

Contents lists available at ScienceDirect

Forest Ecology and Management



journal homepage: www.elsevier.com/locate/foreco

Diversity of growth responses to recent droughts reveals the capacity of Atlantic Forest trees to cope well with current climatic variability

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ARTICLE INFO	A B S T R A C T			
Keywords: Drought recovery Secondary growth Dendrochronology Atlantic Forest Tropical trees Climate change	Understanding the behavior of trees and how they will respond to future climate change is a crucial conservation challenge, especially for tropical species. Despite the high diversity of tree species in Brazil, little is known about their tolerance limits. The study of tree rings is a valuable method for the analysis of growth dynamics with superposed epoch analysis being a good way to understand whether past dry years induce decreased tree growth, how long it takes to recover growth after a dry period, and the resilience of trees. This study investigated seven legume species (deciduous and evergreen) from three different sites in the Atlantic Forest in the state of Rio de Janeiro, Brazil. The studied trees seem to have coped well with the drought periods experienced thus far with no common pattern of recovery among species at the same site. The trees were not affected in a similar way and so different mechanisms are likely involved in preventing significant decreases in growth. These data are important for conservation policies because they reveal that each species requires a unique analysis.			

1. Introduction

Climate change is associated with the failure of individuals and populations. However, not all species or individuals within populations are pressed to their tolerance limits to the same extent and our understanding of these tolerance limits either of species in highly diverse ecosystems or of individuals within populations remains scant and fragmented. In fact, there is a plethora of mechanisms that underlie counterintuitive lack of individual collapses or forest diebacks after severe climatic events such as intense droughts, but their actual relevance to counteract these climatic oscillations under real field conditions deserves extensive attention (Lloret et al., 2013). Forest ecosystems influence the maintenance of the global carbon cycle, by biomass accumulation, and the water cycle mainly within continental environments, with the formation of flying rivers by evapotranspiration process (Davidson et al., 2012; Spracklen and Garcia-Carreras, 2015). In this way, future ecological relationships as well as carbon and water cycling will depend on how plants respond to climate change (Martín-Benito and Pederson, 2015).

Despite intensive study, many uncertainties remain regarding the actual capacity of temperate tree species to cope with current levels of climatic variability (e.g.: Seddon et al., 2016; Thurner et al., 2017; Zywiec et al., 2017). Tropical forests, on the other hand, are gaining attention with an increasing number of studies addressing their actual or potential responses to climate change. However, the extension of tropical forests and their overwhelming biodiversity, together with the proportionally lower research intensity in tropical regions, makes for greater uncertainty regarding these ecosystems (Bustamante et al., 2016; Seddon et al., 2016). This lack of knowledge deserves urgent attention due to the widely recognized importance of tropical forests for the maintenance of global processes involving mass and energy exchange between the biosphere and the atmosphere over the entire earth (Bustamante et al., 2016; Taylor et al., 2017).

The Atlantic Forest biome contains the largest urban concentrations

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https://doi.org/10.1016/j.foreco.2020.118656

Received 17 June 2020; Received in revised form 24 September 2020; Accepted 25 September 2020 Available online 6 October 2020 0378-1127/© 2020 Elsevier B.V. All rights reserved. of Brazil with more than 60% of the nation's population, which has caused the loss of vegetation cover, fragmentation of forests and, consequently, climate impacts (Scarano and Ceotto, 2015). The Atlantic Forest is considered among the three biodiversity hotspots most vulnerable to climate change (Béllard et al., 2014), with vulnerability meaning the degree to which geophysical, biological and socio-economic systems are susceptible to, and unable to cope with, adverse impacts of climate change (Füssel and Klein, 2006; IPCC, 2007). Only 28% of the original extension of the Atlantic Forest remains, yet Rezende et al. (2018) explain that 35% is needed to consider the biome adaptable to climate change. To achieve this, it is necessary to understand the relationship between native plants and extreme climatic events. There is also biological evidence of the "savannization" of rainforest, resulting in a drier and warmer climate (Scarano and Ceotto, 2015).

