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ECOSYSTEMS

Changes in growth and reproductive phenology of *Allagoptera arenaria* (Arecaceae) under climate change scenarios

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Abstract: Climate change has led to shifts in phenology in many species distributed widely across taxonomic groups. It is, however, unclear how we should interpret these shifts without some sort of a yardstick. We assessed climate change effects on *Allagoptera arenaria*, a acaulescent palm, using open top chambers (OTCs) and rain gutters in the field to mimic expected temperature and rainfall changes in this area. In a coastal environment (restinga), using open top chambers (OTCs) and rain gutters in the field to mimic expected temperature and rainfall changes in this area, 40 A. arenaria individuals were selected and randomly allocated to four treatments: control (C), 25% rainfall increase (P), 2 °C temperature increase (T), and 2 °C temperature plus 25% rainfall increase (TP). For 2 years, every two weeks, we measured changes in growth and reproduction phenology to assess whether this species altered allocation patterns in response to new environmental conditions. Increases in aboveground biomass were higher in the TP than in the T treatment, which in turn had more reproductive cycles throughout the experimental period. We conclude that temperature increases may shorten the reproductive cycle of *A. arenaria*.

Key words: Aerial biomass, *Allagoptera arenaria*, climate change, OTC's, reproductive phenology, restinga.

INTRODUCTION

Evidence showing that global climate is changing is now strong and there is growing concern about its consequences for natural ecosystems (Hof et al. 2011, IPCC 2014, Lacerda et al. 2015, Scarano & Ceotto 2015, IPCC 2018). Increasing levels of carbon dioxide in the atmosphere will rise temperatures 2-5°C over this century, with parallel changes in other environmental variables, such as rainfall and soil humidity (IPCC 2014). The impact of these changes on plant phenology have been widely reported (e.g., Fang & Chen 2015, Rai 2015, Keyzer et al. 2017, Mendoza et al. 2017, Prevéy et al. 2017) and include changes in life cycles (Parmesan & Yohe 2003, Menzel et al. 2006, Rosenzweig et al. 2008, Gordo & Sanz 2010, Wolkovich et al. 2012) and plant reproduction and productivity (De Valpine & Harte 2001, Kardol et al. 2010).

Temperature and rainfall influence overall plant growth in terrestrial ecosystems (Kardol et al. 2010). Warming impacts plant biomass (Shaver et al. 2000, Rustad et al. 2001, Pugnaire et al. 2020), increasing (Rustad et al. 2001, Wan et al. 2005, Sullivan et al. 2008) or decreasing productivity (De Boeck et al. 2008, Sherry et al. 2008, Carlyle et al. 2014). There is ample evidence showing that plant biomass responds positively to increased rainfall (Huxman et al. 2004, Spence et al. 2016). However, how changes in temperature and rainfall interact with each other and their influence on plant growth and phenology are less known (Badeck et al. 2004, Kardol et al. 2010, Rai 2015). Temperature is also one of the main factors controlling plant phenology (Estrella & Menzel 2006, Lu et al. 2006, Menzel et al. 2006) and high temperatures speed up the life cycle of plants (Saxe et al. 2001, Walther et al. 2002, Badeck et al. 2004, Solomon et al. 2007) which are further conditioned by rainfall patterns (Badeck et al. 2004, Gordo & Sanz 2010).

In the *restinga*, a coastal ecosystem within the Atlantic Forest biome in SE Brazil, low nutrient and water contents in the sandy substrate, high salinity, and high temperature and irradiance are the main factors limiting plant establishment and performance (Menezes et al. 2017). In such environments, a acaulescente palm, *Allagoptera arenaria* (Gomes) Kuntze, plays a key role in secondary succession, as it is able to colonize open areas (Zaluar & Scarano 2000, Scarano et al. 2004, Carvalho et al. 2014), acting as facilitator for other species (Menezes et al. 2017) by providing soil nutrients under its canopy while decreasing irradiance and temperature through shade (Menezes & Araujo 2000).

It is true that climate change can bring serious risks to the Atlantic forest biome, including the vegetation of coastal ecosystems such as the restinga (Knupp et al. 2021). Projections for 2041-2070 indicate a temperature increase of 1.5-2 °C and rainfall of 15-20% for the southeastern region of Brazil (Scarano & Ceoto 2015). Since climate change will affect rainfall and temperature patterns (IPCC 2018), we need to understand its effects on this species' performance to anticipate its responses to new climate conditions (Meineri et al. 2015, Parmesan & Hanley 2015, Moran et al. 2016). Combined or isolated changes in temperature and rainfall may have different effects on *A. arenaria* biomass and phenology, with consequences for plant fitness and plant community dynamics.

