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ORIGINAL PAPER

The effects of resource availability on sprouting: a key trait influencing the population dynamics of a tree species

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Abstract

Key message **Sprouting is a key component of the population dynamics of woody species. Regeneration via sprouting contributes substantially to population growth when resource availability varies.**

Abstract Basal sprouting is an important trait that facilitates the persistence of woody species under different environmental conditions. Environmental heterogeneity can have variable effects on allocation to sexual reproduction and vegetative growth over an individual's ontogeny; consequently, environmental heterogeneity can influence the dynamics of woody plant populations. However, the effects of environmental factors on the ramet and genet dynamics of woody species have yet to be fully explored. This study investigated the population dynamics of *Curatella americana* L. (Dilleniaceae), an abundant tree species with a wide geographic distribution. The following hypotheses were tested: (1) density, vital rates and population growth rate are constrained by low rainfall and low soil fertility and (2) ramet production contributes more than seedling production to population growth at low rainfall levels and low soil fertility. Population dynamics were evaluated at two soil types (low and high fertility) over 3 years (2010, 2011 and 2012) with varying rainfall levels (average, average and low rainfall levels, respectively). Both hypotheses were supported. Vegetative growth and the population growth rate were limited by low rainfall and low soil fertility. The survival rates of adults and immature ramets had the largest effect on population growth. Although sprouting was limited by resource availability, this regeneration mode contributed more than seedlings to population growth. Basal sprouting not only ensures species persistence but also, as indicated by these results, permits a species to tolerate a lack of seedling recruitment. Basal sprouting was, therefore, determined to play an important role in the population growth of woody species in heterogeneous environments.

Keywords Life table response experiment · Matrix model · Regeneration mode · Resource availability

Introduction

Population size fluctuations have long interested ecologists (Sarukhan 1974; Silvertown 2008; De Kroon et al. 2000). A large number of studies have focused on the processes underlying population dynamics, particularly in herbaceous and woody species that lack vegetative growth. In contrast, persistence is a topic that has long been neglected in the field of plant demography (Bond and Midgley 2001).

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Population biology studies suggest that vegetative growth increases plant abundance (Herben et al. 2014) and promotes resilience to stressful conditions (Muñoz-Costa and Calleja-Alarcon 2013).

Sprouting is a common form of vegetative growth in woody species (Jeník 1994; Dodd et al. 2013) and has been described for plants in the Australian, African and Brazilian savannas (Jeník 1994; Hoffmann 1999, Bond and Midgley 2001). Sprouting (used synonymously with "resprouting"), is defined as the production of ramets from new vegetative growth, induced by injury (e.g., stem removal near the root surface) or a substantial change in growth conditions (Del Tredici2001). In terms of aboveground structure, basal sprouting results in a genet comprised of multiple ramets (Matsuchita et al. 2012). However, the influence of environmental conditions on the population dynamics of sprouting woody plants is still not well known, especially in tropical areas (Bond and Midgley 2001). The relative contribution of sprouting to the population growth rate is not well described and often hard to evaluate (Dodd et al. 2013), as this contribution may change with environmental conditions (Mandujano et al. 2001). To address this question, the buds-protection-resources conceptual framework was proposed; within this framework, the effect of environmental resources on the role of sprouting can be explored (Clarke et al. 2013). Hoffman et al. (2012) states that sprouting plants are more common in low resource sites. Resource allocation may vary among individuals of the same species under different environmental conditions (Xiao et al. 2011). Variation in environmental conditions may also unevenly affect fecundity, survival or growth at different ontogenetic stages (Caswell 2001; Soliveres et al. 2010; Dahlgren and Ehrlén 2009).

Soil type and water availability play major roles in plant population dynamics. For example, soil nutrient availability alters tree biomass (Davidson et al. 2004; Sardans et al. 2006) and significantly affects population growth rate (Brys et al. 2005; Dahlgren and Ehrlén 2009). Water availability is another limiting factor and is inversely related to mortality rates in tree species (Nepstad et al. 2007). At dry sites, sprouting is less vigorous than at wet sites (Grady and Hoffmann 2012). The relative proportion of sprouting woody plants is expected to increase with increasing soil fertility and rainfall (Clarke et al. 2013). However, it remains unknown whether sprouting can be described as a major life-history attribute of trees and incorporated into plant demographic theory (Loehle 2000).