Alternating dry and wet periods on an interannual or decade timescale produce cyclical droughts (Rodrigo et al., 1999) that can affect tree growth. Tree rings provide a detailed record of climatic change in a given region and growth is a key feature that is directly related to fitness of long lived species such as trees. Dendrochronological studies also allow the reconstruction of historical growth patterns and thus relate growth with unusual climatic events over extended periods of time. Such studies are very valuable for assessing the suitability of tree species to cope with current climatic variability, to estimate their vulnerability to increased variability forecasted by global climatic models, and to understand forest dynamics. Models of climate change throughout the world predict wide-spread increased precipitation in response to global warming (Pendergrass et al., 2017). As a result, the frequency of the most intense tropical cyclones is expected to increase, contributing substantially to precipitation in several areas of the world but mainly off-equatorial land (O'Gorman, 2015).

We aimed to explore the sensitivity of tropical trees to increased climatic variability by quantifying growth responses of seven species at three Atlantic Forest locations in Brazil that differ in annual rainfall. We hypothesize that (i) past dry years have induced a significant decrease in the secondary growth of all species and at all sites, which did not fully recover in the subsequent three years; (ii) deciduous species are more resilient to dry years than evergreen species; and (iii) trees at the driest site are the most resilient to dry years.

2. Material and methods

2.1. Study areas and climate data

The research was conducted at three sites with different vegetation cover (IBGE, 2012) and environmental heterogeneity in the Atlantic Forest of the state of Rio de Janeiro, Brazil (Fig. 1). Reserva Biológica de Poço das Antas (Biological Reserve of Poço das Antas, PA) encompasses approximately 5,000 ha in the municipality of Silva Jardim $(22^{\circ}30'-22^{\circ}33'S, 42^{\circ}15'-42^{\circ}19'W)$. The vegetation is sub-montane and alluvial ombrophilous dense forest (Lima et al., 2006). The relief is composed of plains and hills with rounded profiles, the height of which ranges 19-200 m above sea level, separated by floodplains, while the soil is classified as Fluvic Neossol (Moraes et al., 2008). The climate is tropical with a dry season in winter, or Aw by the Köppen system, with average annual rainfall of 1995 mm and an average annual temperature of 25.5 °C (Bernardes, 1952; Lima et al., 2006; Moraes et al., 2006). Precipitation data used in the analysis were obtained from Quarteis meteorological station for 1968-2004, provided by Agência Nacional de Águas (National Agency of Waters - ANA, 2019), while temperature data were obtained and provided by Atlantic Forest Project station for 1984-2007 (Fig. 2A).

Parque Nacional do Itatiaia (Itatiaia National Park, IT) encompasses approximately 28,156 ha (Morim, 2006) in the municipality of Itatiaia (22°15′–22°30′S, 44°30′–44°45′W). The vegetation is a montane ombrophilous dense forest. Samples were collected between 700 m and 1100 m of altitude. The average annual rainfall is 1699 mm and the average annual temperature is 18.2 °C. The soil is characterized by Oxisols, Argisols and Nitossols (IBAMA, 2014). The climate is temperate humid with a cold dry season between June and August, Cfb by the Köppen system (Segadas-Vianna and Dau, 1965). Temperature and



Fig. 1. Map of the study area in the State of Rio de Janeiro, in the Southeastern Brazil. Black points indicate the georeferenced locations of the sampled trees. CF: Cabo Frio center of plant diversity. IT: Itatiaia National Park. PA: Biological Reserve of Poço das Antas.



Fig. 2. Climate diagram according to Walter and Lieth of Poço das Antas (PA) (A), Itatiaia National Park (IT) (B) and Cabo Frio center of plant diversity (CF) (C). Mean annual temperature was 23.8C, 20.1 $^{\circ}$ C, 22.6 $^{\circ}$ C and total annual precipitation was 2370 mm, 1535 mm, 814 mm, respectively.

precipitation data used in the analysis were obtained from Resende meteorological station for 1961–2007 and 1925–1998, respectively, and were provided by Instituto Nacional de Meteorologia (National Institute of Meteorology – INMET, 2019) (Fig. 2B).

