PLANT MORPHO-PHYSIOLOGICAL VARIATION UNDER DISTINCT ENVIRONMENTAL EXTREMES IN RESTINGA VEGETATION

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ABSTRACT

(Plant morpho-physiological variation under distinct environmental extremes in restinga vegetation) This paper is a synthesis of over ten years of research on inter- and intra-population variation in morpho-physiology of six plant species at the Jacarepiá restinga: the shrubs *Alchornea triplinervia*, *Andira legalis, Clusia fluminensis* and *Myrsine parvifolia*, the bromeliad *Aechmea maasii* (formerly identified as *Aechmea bromeliifolia*, now recognized as a species only found in Central Brazil) and the geophyte palm *Allagoptera arenaria*. Individual shape, stature and growth, leaf anatomy, photoinhibition, and carbon, nitrogen and water use were the main parameters studied. The isolated study of intra-specific variation in one or a few of the above-mentioned traits often does not allow a distinction between acclimation and stress symptoms. Thus, we used an approach that integrated morphology, anatomy, physiology and also population parameters. Variation in morphological, anatomical and physiological traits was found for the majority of these species, and often indicated great acclimation capacity to distinct environmental extremes. This acclimation capacity may be partly responsible for the broad colonization success of extreme habitats in restingas, by species often originating in mesic forest environments. This phenomenon is an additional element to be accounted for as an important component of the high biodiversity of the Atlantic forest complex. Finally, we discuss implications for biodiversity conservation of intra-specific variation at the population level.

Key words: acclimation, clonal growth, intraspecific variation, leaf anatomy, photoinhibition, restinga.

RESUMO

(Variação morfo-fisiológica em plantas sob distintos extremos ambientais em vegetação de restinga) Este trabalho é uma síntese das informações obtidas em mais de dez anos de pesquisas sobre variação morfo-fisiológica entre populações e dentre indivíduos de uma mesma população para seis espécies da restinga de Jacarepiá: os arbustos *Alchornea triplinervia*, *Andira legalis, Clusia fluminensis* e *Myrsine parvifolia*, a bromélia *Aechmea maasii* (anteriormente identificada como *Aechmea bromeliifolia*, que agora é como são denominadas plantas ocorrentes no Brasil central) e a palmeira geófita *Allagoptera arenaria*. Forma, porte e crescimento de indivíduos, anatomia foliar, fotoinibição da fotossíntese e uso de carbono, nitrogênio e água foram os principais parâmetros estudados. Com freqüência, a análise isolada da variação de um desses parâmetros não permite distinguir aclimatação de sintoma de injúria. Logo, os estudos aqui revisados apresentam uma abordagem que integra os diferentes parâmetros auto-ecológicos mencionados, assim como estes a parâmetros populacionais. Variação em caracteres morfológicos, anatômicos e fisiológicos foi detectada para a maioria destas espécies e, em geral, apontou para uma grande capacidade de aclimatação das mesmas a distintas circunstâncias ambientais. Tal capacidade de ajuste deve ter sido essencial para que várias destas espécies, na maioria oriundas de ambientes florestais, pudessem vir a colonizar um ambiente extremo como as restingas. Esta mesma capacidade é um elemento a mais a ser contabilizado como componente da grande biodiversidade existente no complexo vegetacional atlântico. Por fim, discutimos as implicações para conservação da biodiversidade da variação intra-específica encontrada ao nível populacional.

Palavras-chave: aclimatação, anatomia foliar, crescimento clonal, fotoinibição, restinga, variação intra-específica.

Artigo recebido em 05/2008. Aceito para publicação em 02/2009.

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INTRODUCTION

Coastal habitats are subjected to a myriad of environmental factors that are often limiting to the survival of many plant species, such as salinity, desiccation, oligotrophy, burial, flooding, high temperature and solar radiation, and large daily thermal amplitude (Crawford 2008). These factors vary in intensity and frequency in time and space, which results in the formation of a habitat mosaic. Thus, each of these habitats has a flora that is largely determined by the combination of locally predominant abiotic features. Brazilian restingas, i.e. vegetation mosaics that grow on sandy coastal plains of Quaternary origin, display, side by side, distinct environmental extremes that harbour plant communities ranging from terrestrial to aquatic, and from reptant herbs to forests. Paradoxically, this combination of limiting factors has not prevented the establishment and fixation of high species richness and a diversity of life forms in the Brazilian sandy coastal plains (*e.g.*, Pereira & Araujo 2000). Structural complexity and biological diversity may, in some cases, be comparable to tropical rainforests (*e.g.*, Pimentel *et al*. 2007).

