

# Caatinga, the Brazilian dry tropical forest: can it tolerate climate changes?

Mauro G. Santos · Marciel T. Oliveira · Karla V. Figueiredo ·  
Hiram M. Falcão · Emília C. P. Arruda · Jarcilene Almeida-Cortez ·  
Everardo V. S. B. Sampaio · Jean P. H. B. Ometto ·  
Rômulo S. C. Menezes · Antônio F. M. Oliveira ·  
Marcelo F. Pompelli · Antônio C. D. Antonino

Received: 17 September 2013 / Accepted: 7 January 2014  
© The Author(s) 2014

**Abstract** Our review focuses on the projections of climate change in the Brazilian semiarid region, the Caatinga, based on recent publications about global climate change and biology. We found several vulnerable points in the initial estimates, the main one being that the data were collected and analyzed without a multidisciplinary knowledge. This review discusses several studies that show the current knowledge in many semiarid regions around the world. Some of these studies argue for the increase in vegetation greenness responses even under severe and prolonged drought, based on the high resilience the Caatinga native species show under severe drought conditions over the years. Additionally, we include in this review recent data produced by our group on key ecophysiological variables under drought conditions.

We also show successful examples of deforested areas recovery in the semiarid region of the Central America. It is critical that the recovery of semiarid areas is coupled with the implementation of socio-environmental policies, engaging the local population and providing subsidies for life wealth improvement. These are key aspects for a long-term recovery and conservation of the Brazilian dry tropical forest.

**Keywords** Caatinga · Drought tolerance · Gas exchange · Global warming · Plant ecophysiology · Semiarid recovery

## 1 Introduction

In the tropical regions, rainforests have been more widely studied than dry forests, even though approximately 42 % of tropical forests around the world are dry tropical ones (Murphy and Lugo 1986; Miles et al. 2006; Quesada et al. 2009; Espírito-Santo et al. 2009; Santos et al. 2011).

The semiarid region in Northeast Brazil covers 735,000 km<sup>2</sup>, and it comprises one of the major national ecosystems, namely Caatinga (Rodal and Sampaio 2002; Silva et al. 2004a, b; Giullieti et al. 2006; Gariglio et al. 2010; Santos et al. 2011; Albuquerque et al. 2012; Lopes et al. 2012). The word refers to a large geographical area comprising different vegetation types under a dry tropical climate. This is one of the most populated and biologically diverse semi-arid regions in

---

M. G. Santos (✉) · M. T. Oliveira · K. V. Figueiredo ·  
H. M. Falcão · E. C. P. Arruda · J. Almeida-Cortez ·  
A. F. M. Oliveira · M. F. Pompelli  
Departamento de Botânica, Universidade Federal de  
Pernambuco, Centro de Ciências Biológicas, Recife, PE,  
Brazil  
e-mail: mauro.g santos@ufpe.br

E. V. S. B. Sampaio · R. S. C. Menezes ·  
A. C. D. Antonino  
Departamento de Energia Nuclear, Universidade Federal  
de Pernambuco, Centro de Tecnologia, Recife, PE, Brazil

J. P. H. B. Ometto  
Instituto Nacional de Pesquisas Espaciais, Centro de  
Ciências do Sistema Terrestre, São José dos Campos, SP,  
Brazil

the world. Much research has been carried out in the region, particularly regarding the systematic of flora and fauna, but much remains to be studied in all fields, especially over long periods. A variety of anatomical, morphological and ecophysiological features combine to ensure great water use efficiency and to support a slow and safe growth of the plants (Machado et al. 1997, Mansur and Barbosa 2000; Silva et al. 2004b; Giullieti et al. 2006; Souza et al. 2009; Figueiredo et al. 2012; Lima et al. 2012).

According to the Forth Assessment Report by the Intergovernmental Panel on Climate Change (AR4 IPCC 2007), the climate scenarios suggest the main threat to the Caatinga is increasing in aridity. The semiarid region of northeastern Brazil is densely populated with approximately 27 million habitants distributed with sub region averages of 20–30 inhabitants per km<sup>2</sup> (Gariglio et al. 2010). The main energy source for most of those people is burning wood from the native vegetation. As a consequence, large areas are threatened by high rates of anthropic damage (Silva et al. 2004a, b; Gariglio et al. 2010; Griscom and Ashton 2011). The implementation of proper management systems, which could guarantee a reasonable degree of preservation and also sustainable uses, suffers from the lack of long-term multidisciplinary studies (Quesada et al. 2009; Stoner and Sánchez-Azofeifa 2009; Santos et al. 2011; Albuquerque et al. 2012; Lopes et al. 2012).

This review presents some of the ecophysiological characteristics that allow the development of most plants in Caatinga and discusses how they may be important in an increasingly unstable climate.

### 1.1 Global climate change and forest ecosystems

Some scenarios are presented in the literature on the response of plant species to global climate change: (i) C<sub>3</sub> crops have increased CO<sub>2</sub> assimilation rates as shown by several controlled studies (Leakey et al. 2009), under non-limiting conditions, (ii) increased mortality of tree species in all continents around the world, especially in wet forests, but also in dry forests (Allen et al. 2010; Phillips et al. 2010; Suresh et al. 2010), and (iii) increased biomass in the last 20 years in dry regions (Donohue et al. 2013). The subject of debate around the world is the cause of these three different situations, and a consensus has not been reached because contradictory results have been

reported due to different experimental setups in the same study area (Büntgen and Schweingruber 2010).

Tree species of rainforests have low tolerance to water stress due to their adaptation to high precipitation, and more homogeneous occurrence, throughout the year. In the last two decades, some prolonged drought events led to the death of several species in different forests on all continents, including the Amazon (Marengo et al. 2008; Allen et al. 2010; Costa et al. 2010; Markewitz et al. 2010; Phillips et al. 2010; Marengo et al. 2011; Liu et al. 2013). For 7 years, an experiment was conducted in the Amazon rainforest, excluding rainwater on the ground, which produced several sets of published data (Asner and Alencar 2010; Costa et al. 2010; Markewitz et al. 2010; Metcalfe et al. 2010; Phillips et al. 2010). This experiment showed the effects of prolonged drought on tropical rainforest plants, including rare data on the deep root system of trees (Markewitz et al. 2010). Notably, this study is the only long-term study assessing root traits in the most important tropical rainforest in the world. Long-term multidisciplinary studies are necessary to make reliable predictions of the plant's adaptation strategies and responses to climate variation in a dry forest. Isolated case studies are critical to evaluate responses at species level, although it is hard to predict what will happen to the ecosystem in the long term without an integrated multilevel approach.

As confirmed by analysis of satellite images between 1982 and 2010, increased green areas in the last two decades have been reported in arid and semiarid regions on different continents, in spite of more than usual prolonged drought events occurring in some of these areas, including the Brazilian semi-arid region (Donohue et al. 2013). These authors argued that the data might be explained by increases in air CO<sub>2</sub> concentration, which would provide greater intrinsic water use efficiency, i.e., higher CO<sub>2</sub> uptake with lower stomatal conductance. Several studies have concluded that dry tropical forests are an important sources of stored carbon (Gibbs et al. 2007; Chaturvedi et al. 2011; Harris et al. 2012). Furthermore, the tropical dry forest represents 41 % of the land surface hosting approximately 38 % of the world population, when considering all the subtypes of the dry areas around the world. Moreover, at least 20 % of the major hotspots for plant diversity worldwide belong to dry tropical forests (Huber-Sannwald et al. 2012; Maestre et al. 2012).

After 2003, a network of collaborative research started a long-term study in different dry tropical forests in neotropical regions, including Caatinga (TROPIDRY project). Our group, which includes ecophysiologicalists, plant ecologists, animal ecologists, and soil researchers, is a multidisciplinary team that collected data for the first long-term project to assist in the discussion of the current and future behavior of Caatinga (see acknowledgments). Furthermore, we would like to emphasize that experimental and model studies need to be complementary and that projects and their specific objectives have been planned together to reduce the level of uncertainty (Friend 2010).

Campos et al. (2013) using satellite mapping, discussed the variation in rainwater use efficiency and vegetation resilience after prolonged drought periods. Discussions in other dry forests in the world contrast in terms of carbon sequestration in these regions (Prince et al. 2007). These research groups diverge when discussing the importance of carbon sequestration in semiarid areas. Vegetation in these areas has been classified as unable to mitigate the greenhouse effect (Rotenberg and Yakir 2010). In contrast, Donohue et al. (2013) suggested that climate change has benefited plants with increasing green mass in semiarid regions and carbon gain in some areas. Furthermore, mature forest have been suggested to be important stocks of carbon (Chaturvedi et al. 2011) mitigating global climate change (Gibbs et al. 2007; Harris et al. 2012).

After 19 years evaluating a tropical dry forest in Indian Territory, researchers have concluded that the main cause of death of adult trees is fire, followed by elephant attacks as the main herbivore damage (Suresh et al. 2010). Events of prolonged drought in this area have also caused plant death but in a longer time interval than that observed in other types of forests. This study reinforced the importance of a long-term study when evaluating forest ecosystems, especially dry tropical forests because many years are necessary to detect climatic changes in semiarid areas.