Centro de Diversidade Vegetal de Cabo Frio (Cabo Frio Center of Plant Diversity, CF) encompasses approximately 150,000 ha of the municipalities of Araruama, Armação dos Búzios, Arraial do Cabo, Cabo Frio, Iguaba, São Pedro da Aldeia and Saguarema (22°30'-23°00'S, $41^{\circ}52'-42^{\circ}42'W$). The topography is mostly flat, with the exception of some coastal hills ranging 50-100 m in altitude. The vegetation includes seasonal semideciduous forest, ombrophilous dense forest, and pioneer vegetation with maritime influence (Lima, 2000). The soil is characterized by Quartzarenic Neossol or as clayey-sandy (Dantas et al., 2009). The climate is tropical with a dry season in the winter, Aw by the Köppen system, with average annual rainfall of 820 mm and an average annual temperature of 23.5 °C. Samples were collected in seasonal semideciduous forest of lowlands on slightly sloping hills in the cities of Cabo Frio and Armação de Búzios. Temperature and precipitation data, for 1970-1987 and 1941-1987, respectively, used in the analysis were obtained from the NOAA weather database (Kalnay et al., 1996) as the NCEP/NCAR Global Reanalysis product and also from Cabo Frio (Alcális) meteorological station and shared by Instituto Nacional de Meteorologia (National Institute of Meteorology - INMET, 2019) (Fig. 2C).

2.2. Study species (Table 1)

Seven tree species of the family Leguminosae were chosen for the study because they present distinct growth rings and are important components of the studied patches of Atlantic Forest (Brandes, 2011; Macedo et al., 2020; Lima, 2000; Lima et al., 2006; Morim, 2006). Apuleia leiocarpa (Vogel) J.F. Macbr. is a pioneer, early secondary, late secondary or climax light-demanding species. It is a deciduous tree and, in the state of Rio de Janeiro, flowers from September to October with fruits ripening from February to May (Carvalho, 2003). In PA the leaves fall from June to September and budding occurs from September to October (Pereira et al., 2008). The wood anatomy of the species was described by Mainieri and Chimelo (1989) and showed distinct growth rings marked by a fibrous zone and marginal parenchyma. Centrolobium tomentosum Guillemin ex Benth. is an early secondary, late secondary or climax shade-tolerant species that occurs in PA. It is a deciduous tree and, in the state of Rio de Janeiro, flowers from November to March and fruits from July to September. Leaf fall occurs in winter (June-August) and budding from September to December (Carvalho, 2005). The species shows distinct growth rings marked by marginal parenchyma and a fibrous zone (Lisi et al., 2008). Lonchocarpus cultratus (Vell.) A.M.G.Azevedo & H.C.Lima is deciduous, with leaf fall in PA occurring from October to December and budding from December to January. Flowering occurs from February to March and fruiting from July to September (Pereira et al., 2008). The species has distinct growth rings marked by thick-walled latewood fibers and marginal parenchyma (Callado et al., 2001). Pseudopiptadenia contorta (DC.) G.P. Lewis & M.P. Lima is a perennial species, but in IT it presents some intensity of leaf fall from June to October and budding in September (Pires, 2006). Budding in PA occurs in October, flowering from November to December and fruiting from April to October (Pereira et al., 2008). Growth rings are marked by thick-walled and radiallyflattened latewood fibers (Barros and Callado, 1997). Pseudopiptadenia leptostachya (Benth.) Rauschert only occurs in montane dense ombrophilous forest in the states of Minas Gerais, Rio de Janeiro and São Paulo (Morim, 2006). Leaf fall is perennial, but in IT it presents some intensity of leaf fall from June to October and budding in September (Pires, 2006). The species has distinct growth rings marked by thickwalled and radially flattened latewood fibers (Barros et al. 2008). Pterocarpus rohrii Vahl is a deciduous species and occurs in CF. Leaf fall occurs from October to November and budding in November (Pereira