Marine regression and transgression movements have gradually shaped the restingas of southeast Brazil over the past 100,000 years (Martin *et al*. 1993), and these sandy coastal plains are currently covered by vegetation where species also found in the adjacent rainforest predominate (Araujo 2000). Thus, as predicted by Hubbell's neutral theory (Hubbell 2001), the high richness of the regional species pool (*i.e*., the Atlantic rainforest) must have determined the large number of potential immigrants, which over long periods of time since the Pleistocene, possibly increased the chances of colonization of the sandy marine deposits. It remains puzzling nevertheless that many plant species originating in a mesic forest environment have become successfully established in these geologically younger coastal areas. Moreover, despite the marked environmental differences between restinga and rainforest, there are still very few cases of endemism in the restinga flora, which means that speciation processes in the restinga environment have not taken place in a significant proportion. In order to understand why this is so, clearly a combination of ecological and evolutionary studies would be needed.

Our group has focused mostly on ecological studies within a niche perspective that provided evidence showing that, for a restinga vegetation type common in the state of Rio de Janeiro (SE-Brazil), facilitation processes could partly explain local plant diversity (Scarano 2002, 2009; Dias & Scarano 2007). Facilitation in this vegetation type consists of a process whereby a few key species create vegetation islands that offer regeneration niches similar to those found in forests, which in turn attenuate environmental filters imposed by these coastal habitats. However, these facilitation studies took place in one among many restinga vegetation types, and are therefore insufficient to explain diversity in the restingas alone. Another possible line of investigation was forwarded by Scarano (2002), who speculated that rainforest - originated colonists of the restingas should consist of a pool of highly environmentally plastic species. Recent studies on ecological fitting in plant communities by species with phenotypically flexible genotypes (Agosta & Klemens 2008) point to the potential relevance of pursuing such a line of study to provide a deeper understanding of colonization and diversity of restinga vegetation. Along with plant genotypic vs. phenotypic plasticity, data on dispersal processes and breeding barriers, largely unavailable to date, shall prove necessary to enhance knowledge on plant biogeography of the restingas.

This paper reviews evidence *potentially* related to phenotypic flexibility of six plant species that occur in the restinga of the Jacarepiá State Ecological Reserve, Saquarema municipality, Rio de Janeiro state, southeast Brazil. The word *potentially* is highlighted because the data reviewed refer to morpho-physiological variation at the population (intra- or inter-) level in the field, whereas phenotypic plasticity is an *individual* property rather than a *population* property, i.e. it is the capacity of a given *individual* to adjust its morpho-anatomy or physiology according to the situation in which it finds itself (Pigliucci 2001). Thus, it remains to be seen whether or not the variation found at the population level for our study species results from phenotypic plasticity at the individual level. The fact that some of the classic studies on 'phenotypic plasticity' have been performed on populations, families or higher taxonomic groups (see discussion in Fuller 2003) suggests that the variation found in the plants examined here shall provide a solid background for future plasticity studies. Nevertheless, and perhaps more importantly, we will focus less on the uncertainty concerning the evolutionary triggers of the intra-specific variation found or the epistemological problems surrounding the concept of phenotypic plasticity and more on the possible implications of such variation for conservation of restinga flora and in particular, our study site.

VARIATION AND PHENOTYPE

Before we discuss the case studies of morpho-physiological variation at the Jacarepiá restinga, it is important to define the scope of two concepts widely used in this paper, i.e. *variation* and *phenotype*. Variation is used here in the sense of *phenotypic variation* and regards morpho-physiological differences detected between individuals of a given population or between individuals of distinct populations of a given species. Thus, while both situations are intra-specific, the former is within-population while the latter is between-populations. Short-term responses to natural selection depend on within-population variation (Schlichting & Pigliucci 1998). It is also important to highlight that, for a given species, a broad between-population phenotypic variation does not necessarily mean that large phenotypic variation should also be found within each population separately.

The *phenotype*, according to Schlichting & Pigliucci (1998), results from the interaction of three components: (*i*) phenotypic plasticity (genetically-mediated responses to environmental variation); (*ii*) epigenetics (set of processes that propagate phenotypic traits throughout development; such processes derive from indirect effects of genetic activity and of non-genetic phenomena such as hormonal activity); and (*iii*) allometry (the way by which various internal and external responses are coordinated to produce a coherent whole). Thus, each morphotype of the species studied is the result of a smaller or larger contribution of each of these three components.