Curatella americana L. (Dilleniaceae) is a woody plant that sprouts prolifically from the root collar. This species is considered to be the most abundant tree in savannas (Devillers and Devillers-Terschuren 1996) and can store a large portion of the energy, carbon and water reserves in this biome (Baruch 2011). *C. americana* has a wide geographic distribution, from Central to South America. Although this species may grow on different soil types, it is often found on acidic and infertile soils (Baruch 2011) or poorly drained soils (e.g., wetlands) (Dalmagro et al. 2014). The physical factors that determine variations in *C. americana* phenology and physiology across rainfall and fertility gradients have been identified. Annual variation in water availability, periodic fires and herbivorous insects primarily influence this species' phenology (Foldats and Rutkis 1975). Specific leaf area and photosynthesis rates are positively associated with rainfall, whereas water use efficiency is negatively associated with rainfall (Baruch 2011). Specific leaf area also decreases with low soil phosphorus (Baruch 2011). However, the effects of environmental resources on this species' population dynamics remain unknown.

This study reports the demographic patterns of *C. americana* under contrasting conditions of resource availability. It was hypothesized that the density, vital rates (i.e., survival, growth and reproductive rates) and the population growth rate (λ) of this species are limited by rainfall and soil fertility. In environments where soil type and rainfall result in resource limitations, ramet production was predicted to affect population growth rate more than seedling production. We analyzed the density, growth, survival and production of *C. americana* ramets and seedlings in years with different rainfall and soil fertility levels. We specifically addressed three questions. (1) Do soil fertility and rainfall conditions affect the density, vital rates and population growth rate (λ) of *C. americana*? (2) Which vital rate most affects λ? (3) What are the relative contributions of sexual reproduction and vegetative growth rate to population size in years with different rainfall and soil fertility conditions?

Methods

Study site

The study site was located in the Cuiabá municipality, Mato Grosso State, Brazil (15°43′ to 15°44′S; 56°04′ to 56°06′W). According to Alvares et al. (2013), the regional climate was classified as Tropical with dry winter (Aw), and the average monthly temperature ranged from 22.3 to 27.0 °C. Altitude was between 165 and 189 m above sea level. This site has been protected from fire for 20 years. The study site is located within an 54,522 km^2 area (Arruda et al. 2008) of an ecotone between the Cerrado, one of the world's biodiversity hotspots (Myers et al. 2000), and the Pantanal, which is extremely biodiverse and is the world's largest freshwater wetland (Carter et al. 2004).

Study species

Curatella americana is a perennial, xerophytic, and fire-tolerant woody species. It can be shrubby or arboreal and reaches up to 10 m in height (Baruch 2011). This species reproduces sexually using hermaphroditic flowers and abundant pollen; it may also reproduce vegetatively via basal sprouting. Production of flowers, fruits and shoots begins between the middle to the last third of the dry season. Seeds are long-lived (Medina and Francisco 1994) and may remain dormant until the beginning of the rainy season, which is a more favorable time for seedling establishment (Garwood 1983). Basal sprouting is the production of sprouts from dormant stem buds near the root collar (Bellingham and Sparrow 2000; Bond and Midgley 2001; Matsuchita et al. 2012; Dodd et al. 2013). Following total aerial biomass loss, a genet (i.e., an individual plant) can produce one or more stems (ramets) by basal sprouting. In this study, the term "ramets" is used according to the definition of Matsuchita et al. (2012). In adult trees, the collar develops at or just below the ground (Del Tredici 2001); thus, basal sprouting can be identified by observing the presence of buds protruding from the trunk. Thicker stems sprout following fire than under undisturbed conditions. As our study site has been protected from fire for 20 years, field observations are consistent with this generalization. Therefore, in this study, sexual reproduction refers to the production of seedlings, whereas vegetative growth refers to the production of ramets by basal sprouting.

Soils, sampling design and rainfall

In 38 ha of native area, two soil classes were identified [Petric Plinthosol (PP) and Yellow Latosol (YL) (Lucena et al. 2014)] according to Empresa Brasileira de Pesquisa Agropecuária (2006). A previous analysis of the surface layers (0–20 cm) of 60 randomly selected plots located in each of the two soil types revealed significant differences in the physical, chemical and hydrological attributes (Table 1). Compared to YL, PP was rich in nutrients and has a low permanent wilting point. Although field capacity and water availability did not statistically differ between these soil types, these values tended to be lower in PP than in YL (Table 1).

This study consisted of 150 plots (replicates) of 10 m × 10 m for each soil type, resulting in a total sampled area of 3.0 ha. *C. americana* individuals were identified and measured. Rainfall was taken into account by incorporating data from three different years (2010, 2011 and 2012). Annual rainfall values were obtained from a micrometeorological station that was at the study site. During 95 years of data, the average rainfall was 1380.11 ± 210.14 mm at the study region (Diniz et al. 2008). According to a classification based on these years, the annual rainfall was average in 2010 (1476.61 mm) and 2011 (1188.81 mm) and low in 2012 (733.22 mm).