et al., 2008). Growth rings are marked by thick-walled latewood fibers and marginal parenchyma (Barros et al., 2008). *Paubrasilia echinata* (Lam.) E. Gagnon, H.C. Lima & G. P. Lewis is a deciduous species and occurs in CF. Leaf fall occurs from September to December and budding occurs from October to January (Borges et al., 2009). The species is considered "Endangered" (Varty, 1998). The annual growth rings are marked by marginal parenchyma, but also by combinations of locally distended rays, latewood thickness and radially flattened fiber walls, as well as differences in vessel and parenchyma frequency between contiguous rings (Macedo et al., 2020).

2.3. Dendroecological analyses and superposed epoch analysis (SEA)

Two to four increment cores were sampled from each tree at breast height (1.30 m). The cores were air dried, glued onto wooden mounts and polished with sandpaper of decreasing granulometry (80-2000 grit size). Wood dust was removed from vessels with compressed air to improve visibility of growth zone boundaries. All samples were scanned at 1200–3200 dpi resolution and growth ring measurements and image processing were performed with Image Pro Plus (version 3.0 for Windows), with a precision of 0.01 mm. Each ring was assigned to the calendar year in which ring formation began according to the dating convention for the Southern Hemisphere (Schulman, 1956). Crossdating of the temporal series was performed following the recommendations of Stokes and Smiley (1996) and Fritts (1976) and statically checked using the program COFECHA (Holmes, 1983). The cross-dated ring width series was detrended and standardized to remove age-related growth trends (Fritts, 1976; Cook and Kairiukstis, 1990). All correctly dated series were standardized using the best functions fitted to the data using the ARSTAN program (Cook, 1985). Standard and residual chronologies of tree ring width were produced for each species and site with the best correlated series using the ARSTAN program (Cook and Kairiukstis, 1990; Cook and Holmes, 1996). Pearson's correlation analysis was used to evaluate relationships between tree-ring-width chronology and monthly and annual precipitation and mean temperature, as well as between tree-ring-width chronology and precipitation for December–January–February (summer), March-April-May (autumn), June-July-August (winter), and September-October-November (spring). Linear regressions were used to test climatic trends (temperature and precipitation).

The nonparametric technique of superposed epoch analysis (SEA) was used to assess the relationship between dry periods and tree growth and a strength of the response in the corresponding year (Lough and Fritts, 1987). In this paper, extreme dry periods were defined as years with precipitation lower than 25th percentile of the total precipitation (Muza et al., 2009), during the growing season (September – August). The selected dry years were 1975, 1986, 1999 at PA, 1963, 1976, 1989 at IT, 1962, 1972, 1979 at CF, which total water availability values were 2008 mm, 2055 mm, 1789 mm at PA, 1094, 1238, 1038 at IT, 526, 624, 470 at CF respectively. These years also showed decrease in tree-ring width index (Brandes, 2011; Macedo et al., 2020). Centered in the year of the drought, 3 years before and 3 years after were taken as background years for comparisons. Pearson's correlation analysis and SEA were performed in the R statistical environment ver. 3.0 (R Core Team, 2019).

3. Results

Seven tree-ring width chronologies were produced covering the interval between 1928 and 2012 and ranging in timespan from 49 to 82 years (Fig. 3). The timespan, intercorrelation, mean sensitivity, Rbar and EPS for each species are given in Table 1. Intercorrelations were highest for *C. tomentosum* while mean sensitivity was highest for *P. echinata*. The oldest tree (82 years) was a *P. leptostachia* while the youngest was a *L. cultratus* (49 years), both from Itatiaia.

The correlation analysis of precipitation and temperature with



Fig. 3. Ring width index chronologies of all individual trees (gray line) and mean series (back line). Apuleia leiocarpa (A), Centrolobium tomentosum (B), Lonchocarpus cultratus (C), Pseudopiptadenia contorta (D), Pseudopiptadenia leptostachya (E), Pterocarpus rohrii (F), Paubrasilia echinata (G).