STUDY SITE AND SPECIES

The Jacarepiá State Ecological Reserve has an area of 12.5 km^2. This reserve is an integral part of the Massambaba Environmental Protection Area, with some 600 species of vascular plants distributed in 118 families along, at least, ten distinct restinga vegetation types (Araujo *et al.* 2009). Table 1 shows a comparison of climatic and vegetation features of Jacarepiá with other restingas mentioned in this paper. Table 2 lists the six species that were studied in Jacarepiá in regard to morpho-physiological variation and survival strategies. The choice of these species was related to the fact that they belonged to distinct life-forms (herbs, shrubs, trees) or represented distinct modes of photosynthesis (C_3, CAM). As is often the case for restinga species, all species studied are also common to forest habitats or other restingas.

Among the woody plants studied, *Alchornea triplinervia* (Spreng.) Müll. Arg. is found in seasonally flooded forests (*várzeas*) in the Amazon, gallery forests of Central Brazil, montane and lowland Atlantic rainforest, and swamp forests within rainforest lowlands or in the coastal restingas, spreading to Rio Grande do Sul state in southern Brazil (Rôças *et al.* 1997). *Myrsine parvifolia* A. DC. also has a broad

Table 1 – Main characteristics of the study sites and denotations used throughout the text. Open restingas have a patchy structure and 'cover' indicates the percentage of terrain covered by vegetation. The wet restinga is closer to the sea and the dune forest further inland.

Location	**Habitats**	**Rainfall (mm/year)**	**Water table**	**Vegetation structure**		**Denotation**	**References**
				Cover (%)	**Height (m)**		
Massambaba Environmental Protection Area (22°56'S, 42°13'W)	Open restinga	800	High (0.9–1.2 m), partly saline	30	3–4	Dry restinga	Scarano *et al.* (2001; 2005a); Duarte *et al*. (2005)
Restinga de Jurubatiba National Park (22°23S, 41°45W)	Open restinga	1164	Low (2–3 m)	50	5–6	Intermediate restinga	Duarte *et al*. (2005); Scarano *et al*. (2005a)
Jacarepiá State Ecological Reserve (22°47S, 42°20W)	Open restinga	1000	High (0.5–1.0 m)	70	2–3	Wet restinga	Cirne & Scarano (2001); Scarano *et al.* (2001; 2005a); Duarte *et al.* (2005)
	Restinga forest		Low (2–6 m)	100	15–20	Restinga forest	

Table 2 – Study species at Jacarepiá and traits measured as regards intra-specific variation: leaf and whole-plant morphology, leaf anatomy (structure –S and ultrastructure – U), plant physiology (chlorophyll *a* fluorescence –fluor.; stable isotopes: carbon –C and nitrogen-N), clonal growth and respective references.

	Morphology		**Leaf anatomy**		**Leaf physiology**			**Clonal growth**	**References**
Species	**Plant**	**Leaf**	**S**	**U**	**C**	**N**	**Fluor.**		
Aechmea maasii Gouda & W. Till (Bromeliaceae)	✓	✓	✓	-	✓	-	✓	✓	Scarano *et al.* (2002)
Alchornea triplinervia (Spreng) Müll. Arg. (Euphorbiaceae)	✓	✓	✓	✓	-	-	-	-	Barros (1998); Rôças *et al*. (1997, 2001)
Allagoptera arenaria (Gomes) Kuntze (Arecaceae)	-	-	-	-	✓	✓	✓	-	Scarano *et al.* (2001)
Andira legalis (Vell.) Toledo (Fabaceae)	✓	-	✓	-	✓	✓	✓	✓	Cirne & Scarano (2001); Cirne *et al*. (2003); Scarano *et al*. (2001); Geβler *et al.* (2005); Pereira *et al*. (2009)
Clusia fluminensis Planch & Triana (Clusiaceae)	-	-	-	-	✓	✓	✓	-	Scarano *et al*. (2001, 2005a)
Myrsine parvifolia A. DC. (Myrsinaceae)	-	-	-	-	✓	✓	✓	-	Scarano *et al*. (2001, 2005a)

geographic range throughout the neotropics, where it occurs in various habitat types. *Andira legalis* (Vell.) Toledo is restricted to coastal vegetation from southeast to northeast Brazil (Rio de Janeiro, Espírito Santo, Bahia and Ceará states), in both forest and open habitat types. *Clusia fluminensis* is restricted to southeast Brazil, where it is found in forests, in open restingas and on rocky outcrops (Scarano *et al*. 2001). Finally, two plants that belong to the herb layer are covered by the studies revised here: *Aechmea maasii* is geographically restricted to restingas and coastal forests in southeast Brazil, from northern Rio de Janeiro to Espírito Santo (Faria 2006); and *Allagoptera arenaria* is a strictly coastal palm occurring in restingas and on sandy soils up to 100 m altitude in the states of Bahia, Espírito Santo and Rio de Janeiro (Morais 1996).