Here we report on the variability of aboveground growth and reproductive phenology patterns of *A. arenaria* in response to increased temperature and rainfall, and analyze how the isolated and combined effects of both climatic factors influence plant growth and reproductive output in this species. For this purpose, we used open top chambers (OTCs) and rain gutters to manipulate microclimate conditions in the field to mimic the expected climate changes for this region, including daily and seasonal fluctuations (Pritchard & Amthor 2005, Lessin & Ghini 2009). We expect that increases in temperature and rainfall will influence to the growth of this species, whereas increases in just one of these factors would have smaller effects on growth and phenology.

MATERIALS AND METHODS

Field site and species

The experiment was carried out in the Itaúnas State Park, Espírito Santo, Brazil (18°24'21" S and 39°42'8" W) in an open, non-flooded *restinga* shrub formation (Monteiro et al. 2014). The region has a tropical humid climate, Aw type in Köppen classification, with annual rainfall around 1100 mm, mean annual temperature of 23.8°C, and mean air relative humidity of 84%. The highest rainfall occurs in summer, with monthly means of 185 mm, and the lowest in winter, with rainfall means of 50 mm. The average temperature in summer is about 26°C, and 21°C in winter.

A. arenaria is a palm typical of the Brazilian *restingas*, up to 2.5 m high and 2 m in canopy diameter (Menezes & Araujo 2005), which is distributed from Sergipe to Paraná States (Moraes & Martins 2017), forming dense populations in certain parts of the sandy shoreline (Menezes & Araujo 1999). This acaulescent palm has an underground stem which makes it able to resprout after fire (Menezes & Araujo 2005).

There is ample information on *A. arenaria* reproductive biology, seed predation (Grenha et al. 2008), and its effects on plant community structure (Menezes & Araujo 1999, 2000, 2005). *A. arenaria* is the main facilitator species through an accumulation of organic matter and nutrients in its understory, lowering the temperature in soil and air underneath, and decreasing wind intensity (Menezes & Araujo 2000).

Flowering and fruiting of *A. arenaria* occur several times throughout the year, mainly in June and July (Menezes & Araujo 2000). Flowers appear grouped like spikes, the female inserted at the base and the male just above. Male flowers open before females. Fruits, usually with a single seed, are orange yellow when ripe, with very aromatic and sweet pulp (Lorenzi et al. 2010). Seeds germinate between 60 and 120 days and fruiting occurs after 4 years.

Experimental design

A total of 40 *A. arenaria* individuals with ca. 2.0 m canopy diameter and 1.20 m in height, randomly distributed in a ~4 ha plot, were selected in June 2015. Open top chambers (OTCs) modified from Pritchard & Amthor (2005), were constructed to induce ~2°C increase in air temperature. OTCs were built as trunked cones with ca. 2.5 m diameter in the base, 1.0 m at the top, and 1.40 m in height; they were made of 0.20 mm thick, clear PVC with an iron frame. OTCs were kept 5 cm above the soil to ease pollinators and fruit dispersers movement.

To simulate the increase in rainfall expected by global circulation models in this region, 244.0 x 50.0 cm rain collectors were directed to the base of *A. arenaria* individuals to reach a 25% increase in rainfall (Pugnaire et al. 2020, Morillo et al. 2022). The experiment was conducted following a completely randomized design with four treatments with ten replicates each; without OTC or gutter (control, C); with gutter (P); with OTC (T), and with OTC and gutter (TP) (Figures 1a, b, c and d).

Monitoring of environmental variables

Temperature and relative humidity were recorded with a data logger (Environment Meter 4-IN-1, PeakTech, Salerno, Italy) every day at noon along August 2016, the month leading up to the rainy season. Measurements were taken 50 cm above the soil surface in a central point of the projected *A. arenaria* canopy, to compare temperatures and relative humidity inside and outside OTCs. Daily variations in temperature and relative humidity were monitored from 8:00 am to 4:00 pm in October 2016 using 20 external data loggers (HOBO U12, Onset, Bourne, MA, USA). The devices were placed below *A. arenaria* crowns in all treatments, with 5 replicates per treatment. Climate data were obtained from the database of the National Institute of Meteorology (INMET 2017).

Aboveground biomass

Aboveground biomass changes were assessed using *A. arenaria* data from the beginning (June 2015) and end (November 2016) of the experiment. Biomass was determined using the equation of Hay et al. (1982); $y = 4.35e^{2.82x}$, where y is the biomass in grams, and x the largest diameter of *A. arenaria* canopy.

