{C}$ and N₂ in air for $\delta^{15}\text{N}$), respectively.

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

$$\Delta = \frac{\delta_a - \delta_p}{1000 + \delta_p} 1000\%, \quad (1)$$

where δ_a and δ_p (in ‰) are carbon isotope composition of the ambient air (–8‰) and dried plant/soil material, respectively (Farquhar et al., 1989a). For C₃ plants this parameter is related to the overall ratio of internal to external CO₂ partial pressure (e_i/e_a) during

photosynthesis, averaged over the life of the plant material analysed as follows:

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

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

Chlorophyll a fluorescence

We used a miniaturised pulse-amplitude modulation fluorometer, Mini-PAM (H. Walz, Effeltrich, Germany) equipped with a standard 2030-B leaf-clip holder to measure potential quantum yield (F_v/F_m) of photosystem II (PSII) (Bilger et al., 1995; see also Rascher et al., 2000). F_v/F_m was measured at the end of the night (predawn values) and during the day after darkening the leaves for 30 min, where F_v is maximum variable fluorescence and F_m is maximum fluorescence of the dark-adapted leaf under a light saturating flash ($F_v = F_m - F_0$; where F_0 is the ground fluorescence of the dark-adapted leaves). Instant light-response curves of $\Delta F/F'_m$ were obtained using the light-curve programme of the Mini-PAM, where actinic light intensity was increased during 4 min in eight steps following each other within 30 s. The internal halogen lamp of the instrument, using the fibre-optics and the leaf-clip holder, provided the light. All light-response curves were taken on leaves that were exposed to high irradiance conditions during the day. Measurements of photosynthetic active radiation (PAR, $\lambda = 400 - 700\text{ nm}$) close to the leaf surface were taken by the micro-quantum sensor of the leaf-clip calibrated against a LI-COR 190 quantum sensor (Li-Cor, Lincoln, NE, USA). The parameters obtained from the light-response curves were: the apparent maximal electron transport rate (ETR_{max}) and effective quantum yield of PSII ($\Delta F/F'_m$) at ETR_{max} , and at $\frac{1}{2}\text{ETR}_{\text{max}}$, and PAR at saturation and at half-saturation of photosynthesis. $\Delta F/F'_m$ was calculated as $(F'_m - F)/F'_m$, where F is the fluorescence yield of the light-adapted sample and F'_m is the maximum fluorescence obtained when a light pulse of 800 ms duration (intensity $\approx 3000\ \mu\text{mol m}^{-2}\text{ s}^{-1}$) is superimposed on the prevailing environmental light levels (Schreiber and Bilger, 1993). ETR was calculated as $0.5 \times 0.84 \times (\Delta F/F'_m) \times \text{PAR}$. This assumes an equal distribution of light energy between PS I and PS II and a leaf absorbance of 0.84.

Results

Carbon and nitrogen contents

C contents in leaves are rather similar for all species and sites except for the low values of *C. compressus* in the dry forest (Table 1), which may be related to ecophysiological performance (see below). C contents in roots of *St. dichotoma* are higher than in the other species. *C. compressus* shows the site effect for both wood and roots as well. N content is comparatively high in leaves and roots of *St. dichotoma* and *C. compressus* and for *St. dichotoma* also in the wood. For N contents there was no site effect in *C. compressus*, but light exposure in *M. gardneriana* significantly affected N content in leaves with lower levels in the shade. Overall, however, the species studied were not very conspicuously different in structural components (as indicated by C and N contents) and allow comparison of possible taxon and site-dependent effects on ecophysiological performance for the woody life form.

Photosynthetic performance

Comparison of the different species at the different sites can be based on the cardinal points of light-use characteristics obtained from the instant light-response curves (Table 2). Due to considerable standard deviations between the performance of individual leaves, there were no conspicuous statistically significant differences in ETR_{max} between the six species. At ETR_{max} , $\Delta F/F'_m$ was somewhat lower in *C. brasiliense* and *R. brasiliensis* than in the other species, a difference which, however, was less pronounced at $\frac{1}{2}\text{ETR}_{\text{max}}$.

There was, however, a clear site effect for *R. brasiliensis* where ETR_{max} increased from swamp forest to intermediate and to dry restinga. It is possible that in part this may be related to water availability because there is a similar trend in $\Delta^{13}\text{C}$ values (see below Table 4). However, the site effect may be dominated by the very large differences in saturating PAR. Increasing saturating PAR (PAR at ETR_{max}) indicates increasing sun-plant nature of the plants. A similar site effect is seen for *M. parvifolia* when ETR_{max} in the dry restinga is compared to that in the dry forest and second (but not first) beach ridge of the intermediate restinga. However, this is not much seen in the $\Delta F/F'_m$ values. *M. gardneriana* showed the expected strong effects of PAR in the light-exposed and shaded sites in the mountain ecosystem. *C. compressus* showed lower ETR_{max} in the dry forest but without lower saturating PAR.

Photoinhibition is indicated by measurements of potential quantum yield of PS II. Although the term photoinhibition is currently much debated, predawn values of F_v/F_m below 0.83–0.80 can be used as an

Table 1. C and N contents (dry-weight %) in different organs of the species studied at the different sites

Species and sites	Leaves		Roots		Wood	
	C (%)	N (%)	C (%)	N (%)	C (%)	N (%)
Restinga complex						
<i>Calophyllum brasiliense</i>						
Jurubatiba swamp forest	47.6 ± 0.6 ^{AA}	1.1 ± 0.2 ^{AA}	49.8 ± 1.8 ^{AA}	1.3 ± 0.3 ^{AB}	46.2 ± 0.5 ^{AA}	0.2 ± 0.01 ^{AA}
<i>Rheedia brasiliensis</i>						
Mean	47.9 ± 1.8 ^A	1.0 ± 0.2 ^A	50.0 ± 8.7 ^A	0.7 ± 0.2 ^A	45.2 ± 2.0 ^A	0.4 ± 0.7 ^A
Jurubatiba swamp forest	46.1 ± 1.4 ^{aA}	1.1 ± 0.1 ^{Aa}	51.0 ± 1.7 ^{Aa}	0.9 ± 0.1 ^{Aa}	45.1 ± 1.8 ^{Aa}	0.3 ± 0.02 ^{Aa}
Jurubatiba (intermediate restinga) first beach ridge	48.4 ± 0.7 ^{ab}	1.0 ± 0.1 ^a	46.1 ± 1.3 ^a	0.7 ± 0.04 ^a	44.5 ± 0.4 ^a	0.7 ± 0.7 ^a
Massambaba dry restinga	49.1 ± 0.8 ^b	0.9 ± 0.1 ^a	52.7 ± 8.5 ^a	0.6 ± 0.1 ^a	45.8 ± 0.6 ^a	0.1 ± 0.02 ^a
<i>Myrsine parvifolia</i>						
Mean	47.5 ± 3.6 ^A	1.0 ± 0.4 ^A	46.1 ± 4.7 ^A	0.4 ± 1.3 ^A	44.3 ± 5.4 ^A	0.3 ± 0.3 ^A
Jurubatiba (intermediate restinga) first beach ridge	47.5 ± 1.7 ^a	1.0 ± 0.04 ^a	43.1 ± 2.6 ^a	0.4 ± 0.1 ^a	43.6 ± 3.2 ^a	0.2 ± 0.04 ^a
Jurubatiba (intermediate restinga) second beach ridge	47.4 ± 2.4 ^a	0.9 ± 0.2 ^a	47.1 ± 0.9 ^a	0.4 ± 0.03 ^a	41.9 ± 0.2 ^a	0.2 ± 0.1 ^a
Jurubatiba dry forest	47.0 ± 1.6 ^a	1.0 ± 0.2 ^a	46.2 ± 1.8 ^a	0.3 ± 0.1 ^a	46.0 ± 3.9 ^a	0.2 ± 0.02 ^a
Massambaba dry restinga	48.0 ± 1.2 ^a	1.1 ± 0.3 ^a	48.0 ± 3.3 ^a	0.6 ± 0.2 ^a	46.0 ± 1.7 ^a	0.4 ± 0.3 ^a
Mountain						
<i>Myrsine gardneriana</i>						
Mean	52.2 ± 2.9 ^A	1.6 ± 0.3 ^A	49.7 ± 3.0 ^A	0.7 ± 0.3 ^A		
Light-exposed	51.7 ± 1.0 ^a	2.0 ± 0.2 ^b	49.4 ± 0.8 ^a	0.6 ± 0.2 ^a		
Shaded	50.6 ± 2.8 ^a	1.2 ± 0.1 ^a	49.9 ± 2.8 ^a	0.7 ± 0.2 ^a		
Inselberg						
<i>Stylingia dichotoma</i>						
Inselberg	50.3 ± 1.9 ^{zA}	2.7 ± 0.2 ^{zB}	58.2 ± 3.1 ^{βB}	1.9 ± 0.7 ^{zB}	47.4 ± 9.6 ^{zA}	1.1 ± 0.6 ^{βB}
<i>Croton compressus</i>						
Mean	47.0 ± 2.2 ^A	3.0 ± 0.5 ^B	45.9 ± 5.7 ^A	1.7 ± 0.3 ^B	51.7 ± 2.0 ^A	0.3 ± 0.2 ^A
Inselberg	53.5 ± 2.0 ^{ab}	3.1 ± 0.4 ^{za}	53.1 ± 0.6 ^{zb}	1.8 ± 0.3 ^{βa}	55.6 ± 1.9 ^{zb}	0.3 ± 0.1 ^{za}
Dry forest						
<i>Croton compressus</i>						
	40.4 ± 1.7 ^a	2.8 ± 0.2 ^a	38.7 ± 5.5 ^a	1.5 ± 0.2 ^a	47.7 ± 0.7 ^a	0.3 ± 0.1 ^a