PHENOTYPIC VARIATION: RESTINGA SPECIES

Shape and size

Shape and size variations within and between populations are possibly the easiest to observe. At Jacarepiá, the woody plants *Alchornea triplinervia* and *Andira legalis*, and the tank bromeliad *Aechmea maasii* were studied in this respect. Four distinct populations of *Alchornea triplinervia* in three different plant communities (montane forest, swamp forest and open, flooded restinga) within the Atlantic forest complex of Rio de Janeiro state were compared and ranged from treelets 3–5 m tall with small (5–10 cm long), green-yellowish leaves, in sun-exposed, flooded conditions at Jacarepiá, to 15–20 m tall trees, with large (20–25 cm long), dark-green leaves in the montane forest (Rôças *et al*. 1997, 2001). *Andira legalis* is a striking example of within-population variation. In a restinga forest in Jacarepiá, under shaded conditions, *Andira* plants are trees reaching 5–6 m in height, however, on an adjacent spit of sandy soil, fully-exposed, they are shrubs reaching a maximum height of 1.5 m (Cirne & Scarano 2001). In another restinga (Restinga de Jurubatiba National Park), some 200 km north, *Andira* shrubs reach up to 2.9 m tall (unpublished data).

There are many reports of morpho-physiological variation within and between bromeliad species (e.g., Martin 1994; Zotz *et al*. 2004; Barbará *et al*. 2007) and *Aechmea maasii* is no exception. It displays both within- and between-population variation in size and shape for four distinct populations at Jacarepiá, mostly in regard to rosette height and ground cover. In the two forest habitats (a swamp forest and a dry forest) rosettes were greener and larger in height and ground cover than in the two open habitats (marsh and open restinga; Scarano *et al.* 2002). This variation implies that sun-plants avoid direct incidence of sunlight on most of the leaf area and simultaneously store larger quantities of rain water in the central tank. Shade-plants, with a broader rosette canopy area, have a greater chance of acquiring sun radiation in the forest environment by reducing leaf overlap.

Clonal growth

Clonal growth is the capacity some plant species have of growing horizontally while vegetatively producing modular units, called *ramets*, which are genetically similar and potentially independent from the mother-plant. The resulting growth pattern (organ from which the ramet originated, number of branches, ramet density, distance between ramets, *etc*.) frequently reflects plant foraging strategy for resource capture (Macek & Lepš 2003). Ramets remain connected physically and functionally to the mother-plant for at least part of their life-cycle and, once established, they may form new units. For these plants, the period of integration with the mother-plant is related to a higher capacity to exploit, store and rapidly mobilize limited resources, which often confers significant advantages to the occupation of heterogeneous or stressful habitats. When ramet separation takes place, this process is known as asexual reproduction, where the new individual is genetically identical to the mother-plant (see review in Hutchings & Kroon 1994).

Many restinga species have clonal growth and asexual reproduction, which has often been related to persistence (Araujo & Peixoto 1977), colonization after disturbance (Cirne & Scarano 2001) and population growth of plants where sexual reproduction is irregular (Sampaio *et al*. 2005). At Jacarepiá, ramet (*i.e.*, tank-forming rosettes) distribution of *Aechmea maasii* was related to light regime (Scarano *et al*. 2002). Two sun-exposed populations (maximum values of photon flux density – PFD – reach up to 2500 mmol m^{-2} s^{-1} in the summer) formed island-shaped colonies of various sizes, well separated from one another. Two shade populations (PFD = 5–100 mmol m^{-2} s^{-1}), on the other hand, showed ramet confluence to an extent that these bromeliads often covered the soil entirely. Light quality strongly affects morphology and foraging behaviour of clonal plants: light environments favour a greater number of branches, which results in intensive foraging, whereas shade favours linear expansion of ramets and extensive foraging (Kroon & Hutchings 1995).

While in *Aechmea maasii* clonal growth variation might have maximised the efficiency of resource capture in different habitats, for the legume shrub *Andira legalis* this same feature has not only favoured persistence but was also related to rapid demographic growth after disturbance. In one of the four habitats where *Aechmea maasii* was also found at Jacarepiá (sun-exposed, nonflooded), a population of c. 90 individuals of *Andira legalis*, within 0.3 ha, increased three-fold after a manmade fire (Cirne & Scarano 2001; Cirne *et al*. 2003). Although fire is an extreme alien type of disturbance in restingas, both *Andira legalis* and *Aechmea maasii* were considerably resistant. Moreover, the former had rapid, prolific resprouting after fire. Plants with different numbers of connected, resprouted ramets were equivalent in average size to new ramets two years after the fire (Cirne & Scarano 2001). This pattern revealed that mechanisms of individual regulation and physiological integration between ramets were present. This is related to a reduction or total absence of competition between ramets, unlike the common pattern of intraspecific competition reported for the seed-originated offspring of many plant species (Pennings & Callaway 2000).