Reproductive phenology

To assess the effects of climate alterations on *A. arenaria* phenology, we recorded flowering (presence of inflorescences with anthetic flowers) and fruiting (presence of green and/or mature infructescences) monthly between June 2015 and November 2016. Fournier (1974) intensity percentage was used to estimate the intensity of the phenophases, from a

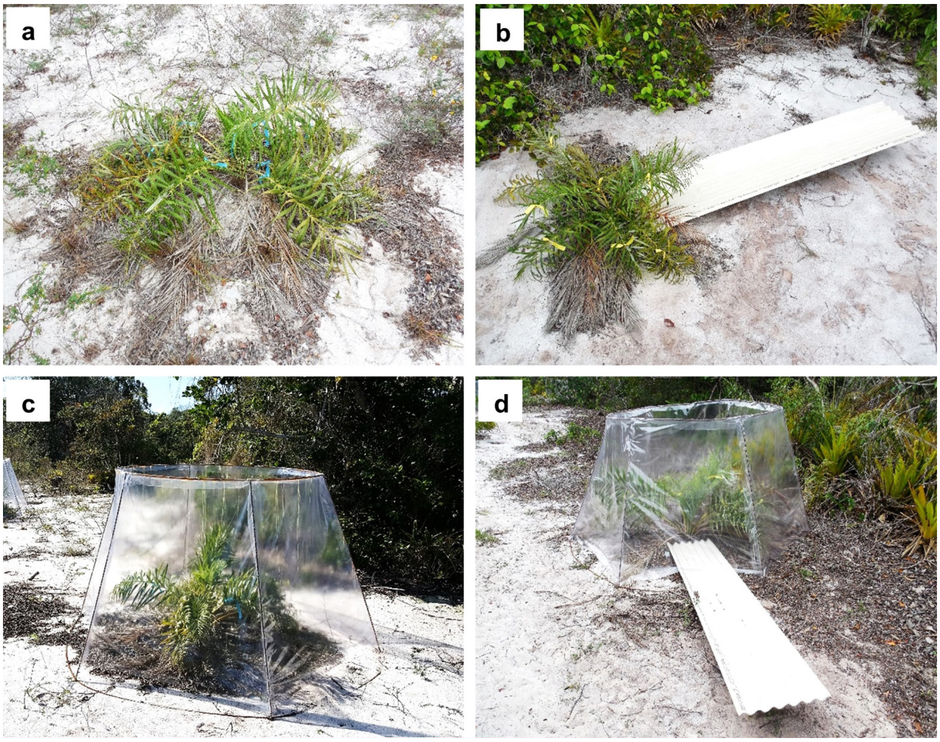

Figure 1. ***Allagoptera arenaria*** **individuals under several environmental treatments; control (a), 25% increase in rainfall volume (b), 2°C increase in temperature (c), and 2°C temperature and 25% rainfall volume increase (d).**

semi-quantitative scale from 0 to 4 (Morellato et al. 2010). To determine the percentage of individuals sampled in each phase, we used the activity index proposed by Bencke & Morellato (2002). This index was also used to estimate the synchrony among sampled individuals (Fournier 1974), assessing the number of individuals that were in the same phenophase at any given time.

Statistical analyses

Statistical analyses were performed using the Infostat software (Di Rienzo et al. 2014). The Shapiro-Wilks test was used to check the normal distribution of means of all analyzed data. Aboveground biomass data were normalized by applying a natural log, and ANOVA followed the Tukey test ($p < 0.05$) was used to compare means of biomass, temperature, and humidity. For phenology, we used the Duncan test ($p < 0.05$) to compare means. Data are shown as mean ± 1 standard error throughout the manuscript.

We applied statistics designed for phenological analyses (Zar 1996) and widely used (Morellato et al. 2010). The experimental period (2015-2016) was represented by a circle, and months by 20° sectors. The mean angle (μ); mean vector length (r) showing the concentration of individuals around the mean angle (values between 0 and 1) and the mean angle significance were verified by the Rayleigh test (Z). Phenophases with significant differences in mean angle ($p < 0.01$) were converted to mean date, i.e., the peak date of the phenophase occurrence during the period recorded. To test the occurrence of different seasonal phenophases and the degree of seasonality, we looked at the significance of the mean angle (μ) and r vector length with the Rayleigh test (Z). The vector r ranges from 0 (when dates are evenly distributed throughout the year) to 1 (when dates concentrate around a single date) (Morellato et al. 2000). Circular distribution analyses were obtained with the ORIANA 4.0 software (Kovach 2009). Using circular statistics, it was possible to test the effect of climatic variations on phenology.

RESULTS

Environmental variables

Annual rainfall in 2015 was 797.3 mm and 822.9 mm in 2016, which are about average. Mean temperature ranged 23-28°C in both 2015 and 2016. Dry periods, where rainfall was less than twice the mean temperature, were recorded mostly from September to December 2015, and in February, April, May, August and September in 2016 (Figure 2).