Values are means ± standard deviation from three to six individuals analysed twice ($n = 3-6$). Mean: average for given species in different habitats. Intra- and interspecific comparisons were made by ANOVA followed by Tukey HSD post-hoc test. Additional comparisons between *C. brasiliense* and *R. brasiliensis*, both from the swamp forest, and between *St. dichotoma* and *C. compressus*, both from the Inselberg, were performed applying Student's *t*-test. Different letters (a,b: intraspecific; A,B: interspecific; A,B: interspecific swamp forest; α,β: interspecific Inselberg) within columns indicate significant differences at $p < 0.05$.

indicator of a sustained decrease in the efficiency of photosynthetic quantum conversion (Björkman and Demmig, 1987). We note, however, that photoinhibition in principle may be both photoprotective and photo-destructive. For field studies as it is the case here, it is useful to follow Thiele et al. (1998). Depressions of F_v/F_m reversible within up to 60 min are considered to result from the build-up of an electrical gradient across the thylakoid membranes (reversible within 10 min) and energy dissipation as heat (reversible within 60 min). Photoprotective energy dissipation as heat involves xanthophylls (Schindler and Lichtenthaler, 1996); zeaxanthin itself may divert chlorophyll excitation from the reaction-centre chlorophyll *a* in the light harvesting complex of PS II (Horton et al., 1994), or the futile cycle of epoxidation/de-epoxidation of zeaxanthin via antheraxanthin and violaxanthin may dissipate energy (Dem-

mig-Adams, 1990; Demmig-Adams and Adams, 1992; Pfündel and Bilger, 1994). Thus, we measured F_v/F_m before dawn and also at times during the day when irradiance levels would reach maximum values (Table 3).

Predawn values were very close to 0.80 for *C. brasiliense* in the swamp forest and for *M. parvifolia* in the intermediate restinga and its dry forest. The values were visually significantly lower for *R. brasiliensis*, *St. dichotoma*, *C. compressus* and for *M. parvifolia* in the dry restinga. At noon all species at all sites were more or less strongly inhibited except *M. parvifolia* in the intermediate restinga and its dry forest. Due to logistic constraints, predawn values of F_v/F_m could not be obtained for *M. gardneriana*. Values found between 08:00 and 16:00 h were consistently around 0.70 (i.e., 0.71 ± 0.03 on average, $n = 29$) showing photoinhibition

Table 2. Apparent maximum electron transport rate (ETR_{max}), effective quantum yield of photosystem II ($\Delta F/F_m'$), and PAR at saturation and at $\frac{1}{2}$ saturation obtained from light curves of leaves of the species studied at the different sites

Species and sites	ETR_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		$\Delta F/F_m'$		PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
	at ETR_{max}	at $\frac{1}{2}ETR_{max}$	at ETR_{max}	at $\frac{1}{2}ETR_{max}$	at ETR_{max}	at $\frac{1}{2}ETR_{max}$
Restinga complex						
<i>Calophyllum brasiliense</i>						
Jurubatiba swamp forest	102 ± 21^A		0.15 ± 0.02^A	0.42 ± 0.03^A	1438 ± 114^A	237 ± 51^A
<i>Rheedia brasiliensis</i>						
Mean	98 ± 51^B		0.17 ± 0.02^B	0.46 ± 0.03^B	1252 ± 717^A	203 ± 113^A
Jurubatiba swamp forest	63 ± 20^{eB}		0.18 ± 0.02^{aA}	0.44 ± 0.12^{aA}	823 ± 200^{bB}	133 ± 46^{bB}
Jurubatiba (intermediate restinga) first beach ridge	90 ± 20^b		0.15 ± 0.01^b	0.49 ± 0.03^a	995 ± 503^b	173 ± 57^b
Massambaba dry restinga	176 ± 18^a		0.15 ± 0.02^b	0.48 ± 0.06^a	2368 ± 92^a	373 ± 58^a
<i>Myrsine parvifolia</i>						
Mean	147 ± 42^A		0.22 ± 0.04^A	0.56 ± 0.03^A	1460 ± 401^A	265 ± 90^A
Jurubatiba (intermediate restinga) first beach ridge	146 ± 30^b		0.18 ± 0.01^b	0.56 ± 0.03^a	1625 ± 338^{ab}	245 ± 63^{ba}
Jurubatiba (intermediate restinga) second beach ridge	125 ± 12^b		0.26 ± 0.04^a	0.59 ± 0.02^a	1035 ± 72^c	207 ± 27^b
Jurubatiba dry forest	120 ± 21^b		0.21 ± 0.02^b	0.54 ± 0.02^a	1335 ± 231^{bc}	258 ± 62^{ba}
Massambaba dry restinga	198 ± 46^a		0.21 ± 0.02^b	0.57 ± 0.04^a	1847 ± 347^a	351 ± 123^a
Mountain						
<i>Myrsine gardneriana</i>						
Light-exposed	110 ± 16^a		0.22 ± 0.06^z	0.43 ± 0.06^z	906 ± 209^z	187 ± 62^z
Shaded	65 ± 2^b		0.24 ± 0.01^z	0.57 ± 0.04^z	491 ± 26^z	79 ± 5^z
Inselberg						
<i>Stylingia dichotoma</i>						
	138 ± 33^{ab}		0.18 ± 0.02^a	0.44 ± 0.07^b	1180 ± 230^a	248 ± 67^{ab}
<i>Croton compressus</i>						
	191 ± 54^a		0.24 ± 0.11^a	0.54 ± 0.03^a	1307 ± 381^a	293 ± 86^a
Dry forest						
<i>Croton compressus</i>						
	120 ± 18^b		0.25 ± 0.03^a	0.57 ± 0.01^a	1140 ± 104^a	187 ± 30^b

Values are means \pm standard deviation from six light curves of leaves of six different plants. Statistics as for Table 1.

throughout the day. Hence, we note that there are both site and taxon (species) effects on the susceptibility of these plants to chronic photoinhibition not reversible overnight.

Dynamically, $\Delta^{13}\text{C}$ and c_i/c_a are determined by stomatal width and photosynthetic capacity. For C_3 species exposed to comparable environmental conditions as prevailing at a given site, carbon isotope discrimination (Δ) and internal to external CO_2 partial pressure (c_i/c_a) of leaves, derived from $\delta^{13}\text{C}$ values of dried leaves comprising mainly structural carbon are related to long-term average stomatal opening and indicative of intrinsic WUE (Duquesnay et al., 1998) over the life-time of the leaves sampled (Broadmeadow et al., 1992; Farquhar et al., 1989a, b). There are no conspicuous species differences in the data obtained (Table 4). However, as for ETR_{max} (see above Table 2) there are clear site effects. $\Delta^{13}\text{C}$ was lower for *R. brasiliensis* at the drier sites and it was particularly low for *C. compressus* in the dry forest. However, it was similar for light-exposed and shaded plants of *M. gardneriana*. Hence, *R. brasiliensis* and *C. compressus*

operated with higher WUE and lower c_i/c_a at the drier sites. Overall site effects were more pronounced than taxon effects.