Table 1 Mean attributes of Petric Plintosol (PP) and Yellow Latosol (YL) topsoils

Soil attributes	PP	YL
Aluminum saturation (m %)	22.18^{a}	27.44^{b}
Magnesium (cmolc dm^{-3})	0.74^{a}	0.49^{b}
Calcium (cmolc dm^{-3})	1.09^{a}	0.58^{b}
pH (H_2O)	5.23^{a}	5.13^{b}
Cation exchange capacity (pH 7)	5.31^{a}	3.36^{b}
Organic matter (g dm^{-3})	19.07^{a}	11.37^{b}
Sulfur (mg kg^{-1})	8.83^{a}	6.55^{b}
Potassium (cmol$_c$ dm^{-3})	0.20^{a}	0.13^{b}
Silt (g kg^{-1})	39.3^{a}	27.1^{b}
Phosphorus (mg dm^{-3})	4.94^{a}	2.62^{b}
Zinc (mg kg^{-1})	1.52^{a}	1.43^{b}
Copper (mg kg^{-1})	0.46^{a}	0.44^{b}
Iron (mg kg^{-1})	77.12^{a}	79.7^{a}
Manganese (mg kg^{-1})	88.82^{a}	56.02^{b}
Boron (mg kg^{-1})	0.37^{a}	0.35^{a}
Pebble (%)	13.47^{a}	4.37^{b}
Gravel (%)	43.31^{a}	17.97^{b}
Clay (mg kg^{-1})	119^{a}	132.7^{b}
Permanent wilting point (%)	2.14^{a}	2.95^{b}
Field capacity (%)	13.65^{a}	16.57^{a}
Plant available water (%)	11.66^{a}	13.61^{a}

Letters indicate significant differences between mean values (permutation *t* test, $p < 0.05$)

Petric Plinthosol soil and YL soil were, therefore, examined during average and low rainfall years. Every April (i.e., the end of the rainy season), all individuals found in the plots on both soil types were identified, numbered, and measured for height, diameter and several morphological characteristics. Each individual was classified by its ontogenetic stage using the following criteria: (1) whether the individual originated through sexual reproduction or vegetative growth and (2) the presence or absence of external morphological characteristics defined by Gatsuk et al. (1980). According to Gatsuk et al. (1980), the presence of cotyledons can be used to indicate the developmental or ontogenetic stage of a given individual. In this study, ontogenetic stages were therefore classified as seedlings (S; plants possessing cotyledons), young seedlings (Y_s; plants lacking cotyledons, with or without branching), immature seedlings (I_s; plants possessing branching and having late-stage reiterations caused by the activation of a latent lateral meristem, Hallé et al. 1978), young ramets (Y_r; plants lacking cotyledons, that have or lack branching, and that originated from stem buds near the root collar of an adult individual), immature ramets (I_r; plants with branching and reiterations that originated from stem buds near the root collar of an adult individual), and adult (*A*; any plant with a diameter and height equal to or greater than those of the smallest reproductive individual, i.e., height $\geq$1300 mm and stem diameter at soil level $\geq$125 mm). For each ontogenetic stage, we annually calculated the number of plants that survived and remained in the same stage, the number of plants that grew to the next stage and the number of plants that returned to the previous stage.

Data analysis

The density (i.e., the number of individual per ha) of each ontogenetic stage on the two soil types over 3 consecutive years (2010, 2011 and 2012) was compared using a permutation test of the equality of means using the *t* statistic ($n = 1000$). This is non-parametric test, and the *t* test was only used after a normal distribution was confirmed. A level of $p < 0.05$ was considered to be significant.

For each ontogenetic stage, vital rates were calculated using matrix models of woody plant species demography (Zuidema et al. 2010). Matrix projections allow the quantification of the vital rates that describe the life cycle of a population (Silvertown et al. 1993) or subpopulation (Zuidema et al. 2010) within different habitats. Using a matrix, it is possible to project the composition of the population or subpopulation at future time intervals (Gurevitch et al. 2009). Before the parameterization of the matrix population model, matrix elements (Eq. 1) were defined for each ontogenetic stage (*i*) in each soil type and annual rainfall level, according to the Lefkovitch matrix models (Caswell 2001).

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{bmatrix} (t+1) = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & S_6 \\ G_1 & P_2 & R_3 & 0 & 0 & V_6 \\ 0 & G_2 & P_3 & 0 & 0 & V_6 \\ 0 & 0 & 0 & P_4 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & R_6 \\ 0 & 0 & G_3 & 0 & G_5 & P_6 \end{bmatrix} \times \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{bmatrix} \qquad (1)$$

Equation 1 corresponds to a general matrix representation of $n\ (t + 1) = An\ (t)$, where *n* describes the numbers of individuals in each stage at times *t* and *t + 1*, and *A* is the transition matrix for the following vital rates: (1) survival rate (*Pi*; the number of plants that survived and remained in the same stage (*i*), divided by the total number of living plants of stage *i* at each annual interval), (2) growth rate (*Gij*; the number of plants of class *I* that moved to the next stage (*j*), divided by the number of living plants of class *i* during the annual interval), (3) retrogression rate (*Rji*; the number of plants of class *j* that returned to the previous stage (*i*), divided by the number of living plants of stage *j* in the annual interval), (4) sexual reproduction rate [*Si*; the number of new seedlings divided by the number of surviving adults in the annual interval (F_6)], and (5) vegetative growth rate (*Vi*; the number of new ramets, young (Y_r) or immature (I_r), produced by all adult individuals in the annual interval).