The majority of forecasts on climate change has highlighted frequent and extensive drought events and also rises in the average temperature by 2050 (IPCC 2007), which would lead to behavior changes of some species and increased desertification in some regions, including the Caatinga region. However, further analysis taking into account other variables that the most common models do not use, such as wind speed,

relative humidity and longwave solar radiation (calculated by using the Penman–Monteith method), has shown little change in areas affected by drought in the last 60 years (Sheffield et al. 2012). The IPCC revised the forecasts in early 2012, and most of the authors involved agreed that there were several sources of uncertainty in these data. Almost one decade of results in the drought controlled experiment in the Amazon rainforest contradict many predictions based on different dynamic global vegetation models (DGVMs), indicating the importance of long-term field studies.

This review is focused on the Caatinga, the Brazilian dry tropical forest (DTF), looking at the plant morphological, anatomical and ecophysiological traits that may confer drought tolerance. We suggest that the native vegetation is able to support long drought events together with high temperature and we present data from ongoing and mostly unpublished studies from two locations in two states in the Northeastern region of Brazil (Fig. 1).

## 1.2 Plant species, study site and growth conditions

### 1.2.1 Plant species

We studied the following eight species, including among them four trees, three shrubs and one herbaceous plant: *Sida galheirensis* Ulbr., Malvaceae, *Hyptis suaveolens* Poit., Lamiaceae, *Poincianella pyramidalis* [Tul.] L. P. Queiroz, Fabaceae, *Anadenanthera colubrina* [Vell.] Brenan, Fabaceae, *Cynophalla flexuosa* [L.] J. Presl, Capparaceae, a broadleaf evergreen, *Jatropha mollissima* [Pohl] Baill., Euphorbiaceae, the exotic *Jatropha curcas* L., Euphorbiaceae, and *Prosopis juliflora* [Sw.] DC., Fabaceae, an invasive species.

### 1.3 Serra Talhada: site of study in the state of Pernambuco, Brazil

The studies were carried out at the Saco Farm located at the Agronomic Institute of Pernambuco (IPA)—7°54′35″S and 38°17′59″W and 430 m altitude. The climate is BSh type according to Köppen classification, with the average annual precipitation of 750 mm, occurring during the summer and fall rainy season. The studied vegetation has approximately 20 years of spontaneous recovery after using the area as pastureland.

**Fig. 1** Map of the Caatinga region in the northeastern Brazil. The spatial localization of the two studied sites is shown: Serra Talhada PE, and Santa Terezinha PB

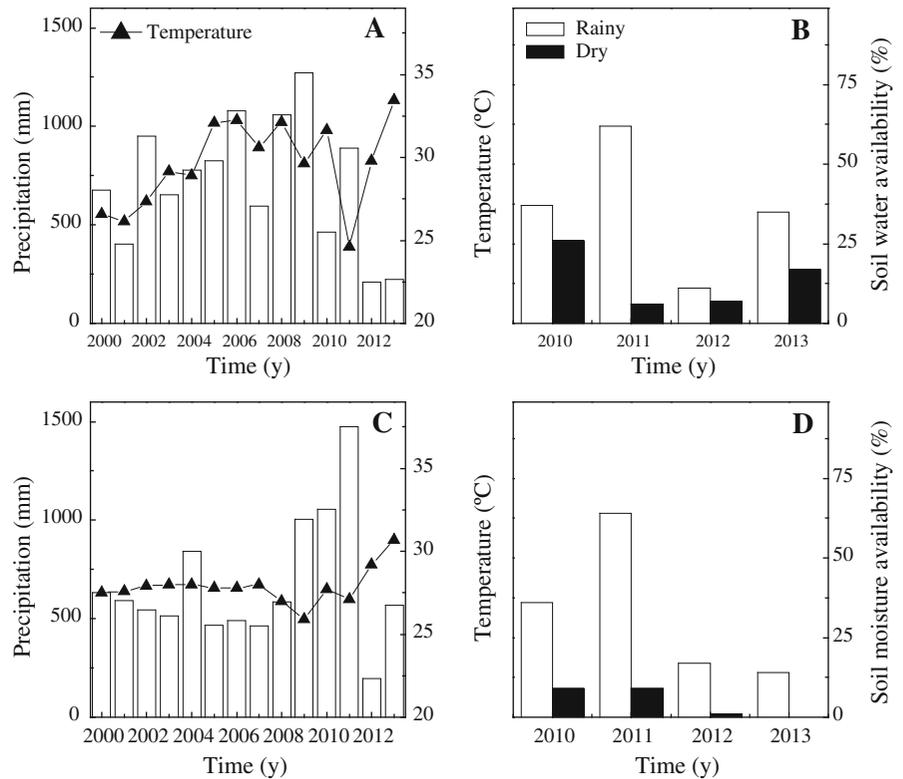


Since the beginning of the millennium rainfall in this region had been in the usual range, not far from the long-term average. However, rainfall was above the average from 2009 to 2011 and far below the average in 2012 and 2013 (Fig. 2a). In 2013, 500 mm of rainfall occurred from January to June, which was an extremely irregular rain pattern, impairing the development of some tree species and turning local agriculture impossible for two consecutive years. Our study began in this location in 2010 and the lowest soil moisture availability was noticed in 2011 (Fig. 2b). The average air temperature varied in accordance to the annual precipitation, and an increase of approximately 4 °C was noticed since 2002. A slight temporary decrease in air temperature was found in 2011 when rainfall was double the recorded average.

#### 1.4 Santa Terezinha: site of study in the state of Paraíba, Brazil

The studies were carried out at the Tamanduá Farm located in the county of Santa Terezinha, Paraíba State, Brazil, 400 km from the coast and at an altitude of 240 m (7°1'31"S and 37°23'31.8"W). The owner has preserved the native vegetation in an area larger than 900 ha, approximately 1/3 of the farm area, and established a legal reserve and a Private Reserve of Natural Patrimony (RPPN) in July 1998. The climate is characteristic of semiarid regions with an average annual rainfall of 800 mm concentrated in a short period of 2–4 months. Measurements were performed in plots set up in areas at an early successional stage (15 years of regeneration after land use as pasture), an intermediate stage (37 years of regeneration after land

**Fig. 2** Climate conditions at Serra Talhada PE Brazil (a, b) and Santa Terezinha PB Brazil (c, d) from 2000 to 2013 (until June) (unpublished results)



use as pasture) and a late stage of regeneration (at least 60 years after land use as pasture).

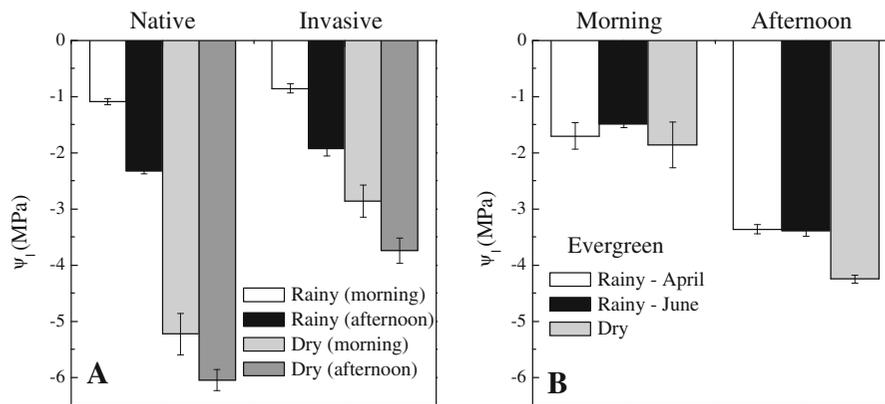
During the past 13 years, the rainfall was lower than the average in 2001, 2010, 2012 and 2013. In the last 2 years, it rained only 1/3 of the expected amount and the highest rainfall occurred in 2009 (Fig. 2c). Extremely low rainfall in two consecutive years, 2012/2013 was directly reflected in the soil moisture availability (Fig. 2d). Herbaceous and tree species were monitored in different areas during this period, and some of them failed to complete the reproductive cycle, but survived. In both locations, some of the seasonal small rivers did not run in the last 2 years, which directly influenced the groundwater reserve. The average air temperature remained stable with only a slight increase in the last 2 years, which was not observed in Serra Talhada.

### 1.5 Tolerance to reduced leaf water potential in native species

The two main environmental factors that directly influence the leaf water potential are the air vapor pressure deficit (VPD) and soil moisture. Caatinga

plants experience 8–10 dry months a year, and the soil of most areas are very shallow. Moreover, a high VPD exists in this region most of the year. Most of plants in the Caatinga are deciduous, that is, lose all their leaves during the dry season as a strategy to cope water loss (Machado et al. 1997; Barbosa et al. 2003; Lima et al. 2012). Moreover, the xylem of most of these species tolerates high negative pressure (Mansur and Barbosa 2000; Silva et al. 2004b), which can reach  $-6.0$  MPa during the dry period (Fig. 3).

In the Caatinga diverse vegetation, plants have different strategies to deal with extreme conditions, e.g. water storage capacity in the stem (Borchert 1998; Borchert and Pockman 2005; Lima et al. 2012). These authors showed that wood density directly influences the amount of water stored. Plants with lower wood density hold more water, resulting in leaf water potentials that vary less throughout the year. Contrastingly, high-density wood species are more stressed during the dry season. In humid tropical forests, mortality after severe drought events is higher in arboreal species with low wood density, regardless the stem diameter (Phillips et al. 2010). In contrast, the



**Fig. 3** Leaf water potential ( $\Psi_l$ ) of three species in Serra Talhada PE Brazil, during the rainy (February) and dry (December) seasons, from 2010 to 2012. **a** Native (*A. colubrina*); invasive (*P. juliflora*). The values are means of February 2010–2012 and December 2010–2011. **b** Evergreen *C.*

*flexuosa*. The values are means of December 2012 (dry season) as well as April and June 2013 (rainy season). *Morning* and *afternoon* represent measurements taken at 6:00 am and 1:30 pm, respectively. Each value is the mean of five trees ( $\pm$ SE) (unpublished results)

few evergreen species observed in the Caatinga have high wood density and do not reach extremely negative water potential like the deciduous species (Lima et al. 2012) (Fig. 3b). This small group of evergreen species has other characteristics besides the wood density to keep their leaves during the dry season. As we will discuss later, these species maintain high resilience of gas exchange even under severe drought.