Midday air temperature under the canopy of *A. arenaria* was significantly higher in treatments T (33.6°C) and TP (33.5°C) than in treatments C (31.6°C) and P (30.9°C), reflecting the expected increase of ca. 2°C within OTCs (Figure 3). Relative

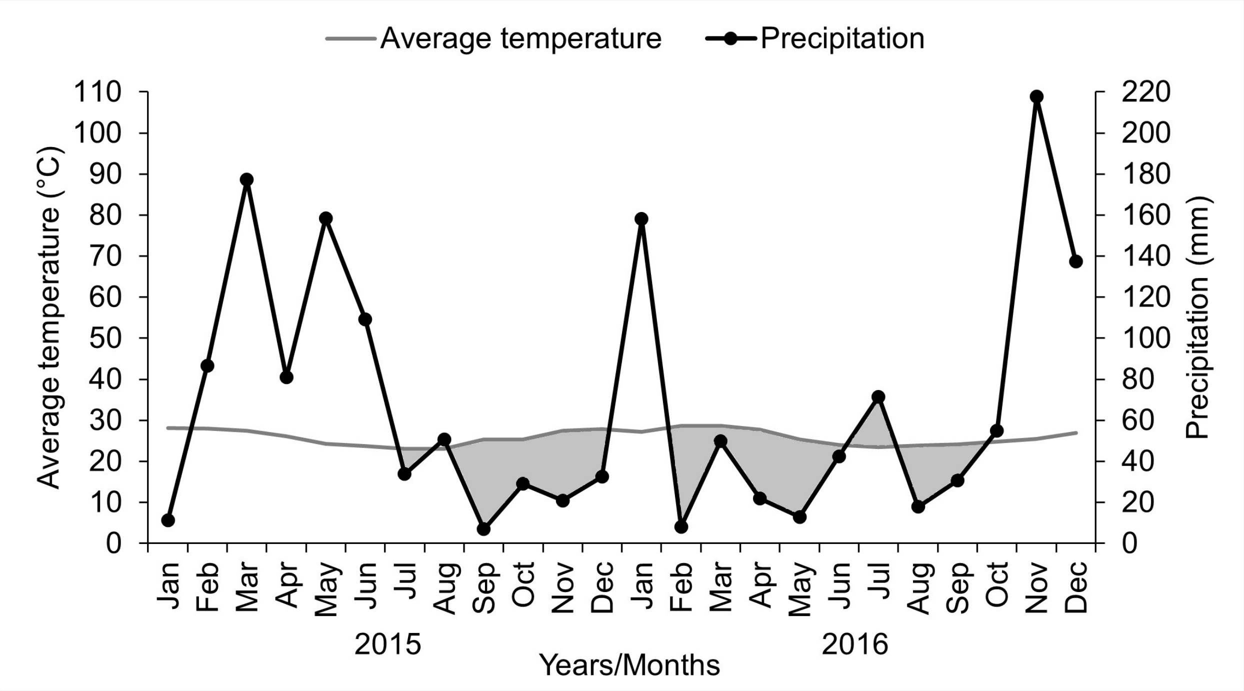

Figure 2. Climate diagram from January 2015 to December 2016 for the northern region of Espírito Santo state, Brazil. The highlighted regions refer to dry periods (P<2T).

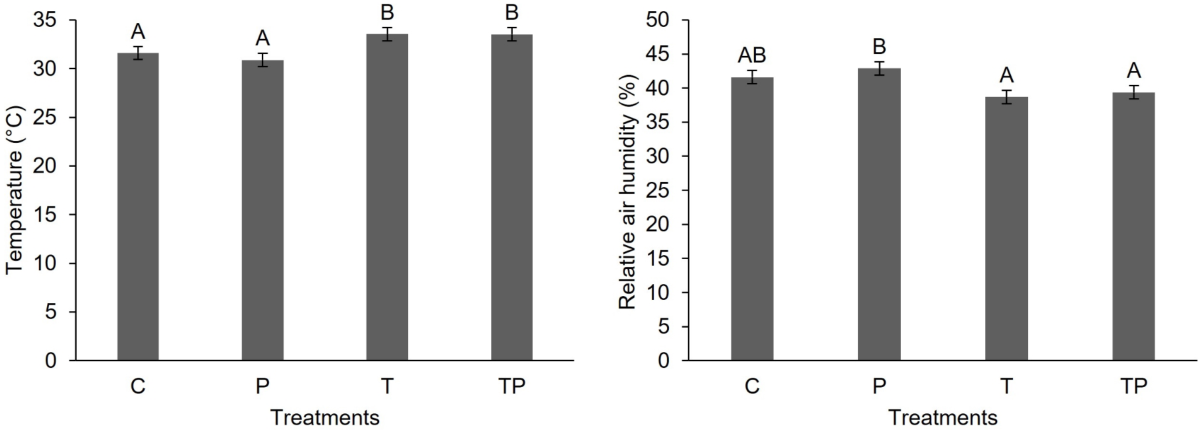

Figure 3. Temperature and relative air humidity under *Allagoptera arenaria* canopies in control treatments (C); with 25% increase in rainfall (P); 2°C increase in temperature (T), and 2°C temperature plus 25% rainfall increase (TP), estimated in August 2016 at midday.

humidity was slight but significantly lower in treatments T (38.7%) and TP (39.4%) than in treatment P (42.9%). Treatment C (41.6%) did not differ significantly from other treatments (Figure 3).