The annual population growth rate (λ) quantifies changes in the number of individuals over time within the tested groups of plants. This rate was calculated as the dominant eigenvalue of the matrix, based on all vital rates. A bootstrap analysis (with 5000 permutations) was conducted to calculate the variability and 95 % confidence intervals of the vital rates; these values were used to evaluate whether λ and the vital rates differed between YL and PP, given the same stage and annual rainfall level. Confidence intervals were not calculated for the sexual reproduction or vegetative growth rates because the numbers of seedlings and ramets produced by each adult individual could not be determined. Therefore, the same sexual reproduction rate and vegetative growth rates were used for all adult individuals. We also used a permutation test (with 5000 permutations) to compare the vital rates and λ between the two groups of plants (Manly 2007).

Elasticity analysis was conducted to evaluate the proportional change in growth rate of the studied group in response to a proportional change of matrix elements (De Kroon et al. 2000). A life table response experiment (LTRE) analysis was used to quantify the contributions of soil type (YL and PP), rainfall (average and low), and their interaction to observe differences in the growth rates of the studied groups. The results of this analysis identify the importance of each factor on the population growth rate (Caswell 2001).

All analyses were performed in R (Popbio package, R Development Core Team 2012).

Results

High values of density were recorded for adults (*A*), immature seedlings (I_s), young seedlings (Y_s), and young ramets (Y_r). The lowest density value was recorded for immature ramets (I_r) (Table 2). At both rainfall levels, adult density was higher in more fertile soil (PP). The densities of I_s and of I_r did not appear to be affected by rainfall condition or soil type.

Table 2 Mean density (individuals ha^{-1}) of *Curatella americana* originating from sexual reproduction and clonal growth (ramets)

Year	Rainfall	Soil	Stages							
			S_l	Y_s	I_s	Ramet production	Y_r	I_r	A	Total
2010	1476.61[a]	PP	–	227*	80	–	200	16	599*	1123*
		YL	–	154	80	–	154	25	459	873
2011	1188.81[a]	PP	27*	104*	114	186*	103*	41	599*	1175*
		YL	6	66	99	121	70	42	462	873
2012	733.22[b]	PP	6	70*	93	134*	61	35	588*	988
		YL	2	41	82	86	84	35	453	868

Year: sampling year; Rainfall: rainfall in mm; Soil: soil type, PP (Petric Plintosol) and YL (Yellow Latosol); Stages: densities of seedlings (S), young seedlings (Y_s), immature seedlings (I_s), young ramets (Y_r), immature ramets (I_r), and adults (A). Ramet production: density of young and immature ramets produced each year; Total: total number of individuals in each soil type

An asterisk (*) indicates a significant difference in the mean density of individuals of the same stage between soil types ($p < 0.05$). The density of seedlings and the production of ramets were not recorded in 2010