In some areas, the most drastic drought in 50 years occurred during 2012 and 2013, affecting significantly the behavior of the groups of species mentioned above. Evaluation of water potential under two VPD conditions during the day in one herbaceous *H. suaveolens*, one shrub *S. galheirensis* and one tree *P. pyramidalis* species showed that water potential varied with the area conservation state (Fig. 4). Areas with more than 60 years of regeneration maintained the highest soil water availability (data not shown), which allowed the occurrence of the highest leaf water potential in the three species. Under the severe and prolonged drought of 2012, these areas had the lowest soil moisture availability and *P. pyramidalis* had the lowest leaf water potential (Fig. 4a).

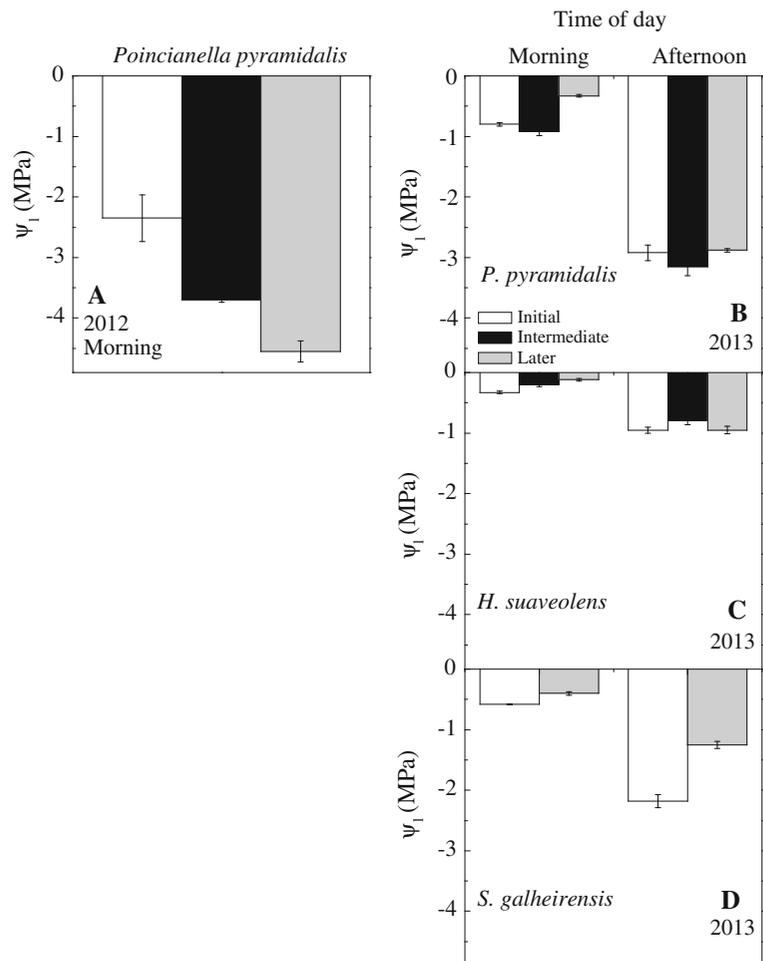
In a tropical dry forest area, variation of soil physical structure has a significant influence on both soil and plant water potentials (Markesteyn et al. 2010). Another factor contributing to the low values of soil moisture in this type of forest is the increased soil evaporation due to leaf loss of plants during the dry season (Markesteyn et al. 2010; Lima et al. 2012).

For two consecutive years, a native (*A. colubrina*) and invasive (*P. juliflora*) species of the Caatinga were evaluated during the dry and rainy seasons. Both species have high wood density, but differed in leaf water potential in the dry season (Fig. 3a). The native species lost its leaves early in the dry season, and the invasive species showed partial leaf loss throughout this season. Although *A. colubrina* has lost completely its leaves at the end of the rainy season, it shows lower leaf water potential during the dry season when compared to *P. juliflora*. Borchert and Pockman (2005) argued that the diameter of xylem vessels varies among species and influences the xylem hydraulic conductivity. The hydraulic conductivities of xylem and leaves have been identified as key features of drought tolerance in several species (Chapotin et al. 2003; Brodrribb et al. 2010; Bartlett et al. 2012).

The maintenance of cell turgor is critical in semiarid conditions and the ability to maintain this state for longer periods is an important trait to differentiate tolerance and growth rate among species. Baobab trees (*Adansonia* spp.), common in African semiarid regions, are able to store water and use it over long periods of drought. This species exhibits a strong reduction of leaf gas exchange at noon, reducing the water loss and increasing the water use efficiency (Chapotin et al. 2006).

The tolerance of dry forest native plants to low water potential has multiple factors involved, not only

**Fig. 4** Leaf water potential ( $\Psi_l$ ) of three species in Santa Terezinha PB Brazil, during the rainy season of 2012 and 2013. Measurements were performed in areas with three increasing recovery stages: initial, intermediate and later. **a**, **b** *P. pyramidalis*, a woody species; **c** *H. suaveolens*, a herbaceous; and **d** *S. galheirensis*, a shrub. *Morning* and *afternoon* represent measurements taken at 6:00 am and 1:30 pm, respectively. Each value is the mean of five plants ( $\pm$ SE) (unpublished results)



including the stomatal control but also morpho-anatomical and hydraulic characteristics, photosynthetic efficiency and maintenance of leaf metabolism under low water availability through photo-protective mechanisms and high water use efficiency.

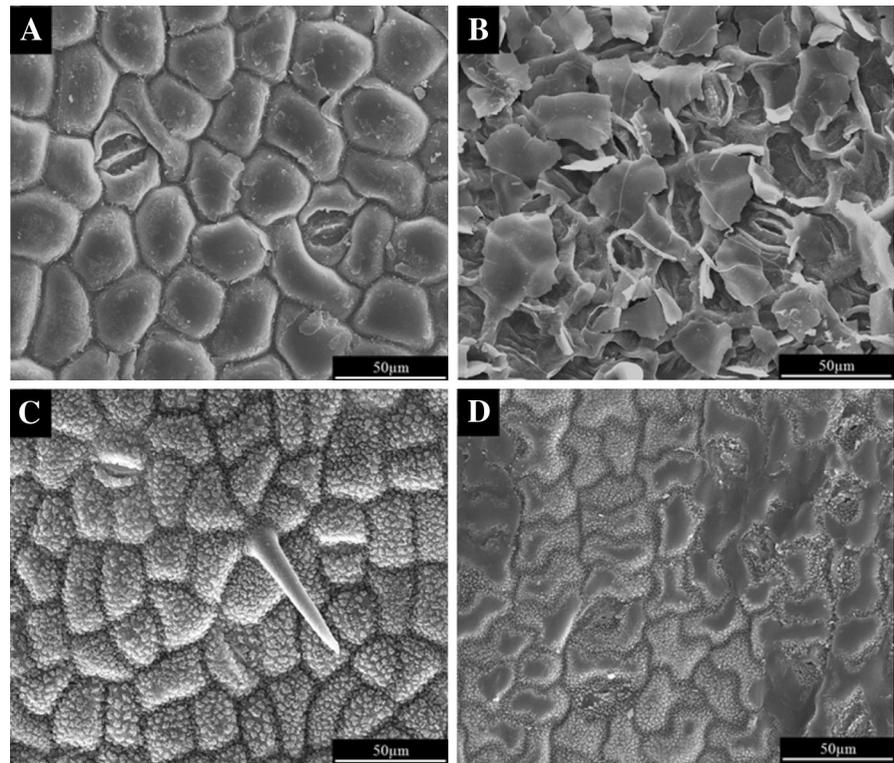
#### 1.6 Cuticle composition: importance to mitigate leaf turgor loss

The maintenance of cell plant turgor depends on both the root system and shoots with the former involved in water uptake from the ground and the latter avoiding excessive water loss to the atmosphere. In this context, Caatinga plants have large variation in the composition of epicuticular wax (Oliveira and Salatino 2000; Oliveira et al. 2003; Figueiredo et al. 2012) as well as morphological and anatomical characteristics

(Fig. 5a, b). The cuticle plays a fundamental role against water loss, but little has been reported under field conditions with respect to its ecophysiological role. The cuticle is composed of three major constituents, being one of the main barriers for diffusion located within the waxy skin and having less than 1- $\mu$ m thick (Kerstiens 1996).

The association of morpho-anatomical and ecophysiological studies has improved our understanding of plant tolerance to adverse semiarid conditions. When present in the same semiarid region, two species of Euphorbiaceae, the native *J. mollissima* and the exotic *J. curcas* showed different morphological and anatomical leaf characteristics (Fig. 5a, b). The native species had different epicuticular wax composition and morphology and larger leaf surface trichomes than the exotic species (data not shown). Under controlled

**Fig. 5** Electron microscopy of the adaxial epidermis of leaves. **a** *J. curcas*; **b** *J. mollissima*; **c** *P. juliflora*; and **d** *A. colubrina*. The leaves were sampled during the rainy season of 2011 in Serra Talhada PE Brazil (unpublished results)



conditions with removal of the leaf surface epicuticular wax, the species mentioned above showed different leaf gas exchange and leaf relative water content values. Such differences occurred not only between the two species but also among different leaves of the same individual (Figueiredo et al. 2012). Higher leaf gas exchange was reported in the native species when the wax was present under drought stress, emphasizing its importance under semiarid conditions.