Carbon metabolism

Our analyses of soluble carbohydrates and the $\delta^{13}\text{C}$ values allude to some aspects of carbon metabolism of the plants studied at different sites.

There were interspecific differences in the concentrations of soluble carbohydrates in leaves and roots (Table 5) which were, however, not related to differences in photosynthetic capacity (Table 2). In both tissues highest concentrations were observed for *R. brasiliensis*. In the leaves the next lower concentrations were detected in *C. brasiliense* followed by *M. gardneriana*. Minimum concentrations were found in *M. parvifolia* and *St. dichotoma*. In roots, minimum soluble carbohydrate concentrations were observed in *C. brasiliense*. Significant intraspecific differences between sites were not present in leaves of the plants. Roots of *R. brasiliensis* in

Table 3. Potential quantum yield of photosystem II, F_v/F_m , predawn and of 30 min dark-adapted leaves at noon of the species studied at the different sites

Species and sites	Predawn 05:00–06:00 h	Noon 11:30–13:30 h
Restinga complex		
<i>Calophyllum brasiliense</i>		
Jurubatiba swamp forest	0.78 ± 0.06 (33)	0.71 ± 0.09 (09)*
<i>Rhedia brasiliensis</i>		
Jurubatiba swamp forest	0.73 ± 0.02 (17)*	0.76 ± 0.05 (09)*
Jurubatiba (intermediate restinga) first beach ridge		0.74 ± 0.03 (09)*
Massambaba (dry restinga)	0.67 ± 0.04 (39)*	0.66 ± 0.04 (16)*
<i>Myrsine parvifolia</i>		
Jurubatiba (intermediate restinga) first beach ridge	0.78 ± 0.02 (40)*	0.77 ± 0.03 (09)*
Jurubatiba (intermediate restinga) second beach ridge	0.79 ± 0.02 (30)*	0.78 ± 0.02 (18)*
Jurubatiba dry forest	0.79 ± 0.01 (30)*	0.79 ± 0.02 (15)*
Massambaba dry restinga	0.72 ± 0.04 (39)*	0.71 ± 0.03 (15)*
Inselberg		
<i>Stylingia dichotoma</i>		
	0.60 ± 0.08 (15)*	
<i>Croton compressus</i>		
	0.65 ± 0.02 (15)*	
Dry forest		
<i>Croton compressus</i>		
	0.72 ± 0.02 (24)*	

Values are means ± standard deviation (*n*). * Indicates values significantly smaller than 0.80 at $p < 0.05$ using Student's *t*-test.

the Jurubatiba restinga habitat contained the highest concentrations of soluble carbohydrates compared to individuals from the dry restinga and the swamp forest. In the phloem of *R. brasiliensis*, carbohydrate concentrations increased from the wettest site (swamp forest) to the driest site (dry restinga in Massambaba). Comparable patterns were observed for *M. parvifolia* where phloem carbohydrate concentrations showed a maximum in the dry restinga and for *C. compressus* where values were higher in the dry forest than on the inselberg. Lowest values were obtained in *St. dichotoma*.

The composition of soluble carbohydrates in leaves showed strong species-specific patterns (Fig. 2). While sucrose was the most abundant sugar in *C. brasiliense*, *R. brasiliensis* and *M. gardneriana* and made up about 50% in *C. compressus*, glucose and fructose dominated in *St. dichotoma*. Glucose and fructose were also dominant in leaves of individuals of *M. parvifolia* growing at the first beach ridge in the Jurubatiba restinga, whereas sucrose made up 50% and more of soluble carbohydrates in the other habitats. In the roots of all species at all sites, sucrose was the dominant soluble carbohydrate with a relative contribution between 62% and 90%. In the majority of species examined, sucrose was also the most abundant soluble carbohydrate in the phloem. However, in *C. brasiliense* and *R. brasiliensis*, both growing in the swamp forest, glucose and fructose together contributed to 82% and 63% of soluble carbohydrates. While the abundance of other soluble carbohydrates was low in leaves and roots,

myo-inositol and raffinose contributed together to up to 12% of soluble carbohydrates in the phloem.

Carbon isotope effects are due to both diffusion of CO₂, especially via stomatal pores, and to metabolic reactions and partitioning of different metabolites, e.g., from leaves to roots and wood. All $\delta^{13}\text{C}$ values detected in leaves were highly negative indicating performance of C₃ photosynthesis by all species at all sites (Table 6). Differences may be due to stomatal regulation and water-use characteristics as described above in relation to the parameters of $\Delta^{13}\text{C}$ and c_i/c_a (Table 4), derived from the $\delta^{13}\text{C}$ values. Mainly there were no important differences of $\delta^{13}\text{C}$ between different organs of the plants. For *M. parvifolia* at some of the locations values were less negative in roots and wood than in leaves (see Table 6).

Nitrogen metabolism

Our analysis of soluble non-protein nitrogen compounds alludes to some aspects of nitrogen metabolism of the plants studied at the different sites.

For the total concentrations of soluble non-protein N compounds in the various plant organs (Table 7), there were no statistically significant trends of intraspecific differences at the different sites. For the leaves there was only the clear and expected difference in shaded as compared to light-exposed plants of *M. gardneriana*. In the restinga, complex roots of *R. brasiliensis* had the

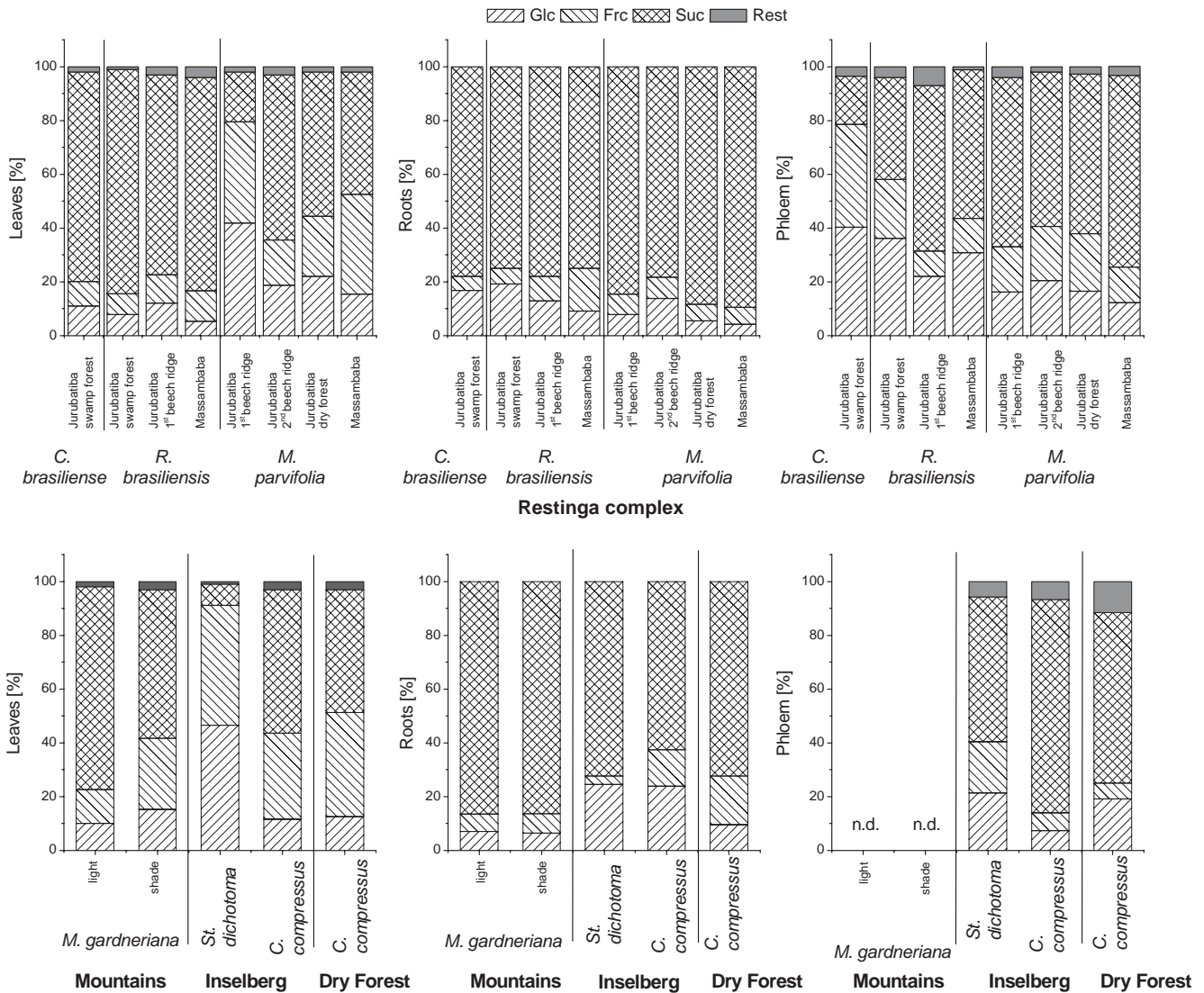


Fig. 2. Relative contributions of single sugars to total soluble carbohydrate carbon in leaves, roots and phloem of the different species studied at the different sites. Light: light exposed; shade: shaded; n.d.: not determined; Glc: glucose; Frc: fructose; Suc: sucrose; rest: sum of sugars present in trace amounts (mainly raffinose and myo-inositol).