Table 1

Species, leaf fall behavior, collection site, tree-ring width chronologies data and years for growth recovery after drought year.

Chronology/species	Apuleia leiocarpa	Centrolobium tomentosum	Lonchocarpus cultratus	Pseudopiptadenia contorta	Pseudopiptadenia leptostachia	Pterocaupus rohrii	Paubrasilia echinata
Leaf fall	deciduous	deciduous	deciduous	perennial	perennial	deciduous	deciduous
Site	Poço das Antas	Poço das Antas	Itatiaia	Cabo Frio	Itatiaia	Cabo Frio	Cabo Frio
Number of trees	7	5	4	6	7	4	8
Number of series	14	15	9	7	8	9	10
Chronology extension	1942-2007	1937–2007	1959–2007	1959–2009	1928–2009	1954–2009	1953–2012
Age	66	71	49	51	82	56	59
Radial increment (mm)	1.85	2.04	2.43	1.47	2.32	1.52	2.4
Chronology	STD	STD	STD	STD	STD	STD	RES
Intercorrelation	0.382	0.551	0.513	0.525	0.424	0.48	0.41
Mean sensitivity	0.509	0.482	0.491	0.665	0.396	0.615	0.71
Rbar	0.32	0.179	0.107	0.193	0.153	0.424	0.159
Rbar window overlap	50–25	30–15	20–10	20–10	20–10	20–10	10–5
EPS	0.809	0.635	0.419	0.626	0.474	0.787	0.65
Years	3	1	1	1	x	2	x

chronology showed distinct results that are presented in Table 2. Neither climatic feature was significantly correlated with *L. cultratus* growth. Temperature was not significantly correlated with the chronologies of *C. tomentosum* and *P. echinata*, but was negatively correlated with those of *A. leiocarpa* and *P. contorta* and positively correlated with those of *P. leptostachia* and *P. rohrii*. Several precipitation variables were positively correlated with chronologies during current or previous growth years.

Superposed epoch analysis (SEA) allowed us to understand the growth responses among different species and sites of the Atlantic Forest, but none of the species exhibited statistically significant growth reductions after the drought period. There was no common drought response across species, with some species growing slowly while others exhibiting no growth decrease after the drought period (Fig. 4).

Time of recovery differed among species, with most varying between one and three years but with some not exhibiting growth recovery after three years (Table 1). Time of recovery was not correlated with leaf phenology or site. There was no growth reduction during the drought year for *A. leiocarpa* of PA, but it was observed the following year with recovery in the third year (Fig. 4A). *Centrolobium tomentosum* of PA revealed a growth reduction during the drought year and recovered its growth the following year (Fig. 4B). The species of IT also differed in their responses. *L. cultratus* exhibited a growth reduction during the

Table 2

Statistically significant correlation values between precipitation, temperature and chronologies. p = previous.

Species	Precipitation	Temperature
Apuleia leiocarpa PA	Dec ($r = 0.476$, $p = 0.003$); annual ($r = 0.463$, $p = 0.003$)	pApr (r = -489, p = 0.018)
Centrolobium tomentosum PA	pFeb ($r = 0.421$, $p = 0.009$); annual ($r = 0.339$, $p = 0.037$)	X
Lonchocarpus cultratus IT	X	х
Pseudopiptadenia contorta CF	May (r = 0.412, p = 0.029); Jul (r = 0.446, p = 0.017)	Dec (r = -0.592 , p = 0.010); summer (r = -0.496 , p = 0.043)
Pseudopiptadenia leptostachia IT	pMar ($r = 0.308$, $p = 0.009$); annual ($r = 0.363$, $p = 0.002$); psummer ($r = 0.282$, $p = 0.017$); pautumn (0.254, $p = 0.033$)	pJul (r = 0.409, p = 0.005); pMay (r = 0.313, p = 0.032)
Pterocarpus rohrii CF	pFeb (r = 0.409, p = 0.016)	pMar (r = 0.556 , p = 0.016); pOct (r = 0.509 , p = 0.031)
Paubrasilia echinata CF	pApr (r = 0.28); Nov (r = 0.27); Jan (0.25)	x