The highest temperature and lowest relative air humidity were recorded below *A. arenaria* canopies in all treatments usually between 11:00 a.m. and 01:00 p.m. (Figure 4).

Aboveground biomass

The increase in aboveground biomass between June 2015 and November 2016 was higher in *A. arenaria* individuals in the TP treatment (6.77 g) than in individuals in the T treatment (5.32 g). The other treatments were in between (C: 5.49 g; P: 5.71 g; Figure 5).

Reproductive phenology

Phenology showed an intra-annual pattern in all treatments, with phenology events occurring more than once per year. The duration of phenophases ranged 5-20 weeks, with shorter duration in treatment T. Flowering synchrony (i.e., when individuals show inflorescences at the same time) was low, being recorded in 20-40% of cases. Fruiting was not synchronized, and only 10% of *A. arenaria* individuals were in this phase at any given time. The highest intensities of flowering events, obtained by the Fournier Index for *A. arenaria* individuals, occurred in February 2016 for treatment C, April 2016 for P and T, and September 2016 for TP treatment. For fruiting events, activity peaks were between February and April 2016 for individuals in treatment C, May 2016 for P, November 2015 for T and September 2015 for TP. In treatment T, *A.*

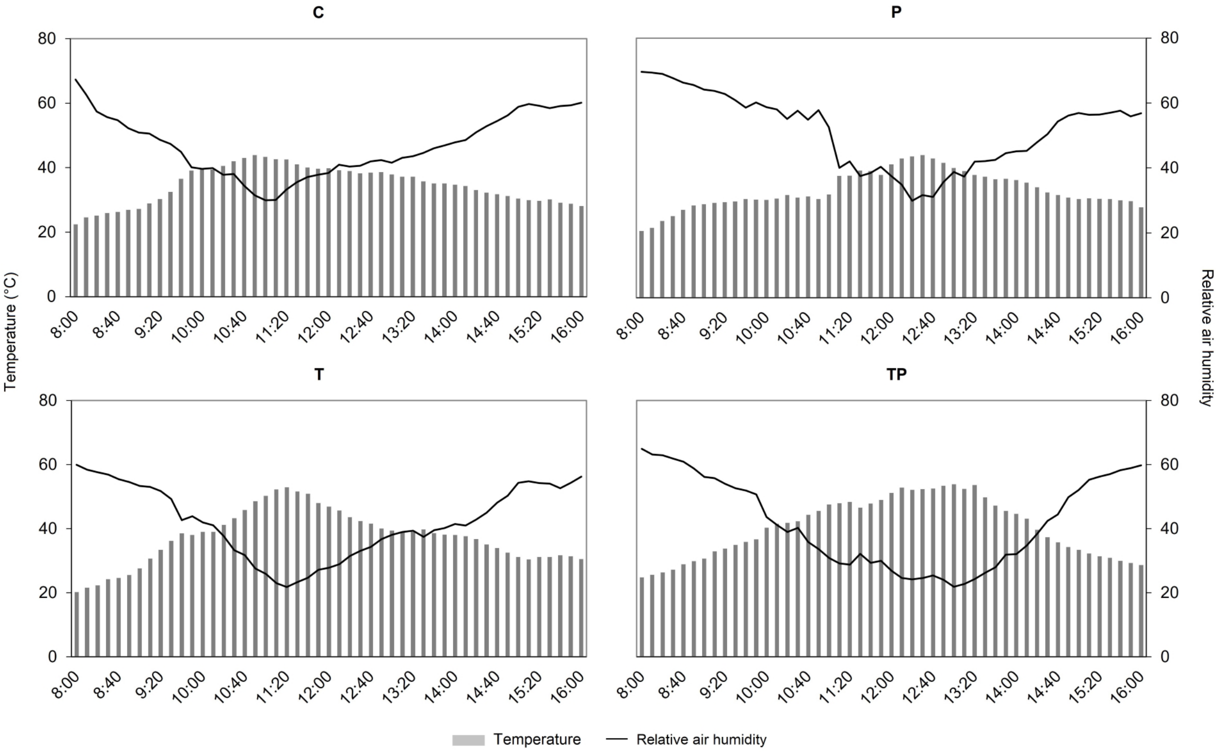

Figure 4. Daily variation in temperature and relative humidity below *Allagoptera arenaria* canopies in control treatments (C), with 25% rainfall increase (P); 2°C increase in temperature (T), and 2°C temperature plus 25% in rainfall volume increase (TP), between 08:00 am and 04:00 pm in October 2016.

arenaria individuals presented higher number of inflorescences and infructescences than in C and TP treatments, not differing from treatment P (Table I). Similarly, the frequency of *A. arenaria* individuals recorded in flowering and fruiting phenophases per month presented higher values in treatment T than in treatments C and TP, and did not differ significantly from P (Table I).