Kruger *et al.* (1997) explained that between areas with distinct light regimes there is often a trade-off between resource allocation for seed production and apical growth *vs*. ramet production and horizontal growth via maintenance and protection of a bud bank. In the case of *Andira legalis*, indeed, forest individuals are erect trees and there was no evidence of ramet profusion in a single plant, as opposed to the contiguous sun-exposed habitat. This capacity to allocate resources differentially under distinct environmental regimes is expected to confer advantages in regard to foraging efficiency for limiting resources.

The relevance of clonal growth plasticity to maintenance and expansion of populations of *Aechmea maasii* and *Andira legalis* is further highlighted by the fact that in 10 years of observation no plant recruitment from seeds has been observed although annual fruit production was observed in the former and supra-annual production in the latter.

Leaf anatomy

Comparative leaf anatomy studies were carried out in (1) *Aechmea maasii* (Scarano *et al*. 2002), for four populations under distinct environmental regimes (different combinations of light and flooding regimes), all of which were inside our study site; (2) *Alchornea triplinervia* (Rôças *et al.* 2001), for five distinct populations along gradients of altitude, light regime and flooding, including two locations in our study site; and (3) *Andira legalis* (Pereira *et al.* 2009), along a forest-open restinga gradient in our study site. For all three species, between-population variation in leaf anatomy was large.

Two shaded populations of *Aechmea maasii* plants did not differ from each other, irrespective of flooding regime, and had lower stomatal density at leaf base and mid-section when compared to sun-exposed plants. Sun-exposed/flooded plants showed the highest values of width and number of cell layers in the chlorophyll parenchyma and stomatal density, both at leaf base and mid-section. Sun-exposed/unflooded plants showed the lowest values for this parameter. Interestingly, the latter population also showed the lowest values of width and number of cell layers of water parenchyma, which suggests stress and malfunction (see Tood *et al.* 1974) since light acclimation is related to an increase in mesophyll width (chlorophyll + water parenchyma; *e.g.*, Chazdon & Kaufmann 1993). Since the sun-exposed/flooded population had greater mesophyll width, it is likely that stress in the sun-exposed/nonflooded population might have been due to a combination of sun exposure and drought.

Alchornea triplinervia was found in two distinct habitats at the study site, semi-exposed/flooded and exposed/nonflooded. Leaf anatomy was compared for these two cases, as well as for plants sampled elsewhere in shaded, nonflooded hillside forest and in a swamp forest (Rôças *et al.* 2001). Plants from the two populations at the study site differed from each other in terms of quantitative leaf-anatomy parameters, most likely related to differences in light regime, but showed marked qualitative differences when compared to forest plants. Study site plants had anticlinally elongated cells in the bottom layer of the spongy parenchyma, which resulted in the formation of a palisade layer by the abaxial epidermis thus constituting an isobilateral mesophyll. Plants from the forest populations had a dorsiventral mesophyll. Leaves that develop under high light incidence are indeed known to be thicker and to present well-developed palisade cells (*e.g.*, Brooks *et al.* 1996). Moreover, the columnar shape of these cells facilitates light penetration in the spongy parenchyma (Vogelmann & Martin 1993). Epidermal cells were also studied in more detail for these populations so as to assess phenotypic variation at the ultrastructural level (Barros 1998). These cells perform important functions related to transpiration restriction, to protection against excessive radiation and to the direction of light incidence to photosynthetic tissue. Sun-exposed plants had wider outer epidermal cell walls, particularly in the wall regions impregnated with cutin (cuticule and cuticular strata), while the wall regions richer in polysaccharides did not differ significantly. These results suggest greater restriction for transpiration in the sun-plants (*e.g.*, Riederer & Schreiber 2001). The outer periclinal epidermal cell walls of sun-exposed plants were flat and the epicuticular wax was granular, whereas outer epidermal cell-walls of shade plants were convex and the epicuticular wax was smooth with no ornamentation. Increased light intensity is related to the occurrence of flat outer periclinal epidermal cell walls and to various forms of epicuticular wax, which confer to the epidermis important reflexive traits that prevent chloroplast photo-oxidation (Juniper & Jeffree 1983). Convex cells are related mainly to light convergence towards the chlorophyll tissue, particularly in shade plants that need to use the diffuse light of the forest understorey (Vogelmann & Martin 1993).