In fact, the importance of the cuticle has been emphasized in the literature not only for Caatinga plants (Oliveira and Salatino 2000; Oliveira et al. 2003; Costa Filho et al. 2012; Figueiredo et al. 2012) but also for species of other vegetations (Jeffree et al. 1971; Jetter and Schäfer 2001; Ni et al. 2012). The wax buildup around the stomatal pore is species-dependent and has been observed to reduce water loss (Jeffree et al. 1971; Jetter and Schäfer 2001, Shope et al. 2008). The chemical composition of n-alkane chains and the amount of accumulated wax are key to the efficiency of reducing epidermis transpiration, affecting the stomatal conductance (Figueiredo et al. 2012). The composition and amount of wax varies when the plants

are submitted to water stress and under various seasonal conditions as shown for the four species (two native, one exotic and one invasive species) grown in the same field (Fig. 5).

### 1.7 Gas exchange, carbon emission and stock under tropical forest

The water flow through plant tissues to the atmosphere is at the order of  $40,000 \text{ km}^3 \text{ year}^{-1}$  representing, approximately, 70 % of global terrestrial evaporation (Brodribb et al. 2010). Water mechanical conductivity through leaves is a complex issue and is difficult to understand, especially if it is analyzed with isolated tools. Studies involving anatomy, morphology and ecophysiology are needed. In such context, the stomatal behavior is a key adaptation factor among dry tropical forest plants, influencing the primary productivity, growth rate and carbon storage.

Efficiency of carbon uptake and storage in forest ecosystems is an important research issue, enhanced by the difficulty in correctly measure the flux and stock changes in both soil and vegetation. A comparison among different forest types around the world showed

that the total carbon stored in forests is 1150 Gt, with 49 % in boreal forest, 14 % in temperate forests and 37 % in tropical forests (Malhi et al. 1999). Boreal forests accumulate most of the carbon in the soil as organic matter and, whereas the vegetation is the big compartment in humid tropical forest. The vulnerability of these stocks has been debated due to changes in climate and land use (Malhi et al. 1999; Chaturvedi et al. 2011).

One recent study using satellite images showed that the carbon emission from deforestation in a tropical region between 2000 and 2005 was 25–50 % of previously published data (Harris et al. 2012). This study showed carbon emissions and forest cover loss in Latin America, the Caribbean, Sub-Saharan Africa, South Asia and Southeast Asia. Out of 15 countries, Brazil had the highest carbon emission during this period. Brazil and Indonesia accounted for 55 % of total emission from tropical deforestation. This study concluded that the main source of Brazilian emission is the Amazon Forest. Nevertheless, the intensification of new approaches in the Brazilian agricultural system has reduced the deforestation in some regions, at least in the Southeast region. However, the analysis of data since 1960 has shown that new areas are being occupied in the Cerrado ecosystem (central/western region) and that deforestation has decreased due to economic reasons (Barretto et al. 2013). Recent data published by the Brazilian Government has shown a reduction of deforestation in the last decade for most biomes. However, among the biomes Cerrado, Atlantic Forest, Caatinga, Pantanal and Pampa, the Caatinga was the third largest emitter of carbon during the period 1994–2002 (MCTI 2013).

The following two possibilities can be used to mitigate carbon emission: create new carbon drains and/or preserve existing ones. The speed with changes is occurring endangers the fragile biodiversity of various ecosystems. The need for protection of these as well as an increased number of protected areas is clear as an emergency solution in the short-term (Silva et al. 2003; Loarie et al. 2009). This endangerment reinforces the need for changes in Caatinga, where deforestation is the main cause of damage to the ecosystem and results mainly from the consumption by poor people of wood as a fuel source (Gariglio et al. 2010). Burning plant residues after deforestation reduces biomass and biodiversity of the regenerating vegetation (Sampaio et al. 1998), and contributes

directly to the greenhouse effect. Suppression of fire is the most important practice to regenerate dry tropical forests, as has been observed in Costa Rica (Powers et al. 2009).

Some of the greatest paucities among published data on Caatinga are values of leaf gas exchange and carbon storage in vegetation and soil (Sampaio et al. 2010). The discussion on the efficiency of carbon sequestration by tree canopy is extensive and controversial (Buitenwerf et al. 2012; Donohue et al. 2013), as occurs for the largest tropical rainforest in the world, the Amazonia (Asner and Alencar 2010; Marengo et al. 2011), and especially for dry forests (Rotenberg and Yakir 2010; Donohue et al. 2013; Newingham et al. 2013).

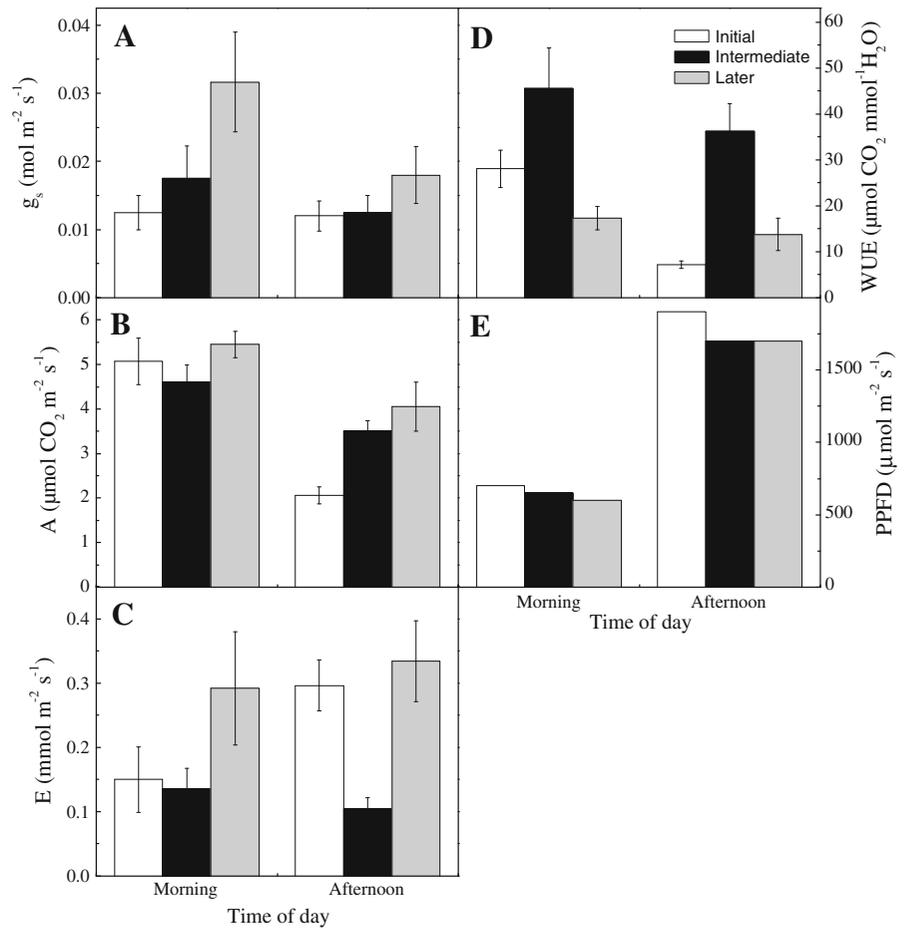
The impacts of extreme drought events, causing extensive death of tree species, are reported for both tropical rain (Phillips et al. 2010; Liu et al. 2013) and dry tropical forests (Rotenberg and Yakir 2010). However, due to the different study types and scales used to evaluate the different ecosystems, there is controversy about the importance of the death rates in dry forests. Therefore, dry forest can be of great importance in the chain of carbon sequestration (Buitenwerf et al. 2012; Donohue et al. 2013; Newingham et al. 2013).

In general, the use of wood as a fuel source and subsequent land use as pasture in the Brazilian areas occupied by dry forest has frequently led to the abandonment of the areas (Silva et al. 2003; Gariglio et al. 2010). In many places, soil erosion and salinization results in degraded soils and desertification may be the consequent evolution in many of these places. In Brazil, 62 % of the areas subject to desertification are within the Caatinga region (MMA 2007).

Although not quantified, the increase in net photosynthetic rates of plants due to increase in air CO<sub>2</sub> concentration has been pointed as the main cause of increased green areas between 1982 and 2010 in semiarid regions (Donohue et al. 2013). If plants in these regions are considered to maintain high intrinsic water use efficiency, i.e., the maximum CO<sub>2</sub> assimilation under minimum stomatal conductance, the increase of CO<sub>2</sub> in the atmosphere could benefit these plants (Leakey et al. 2009).