highest levels at the first beach ridge at Jurubatiba while roots of *M. parvifolia* had the highest levels at the dry restinga of Massambaba. This was not correlated with soil nitrogen. For the restinga complex at a soil depth of 0–5 cm in the rooting zone of the plants the highest N contents (in % of soil dry weight) were found in the swamp forest at Jurubatiba, i.e., $2.1 \pm 0.3\%$, while all the other restinga soils had levels of $0.1\text{--}0.2 \pm 0.1\%$. Levels of soluble non-protein N compounds varied greatly between species. For the leaves there was a tenfold difference between the lowest and the highest levels obtained, and this factor was even larger for roots and phloem. Highest levels were found for leaves, roots and phloem in *C. compressus* and for wood in *St. dichotoma*.

In leaves from all species in the restinga complex aspartate (Asp), asparagine (Asn), glutamate (Glu),

glutamine (Gln) and alanine (Ala) were the most abundant amino compounds contributing together to 32–60% of total soluble non-protein N (Fig. 3). For comparison, a general dominance of Asp, Asn, Glu and Gln was also observed in the foliage of European beech (Gebler et al., 1998). Fotelli et al. (2002a) observed that the Gln and Asn contents in beech leaves were directly indicative for the soil nitrogen content and availability. In the present study, foliar Asn contents of all three species were also highly correlated with total soil nitrogen content ($R^2 = 0.893$; $p < 0.001$). Nitrate was not detectable in leaves, but ammonium was present in significant amounts in leaves of plants from the restinga complex. Ammonium made up ca. 30% of soluble N in leaves of *M. parvifolia* and *R. brasiliensis* at the dry restinga of Massambaba, and between 8% and 15% in

Table 4. Carbon isotope discrimination (Δ) and internal to external CO₂ partial pressure (c_i/c_a) in leaves of the species studied at the different sites

Species and sites	Δ (‰)	c_i/c_a
Restinga complex		
<i>Calophyllum brasiliense</i>		
Jurubatiba swamp forest	21.4 ± 0.4^{AA}	0.75 ± 0.02^{AA}
<i>Rhedia brasiliensis</i>		
Mean	20.5 ± 0.9^A	0.71 ± 0.03^A
Jurubatiba swamp forest	21.7 ± 0.8 ^{Aa}	0.77 ± 0.04 ^{Aa}
Jurubatiba (intermediate restinga) first beach ridge	20.4 ± 0.3 ^b	0.71 ± 0.01 ^b
Massambaba dry restinga	19.2 ± 0.1 ^c	0.66 ± 0.01 ^c
<i>Myrsine parvifolia</i>		
Mean	22.4 ± 2.4^{AB}	0.79 ± 0.09^{AB}
Jurubatiba (intermediate restinga) first beach ridge	21.9 ± 0.9 ^a	0.78 ± 0.04 ^a
Jurubatiba (intermediate restinga) second beach ridge	21.6 ± 1.2 ^a	0.76 ± 0.05 ^a
Jurubatiba dry forest	23.3 ± 1.9 ^a	0.84 ± 0.09 ^a
Massambaba dry restinga	22.4 ± 0.7 ^a	0.80 ± 0.03 ^a
Mountain		
<i>Myrsine gardneriana</i>		
Mean	24.5 ± 1.9^B	0.89 ± 0.07^B
Light-exposed	24.4 ± 1.7 ^a	0.88 ± 0.06 ^a
Shaded	24.5 ± 0.9 ^a	0.89 ± 0.03 ^a
Inselberg		
<i>Stylingia dichotoma</i>		
Inselberg	23.6 ± 0.3^{zB}	0.85 ± 0.01^{zB}
<i>Croton compressus</i>		
Mean	22.9 ± 0.7^B	0.82 ± 0.03^B
Inselberg	25.7 ± 0.6 ^{βb}	0.94 ± 0.02 ^{βb}
Dry forest		
<i>Croton compressus</i>		
	20.1 ± 0.4 ^a	0.69 ± 0.02 ^a

Values are means ± standard deviation ($n = 3-6$). Intra- and interspecific comparisons were made by ANOVA followed by Tukey HSD post-hoc test. Additional comparisons between *C. brasiliense* and *R. brasiliensis*, both from the swamp forest, and between *St. dichotoma* and *C. compressus*, both from the Inselberg, were performed applying Student's *t*-test. Different letters (a,b: intraspecific; A,B: interspecific; A,B: interspecific swamp forest; α,β : interspecific Inselberg) within columns indicate significant differences at $p < 0.05$.

leaves of plants from the other sites. A comparably high relative contribution of ammonium to total soluble N has been observed in *Fagus sylvatica* and *Picea abies* (Fotelli et al., 2002b; Geßler et al., 1998; Schneider et al., 1996) but was not related to soil ammonium or nitrate availability. It is likely that photorespiration contributes to the high amounts of ammonium (Husted et al., 2002). In leaves of *M. gardneriana*, Asn was the strongly dominating amino acid in the light-exposed plants but otherwise no specific amino acids were particularly dominant. In leaves of *St. dichotoma*, arginine (Arg) was most important and in *C. compressus*, in addition to Arg and Glu, proline (Pro) and hydroxyproline (Hpr) made larger contributions to total levels. In *C. compressus*, in the dry forest, Pro was most conspicuous while at the Inselberg Hpr was more dominant.

Soluble N of roots in the restinga complex was made up mainly of the amino acids Asn, Glu, Gln and

arginine (Arg) (60–88% of total; Fig. 3). Nitrate and ammonium contributed together to less than 10%. Glu, Gln and Arg were also important in the roots of *M. gardneriana* and *C. compressus* while in *St. dichotoma* Asn made a relatively large contribution. Nitrate and ammonium (as part of the non-proteinogenic rest) contributed to less than 2% of total non-soluble N in these species.

In the phloem of the restinga species Asp, Asn, Glu, Gln, Ala and Arg were the predominant soluble non-protein N compounds contributing together more than 80% of the total in all species and habitats (Fig. 3). In *C. compressus* in the dry forest, but much less in the Inselberg, Pro and Arg were the most outstanding amino acids, whereas γ -aminobutyric acid (Gaba) was the most abundant N compound in *St. dichotoma*.

In the woody tissue of all restinga species, Arg was the dominant soluble N compound and comprised 40–85% of total. In addition to Arg, proline was again important

Table 5. Concentrations of soluble carbohydrate carbon in different organs of the species studied at the different sites