[a] Average rainfall, [b] Low rainfall

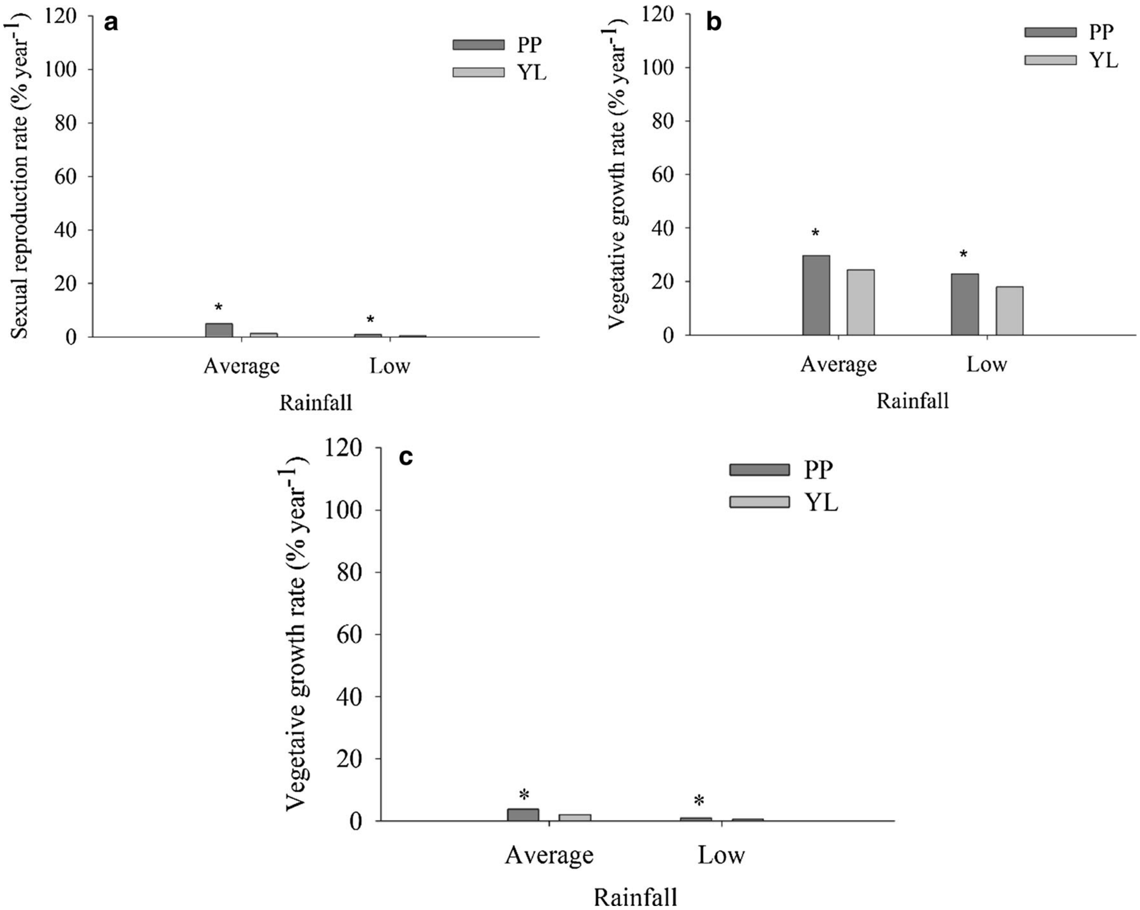


Fig. 1 **a** Sexual reproduction rate, shown as the number of seedlings produced annually per adult, **b** vegetative growth rate, shown as the number of new young ramets produced annually per adult, and **c** vegetative growth rate, shown as the number of new immature ramets produced annually per adult of *C. americana* on Petric Plinthosol (PP) and Yellow Latosol (YL). An *asterisk* (*) indicates significant differences ($p < 0.05$) between the soil classes for average and low rainfall levels