The highest number of flowering and fruiting events across the study occurred in treatment T. For fruiting, the Rayleigh test was significant for all treatments, while flowering was significant for treatments C, T and TP. With the significant Rayleigh test ($p> 0.01$) it was possible to transform mean angles into average dates, indicating the peak occurrence of phenophases for each treatment, C (05 Mar 2016), T (08 Jan 2016) and TP (15 Jul 2015) for flowering, and C (13 Feb 2016), P (24 Feb 2016), T (15 Jun 2016) and TP (06 Jul 2016) for fruiting. Mean vector length (r) values together with the Rayleigh (Z) test values, suggest the influence of seasonality on fruiting and flowering. When comparing the treatments, it is possible to verify that the *A. arenaria* individuals in TP presented higher seasonality intensity for fruiting, since the mean vector (r) length value was greater than 0.5 (Figure 6, Table II).

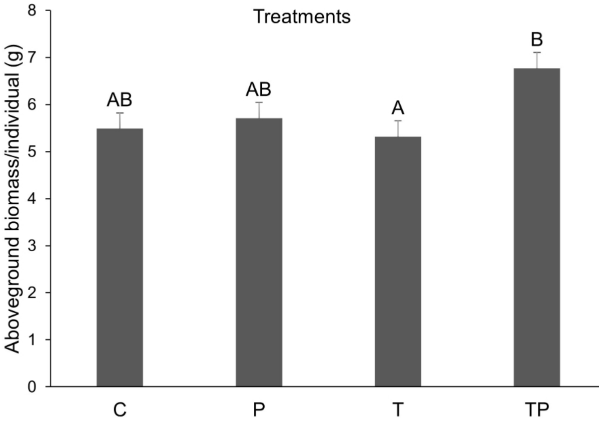

Figure 5. **Changes in aboveground biomass between June 2015 and November 2016 of *Allagoptera arenaria* individuals in control treatments (C); with 25% rainfall increase (P); 2°C increase in temperature (T), and 2°C temperature plus 25% rainfall increase (TP).**

DISCUSSION

As expected, the combined effect of temperature and rainfall increases enhanced *A. arenaria* growth, while increasing only temperature led to more frequent, shorter reproductive cycles with higher number of flowering and fruiting phenophases. Our results showed that OTCs induce the expected T increase at midday, the time of highest irradiance, along with lower relative humidity values inside OTCs than outside. Air temperature and relative humidity (RH) are inversely related, and therefore the

Table I. **Number of structures and frequency of phenophases observed per month for flowering and fruiting of *Allagoptera arenaria* individuals under several environmental treatments; control (C), 25% increase in rainfall volume (P), 2°C increase in temperature (T), and 2°C temperature and 25% rainfall volume increase (TP), from June 2015 to November 2016.**

	Flowering			
	C	**P**	**T**	**TP**
Inflorescence number/month	0.4 ± 0.2^{A}	1.1 ± 0.2^{BC}	1.3 ± 0.2^{C}	0.5 ± 0.2^{AB}
Frequency (%)/month	3.3 ± 2.0^{A}	8.9 ± 2.0^{AB}	10.6 ± 2.0^{B}	4.4 ± 2.0^{A}
	Fruiting			
Infructescence number/month	0.4 ± 0.2^{A}	0.7 ± 0.2^{AB}	1.1 ± 0.2^{B}	0.6 ± 0.2^{A}
Frequency (%)/month	2.8 ± 1.6^{A}	6.7 ± 1.6^{AB}	10.6 ± 1.6^{B}	5.0 ± 1.6^{A}

Equal superscript letters mean treatments do not differ significantly; Tukey test ($p < 0.05$).

increase of T inside OTCs leads to decreases in RH (Buriol et al. 2000). This is in fact one of the potential drawbacks of this method, since strong changes in RH may affect gas exchange and the energy balance of leaves, increasing water vapour deficit and lowering leaf water potential (Hernández-Fuentes et al. 2015).