In fact, native pioneer desert plants showed increased water use efficiency after 10 years under elevated CO<sub>2</sub> concentration in the atmosphere

**Fig. 6** Leaf gas exchange of *P. pyramidalis* during the rainy season (2012) in Santa Terezinha PB Brazil: stomatal conductance ( $g_s$ , in **a**); net  $\text{CO}_2$  assimilation rate (A, in **b**); transpiration (E, in **c**); water use efficiency (WUE, in **d**); photosynthetic photon flux density (PPFD, in **e**). Measurements were performed in areas with three increasing recovery stages: initial, intermediate and later. *Morning* and *afternoon* represent measurements taken at 8:00 am and 2:30 pm, respectively. Each value is the mean of five trees ( $\pm$ SE) (unpublished results)



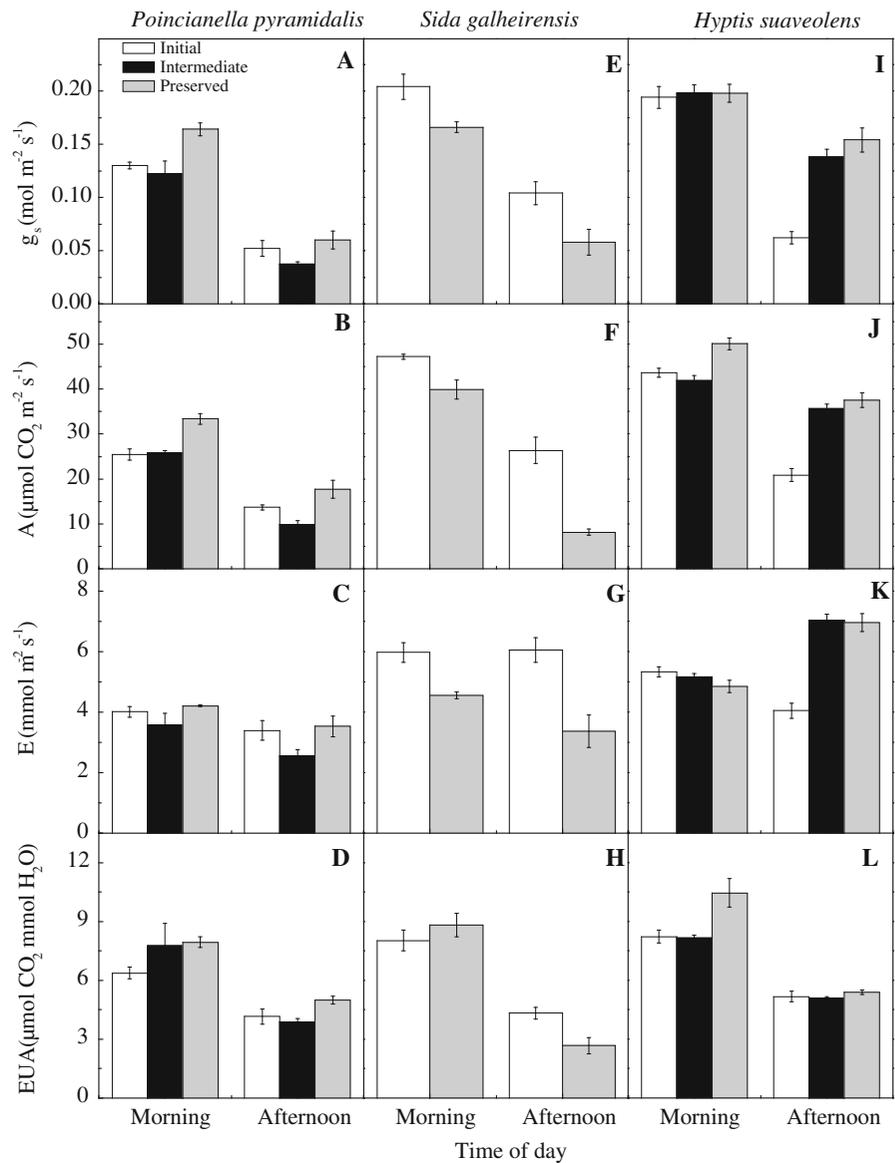
(Newingham et al. 2013), and this situation occurs with some native species of the Caatinga. Under the severe drought in the past 2 years (Fig. 2), the leaf gas exchange of three species of different growth habits were measured during the rainy season in three areas with different conservation status (Figs. 6, 7). The leaf gas exchange of *P. pyramidalis* trees in April 2012 were approximately 10 times lower than those observed in 2013 (Figs. 6a–c, 7a–c) due to low soil moisture (Fig. 2). In April 2013, there was a strong rainfall prior to the sampling, and the rapid response of the native *P. pyramidalis* tree proved the high adaptive capacity, increasing the photosynthetic rate in 5–6 times.

The vegetation successional stage in the Santa Terezinha site affected the gas exchange of shrub and herbaceous species, such as *S. galheirensis* and *H. suaveolens* respectively (Fig. 7e–l). The shrub plants growing in the most recovered area showed lower leaf

gas exchange as compared to plants under initial recovery. In such condition, the herbaceous species had the lowest leaf gas exchange values. The initial ecophysiology assessment of the species indicated a high ability to tolerate prolonged drought events. However a broad scenario cannot be extrapolated, which is another difficulty due to the diversity and reduced ecophysiological studies of this ecosystem (Albuquerque et al. 2012; Lopes et al. 2012). Accordingly, proposed scenarios indicate, out of the increase in mean and extremes temperature, the reduction of precipitation average in Caatinga (Marengo et al. 2009a, b).

Under the climatic conditions of Serra Talhada, *J. mollissima* (a native shrub species), *J. curcas* (an exotic shrub species), *A. columbrina* (a native arboreal species) and *P. juliflora* (an invasive arboreal species) showed different gas exchange behavior between 2010 and 2011 (Fig. 8). *J. curcas* showed higher rate of  $\text{CO}_2$

**Fig. 7** Leaf gas exchange of *P. pyramidalis*, in **a–d** *S. galtheirensis*, in **e–h** *H. suaveolens*, in **i–l** during the rainy season (2013) in Santa Terezinha PB Brazil: stomatal conductance ( $g_s$ , in **a, e, i**); net CO<sub>2</sub> assimilation rate ( $A$ , in **b, f, j**); transpiration ( $E$ , in **c, g, k**); water use efficiency ( $WUE$ , in **d, h, l**). Measurements were performed in areas with three increasing recovery stages: initial, intermediate and later. The photosynthetic photon flux density ( $PPFD$ ) during measurements was 1600, 1300 and 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (morning) and 1900, 1800 and 1600  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (afternoon) at initial, intermediate and later recovery stages, respectively. Morning and afternoon represent measurements taken at 8:00 am and 2:30 pm, respectively. Each value is mean of five trees ( $\pm$ SE) (unpublished results)

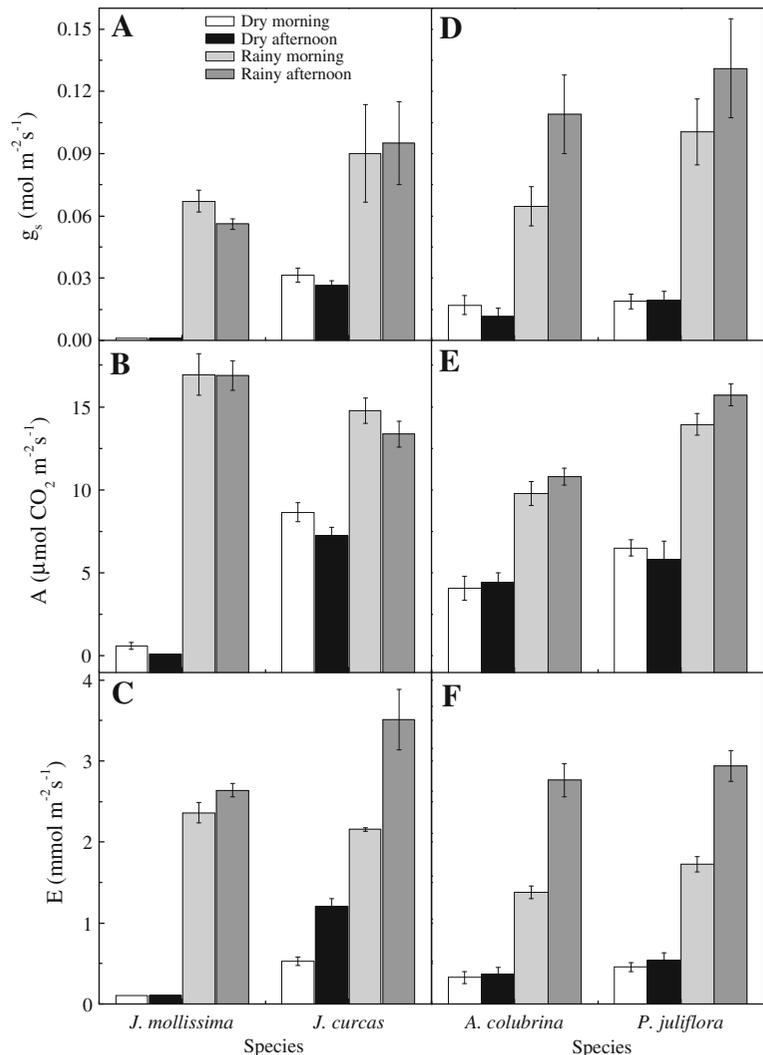


assimilation at the beginning of the dry season and a lower rate of leaf loss than *J. mollissima*, with these trends being supported by an increased stomatal conductance. This strategy generally results in excessive water loss by exotic species. Younger plants of both species presented similar gas exchange under greenhouse conditions (Figueiredo et al. 2012). These shrubs had different epidermis morphological features (Fig. 5a, b) and high stomatal conductance (Fig. 8a), resulting in low leaf relative water content (data not shown) in the exotic species. Among the tree species, the gas exchange was not associated with the leaf

water potential (Figs. 3b, 8d–f) in the invasive species, being a result of other factors such as the amino acid content, sugar content, morpho-anatomical characteristics of leaves (Fig. 5c, d).