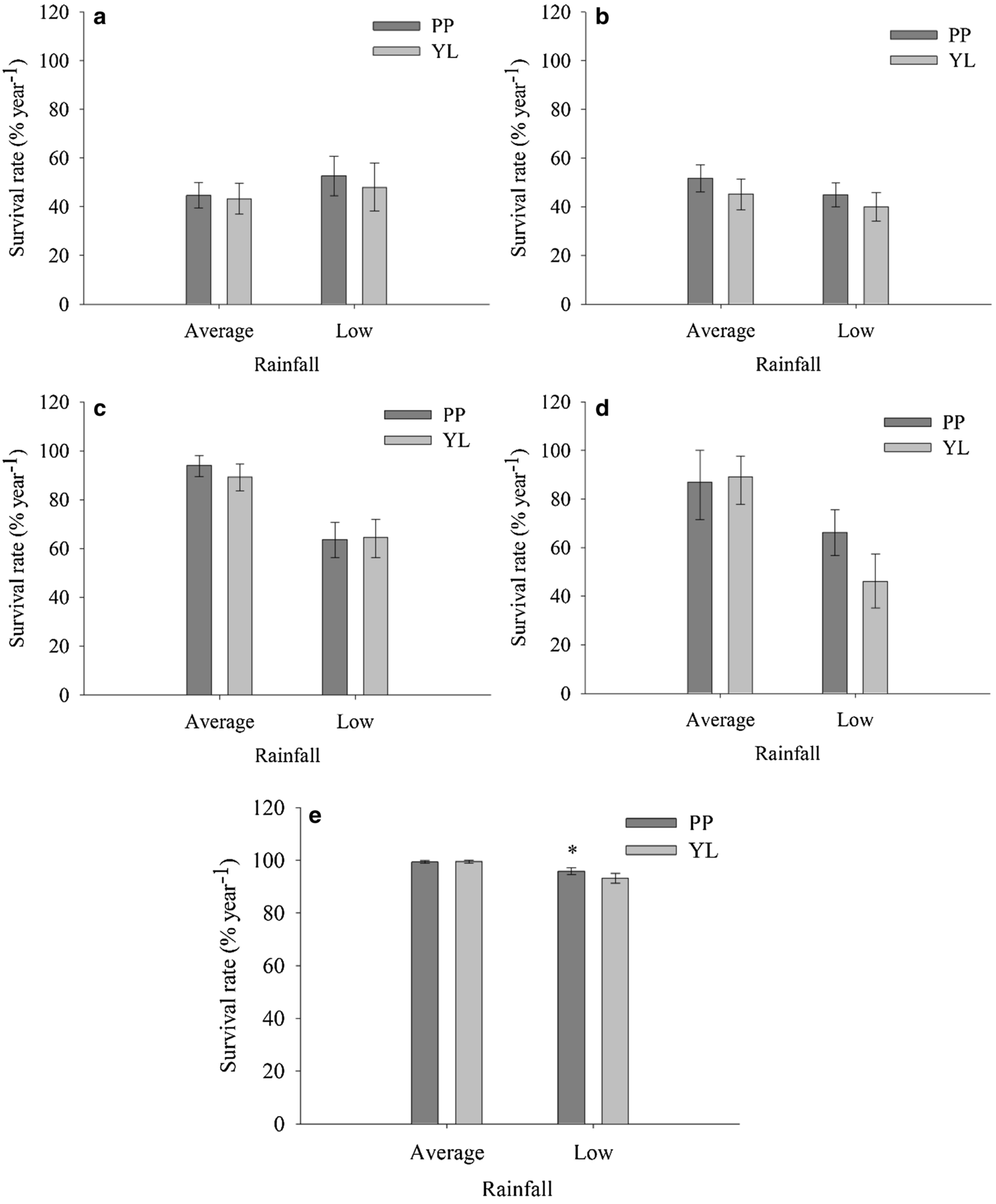


Fig. 2 Survival rates, shown as the annual number of plants that survived and persisted in the same stage divided by the number of living plants, for **a** young seedlings, **b** young ramets, **c** immature seedlings, **d** immature ramets and **e** adults of *C. americana* on Petric Plinthosol (PP) and Yellow Latosol (YL). Values are means ± 95 % confidence interval. An *asterisk* (*) indicates significant differences ($p < 0.05$) between the soil classes for average and low rainfall levels

The density of Y_s was directly related to soil type. At this stage, density was higher in PP at both average and low rainfall levels (Table 2). Y_r density varied with both environmental factors and exhibited its highest value at average rainfall in PP. Of the environmental conditions tested, average rainfall and PP soil were the most suitable for the production of seedlings (S), Y_r and I_r. The annual density of ramet production was higher than that of seedlings.

The vital rates, the rate of sexual reproduction and the annual vegetative growth rate were higher in PP soil at average rainfall (i.e., higher-nutrient soil with a lower permanent wilting point) than in YL soil at low rainfall