Leaf anatomy variation in *Andira legalis* was examined at a very small spatial scale (0.5 ha) by comparing plants of two distinct but adjacent light environments: dense forest (shaded) and contiguous palm scrub (sun-exposed) (Pereira *et al.* 2009). Anatomical features (leaf and mesophyll thickness, thickness of the outer periclinal cell wall, thickness of the adaxial and abaxial epidermis and vascular bundle transverse section area, and also common epidermal cells, and stomata density), except for trichome density, and morphological parameters (leaf specific mass and succulence) were significantly higher for sun-exposed plants. Less expected, however, was the marked qualitative difference between exposed and shaded plants: in the former the mesophyll had unilateral symmetry (*i.e.*, the entire mesophyll occupied by photosynthetic tissue), whereas in the latter there was a dorsiventral symmetry (*i.e.*, partly palisade and partly spongy parenchyma).

Photoinhibition of photosynthesis

The modern techniques available for *in situ* measurements of photosynthesis and photoinhibition by portable high-precision equipment (see review in Schreiber *et al.* 1995) have allowed rapid quantitative and qualitative advances in ecophysiological knowledge about plants in the restingas and other vegetation types adjacent to the Atlantic rainforest (see review in Scarano *et al.* 2005a). At our study site, a number of studies have been conducted on plant chlorophyll *a* fluorescence, which is ultimately indicative of plant vigour since it allows assessment of parameters such as photoinhibition and electron transport rate (for review see Demmig-Adams & Adams 2006). Five of the six species (*Alchornea triplinervia* was the sole exception) reviewed in this paper were studied as regards chlorophyll fluorescence parameters: (1) variation between distinct populations at distinct habitats within our study site was assessed for *Aechmea maasii* (Scarano *et al.* 2002) and *Andira legalis* (Scarano *et al.* 2001; Geβler *et al.* 2005); (2) variation between distinct populations at different study sites (Jacarepiá vs. other restingas) was examined for *Allagoptera arenaria*, *Clusia fluminensis* and *Myrsine parvifolia* and also for *Andira legalis* (Scarano *et al.* 2001, 2005b).

The values of potencial quantum efficiency of photosystem II (measured as the rate of variable to maximal fluorescence, *i.e.* F_v/F_m), in the case of *Aechmea maasii*, were in harmony with the leaf anatomy results described above, *i.e.* the sun-exposed/nonflooded population showed symptoms of stress as indicated by *Fv/Fm* values always below optimal (0.83, *i.e.* 83% of efficiency, according to Björkman & Demmig 1987). After a marked midday depression (c. 0.6), the rest of the day and night showed no recovery to optimal values until the early morning hours of the following day (c. 0.7), which is an indication of chronic photoinhibition in this population. The sun-exposed population, which was flooded, performed better than the nonflooded plants although values were also below optimal (next morning values: c. 0.75). Osmond (1994) calls this reversibility in photoinhibition status 'dynamic photoinhibition', which he defines as a protective mechanism of the plant photosynthetic apparatus. The two shaded populations showed no decrease in *Fv/Fm* throughout the day and maintained high photochemical efficiency. Thus, although this species is a CAM plant (crassulacean acid metabolism, see next section), *i.e.*, plants that are frequently associated with extreme conditions of excess light and water restriction where photoinhibition is often low (Griffiths *et al.* 1989), it was photoinhibited for most of the day in the dry, sun-exposed conditions of Jacarepiá. Therefore, along with many other species of the Bromelioideae subfamily, *Aechmea maasii* can be classified as a shade-adapted CAM plant.

In the case of *Andira legalis*, at Jacarepiá, forest plants, as expected, showed *Fv/Fm* values closer to optimal than sun-exposed plants that were chronically photoinhibited since they showed values lower than optimal throughout the day (Geβler *et al.* 2005). Interestingly, in other restingas where *Andira legalis* is subjected to drier conditions (less rainfall; see Table 1) values were higher and plants displayed a more dynamic and reversible photoinhibition. *Allagoptera arenaria* and *Myrsine parvifolia* showed an opposite trend of more readily reversible photoinhibition in Jacarepiá than in two other study sites with drier conditions (Scarano *et al.* 2001), which, in the case of the latter, was later confirmed by another gradient study (Duarte *et al.* 2005).