Species and sites	mmol C g ⁻¹ FW		
	Leaves	Roots	Phloem
Restinga complex			
<i>Calophyllum brasiliense</i>			
Jurubatiba swamp forest	0.59 ± 0.03^{AC}	0.08 ± 0.04^{AA}	0.22 ± 0.02^{BB}
<i>Rheedia brasiliensis</i>			
Mean	0.87 ± 0.25^D	0.49 ± 0.13^B	0.22 ± 0.15^B
Jurubatiba swamp forest	1.02 ± 0.03 ^{aB}	0.22 ± 0.06 ^{aB}	0.12 ± 0.04 ^{aA}
Jurubatiba (intermediate restinga) first beach ridge	0.84 ± 0.20 ^a	0.88 ± 0.11 ^b	0.20 ± 0.04 ^{ab}
Massambaba dry restinga	0.74 ± 0.14 ^a	0.36 ± 0.02 ^a	0.35 ± 0.14 ^b
<i>Myrsine parvifolia</i>			
Mean	0.18 ± 0.15^A	0.25 ± 0.31^{AB}	0.21 ± 0.17^B
Jurubatiba (intermediate restinga) first beach ridge	0.15 ± 0.04 ^a	0.29 ± 0.20 ^a	0.12 ± 0.01 ^a
Jurubatiba (intermediate restinga) 2nd beach ridge	0.15 ± 0.05 ^a	0.34 ± 0.17 ^a	0.16 ± 0.09 ^a
Jurubatiba dry forest	0.24 ± 0.09 ^a	0.19 ± 0.14 ^a	0.17 ± 0.11 ^a
Massambaba dry restinga	0.19 ± 0.10 ^a	0.16 ± 0.11 ^a	0.40 ± 0.10 ^b
Mountain			
<i>Myrsine gardneriana</i>			
Mean	0.34 ± 0.06^B	0.16 ± 0.05^{AB}	
Light-exposed	0.34 ± 0.03 ^a	0.16 ± 0.04 ^a	
Shaded	0.33 ± 0.06 ^a	0.16 ± 0.03 ^a	
Inselberg			
<i>Stylingia dichotoma</i>			
Inselberg	0.14 ± 0.04^{αA}	0.32 ± 0.07^{zB}	0.04 ± 0.01^{αA}
<i>Croton compressus</i>			
Mean	0.22 ± 0.10^A	0.34 ± 0.12^B	0.24 ± 0.06^B
Inselberg	0.20 ± 0.08 ^{za}	0.27 ± 0.11 ^{za}	0.15 ± 0.04 ^{βa}
Dry forest			
<i>Croton compressus</i>			
	0.23 ± 0.06 ^a	0.41 ± 0.07 ^b	0.32 ± 0.04 ^b

Values are means ± standard deviation ($n = 3-6$). Intra- and interspecific comparisons were made by ANOVA followed by Tukey HSD post-hoc test. Additional comparisons between *C. brasiliense* and *R. brasiliensis*, both from the swamp forest, and between *St. dichotoma* and *C. compressus*, both from the Inselberg, were performed applying Student's *t*-test. Different letters (a,b: intraspecific; **A,B**: interspecific; *A,B*: interspecific swamp forest; α,β : interspecific Inselberg) within columns indicate significant differences at $p < 0.05$.

in *C. compressus* in the dry forest, and Asn and Gln occurred at higher levels in *St. dichotoma*.

Nitrogen-isotope signature showed no significant interspecific differences in leaves, roots or wood within sites of the restinga complex (Table 8), which suggests that at each site individually there are no differences in nitrogen-isotope fractionation as it might result from rooting depth, mycorrhisation, N metabolism and partitioning (Adams and Grierson, 2001; Geßler et al., 2005b). However, in the restinga complex there was a marked intraspecific variation for *R. brasiliensis* and *M. parvifolia* between sites. In both species, leaves, roots and wood were significantly ¹⁵N enriched in the dry restinga of Massambaba compared to the different sites at the Jurubatiba restinga (Table 8). This enrichment reflects differences in ¹⁵N in the bulk soil between the two sites. At the dry restinga of Massambaba soil ¹⁵N was $3.3 \pm 0.8\%$ while it was significantly

lower at all Jurubatiba sites (1.2 ± 0.2 to $1.7 \pm 0.4\%$). The high ¹⁵N values found for these two species in the dry restinga in the present study (1999), however, do not match those found by Scarano et al. (2001) for these same populations sampled 2 yr earlier (1997), in the same season. In 1997, leaves of *M. parvifolia* showed -1.9% vs. $+4.3\%$ in 1999, whereas *R. parvifolia* values were respectively $+1.3\%$ and $+4.3\%$. Intraspecific variation of this magnitude is quite surprising and indicates a wide year-to-year variation. In 1997, this dry restinga showed the largest variation in interspecific values of ¹⁵N ranging from -4.9% (*Philodendron corcovadense*, a climbing Araceae) to $+5.5\%$ (*Mollugo verticillata*, a geophyte) when compared to the other three sites. This was also surprising since variation of up to 10% within sites have been previously reported only for high-latitude systems (Högberg, 1997).

Table 6. Carbon isotope signature ($\delta^{13}\text{C}$) in different organs of the species studied at the different sites

Species and sites	$\delta^{13}\text{C}$ (‰)		
	Leaves	Roots	Wood
Restinga complex			
<i>Calophyllum brasiliense</i>			
Jurubatiba swamp forest	-28.8 ± 0.4^{AA} <u>a</u>	-27.6 ± 1.0^{AA} <u>a</u>	-27.9 ± 0.2^{AA} <u>a</u>
<i>Rheedia brasiliensis</i>			
Mean	-27.9 ± 0.9^A <u>a</u>	-27.0 ± 2.4^A <u>a</u>	-26.1 ± 1.9^A <u>a</u>
Jurubatiba swamp forest	-29.1 ± 0.8^{Ac} <u>a</u>	-27.3 ± 1.6^{Aa} <u>a</u>	-27.5 ± 0.5^{Aa} <u>a</u>
Jurubatiba (intermediate restinga) first beach ridge	-27.8 ± 0.3^b <u>b</u>	-27.3 ± 0.5^b <u>b</u>	-25.5 ± 1.8^a <u>a</u>
Massambaba dry restinga	-26.7 ± 0.1^a <u>a</u>	-26.5 ± 1.7^a <u>a</u>	-25.4 ± 0.1^a <u>a</u>
<i>Myrsine parvifolia</i>			
Mean	-29.7 ± 2.4^{AB} <u>a</u>	-26.7 ± 3.4^A <u>a</u>	-27.8 ± 1.8^A <u>a</u>
Jurubatiba (intermediate restinga) first beach ridge	-29.3 ± 0.9^a <u>b</u>	-25.5 ± 0.6^a <u>c</u>	-27.3 ± 0.1^{ab} <u>a</u>
Jurubatiba (intermediate restinga) second beach ridge	-29.0 ± 1.1^a <u>b</u>	-25.6 ± 2.7^a <u>a</u>	-27.7 ± 1.0^{ab} <u>ab</u>
Jurubatiba dry forest	-30.6 ± 1.8^a <u>a</u>	-29.5 ± 1.8^b <u>a</u>	-29.6 ± 1.5^b <u>a</u>
Massambaba dry restinga	-29.7 ± 0.7^a <u>b</u>	-26.1 ± 0.7^a <u>a</u>	-26.4 ± 0.4^a <u>a</u>
Mountain			
<i>Myrsine gardneriana</i>			
Mean	-31.7 ± 1.9^B	-31.0 ± 0.6^B	
Light-exposed	-31.6 ± 1.7^a <u>a</u>	-31.1 ± 0.5^a <u>a</u>	
Shaded	-31.7 ± 0.9^a <u>a</u>	-30.9 ± 0.6^a <u>a</u>	
Inselberg			
<i>Stylingia dichotoma</i>			
Inselberg	-30.9 ± 0.2^{zB} <u>a</u>	-31.7 ± 0.6^{zB} <u>a</u>	-31.2 ± 0.02^{zB} <u>a</u>
<i>Croton compressus</i>			
Mean	-30.2 ± 0.7^B <u>a</u>	-30.0 ± 1.4^B <u>a</u>	-30.4 ± 0.02^B <u>a</u>
Inselberg	$-32.9 \pm 0.6^{\beta b}$ <u>a</u>	-32.3 ± 0.4^{zb} <u>a</u>	$-32.2 \pm 0.4^{\beta b}$ <u>a</u>
Dry forest			
<i>Croton compressus</i>			
	-27.5 ± 0.4^a <u>a</u>	-27.7 ± 1.3^a <u>a</u>	-28.6 ± 0.5^a <u>a</u>

Values are means \pm standard deviation ($n = 3-6$). Intra- and interspecific comparisons were made by ANOVA followed by Tukey HSD post-hoc test. Additional comparisons between *C. brasiliense* and *R. brasiliensis*, both from the swamp forest, and between *St. dichotoma* and *C. compressus*, both from the Inselberg, were performed applying Student's *t*-test. Different letters (a,b: intraspecific; **A,B**: interspecific; *A,B*: interspecific swamp forest; α,β : interspecific Inselberg) within columns indicate significant differences at $p < 0.05$. Different letters a, b indicate significant differences ($p < 0.05$) between different tissues of a given species.