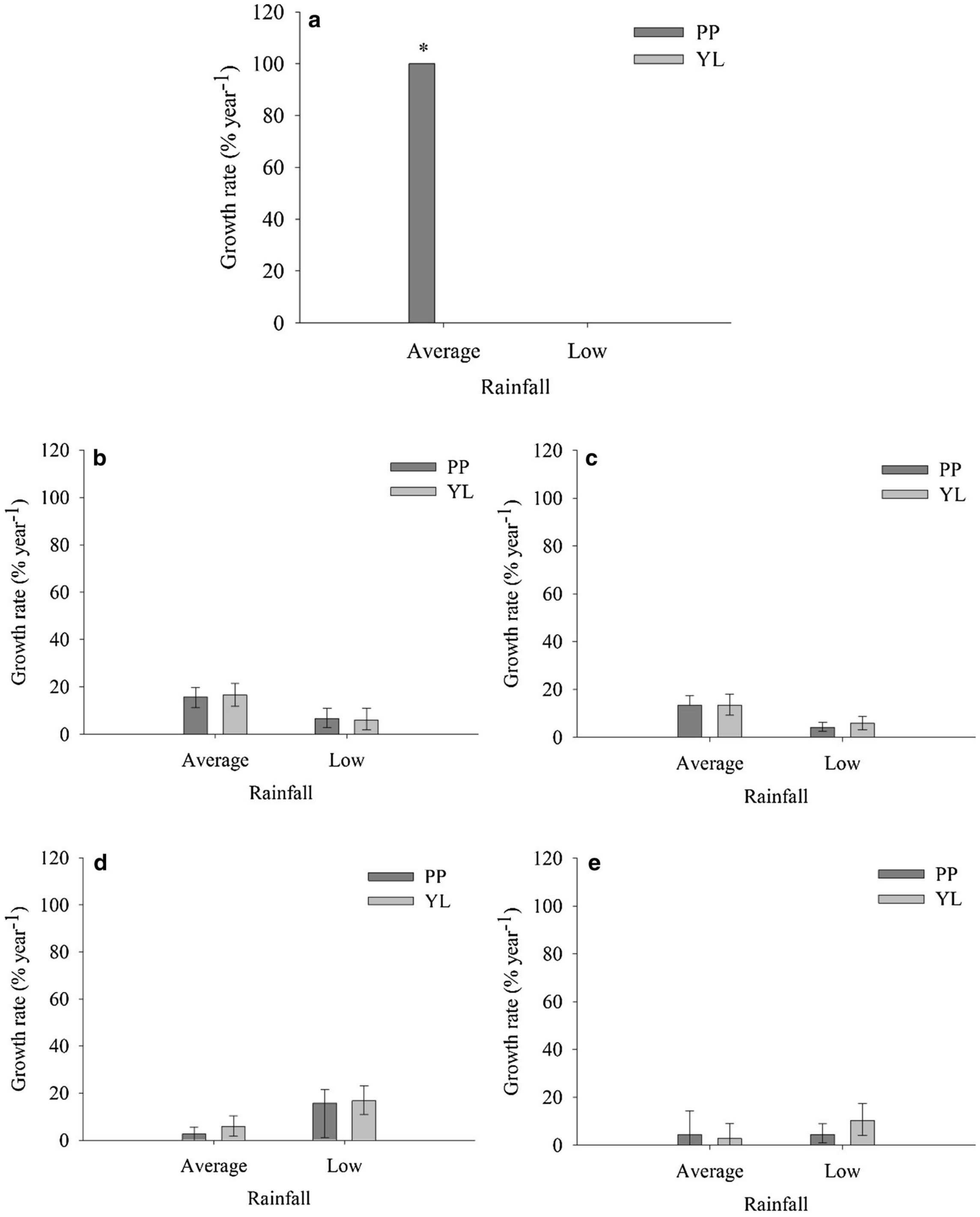


Fig. 3 Growth rates, shown as the proportion of plants that moved from one class to the next in an annual interval, for **a** seedlings, **b** young seedlings, **c** young ramets, **d** immature seedlings and **e** immature ramets of *C. americana* on Petric Plinthosol (PP) and Yellow Latosol (YL). Values are means ± 95 % confidence interval. An *asterisk* (*) indicates significant differences ($p < 0.05$) between the soil classes for average and low rainfall levels. In **a**, only one seedling moved to the next class

(Fig. 1). At low rainfall, adult survival rate was higher in PP than in YL soil (Fig. 2). The growth rates of seedlings were recorded only at average rainfall in more fertile soil (PP) (Fig. 3). The annual regression rates of I_s and I_r were recorded only under low rainfall (Fig. 4). There was an increase in adult regression at low rainfall, and there was a difference in adult regression between soil types. For the remaining ontogenetic stages, there were no