Clusia fluminensis consistently showed lower intrinsic and instantaneous photosynthetic capacity in dry restinga and in a semideciduous dry forest at Búzios municipality, when compared with wet restinga (Scarano *et al.* 2005b). This was partly correlated with soluble carbohydrate content in the leaves which was lowest in dry forest, intermediate in dry restinga and highest in wet restinga. Significantly higher photoinhibition was found also in dry restinga as compared to the other two sites, confirming previous results (Scarano *et al.* 2001). Rainfall and moisture regime could therefore be a strong limiting factor for the photosynthetic behaviour of this species. Arraial do Cabo municipality, where the dry restinga is located, is the driest part of Rio de Janeiro state (Araujo 1997) and is also the northern limit of the distribution of *C. fluminensis*.

Water-, carbon- and nitrogen-use

Carbon and nitrogen isotope analyses were carried out on leaves of *Allagoptera arenaria*, *Andira legalis*, *Clusia fluminensis* and *Myrsine parvifolia*, whereas *Aechmea maasii* was analysed only for carbon isotopes. Carbon isotope ratios ($\delta^{13}C$) of these species indicated that *Clusia fluminensis* and *Aechmea maasii* are obligate CAM, while the others are typical C_3 plants. While *C. fluminensis* values were very similar to another population at Arraial do Cabo municipality, some 100 km northwards, *Aechmea maasii* values varied up to 1 ‰ between neighbouring populations at Jacarepiá.

Carbon isotope discrimination ($\Delta^{13}C$) and the ratio between internal and atmospheric partial CO_2 concentration (c_i/c_a) remained similar between Jacarepiá and Arraial do Cabo plants for *Andira legalis* and *Myrsine parvifolia*. These two parameters are correlated to the ratio between CO_2 assimilation and mean stomatal opening during a leaf's lifetime in C_3 plants and, thus, in given situations they can be used as indicators of water-use efficiency (WUE; see Broadmeadow *et al.* 1992). Therefore, the different rainfall regime between the two sites did not imply differences in WUE. These results found by Scarano *et al.* (2001) are in harmony with similar studies conducted by Schulze *et al.* (1991; 1996; 1998) along rainfall gradients in Namibia, Patagonia and Australia. In the latter study these authors propose that the maintenance of similar WUE for individuals of a given taxonomic group along a rainfall gradient might have been due to a possible pattern of species or ecotype substitution that maintained equivalent assimilation under water and nutrient deficit in more arid zones. Indeed, Scarano *et al.* (2001) found that *Myrsine parvifolia* (Jacarepiá: $\Delta^{13}C$ = 20.25‰, 1000 mm rainfall; Arraial do Cabo: 19.76‰, 800 mm), *Myrsine gardneriana* (Itatiaia, high altitude *campos*: 20.03‰ , 2200 mm) and *Myrsine* sp (Búzios, dry forest: 20.67‰, 800 mm) showed similar $\Delta^{13}C$ values along a rainfall gradient. The CAM tree, *Clusia fluminensis*, also showed similar $\Delta^{13}C$ between wet and dry restinga, unlike *Allagoptera arenaria* that showed values 2‰ higher in the wet than in the dry restinga.

Nitrogen isotope ratios ($\delta^{15}N$) reflect different ecological processes to which a given individual or species have been submitted in a given ecosystem. Högberg (1997) showed that fire consumes the soil surface layer, which implies in nitrogen harvest by plants at deeper soil horizons. As a result, in such cases plants show an increase in $\delta^{15}N$. Indeed, *Clusia fluminensis*, *Andira legalis* and *Myrsine parvifolia* at Jacarepiá, which were subjected to various fire events over the past decade (Cirne & Scarano 2001), showed $d^{15}N$ values that were on average c. 1–1.5 ‰ more positive than conspecifics at other restingas unaffected by fire. In the case of the deep rooted palm, *Allagoptera arenaria*, $\delta^{15}N$ values were c. 3 ‰ more positive at the wet restinga of Jacarepiá than in the dry restingas of Arraial do Cabo (Scarano *et al.* 2001). Finally, our studies have also shown that *Andira legalis* nodulate and fix nitrogen in open restinga habitats, and that this is not found in neighbouring restinga forests, suggesting great plasticity also in this respect (Scarano *et al.* 2001; Geβler *et al.* 2005).

ACCLIMATION OR STRESS SYMPTOM?

Some of the above examples suggest that not all intra-specific morpho-physiological variation is an expression of acclimation and that it might also result from stress in particular habitats. The integration of morphological, anatomical, physiological, and population studies, as in the case of *Aechmea maasii*, allows a more precise assessment of the acclimation value of a given morph at a given environmental circumstance (see also Strauss-Debenedetti & Berlyn 1994). However, although comparative studies of native populations, such as those reviewed here, have been essential to enhance knowledge of phenotypic plasticity (Fuller 2003), they are clearly insufficient to allow a precise assessment of the adaptive value of phenotypic variation. Field studies, as those described here, must rely on laboratory experiments combined with genetic studies to allow further progress in strengthening their explanatory power of processes that operate at an evolutionary scale (Hansen *et al.* 2003; Winn 2004; Valladares *et al*. 2007).