drought year and recovery in the following year (Fig. 4C). In addition, drought reduced the growth of *P. leptostachya*, with no recovery being observed in these analyses (Fig. 4D). The species from CF, the driest site, exhibited growth reduction in the years following the drought year: *P. rohrii* experienced growth reduction during the year immediately after the drought year and recovered in the second year (Fig. 4E); *P. echinata* had decreased growth in the second year after the drought year with no recovery being observed (Fig. 4F); *P. contorta* recovered its growth during the year immediately after the drought year immediately after the drought year with no recovery being observed (Fig. 4F); *P. contorta* recovered its growth during the year immediately after the drought event (Fig. 4G).

4. Discussion

The physiological changes that trees undergo during water stress can affect their growth during drought conditions and encumber their recovery (Kannenberg et al., 2019). These changes, therefore, are important for quantifying the ecosystem responses to global change. Seasonality in rainfall is the main influential factor of cambial activity in the tropics and subtropics (Callado et al., 2013). Tropical species, including those of the Atlantic Forest, frequently exhibit a positive correlation of growth with precipitation during the rainy months in spring and summer (e.g. Brandes et al., 2011; Brienen et al., 2016; Fontana et al., 2018; Macedo et al., 2020). Considering the projected reductions in precipitation and soil moisture content for Atlantic Forest by the end of the century (WMO-UNEP, 2008), and the evidence of the "savannization" of the rainforest (Scarano and Ceotto, 2015), the diversity of growth responses to recent droughts found in the present study reveals that Atlantic Forest trees have the capacity to cope well with climatic change. Although we noted reductions in the growth of trees of the populations analyzed here, most of the reductions were not significant and growth recovered occurred within three years. Other predictions for the end of the century suggest an increase in precipitation in most of the world, including Southeast Brazil (Pendergrass et al., 2017). Even with this scenario, drought years are still likely to occur, but southeast Atlantic Forest trees should cope with these events well.

A positive correlation between growth and precipitation during spring and summer was observed for all the species studied here, with the exception of *Lochocarpus cultratrus*, but responses varied. Granda et al. (2013) showed that water supply, temperature and photosynthetic activity in the previous autumn affect tree ring formation in some Mediterranean tree species. We also observed a positive correlation between precipitation of the previous year and growth in species such as *A. leiocarpa, C. tomentosum, P. leptostachia, P. rohrii* and *P. echinata,* among which only *P. leptostachia* did not exhibit growth recovery after three years. It seems likely that growth recovery is related to a wet period after a drought year, but not for all the analyzed species.



Fig. 4. Superposed epoch analysis showing tree growth departures for the drought year and 3 years before and after the drought event in trees in three different sites of the Atlantic Rain Forest. *Apuleia leiocarpa* (A) and *Centrolobium tomentosum* (B) from Biological Reserve of Poço das Antas (PA). *Lonchocarpus cultratus* (C), *Pseudopiptadenia leptostachya* (D) from Itatiaia National Park (IT). *Pterocarpus rohrii* (E), *Paubrasilia echinata* (F), *Pseudopiptadenia contorta* (G) from Cabo Frio center of plant diversity (CF).

No common pattern of recovery was found for species of the same site, thus our results show that different species are affected in different ways at the same site. Chronology length did not influence studied species since species varied ca. 5 years in PA and ca. 8 years in CF, and even more in IT with ca. 33 years. Neither did the radial increment, the species showed increment between 1.47 and 2.43 mm. Thus, the present results indicate that tropical tree species respond differently to drought periods than do temperate trees, which may be influenced by synergy with other environmental factors such as latitude and water table depth, for example (Martín-Benito and Pederson, 2015; Kannenberg et al., 2019). The effects that drought periods have on growth trends were not similar for all the leguminous tree species analyzed here from Atlantic Forest, which indicates that distinct conservation policies may be required for different species at the same site.