Discussion

Long-term intrinsic water-use efficiency (WUE)

$\Delta^{13}\text{C}$ values of dried leaf material are determined by a variety of factors, such as mode of photosynthesis, photosynthetic capacity and average stomatal width. All species were C_3 plants, and thus differences in $\Delta^{13}\text{C}$ values would be strongly determined by water availability, where lower values indicate lower average stomatal opening, lower average c_i/c_a and higher WUE (Farquhar et al., 1989a). For *R. brasiliense* ecophysiological comparison supports this expectation as $\Delta^{13}\text{C}$ decreases from swamp forest to intermediate restinga and to dry restinga. Of course, these $\Delta^{13}\text{C}$ patterns observed for *R. brasiliensis* could be influenced

by both, water and light availability (Adams and Grierson, 2001). Under light-limiting conditions, photosynthesis and, consequently, c_i depend strongly on irradiation. As a consequence, organic carbon in leaves from the shaded part of the crown of trees is generally more depleted in ^{13}C as compared to the sun-exposed crown (Leavitt and Long, 1986). Indeed, for *R. brasiliense* the site-dependent gradation of $\Delta^{13}\text{C}$ values is also correlated to the sun-plant nature of the plants as indicated by photosynthesis-saturating PAR increasing from swamp forest to intermediate restinga and to dry restinga.

In this respect it is interesting then, that for *C. compressus*, where saturating PAR did not differ between the two sites, $\Delta^{13}\text{C}$ was significantly lower in the dry forest than at the Inselberg. Thus, on the

Table 7. Concentrations of soluble non-protein N in different organs of the species studied at the different sites

Species and sites	$\mu\text{mol N g}^{-1}$ FW			
	Leaves	Roots	Phloem	Wood
Restinga complex				
<i>Calophyllum brasiliense</i>				
Jurubatiba swamp forest	6.79 ± 1.14^{BB}	8.07 ± 0.86^{AA}	4.30 ± 1.31^{AB}	51.97 ± 8.97^{BC}
<i>Rheedia brasiliensis</i>				
Mean	2.87 ± 1.30^A	8.60 ± 4.68^A	2.28 ± 0.73^A	9.51 ± 4.89^A
Jurubatiba swamp forest	2.95 ± 0.53^{aA}	7.59 ± 1.92^{aA}	4.15 ± 0.54^{bA}	16.01 ± 2.56^{bA}
Jurubatiba (intermediaterestinga) first beach ridge	3.17 ± 0.18^a	13.65 ± 4.10^b	1.49 ± 0.43^a	8.80 ± 3.97^a
Massambaba dry restinga	2.50 ± 1.16^a	4.55 ± 1.17^a	1.21 ± 0.22^a	3.74 ± 1.26^a
<i>Myrsine parvifolia</i>				
Mean	2.71 ± 1.74^A	12.91 ± 6.23^A	1.49 ± 1.54^A	22.40 ± 13.37^B
Jurubatiba (intermediate restinga) first beach ridge	3.34 ± 0.71^b	12.38 ± 2.86^b	1.19 ± 0.07^a	8.72 ± 4.18^a
Jurubatiba (intermediate restinga) second beach ridge	1.85 ± 3.89^a	12.63 ± 5.18^b	1.49 ± 1.22^a	23.58 ± 9.39^b
Jurubatiba dry forest	2.14 ± 0.54^{ab}	3.46 ± 1.27^a	1.49 ± 0.53^a	32.93 ± 6.99^b
Massambaba dry restinga	3.53 ± 1.43^b	23.17 ± 1.47^c	1.77 ± 0.77^a	24.37 ± 4.93^b
Mountain				
<i>Myrsine gardneriana</i>				
Mean	4.06 ± 1.56^{AB}	10.18 ± 2.10^A		
Light-exposed	8.24 ± 1.39^b	10.55 ± 1.57^a		
Shaded	3.95 ± 0.63^a	9.81 ± 0.98^a		
Inselberg				
<i>Stylingia dichotoma</i>				
Inselberg	8.31 ± 1.38^{zB}	21.99 ± 2.32^{zB}	0.97 ± 0.21^{zA}	47.76 ± 4.91^{BC}
<i>Croton compressus</i>				
Mean	24.83 ± 3.78^C	51.55 ± 10.20^C	15.65 ± 10.50^C	12.91 ± 8.50^A
Inselberg	$24.96 \pm 2.64^{\beta a}$	$57.75 \pm 6.14^{\beta a}$	$7.75 \pm 4.45^{\beta a}$	7.67 ± 1.59^{za}
Dry forest				
<i>Croton compressus</i>				
	24.69 ± 5.13^a	45.35 ± 7.91^a	23.37 ± 10.13^b	18.15 ± 7.81^b

Values are means \pm standard deviation ($n = 3-6$). Intra- and interspecific comparisons were made by ANOVA followed by Tukey HSD post-hoc test. Additional comparisons between *C. brasiliense* and *R. brasiliensis*, both from the swamp forest, and between *St. dichotoma* and *C. compressus*, both from the Inselberg, were performed applying Student's *t*-test. Different letters (a,b: intraspecific; A,B,C: interspecific; A,B: interspecific swamp forest; α,β : interspecific Inselberg) within columns indicate significant differences at $p < 0.05$.

inselberg *C. compressus* had a much lower WUE and operated at much higher c_i/c_a than in the dry forest. *St. dichotoma* was in between but somewhat closer to *C. compressus* on the inselberg, where it is sympatric with this species, than in the dry forest. We may expect that with the rapid run-off of water and limited soil depths on the inselberg, water availability to the plants may be an important limiting factor. However, this appears to be even more pronounced in the dry forest due to the very different precipitation regime with 1500 and 800 mm yr⁻¹ on the inselberg and in the dry forest, respectively.

In conclusion, while a comparison between species showed that they all were basically similar in their $\Delta^{13}\text{C}$, these isotope data revealed interesting site effects such as those on *R. brasiliense* in the restinga complex and the comparison of inselberg and dry forest for *C. compressus*.

Photosynthesis

As the $\Delta^{13}\text{C}$ values, ETR_{max} did not vary significantly between species. However, ETR_{max} as well as saturating PAR increased in *R. brasiliensis* in the restinga gradation of swamp forest – intermediate restinga – dry restinga and in *M. parvifolia* in the dry restinga as compared to second beach ridge and dry forest. This indicates an increased sun-plant nature of the plants in the gradations. Sun- and shade-plant nature was strongly expressed in ETR_{max} of light-exposed and shaded plants of *M. gardneriana*. *C. compressus* had lower ETR_{max} in the semideciduous dry forest than at the inselberg. These differences were less pronounced in $\Delta F/F'_m$ values.

In conclusion, it appears that the six shrub and tree species chosen for this comparison were rather similar