In addition to the deciduous species (Machado et al. 1997), there are a small number of evergreens in the Caatinga (Lima et al. 2012). It is unknown how the leaves maintain C<sub>3</sub> photosynthetic metabolism under semiarid climate condition. *C. flexuosa* is an evergreen tree with broad leaves, significant leaf thickness and high wood density, with no variation in leaf water potential throughout the year (Lima et al. 2012), even

**Fig. 8** Leaf gas exchange of native *Jatropha mollissima*, in **a–c** exotic *J. curcas*, in **a–c** native *A. colubrina*, in **d–f** and invasive *P. juliflora*, in **d–f** during the rainy and dry seasons (2010–2012) in Serra Talhada PE Brazil: stomatal conductance ( $g_s$ , in **a, d**); net  $\text{CO}_2$  assimilation rate ( $A$ , in **b, e**); and transpiration ( $E$ , in **c, f**). The photosynthetic photon flux density (PPFD) during measurements was 551 (*morning*) and 1652 (*afternoon*)  $\mu\text{mol m}^{-2} \text{s}^{-1}$  during the dry season and 1088 (*morning*) and 1652 (*afternoon*)  $\mu\text{mol m}^{-2} \text{s}^{-1}$  during the rainy season. *Morning* and *afternoon* represent measurements taken at 8:00 am and 2:30 pm, respectively. Each value is the mean of five trees ( $\pm\text{SE}$ ) in each season (unpublished results)

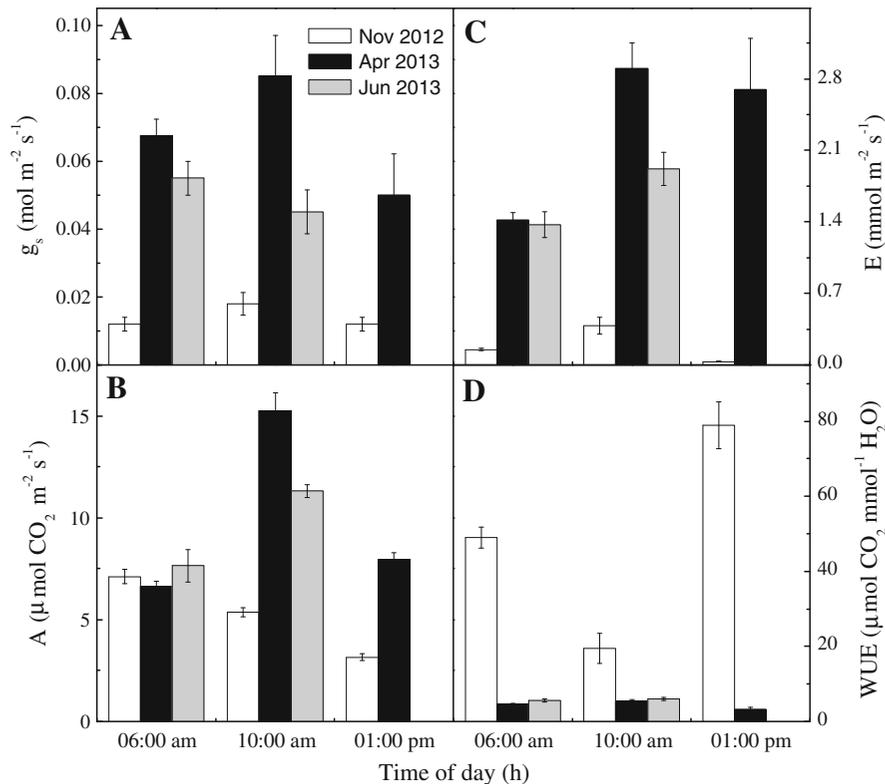


under the severe droughts of 2012 and 2013 (Fig. 2). The leaf water potential of *C. flexuosa* remained relatively high compared to other tree species with different deciduous degrees in the same area (Fig. 3), supporting high gas exchange with high water use efficiency even in the dry season (Fig. 9). In fact, a set of factors acting in an integrated way is probably required to maintain the photosynthetic rates throughout the day and during severe and prolonged droughts. Among the factors, we may cite: biochemical, morphological and anatomical features, including epidermis and stomatal density, hydraulic conductivity, and leaf mesophyll conductance (Borchert 1998; Mott and Buckley 2000; Oliveira et al. 2003; Borchert and Pockman 2005; Souza et al. 2009; Brodrribb et al.

2010; Figueiredo et al. 2012; Rivas et al. 2013; Flexas et al. 2013).

### 1.8 Recovery of degraded areas

There is not enough data to affirm how most Caatinga species will behave under global climate change (Marengo et al. 2009a, b). However, the Brazilian dry forests may disappear, and desertification of these areas may increase, leaving only a few protected areas. The pressure over the native areas might increase without government policies against the poverty imposed to many families, the main cause of deforestation in the region. Among the Brazilian ecosystems, Caatinga is the least protected, hosting only



**Fig. 9** Leaf gas exchange of evergreen *C. flexuosa* during the rainy and dry seasons (2012–2013) in Serra Talhada PE Brazil: stomatal conductance ( $g_s$ , in **a**); net CO<sub>2</sub> assimilation rate (A, in **b**); transpiration (E, in **c**); water use efficiency (WUE, in **d**). Measurements were taken in November 2012 (dry season) and April and June 2013 (rainy season). The photosynthetic photon flux density (PPFD) during measurements was 130, 1500,

2000  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  at 6:00, 10:00 am and 01:00 pm in November; 300, 1100, 1700  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  at 6:00, 10:00 am and 01:00 pm in April; and 1100 and 230  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  at 06:00, 10:00 am in June. The measurements of leaf gas exchange were not possible due to weather conditions at 13:00 h in June. Each value is the mean of five trees ( $\pm$ SE) (unpublished results)

7.1 % of its territory in conservation units and having 0.2 % of its land belonging to Indian groups. Only 1 % of the Caatinga is considered to be under a full protection and the private reserves (RPPN) represent 0.08 % of the ecosystem territory (Silva et al. 2003, MMA 2008).

Recovery of deforested areas is difficult anywhere for many reasons (Miles et al. 2006, Marengo et al. 2009a, b; Quesada et al. 2009; Friend 2010; Phillips et al. 2010; Rotenberg and Yakir 2010), especially in this ecosystem due to climatic conditions, lack of protection for the new reforested areas, and lack of investments in technology for such purpose (Gariglio et al. 2010).

Studies aimed at understanding the ecological, ecophysiological and edaphoclimatic features of this area based on knowledge created by studies of plant

systematics (Machado et al. 1997; Barbosa et al. 2003; Giullietti et al. 2006; Albuquerque et al. 2012; Lopes et al. 2012) should lead to significant advances in the broad knowledge of Caatinga (Benko-Iseppon et al. 2011). Such studies have only been initiated and begin to build a database with lower uncertainty due to multidisciplinary advances. Studies on Caatinga are needed to find alternatives for the local population to explore the natural resources in a sustainable manner (Gariglio et al. 2010; Huber-Sannwald et al. 2012; Maestre et al. 2012). The exploration of new drugs extracted from native species offers promising perspectives (Albuquerque et al. 2012) as well as exploration of oils from seeds, such as licuri palm, for multiple uses (Tadeu et al. 2008; Pinho et al. 2009). Use of exotic species with multiple economic potential may aid in maintaining native forest because they represent a

source of products with high economic added value. The following are examples of such exotic species: *Moringa oleifera* (Rivas et al. 2013) with oil quality and potential to become a source of biofuel on a subsistence scale, *Calotropis procera* (Frosi et al. 2012) as a source of numerous drugs, and *Opuntia ficus-indica* (Falcão et al. 2013) as a forage source to support livestock production. Many native species have high economic potential and some already provide commercial products extracted from the native vegetation but are not cultivated, such as Umbu, whose fruits are largely sold in local markets (Silva et al. 2008).

As has been performed in the last decades in the Amazon rainforest through groups organized in cooperative systems, the Brazilian semiarid region needs policies to operate sustainably. These policies should aim at maintaining the families in rural areas but guaranteeing that they profit from a minimally decent quality of life. Despite several possibilities for coexistence of preservation and exploration in semiarid regions, only few actions have been conducted in relation to Caatinga and the Brazilian semiarid region (Gariglio et al. 2010).

In parallel to the studies aimed at improving the life of thousands of Brazilians in semiarid region, a reforestation program based on scientific knowledge needs to be implemented. If there is not enough data about Caatinga at this time, information can be gathered from dry tropical forests in Central America where the recovery of several areas has been attempted with success. In this region, soil degradation after years of deforestation led many farmers to sell their properties. The new owners are generally interested in attracting tourism to the Pacific Ocean coast and they support reforestation of large areas. Some techniques have shown significant results, such as the use of species that tolerate fire, promote shading and attract dispersers. This provides a favorable environment for the sprouting and or introduction of species to restore biodiversity (Griscom and Ashton 2011). Similar advances have been attained in the recovery of Brazilian Atlantic Forest (Rodrigues et al. 2009). We previously mentioned that fire is a major problem in dry tropical forests, including the Caatinga. So, the first step is to avoid fire, especially in areas of initial recovery after pasture abandonment. Finally, there is a necessity of robust research institutions that integrate the needs of society and ecological care in Brazil (Nobre et al. 2008).