Aboveground biomass

The combined effect of temperature and rainfall increases led to the highest increase in *A. arenaria* aerial biomass in the TP treatment. Similar field manipulations have evidenced the role of rainfall in increasing species biomass (Kardol et al. 2010, Spence et al. 2016). In our case, the combined increase in rainfall and temperature led to large

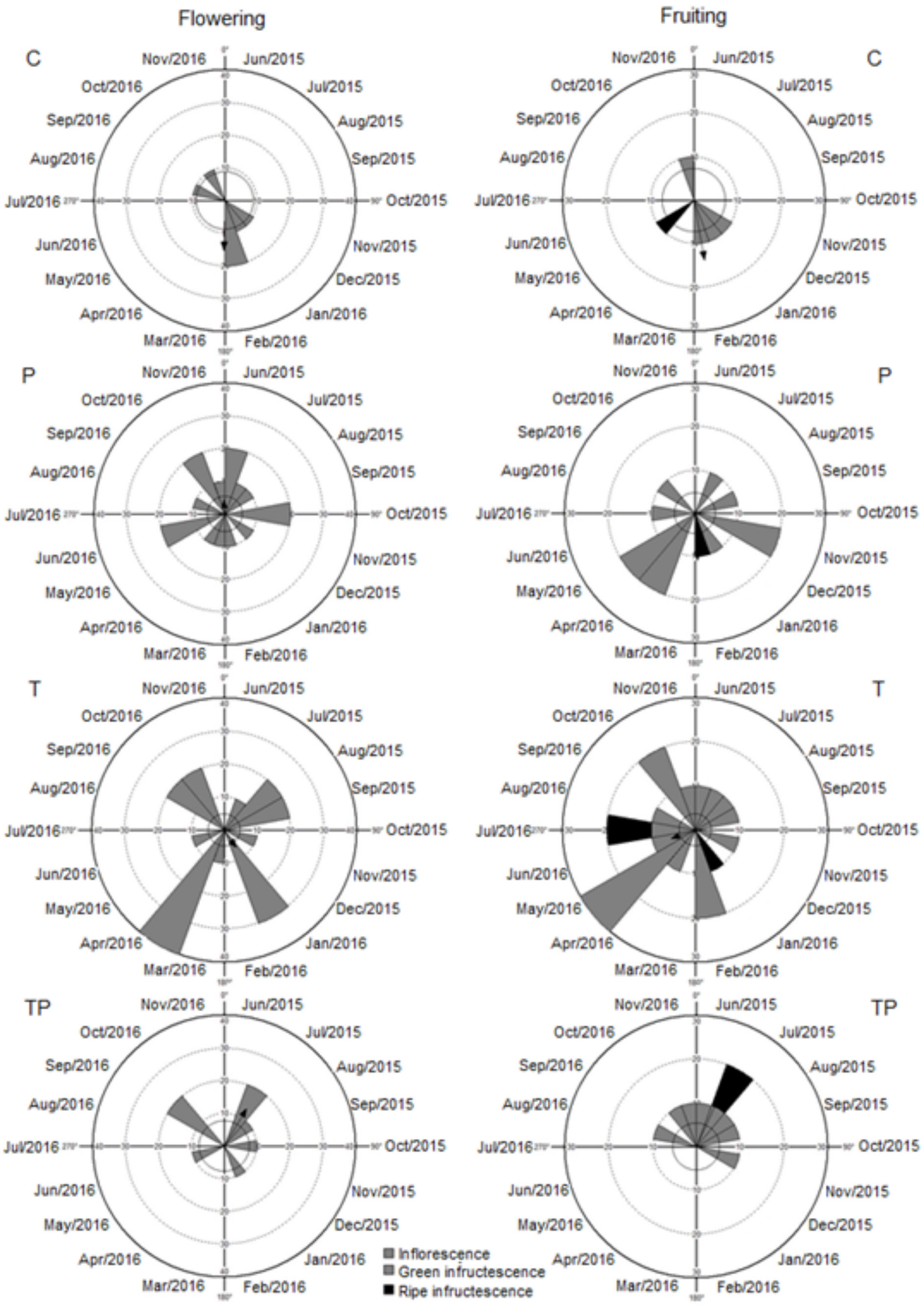

Figure 6. **Circular histograms with the activity index of flowering and fruiting (green and ripe fruit) phenophases of *Allagoptera arenaria* in control treatments (C), with 25% rainfall increase (P), 2°C increase in temperature (T), and 2°C temperature plus 25% rainfall increase (TP) between June 2015 and November 2016.**

increases in aboveground biomass. Growth is controlled by the water balance in the plant, which reflects the relationship between uptake and transpiration. Most likely, in the TP treatment water and temperature allowed for a larger stomatal opening, increasing photosynthetic rates that led to greater growth. By contrast, exposure of *A. arenaria* individuals only to increased air temperature led to substantially lower biomass than in the TP treatment. Previous works also have reported a negative effect of temperature increases on biomass production in nine grassland species, which they attributed to higher abiotic stress (de Boeck et al. 2008). A mechanistic explanation would be that increased temperatures in treatment T increased transpiration rate, causing an internal water imbalance that led to stomatal closure, reduced photosynthesis and smaller growth.

Reproductive phenology

The duration of phenological cycles and the synchronization of flowering and fruiting in *A. arenaria* individuals were in agreement with the data reported by Machado (2013) for this species elsewhere. However, we recorded a certain amount of inflorescences aborted during the monitoring period, most likely caused by low rainfall, which was characterized by several months of drought (Figure 2). The same happened to infructescences, where high abortion rates resulted in few mature fruits. The lack of fruiting synchronization in *A. arenaria* may have been linked to this high abortion rate.