The species analyzed here are known to be drought susceptible and to respond plastically to environmental conditions (Brandes, 2011; Macedo et al., 2020), suggesting that climatic conditions affect tree growth in the tropics (Callado et al., 2013), but growth reduction is not sustained by most. It is, therefore, important to understand the survival potential of tropical trees and time period for recovery in unfavorable future climatic conditions (Venegas-González et al., 2018). The results presented here allow us to infer that P. leptostachya would be the most affected, corroborating Venegas-González et al. (2018) who showed that Atlantic Forest trees at the highest-altitudes are more sensitive to drought. Pterocarpus rohrii was less affected than other tree species, probably because deciduous tropical species in dry areas respond directly to rainfall seasonality by synergistic action between leaf phenology, cambial phenology and water storage (Borchert, 1999). Thus, the response of deciduous species is not only related to global climate events, but also to the complex integration of multiple internal and external factors.

All species that possess diffuse-porous wood, which, according to Kannenberg et al. (2019) is more related to the legacy effects of significant droughts than all other wood anatomies in temperate mesic forests. They also found that species that are more affected by drought experience a long period of recovery and are from sites with higher clay and silt content than sand. The species analyzed here are from different edaphic conditions that likely affect soil water saturation, which can explain some of the observed variability in response to drought. The diversity found in the Atlantic Forest can be related with tree response and time of recovery. These results should improve our capacity to predict ecosystem sensitivity to drought (both during and after drought events) across a region that is expected to experience increasing water stress in the coming decades (Pendergrass et al., 2017; Dai, 2013).

The chronologies described and used in the present study can be considered short, indicating the studied populations are young. Other studies of dendrochronology and age structure in different phytophysiognomies of the Atlantic Forest corroborate this finding by showing that most species do not exceed 150 years of age (Seitz and Kanninen, 1989; Estrada et al., 2008; Callado and Guimarães, 2010; Oliveira et al., 2010; Brandes et al., 2011, 2016; Costa et al., 2015; Vasconcellos et al., 2016; Fontana et al., 2019; Macedo et al., 2020; Albuquerque et al., 2019). The longest chronology obtained for the Atlantic Forest was for 171 years for an individual of Nectandra oppositifolia from a dense rainforest (Granato-Souza et al., 2018). The lack of old trees in this biome may be related to anthropogenic influences during the historical process of occupation of the Brazilian coast. The creation of protected areas in Brazil - the first of which was IT on June 14, 1937 (IBDF (Instituto Brasileiro de Desenvolvimento Florestal), 1982) - contributed to ceasing predatory exploitation of trees in the Atlantic Forest.

5. Conclusion

The disparity of growth responses to dry years or, in other words, the lack of a strong, homogenous climatic signal of the data, suggests that the studied populations are, on average, well suited to deal with the moderate levels of aridity experienced so far. Since many responses to stress are nonlinear and exhibit tipping points and thresholds, our study does not discard growth reductions under increasing aridity. However, our study points to the existence of mechanisms involving either ample genetic variability, individual tolerance and plasticity or local environmental heterogeneity that are effective in preventing general and significant decreases in fitness due to unusually dry years.

CRediT authorship contribution statement

Tahysa Mota Macedo: Methodology, Investigation, Writing - review & editing. Warlen Silva Costa: Investigation, Writing - review & editing. Arno Fritz Neves Brandes: Methodology, Investigation, Writing - review & editing. Fernando Valladares: Conceptualization. Cláudia Franca Barros: Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Laboratório de Botânica Estrutural from Instituto de Pesquisas Jardim Botânico do Rio de Janeiro and the CNPq (Conselho Nacional de Desenvolvimento Científico Tecnológico) for the PDJ and Pesquisador Visitante fellowships, as well as CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), PPBIO (Programa de Pesquisa em Biodiversidade), and FAPERJ (Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro) for the research fellowship grant.

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T.M. Macedo et al.

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