For instance, the fact that some of the morpho-physiologically variable study species have clonal growth may, at first glance, suggest that plants with low genetic variation exploit distinct environmental conditions via phenotypic plasticity (*e.g.*, Jain 1979). Alternatively, wherever genetic variation would be available, one might expect that adaptation should be attained by polymorphism, with distinct genotypes exploiting different environments. Nevertheless, Schlichting & Pigliucci (1998) showed that phenotypic plasticity and genetic variation were not necessarily distinct and mutually exclusive alternatives, since phenotypic plasticity is also genetically regulated. This means that plasticity itself can be the target of natural selection, which would result in the maintenance of a variety of possible phenotypic outcomes as opposed to single morphotypes in the case of canalized (non plastic) characters. Moreover, Eriksson (1993) had also listed a range of existing mechanisms that maintain high genetic diversity in local populations of clonal plants.

Another important point raised by Schlichting & Pigliucci (1998) is that phenotypic variation and phenotypic plasticity have often been studied in regard to specific traits (*e.g.*, plant height, leaf width, photosynthetic rate), although separately they do not necessarily explain plant fitness, as in some of the examples seen here (see also Lüttge & Scarano 2007). If fitness itself is the trait under scrutiny, it is therefore not sufficient to examine various morpho-physiological traits but, instead, their integration, *i.e.* how they correlate and interact with each other (Pigliucci & Preston 2004; Hulme 2008). For the restinga plants studied in regard to morpho-physiological variations, we are not aware of the phenotypic integration of the various traits examined and therefore we know neither the spectrum of reaction norms (*i.e.*, the set of phenotypes that can be produced by a given genotype exposed to distinct environmental conditions) that confer adaptation to these plants nor the genetic variation that promotes such responses. Genetic studies of restinga plants at the population or individual level are still in their infancy (*e.g.*, Salgueiro *et al.* 2004; Martins *et al.* 2007) and shall be necessary to understand the role of genotypic variation vs. phenotypic plasticity in the process of adaptation from a rainforest habitat at their origin to open, coastal, oligotrophic conditions of the restinga (see also Pertoldi *et al.* 2007).

Implications for Conservation

The genetic basis that grants distinct phenotypic expressions under different environmental conditions consists of a great richness which is as unknown as it is unexplored by science in Brazil. We have often proposed (Scarano 2002, 2009) that this might be a key feature of many Atlantic forest plants that is largely overlooked, and the broad phenotypic variation described for the study species here is further evidence in this direction. Conservation often targets rare and/or endemic species, due to the extinction threat they are often but not always exposed to (Mace & Kershaw 1997). On the other hand, common species with broad distribution ranges, as some of the plants reviewed, are supposedly not as easily threatened by extinction. However, local populations of the latter might be locally extinct (McKinney 1997) turning genetic information less available (Harrison 1991) and negatively affecting ecological processes (Scarano 2009).

Phenotypic plasticity, one of the possible evolutionary components underlying the intra-specific variation discussed in this paper, is being increasingly recognized as an individual process that might have great ecological consequences at community and ecosystem level (Miner *et al.* 2005). Moreover, this potential to vary and adapt shall be particularly relevant in a climate-change scenario. We hope that this is a further argument to help restrain the increasing pressure on restinga vegetation, particularly at Jacarepiá.

ACKNOWLEDGEMENTS

We thank D.S.D. Araujo and C.F.C. Sá for introducing us to this beautiful vegetation and for providing guidance and logistic support at the earlier steps of the series of studies reviewed here; G. Ganade for critical reading of an earlier version of the manuscript; Fundação O Boticário, PRONEX/ FINEP, PROBRAL (CAPES-DAAD), and Volkswagen Foundation for providing financial support to various studies reviewed here; CNPq, CAPES, FAPERJ, Fundação Botânica Margaret Mee and Petrobras for research grants; and in particular to all those who took part in field studies or in the papers published regarding Jacarepiá Reserve: E.F. Amado, S.M.B. Barreto, P. Cirne, H.M. Duarte, T. Fontoura, A.C. Franco, A. Geβler, H.R.P. Lima, L.S. López, U. Lüttge, A. Mantovani, D.C. Pereira, P. Peres-Neto, F. Reinert, H. Rennenberg, K.T. Ribeiro, G. Rôças, and H.L.T. Zaluar.

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