The highest flowering and fruiting intensities given by the Fournier Intensity Index occurred in the dry periods for all treatments. This may be partly due to the drought period mentioned above. Thus, the drought event and its influence on the phenophases is not conclusive but becomes a starting point for future analysis, as longer studies are needed to understand responses and preferences of this species.

Allegoptera arenaria in T treatments presented more reproductive cycles, with higher number of flowering and fruiting phenophases over the evaluated period compared to treatments C and TP. In addition, the mean duration of phenological cycles in this treatment was shorter. Most likely, the 2°C temperature increase in treatment T led to even more limiting conditions for *A. arenaria* than in other treatments, leading individuals to invest more in reproductive cycles as a strategy for the species survival (Crosby et al. 2015). There are now reports showing that high temperatures are accelerating the phenological cycles of many species around the world (Prevéy et al. 2017), suggesting that

Table II. Number of observations of phenophases (n), average angle (μ), average vector length (r), Rayleigh test (Z) for flowering and fruiting phenophases of *Allagoptera arenaria* individuals submitted to open-control environment treatments (C), 25% increase in rainfall volume (P), 2°C increase in temperature (T), and 2°C temperature and 25% rainfall volume increase (TP) from June 2015 to November 2016.

	Flowering				Fruiting			
	C	P	T	TP	C	P	T	TP
Number of Observations (n)	6	16	18	8	5	12	19	9
Average angle (μ)	182°	356°	146°	30°	170°	177°	250°	24°
Length of the average vector (r)	0.38	0.11	0.16	0.33	0.46	0.36	0.20	0.62
Rayleigh test (Z)	8.80 *	1.95	4.89 *	8.89 *	10.7 *	15.6 *	7.3*	34.8 *

(*) significant values for the Rayleigh test ($p < 0.01$).

climate changes may significantly alter plant phenology as temperature increases (Cleland et al. 2007).

The recording of phenological events (Figure 4 and Table II) allowed us to register the distribution of phenophases throughout the year and to test their intensity and seasonality. We identified *A. arenaria* seasonal patterns except for flowering in the P treatment, as data were evenly distributed over the monitoring period and there was no seasonal effects on flowering. Seasonality was, however, evident for other treatments and phenophases. The presence of low seasonality in *A. arenaria* was also reported by Machado (2013) in a Rio de Janeiro *restinga*.

The individuals of *A. arenaria* in treatment T, under higher stress conditions imposed by the temperature increase, invested in more reproductive cycles, producing more inflorescences and infructescences and less aboveground biomass. As mentioned above, individuals in treatment T were subjected to high temperatures and water pressure deficits inside the OTC and tried to regulate water loss through stomatal closure, which leads to a marked decline in photosynthetic rate (Katsoulas et al. 2001, Muraoka et al. 2000, Tucci et al. 2010, Zhang et al. 2015). Changes in biomass allocation patterns, trying to produce more reproductive structures, have been reported under stress conditions (Crosby et al. 2015). Therefore, *A. arenaria* individuals in treatment T likely invested more on root biomass (which unfortunately we did not measured) to secure water uptake to meet a larger evaporational demand caused by higher temperatures. On the other hand, *A. arenaria* individuals in the TP treatment allocated more biomass to aboveground parts, maximizing growth instead of reproduction, as they had a smaller number of reproductive cycles over the evaluated period. The biomass allocation patterns, from a physiological perspective, generally reflect the differential investment of photoassimilates induced by abiotic and biotic pressures (Mokany et al. 2006, Szabo et al. 2009, Luo et al. 2013). Biomass is allocated preferentially to the plant organ that harvests the limiting resource (Roa-Fuentes et al. 2012) and the allocation of biomass allows control of resource acquisition. The higher the root biomass, the better the acquisition of nutrients and water from the soil, while a larger photosynthetically active biomass allows for a more efficient collection of radiation (Salazar et al. 2019). Changes in biomass allocation patterns in response to climatic factors can alter the competition regimes between coexisting plants, resulting in changes in community composition, as well as in ecosystem structure and function (Luo et al. 2013).

CONCLUSIONS

We can conclude that combined temperature increases (by 2°C) and rainfall (by 25%) favored aboveground biomass production in *A. arenaria*, while increases only in temperature (2°C) resulted in less growth and more reproductive cycles. Therefore, temperature increases alone may shorten the reproductive cycle of *A. arenaria* and decrease growth. If expected climate changes in the *restinga* affect only temperature, the environment would turn extreme, threatening survival of this species. However, if temperature increases are accompanied by higher rainfall, the new conditions could secure the species future in the restinga environment.

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