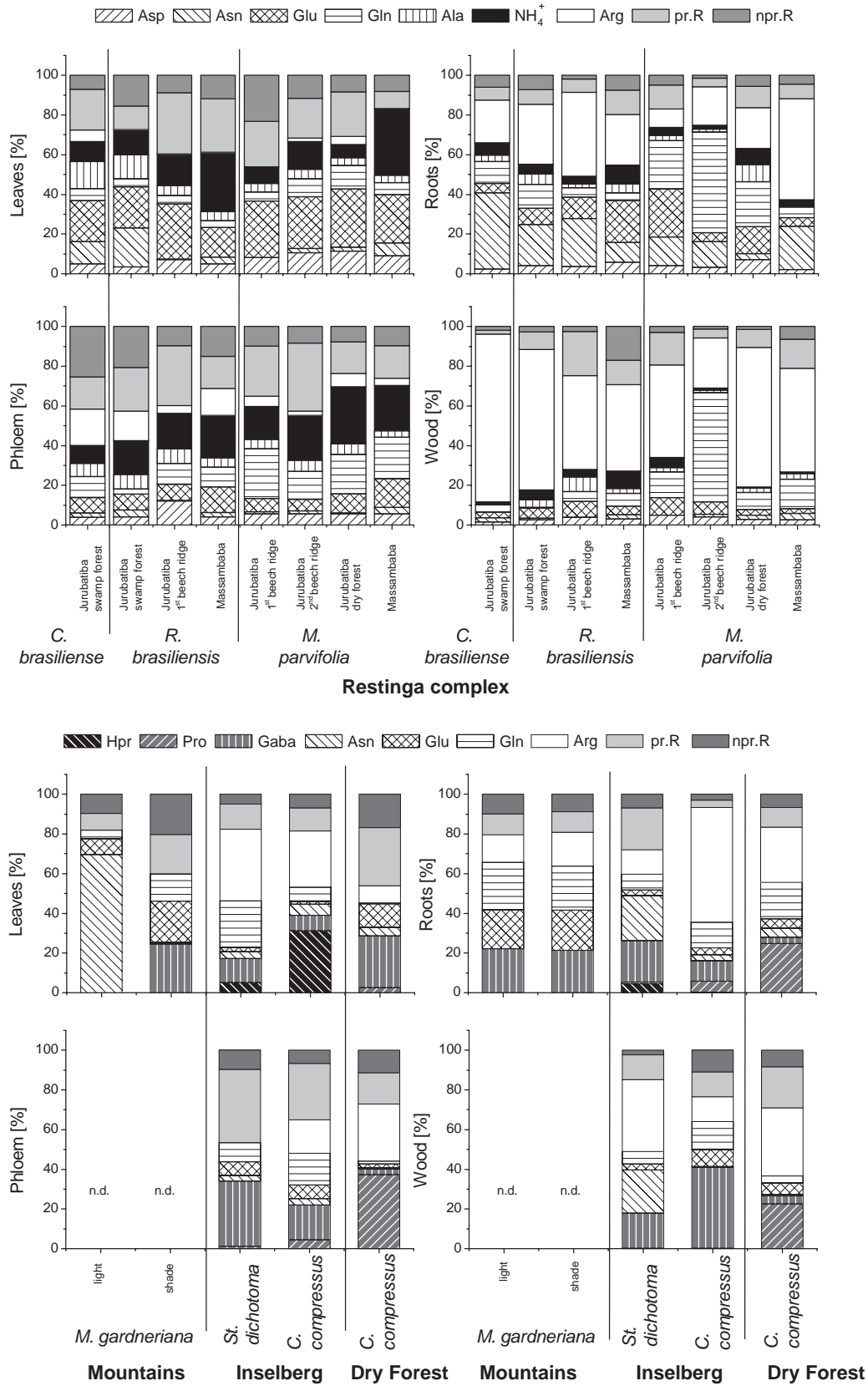


Fig. 3. Relative contribution of single amino acids and ammonium to total soluble non-protein nitrogen in leaves, roots, phloem and wood of the different species studied at the different sites. Light: light exposed; shade: shaded; n.d.: not determined; pr.R: rest of proteinogenic amino compounds; npr.R: non-proteinogenic rest; Hpr: hydroxyproline; Gaba: gamma-aminobutyric acid.

Table 8. Nitrogen isotope signature ($\delta^{15}\text{N}$) in different organs of the species studied at the different sites

Species and sites	$\delta^{15}\text{N}$ (‰)		
	Leaves	Roots	Wood
Restinga complex			
<i>Calophyllum brasiliense</i>			
Jurubatiba swamp forest	1.6 ± 0.1^{AB}	1.8 ± 0.1^{AB}	1.5 ± 0.1^{AAB}
<i>Rhedia brasiliensis</i>			
Mean	2.5 ± 0.3^B	2.4 ± 1.1^B	2.7 ± 0.4^B
Jurubatiba swamp forest	1.5 ± 0.2^{aA}	2.0 ± 0.2^{abA}	1.8 ± 0.2^{aA}
Jurubatiba (intermediate restinga) first beach ridge	1.7 ± 0.3^a	1.8 ± 0.1^a	1.4 ± 0.3^a
Massambaba dry restinga	4.3 ± 0.1^b	3.3 ± 1.0^b	4.7 ± 0.1^b
<i>Myrsine parvifolia</i>			
Mean	2.2 ± 0.5^B	2.1 ± 1.3^B	2.4 ± 0.6^B
Jurubatiba (intermediate restinga) first beach ridge	1.2 ± 0.4^a	1.3 ± 0.5^a	1.6 ± 0.1^a
Jurubatiba (intermediate restinga) second beach ridge	1.8 ± 0.3^b	1.7 ± 0.2^a	2.0 ± 0.5^a
Jurubatiba dry forest	1.6 ± 0.1^{ab}	1.8 ± 0.5^a	1.7 ± 0.3^a
Massambaba dry restinga	4.3 ± 0.1^c	3.5 ± 1.1^b	4.4 ± 0.2^b
Mountain			
<i>Myrsine gardneriana</i>			
Mean	4.3 ± 1.1^C	4.1 ± 1.2^C	
Light-exposed	4.5 ± 0.9^a	4.1 ± 0.8^a	
Shaded	4.1 ± 0.3^a	4.0 ± 1.1^a	
Inselberg			
<i>Stylingia dichotoma</i>			
Inselberg	$0.9 \pm 0.1^{\alpha A}$	$1.0 \pm 0.2^{\alpha A}$	$1.2 \pm 0.1^{\alpha A}$
<i>Croton compressus</i>			
Mean	0.9 ± 0.3^A	1.0 ± 0.5^A	1.2 ± 0.4^A
Inselberg	$0.9 \pm 0.2^{\alpha A}$	$1.1 \pm 0.3^{\alpha A}$	$1.0 \pm 0.3^{\alpha A}$
Dry forest			
<i>Croton compressus</i>			
	0.9 ± 0.2^a	0.9 ± 0.5^a	1.4 ± 0.1^a

Values are means \pm standard deviation ($n = 3 - 6$). Intra- and interspecific comparisons were made by ANOVA followed by Tukey HSD post-hoc test.

Additional comparisons between *C. brasiliense* and *R. brasiliensis*, both from the swamp forest, and between *St. dichotoma* and *C. compressus*, both from the Inselberg, were performed applying Student's *t*-test. Different letters (a, b: intraspecific; A, B, C: interspecific; A, B: interspecific swamp forest; α, β : interspecific Inselberg) within columns indicate significant differences at $p < 0.05$.

in their basic photosynthetic capacity but acclimated to site-dependent conditions.

Photoinhibition

The three species in the restinga complex showed totally different responses with regard to photoinhibition. The swamp-specialist, *C. brasiliense*, showed a typical pattern of photoprotective photoinhibition, i.e., after a midday depression of F_v/F_m at the peak of irradiance, this plant returned to optimal values overnight. This plant is one of the dominant trees in the restinga swamp forests (Henriques et al., 1986). Conversely, *R. brasiliensis*, a habitat generalist with discrete occurrence in swamps, showed F_v/F_m values below the

optimal range particularly at predawn. In the open restingas, where *R. brasiliensis* is fully exposed to high irradiance, F_v/F_m values were also below the optimal range. In the dry restinga, photoinhibition was particularly chronic. A dry spell prior to this study in 1999 has probably been partly responsible for the very low F_v/F_m values at predawn in the dry restinga. For instance, in 1997, the values found for the same population of *R. brasiliensis* also indicated photoinhibition but were in a higher range (0.71–0.75; Scarano et al., 2001) than the ones found now in the dry restinga (0.66–0.67). This could also be due to the fact that in the present study the sampled plants of *R. brasiliensis* in the dry restinga were bearing flowers and fruits, and the reproduction investment may result in lower photosynthetic efficiency. This plant also occurs in low abundance in the

open restingas (Pimentel, 2002; Zaluar, 1997). From these results, it would appear that this typical rain forest plant (Vieira, 1997) is probably not at its optimal performance at the edge of its distribution, in the more stressful conditions of open restingas and swamps. However, although maintenance costs under these circumstances may be high, this species remains capable of growing and reproducing.

The other habitat generalist, *M. parvifolia*, is also originally from the Atlantic rain forest. It seems particularly well adapted to open restingas, where it is often one of the dominant species (Pimentel, 2002; Zaluar, 1997). *M. parvifolia* showed F_v/F_m values very close to optimal throughout the range of habitats studied. Lower values were found in the dry restinga, unlike 1997 when values for this species in this site were also close to 0.8 (Scarano et al., 2001). Thus, none of the plants we measured in the dry restinga in 1999 showed predawn F_v/F_m values in the optimal range (see also Geßler et al., 2005a; Scarano et al., 2005b, for results of *Andira legalis* and *Clusia fluminensis*). This sustained depression of F_v/F_m may be the result of photodamage, but it can also represent the engagement of nocturnally retained zeaxanthin and anteraxanthin in the photoprotective down-regulation of PS II (Barker and Adams, 1997).