Conclusions about possible consequences of global climate changes in semiarid regions have been hastily published. Furthermore, lack of multidisciplinary studies exaggerates these conclusions, especially the statements on factors that require complex analyses, such as behavior of plant species under environmental stresses. The available ecophysiological data lead us to believe that some Caatinga species are prepared to go through periods of severe drought, however, could not support the current level of unsustainable. Finally, the current fragile union between science and politics is the most worrisome among the treats on Caatinga.

**Acknowledgments** The authors are grateful for the financial support provided by FACEPE-FAPESP to the project “Impactos de mudanças climáticas sobre a cobertura e uso da terra em Pernambuco: geração e disponibilização de informações para o subsídio a políticas públicas” (APQ-FACEPE-0077-5.01/09), by FACEPE to the project “Aumento da tolerância em plantas jovens de espécies lenhosas da Caatinga aos estresses salino e seca (APQ-0829-2.03/12)” and by CNPq to the project “Biodiversidade e regeneração natural em florestas tropicais secas brasileiras”—SISBIOTA (CNPq-563304/2010-3). We are also grateful to Fazenda Tamanduá and the Instituto Agrônomo de Pernambuco (IPA) for the logistic support during the studies and to CNPq for the fellowships.

## References

- Albuquerque UP, Lima Araújo E, El-Deir ACA, Lima ALA, Souto A, Bezerra BM, Ferraz EMN, Freire EMX, Sampaio EVSB, Las-Casas FMG, Moura GJB, Pereira GA, Melo JG, Ramos MA, Rodal MJN, Schiel N, Lyra-Neves RM, Alves RRN, Azevedo-Júnior SM, Telino Júnior WR, Severi W (2012) Caatinga revisited: ecology and conservation of an importante seasonal dry forest. *Sci World J* 2012:1–18
- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowelle N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg E, Gonzalez P, Fenshaml R, Zhangm Z, Castro J, Demidova N, Limp JH, Allard G, Runningr SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manag* 259:660–684
- Asner GP, Alencar A (2010) Drought impacts on the Amazon forest: the remote sensing perspective. *New Phytol* 187:569–578
- Barbosa DCA, Barbosa MCA, Lima LCM (2003) Fenologia de espécies lenhosas da Caatinga. In: Leal IR, Tabarelli M, Silva (eds) *Ecologia e Conservação da Caatinga*. Editora Universitária UFPE, Recife, pp 657–693
- Barretto AGOP, Berndes G, Sparovek G, Wirsenius S (2013) Agricultural intensification in Brazil and its effects on land-use patterns: an analysis of the 1975–2006 period. *Glob Change Biol* 19:1804–1815

- Bartlett MK, Scoffoni C, Sack L (2012) The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecol Lett* 15:393–405
- Benko-Iseppon AM, Soares-Cavalcanti NM, Berlarmino LC, Bezerra-Neto JP, Amorim LLB, Ferreira-Neto JRC, Pandolfi V, Azevedo HMA, Silva RLO, Santos MG, Alves M, Kido EA (2011) Prospecção de genes de resistência à seca e à salinidade em plantas nativas e cultivadas. *Revista Brasileira de Geografia Física* 6:1112–1134
- Borchert R (1998) Responses of tropical trees to rainfall seasonality. *Clim Changes* 39:381–393
- Borchert R, Pockman WT (2005) Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. *Tree Physiol* 25:457–466
- Brodribb TJ, Feild TS, Sack L (2010) Viewing leaf structure and evolution from a hydraulic perspective. *Funct Plant Biol* 37:488–498
- Buitenwerf R, Bond WJ, Stevens N, Trollope WSW (2012) Increased tree densities in South African savannas: >50 years of data suggests CO<sub>2</sub> as a driver. *Glob Change Biol* 18:675–684
- Büntgen U, Schweingruber FH (2010) Environmental change without climate change? *New Phytol* 188:646–651
- Campos GEP, Moran MS, Huete A, Zhang Y, Bresloff C, Huxman TE, Eamus D, Bosch DD, Buda AR, Gunter SA, Scalley TH, Kitchen SG, McClaran MP, McNab WH, Montoya DS, Morgan JA, Peters DPC, Sadler EJ, Seyfried MS, Starks PJ (2013) Ecosystem resilience despite large-scale altered hydroclimatic conditions. *Nature* 494:349–352
- Chapotin SM, Holbrook NM, Morse SR, Gutiérrez MV (2003) Water relations of tropical dry forest flowers: pathways for water entry and the role of extracellular polysaccharides. *Plant, Cell Environ* 26:623–630
- Chapotin SM, Razanameharizaka JH, Holbrook NM (2006) Water relations of baobab trees (*Adansonia* spp. L.) during the rainy season: does stem water buffer daily water deficits? *Plant, Cell Environ* 29:1021–1032
- Chaturvedi RK, Raghubanshi AS, Singh JS (2011) Carbon density and accumulation in woody species of tropical dry forest in India. *For Ecol Manag* 262:1576–1588
- Costa Filho LO, Silva MHM, Almeida-Cortez JS, Silva SI, Oliveira AFM (2012) Foliar cuticular n-alkane of some *Croton* species from Brazilian semiarid vegetation. *Biochem Syst Ecol* 41:13–15
- Costa ACL, Galbraith D, Almeida S, Portela BTT, Costa M, Silva-Junior JA, Braga AP, Gonçalves PHL, Oliveira AAR, Fisher R, Phillips OL, Metcalfe DB, Levy P, Meir P (2010) Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytol* 187:579–591
- Donohue RJ, Roderick ML, McVicar TR, Farquhar GD (2013) CO<sub>2</sub> fertilization has increased maximum foliage cover across the globe's warm, arid environments. *Geophys Res Lett* 40:3031–3035
- Espírito-Santo MM, Sevilha AC, Anaya FC, Barbosa R, Fernandes GW, Sanchez-Azofeifa GA, Scariot A, Noronha SE, Sampaio CA (2009) Sustainability of tropical dry forests: two case studies in southeastern and central Brazil. *For Ecol Manag* 258:922–930
- Falcão HM, Oliveira MT, Mergulhão AC, Silva MV, Santos MG (2013) Ecophysiological performance of three *Opuntia ficus-indica* cultivars exposed to carmine cochineal under field conditions. *Sci Hortic* 150:419–424
- Figueiredo KV, Oliveira MT, Oliveira AFM, Silva GC, Santos MG (2012) Epicuticular-wax removal influences gas exchange and water relations in the leaves of an exotic and native species from a Brazilian semiarid region under induced drought stress. *Aust J Bot* 60:685–692
- Flexas J, Niinemets U, Gallé A, Barbour MM, Centritto M, Dias-Espejo A, Douth C, Galmés J, Ribas-Carbo M, Rodriguez PL, Rosselló F, Soolanayakanahally R, Tomas M, Wright IJ, Farquhar GD, Medrano H (2013) Diffusional conductances to CO<sub>2</sub> as a target for increasing photosynthesis and photosynthetic water-use efficiency. *Photosynth Res* 117:45–59
- Friend AD (2010) Terrestrial plant production and climate change. *J Exp Bot* 61:1293–1309
- Frosi G, Oliveira MT, Almeida-Cortez J, Santos MG (2012) Ecophysiological performance of *Calotropis procera*: an exotic and evergreen species in Caatinga, Brazilian semiarid. *Acta Physiologia Plantarum* 35:335–344
- Gariglio MA, Samapao EVSBS, Cestaro LAC, Kageyama PY (2010) Uso sustentável e conservação dos recursos florestais da Caatinga. Ministério do Meio Ambiente. Publicado pelo Serviço Florestal Brasileiro, Brasília
- Gibbs HK, Brown S, Niles JO, Foley J (2007) Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environ Res Lett* 2:1–13
- Giullietti AM, Conceição A, Queiroz LP (2006) Diversidade e caracterização das fanerógamas do semiárido brasileiro. Publicado por Associação Plantas do Nordeste, Recife
- Griscom HP, Ashton MS (2011) Restoration of dry tropical forests in Central America: a review of pattern and process. *For Ecol Manag* 261:1564–1579
- Harris NL, Brown S, Hagen SC, Saatchi SS, Petrova S, Salas W, Hansen MC, Potapov PV, Lotsch A (2012) Baseline map of carbon emissions from deforestation in tropical regions. *Science* 336:1573–1576
- Huber-Sannwald E, Palacios MR, Moreno JTA et al (2012) Navigating challenges and opportunities of land degradation and sustainable livelihood development in dryland social–ecological systems: a case study from Mexico. *Philos Trans R Soc Lond Ser Bot Biol Sci* 367:3158–3177
- IPCC (2007) Climate change: the physical science basis. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge
- Jeffree CE, Johnson RPC, Jarvis PO (1971) Epicuticular wax in the stomatal antechamber of Sitka spruce and its effects on the diffusion of water vapour and carbon dioxide. *Planta* 10:1–10
- Jetter R, Schäfer S (2001) Chemical composition of the *Prunus laurocerasus* leaf surface. Dynamic changes of the epicuticular wax film during leaf development. *Plant Physiol* 126:1725–1737
- Kerstiens G (1996) Signalling across the divide: a wider perspective of cuticular structure–function relationships. *Trends Plant Sci* 1:125–129

- Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR (2009) Elevated CO<sub>2</sub> effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *J Exp Bot* 60:2859–2876
- Lima ALA, Sampaio EVSB, Castro CC, Rodal MJN, Antonino ACD, Melo AL (2012) Do the phenology and functional stem attributes of woody species allow for the identification of functional groups in the semiarid region of Brazil? *Trees* 26:1605–1616
- Liu H, Williams AP, Allen CD, Guo D, Wu X, Anenkhonov OA, Liang E, Sandanov DV, Yin Y, Zhaohuan QI, Badmaeva NK (2013) Rapid warming accelerates tree growth decline in semiarid forests of Inner Asia. *Glob Change Biol* 19:2500–2510
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. *Nature* 462:1052–1055
- Lopes CGR, Ferraz EMN, Castro CC, Lima EN, Santos JMFF, Santos DM, Araújo EL (2012) Forest succession and distance from preserved patches in the Brazilian semiarid region. *For Ecol Manag* 271:115–123
- Machado ICS, Barros LM, Sampaio EVSB (1997) Phenology of Caatinga species at Serra Talhada, PE. *Biotropica* 29:57–68
- Maestre FT, Salguero-Gómez R, Quero JL (2012) It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands. *Philos Trans R Soc Lond Ser Bot Biol Sci* 367:3062–3075
- Malhi Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. *Plant, Cell Environ* 22:715–740
- Mansur RJCN, Barbosa DCA (2000) Physiological behavior in young plants of four trees species of Caatinga submitted the two cycles of water stress. *Phyton* 68:97–106
- Marengo JA, Nobre C, Tomasella J, Cardoso MF, Oyama MD (2008) Hydro-climate and ecological behaviour of the drought of Amazonia in 2005. *Philos Trans R Soc Lond Ser Bot Biol Sci* 363:1773–1778
- Marengo JA, Ambrizzi T, Rocha RP et al (2009a) Future change of climate in South America in the late twenty-first century: intercomparison of scenarios from three regional climate models. *Clim Dyn* 35:1073–1097
- Marengo JA, Jones R, Alves LM, Valverde MC (2009b) Future change of temperature and precipitation extremes in South America as derived from the PRECIS regional climate modeling system. *Int J Climatol* 29:2241–2255
- Marengo JA, Tomasella J, Alves LM, Soares WR, Rodriguez DA (2011) The drought of 2010 in the context of historical droughts in the Amazon region. *Geophys Res Lett* 38:L12703. doi:10.1029/2011GL047436
- Markesteyn L, Iraipi J, Bongers F, Poorter L (2010) Seasonal variation in soil and plant water potentials in a Bolivian tropical moist and dry forest. *J Trop Ecol* 26:497–508
- Markewitz D, Devine S, Davidson EA, Brando P, Nepstad DC (2010) Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake. *New Phytol* 187:592–607
- Metcalf DB, Meir P, Aragão LEOC, Lobo-do-Vale R, Galbraith D, Fisher RA, Chaves MM, Maroco JP, Costa ACL, Almeida SS, Braga AP, Gonçalves PHL, Athaydes J, Costa M, Portela TTB, Oliveira AAR, Malhi Y, Williams M (2010) Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. *New Phytol* 187:608–621
- Miles L, Newton AC, Fries RS, Ravilious C, May I, Blyth S, Kapos V, Gordon JE (2006) A global overview of the conservation status of tropical dry forests. *J Biogeogr* 33:491–505
- Ministério da Ciência e Tecnologia (MCTI) (2013) Estimativas anuais de emissões de gases de efeito estufa no Brasil. MCTI, Brasília
- Ministério do Meio Ambiente (MMA), Secretaria de Recursos Hídricos da Paraíba, Universidade Federal da Paraíba (2007) Altas das Áreas suscetíveis à desertificação do Brasil. Organizador Marcos Oliveira Santana, Brasília
- Ministério do Meio Ambiente: TNC (MMA) (2008) Mapa das Unidades de Conservação e Terras Indígenas do Bioma Caatinga. Org. Shirley Hauff. Coronário, Brasília
- Mott KA, Buckley TN (2000) Patchy stomatal conductance: emergent collective behaviour of stomata. *Trends Plant Sci* 5:258–262
- Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. *Annu Rev Ecol Syst* 17:67–88
- Newingham BA, Vanier CH, Charlet TN, Ogle K (2013) No cumulative effect of 10 years of elevated [CO<sub>2</sub>] on perennial plant biomass components in the Mojave Desert. *Glob Change Biol* 19:2168–2181
- Ni Y, Guo YJ, Han L, Han I, Tang H, Conyers M (2012) Leaf cuticular waxes and physiological parameters in alfalfa leaves as influenced by drought. *Photosynthetica* 50:458–466
- Nobre CA, Lahsen M, Ometto JPHB (2008) Global environmental change research: empowering developing countries. *Anais da Academia Brasileira de Ciências* 80:523–529
- Oliveira AFM, Salatino A (2000) Major constituents of the foliar epicuticular waxes of species from the Caatinga and Cerrado. *Z Naturforsch* 55:688–692
- Oliveira AFM, Meirelles ST, Salatino A (2003) Epicuticular waxes from Caatinga and Cerrado species and their efficiency against water loss. *Anais da Academia Brasileira de Ciências* 75:431–439
- Phillips OL, Van der Heijden G, Lewis SL (2010) Drought–mortality relationships for tropical forests. *New Phytol* 187:631–646
- Pinho RS, Oliveira AFM, Silva SI (2009) Potential oilseed crops from the semiarid region of northeastern Brazil. *Bioresour Technol* 100:6114–6117
- Powers JS, Becknell JM, Irving J, Pèrez-Aviles D (2009) Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. *For Ecol Manag* 258:959–970
- Prince SD, Wessels KJ, Tucker CJ, Nicholson SE (2007) Desertification in the Sahel: a reinterpretation of a reinterpretation. *Glob Change Biol* 13:1308–1313
- Quesada M, Sanchez-Azofeifa GA, Alvarez-Añorve M (2009) Succession and management of tropical dry forests in the Americas: review and new perspectives. *For Ecol Manag* 258:1014–1024
- Rivas R, Oliveira MT, Santos MG (2013) Three cycles of water deficit from seed to young plants of *Moringa oleifera* woody species improves stress tolerance. *Plant Physiol Biochem* 63:200–208

- Rodal MJN, Sampaio EVSBA (2002) Vegetação do bioma Caatinga. In: Sampaio EVSBA, Giuliatti AM, Virginio J, Gamarra-Rojas CFL (eds) *Vegetação e flora da Caatinga*. Publicadopor PNE/CNIP, Recife, pp 11–24
- Rodrigues RR, Lima RAF, Gandolfi S, Nave AG (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biol Conserv* 142:1242–1251
- Rotenberg E, Yakir D (2010) Contribution of semi-arid forests to the climate system. *Science* 327:451–454
- Sampaio EVSB, Araújo EL, Salcedo IH, Tiessen H (1998) Regrowth of Caatinga vegetation after slashing and burning at Serra Talhada, PE, Brazil. *Pesquisa Agropecuária Brasileira* 33:621–632
- Sampaio E, Gasson P, Baracat A, Cutler D, Pareyn F, Lima KC (2010) Tree biomass estimation in regenerating areas of tropical dry vegetation in northeast Brazil. *For Ecol Manag* 259:1135–1140
- Santos JC, Leal IR, Almeida-Cortez JS, Fernandes GW, Tabarelli M (2011) Caatinga: the scientific negligence experienced by a dry tropical forest. *Trop Conserv Sci* 4:276–286
- Sheffield J, Wood EF, Roderick ML (2012) Little change in global drought over the past 60 years. *Nature* 491:435–438
- Shope JC, Peak D, Mott KA (2008) Stomatal responses to humidity in isolated epidermes. *Plant, Cell Environ* 31:1290–1298
- Silva RA, Santos AMM, Tabarelli M (2003) Riqueza e diversidade de plantas lenhosas em cinco unidades de paisagens da Caatinga. In: Leal IR, Tabarelli M, Silva JMC (eds) *Ecologia e Conservação da Caatinga*. EditoraUniversitária da UFPE, Recife
- Silva JMC, Tabarelli M, Fonseca MT, Lins LV (2004a) Biodiversidade da Caatinga: áreas e ações prioritárias para a conservação. MMA—UFPE—Conservation International—Biodiversitas—Embrapa Semi-arido, Brasília
- Silva EC, Nogueira RJMC, Azevedo-Neto AD, Brito JZ, Cabral EL (2004b) Ecophysiological aspects of ten species occurring in “caatinga” dry forest in Cabaceiras County, Paraíba State, Brazil. *Revista Iheringia* 59:201–205
- Silva EC, Nogueira RJMC, Araújo FP, Melo NF, Azevedo-Neto AD (2008) Physiological responses to salt stress in young umbu plants. *Environ Exp Bot* 63:147–157
- Souza BD, Meiado MV, Rodrigues BM, Santos MG (2009) Water relations and chlorophyll fluorescence responses of two leguminous trees from the Caatinga to different watering regimes. *Acta Physiol Plant* 32:235–244
- Stoner KE, Sánchez-Azofeifa GA (2009) Ecology and regeneration of tropical dry forests in the Americas: implications for management. *For Ecol Manag* 258:903–906
- Suresh HS, Dattaraja HS, Sukumar R (2010) Relationship between annual rainfall and tree mortality in a tropical dry forest: results of a 19-year study at Mudumalai, southern India. *For Ecol Manag* 259:762–769
- Tadeu J, Costa DM, Holanda L, Andrade C (2008) Knowledge and use of ouricuri (*Syagrus coronata*) and babaçu (*Orbignya phalerata*) in Buíque, Pernambuco State, Brazil. *Acta Bot Brasilica* 22:1141–1149