C. compressus was chronically photoinhibited at both of its sites and *St. dichotoma* similarly on the inselberg. Chronic photoinhibition was largest in *St. dichotoma* and smaller in *C. compressus* in the dry forest, but the difference between sympatrically growing *St. dichotoma* and *C. compressus* on the inselberg was smaller than the difference between *C. compressus* on the inselberg and in the dry forest, respectively. In a previous study in 1997 (Scarano et al., 2001), the same species of *Croton* in the same dry forest of Búzios showed similar values of ETR_{max} ($118 \mu\text{mol m}^{-2} \text{s}^{-1}$), $\Delta F/F'_m$ at $\frac{1}{2}ETR_{max}$ (0.41) and PAR at ETR_{max} ($1160 \mu\text{mol m}^{-2} \text{s}^{-1}$) as in the present investigation (Table 3). However, in the earlier study it was not photoinhibited and had predawn values of F_v/F_m of 0.84, and it was noted that photosynthetic performance was hardly affected by a strong wilted appearance of the leaves at midday. These differences may be due to different expressions of the dry season which was more pronounced in 1999 than in 1997.

In conclusion, the susceptibility to chronical photoinhibition not reversible overnight appears to be a distinctive trait of the species.

Carbon metabolites

Levels of soluble C compounds, mainly sugars, could be related to primary photosynthetic capacity but also to the secondary physiological functions of sugars in the plants. As far as we can say this from the pool sizes, no

interspecific differences in relation to photosynthetic capacity were detected. Of course, for a full assessment it also would be necessary to know dynamics, especially transport rates in the phloem. Phloem concentrations of carbohydrates may also be responsive to water relations. For example, Cernusak et al. (2003) and Keitel et al. (2003) observed that phloem sugar concentrations increased with increasing drought in *Eucalyptus globulus* and *F. sylvatica*, respectively, in order to adjust osmotic pressure in the sieve tubes. In this respect, the intraspecific site effects on soluble sugar concentrations in the phloem in *R. brasiliensis*, *M. parvifolia* and *C. compressus* appear noteworthy. Levels of soluble carbohydrate C were higher in the drier sites as compared to the wetter ones. These site effects correspond to those of photosynthetic performance and water relations discussed above.

Except for *M. parvifolia* at some of its restinga locations, there were no significant differences between $\delta^{13}\text{C}$ of leaves, roots and wood of a given species. This contrasts with the results obtained for other tree species in the ecosystems marginal to the Atlantic rain forest studied here, such as the legumes *Caesalpinia echinata*, *Caesalpinia ferrea* and *Machaerium obovatum* in the semideciduous dry forest (Geßler et al., 2005b), and the gymnosperm *Araucaria angustifolia* in the mountain site (Franco et al., 2005), as well as European *F. sylvatica* (Damesin and Lelarge, 2003; Fotelli et al., 2001). In those trees, as in some of the *M. parvifolia* plants, leaves were the most ^{13}C depleted organs. This may be due to a larger lipid content of leaves with their membrane-rich chloroplasts, because acetyl residues building up lipids are known to show a metabolic isotope effect discriminating against ^{13}C (Deniro and Epstein, 1977). Differences between organs were also absent in *Clusia* species in the restinga (Scarano et al., 2005b). For *Clusia* and the Clusiaceae *C. brasiliense* and *R. brasiliensis* studied here as well as the Euphorbiaceae *St. dichotoma* potential differences between leaves and the other organs might be masked by the strong latex production in all parts of the Clusiaceae when hydrocarbon chains of latex molecules are synthesised from acetyl residues.

In conclusion, for the ecophysiological perspective there are no major distinctions that could be based on soluble C-compound levels. However, there are some subtle intraspecific responses which appear to be related to environmental parameters such as availability of water.

Nitrogen metabolites

While there were large differences between total soluble non-protein N compounds between species, there were no apparent ecophysiological relevant intraspecific responses in relation to sites. The presence

of arginine (Arg) and proline (Pro) may be most interesting from an ecophysiological perspective. Pro is a solute frequently accumulated in plants in response to osmotic stress and drought (Ain-Lhout et al., 2001; Geßler et al., 2005a, b; Heuer, 1994; McNeill et al., 1999; Samaras et al., 1995). Arg is often considered to be an N storage compound that is accumulated under conditions when N uptake surpasses N demand of plants (Geßler et al., 1998; Nordin et al., 2001). However, Arg has also been observed to accumulate together with proline as a consequence of salt stress or drought (Cramer et al., 2002). As water supply decreased, Fotelli et al. (2002b) observed a significant increase of Arg exclusively in the roots of beech.

In *C. compressus* in all plant parts measured, Pro levels were much higher in the dry forest than at the inselberg. This agrees with the conclusion made above based on the carbon isotope data that *C. compressus* was more drought stressed in the dry forest than on the inselberg. Arg was mainly responsible for the high levels of soluble non-protein N in the roots of *M. parvifolia* in the dry restinga contributing more than 50% of total, and in the roots of *R. brasiliensis* at the first beach ridge compared to its other two restinga sites. The high concentration of total soluble nitrogen in the wood of *C. brasiliense* also mainly consisting of Arg confirms the assumption that this species is well N supplied in the swamp forest, where soil N-levels were highest. The high levels of soluble N in the wood of *St. dichotoma* were also mainly due to Arg.

In conclusion, there are some specific species responses, such as for Pro in relation to water stress in *C. compressus* and for Arg in relation to N supply. These site effects allow some fine-tuned ecophysiological comparisons. However, from N metabolism assessed by comparing total soluble non-protein nitrogen compounds, amino acid patterns and $\delta^{15}\text{N}$ values, largely no conspicuous differences for species performance in the ecosystems are emerging.

Ecophysiological performance related to the community level

As noted in the Introduction, the two Clusiaceae studied in the restinga complex differ in that *C. brasiliense* is a wetland specialist, while *R. brasiliensis* is a generalist, occurring in wetlands but also in rain forests and open, exposed sites of the restingas. In the swamp forest, the specialist appeared to be better adapted to withstand high-irradiance stress. This is well supported by the observation that the generalist had lower predawn F_v/F_m , ETR_{max} and lower saturating PAR in the swamp forest, i.e., less pronounced sun-plant characteristics. The other generalist, *M. parvifolia* overall had a somewhat superior performance over the

other two species. It was better protected against photoinhibition and had higher photosynthetic capacity. Compared with the other generalist, *R. brasiliensis*, it also showed better photosynthetic accomplishment in the open, exposed, unflooded restinga sites. Both generalists resembled each other in that they were more strongly photoinhibited at the dry restinga site, although this was also the site where both species had their highest ETR_{max} and saturating PAR, i.e., higher sun-plant characteristics. Nevertheless, *R. brasiliensis* shows an increase in intrinsic WUE as habitat conditions get drier, whereas *M. parvifolia* does not vary between sites. Thus, it would appear that the more generalist Clusiaceae resorts to distinct ecophysiological behaviour in all sites where it occurs; however, these distinct behaviours are similarly conservative.

Of the two Euphorbiaceae studied, phytogeographically *St. dichotoma* is restricted to inselbergs while *C. compressus* has a larger ecophysiological amplitude. In many aspects performance of *St. dichotoma* and *C. compressus* was similar on the inselberg, and in cases where there were large intraspecific differences for *C. compressus* between the inselberg and the dry forest sites, these were more pronounced than the interspecific differences between the two different species on the inselberg, e.g., intrinsic WUE and photoinhibition. The higher ecophysiological amplitude of *C. compressus* requires ecophysiological plasticity. This is borne out by the data obtained. Although it was evidently more drought stressed in the dry forest than on the inselberg it could cope well with this situation by physiological adaptations at the leaf level with higher long-term intrinsic WUE, and by higher protective production of proline. In the stressed situation in the dry forest the plants of *C. compressus* even showed somewhat lower chronic photoinhibition.

Notwithstanding the very different conditions at 2000 m a.s.l. in the high mountains, the overall performance of *M. gardneriana* was quite similar to that of the shrub species at the lowland sites.

Conclusions

In conclusion, from the wealth of data collected, some overall trends could be detected that relate to the three questions posed. First, generalists and specialists did not always differ in ecophysiological behaviour: for instance, while widespread generalists such as *M. parvifolia* and *C. compressus* were ecophysiological versatile, *R. brasiliense* appeared to perform below optimum in all sampled sites. This pattern agrees with the results found in some of our previous studies within this vegetation complex (Scarano et al., 2001, 2005b). Second, and more expectedly, light and water availability were abiotic

factors which apparently explained most of the intra- and/or interspecific variation found. Third, ecophysiological responses and variation were often more clearly related to individual species rather than to taxonomic affinities in higher hierarchies (family, genus) or habitat. Thus, these results are further evidence that the reportedly high floristic diversity of these vegetation types (Scarano, 2002) is matched by a high ecophysiological diversity and plasticity (see also Lüttge and Scarano, 2004), which shall be of relevance in a global change scenario.

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