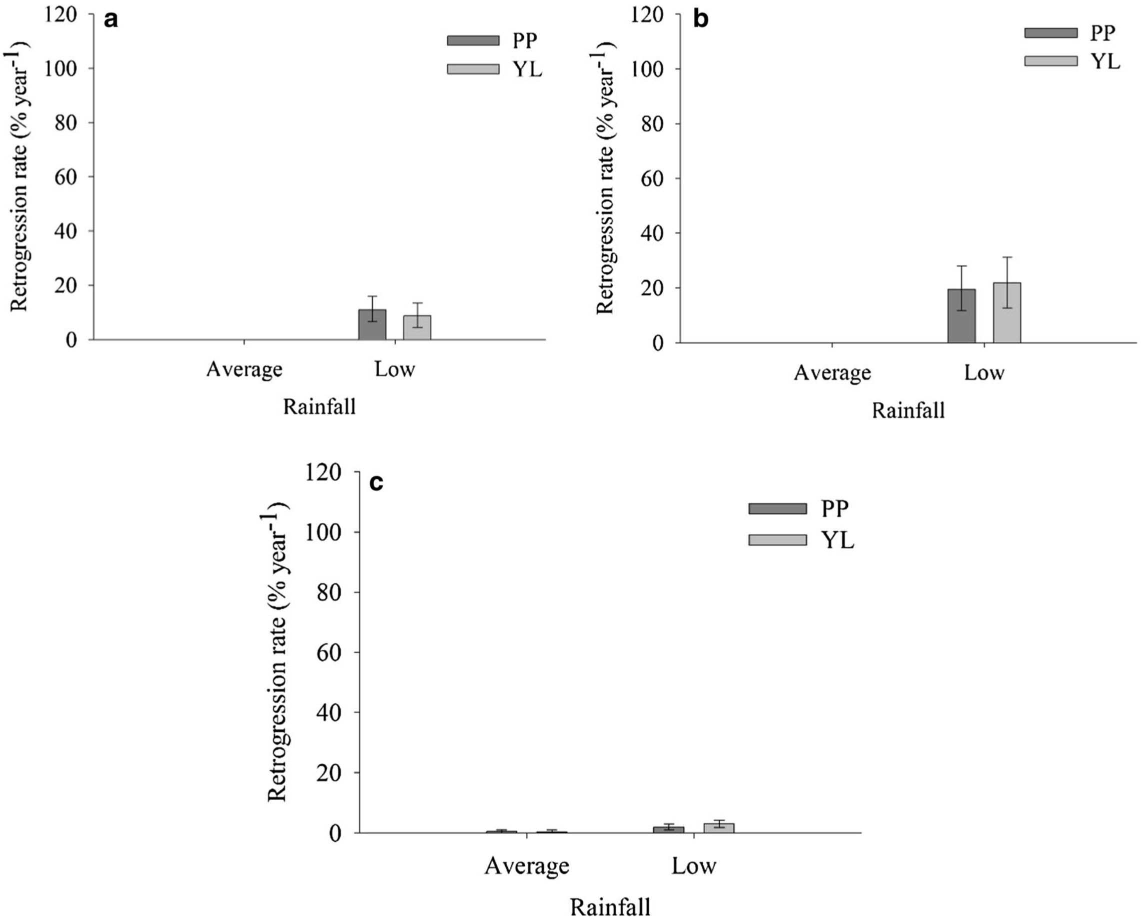


Fig. 4 Retrogression rates, shown as the number of plants from stage *j* that returned to stage *i* divided by the number of living plants in an annual interval, for **a** immature seedlings, **b** immature ramets and **c** adults of *C. americana* on Petric Plinthosol (PP) and Yellow Latosol (YL). Values are means ± 95 % confidence interval. An *asterisk* (*) indicates significant differences ($p < 0.05$) between the soil classes for average and low rainfall levels

statistically significant differences among rainfall levels and soil types.

At average rainfall, λ was similar between soil types, reaching approximately 100 % of growth per year and indicating stabile population growth (Table 3). Low rainfall negatively affected λ, which was significantly lower in YL than in PP soil.

According to the elasticity analysis, adult survival rate mostly affected λ; this effect was greatest at low rainfall levels (Table 3). At average rainfall, λ was next most affected by I_r survival rate, with values of 12.6 % in PP and 10.3 % in YL soil. Although the values of sexual reproduction and vegetative growth were relatively low, it is possible that vegetative growth had a greater effect on λ than did sexual reproduction.

Of the factors evaluated, low rainfall most limited λ (Fig. 5). Average rainfall most favored λ, followed by more fertile soil (PP). The interaction of soil and rainfall had little effect on λ.

Discussion

Differences in density and vital rates confirmed that rainfall and soil fertility affect genets and ramets of several ontogenetic stages in *C. americana*. This result is consistent with the recent studies that describe weak associations between environmental factors; for example, soil fertility and soil water content can have substantial long-term effects on growth rate (Dahlgren and Ehrlén 2009).

Seedling establishment represents a demographic bottleneck, not only because of the limitations in seed dispersal and production but also because of the environmental importance of this vulnerable stage (McCarthy-Neumann and Ibáñez 2012). This seedling-establishment bottleneck emphasizes the importance of local environmental conditions on the population performance of a widespread plant species (Villlellas et al. 2013). Therefore, investing very little into sexual reproduction (as evidenced by low density and low rates of reproduction and

Table 3 Elasticity matrix for *Curatella americana* at different rainfall levels and soil types

Time interval and environmental condition	λ and CI	Stages						
		Stages	S_l	Y_r	I_r	Y_s	I_s	A
2010–2011	$\lambda = 1.03$	S_l	0	0	0	0	0	0
Average rainfall	CI: 0.99–1.04	Y_r	0	0.009	0	0	0	0.01
Yellow Latosol		I_r	0	0.011	0.104*	0	0	0.00
		Y_s	0	0	0	0	0	0
		I_s	0	0	0	0	0.011	0.002
		A	0	0	0.014	0	0.002	0.834*
2010–2011	$\lambda = 1.02$	S_l	0	0	0	0	0	0.003
Average rainfall	CI: 0.99–1.06	Y_r	0	0.016	0	0	0	0.016
Petric Plintosol		I_r	0	0.016	0.127*	0	0	0.008
		Y_s	0.003	0	0	0.002	0	0
		I_s	0	0	0	0.003	0.038	0.001
		A	0	0	0.023	0	0.004	0.743*
2011–2012	$\lambda = 0.95$	S_l	0	0	0	0	0	0.000
Low rainfall	CI: 0.93–0.96	Y_r	0	0.003	0	0	0	0.004
Yellow Latosol		I_r	0	0.004	0.005	0	0	0.001
		Y_s	0	0	0	0.001	0.001	0
		I_s	0	0	0	0.001	0.035	0.016
		A	0	0	0.005	0	0.016	0.908*
2011–2012	$\lambda = 0.97$	S_l	0	0	0	0	0	0.000
Low rainfall	CI: 0.96–0.98	Y_r	0	0	0	0	0	0.003
Petric Plintosol		I_r	0	0	0.009	0	0	0.001
		Y_s	0	0	0	0.001	0.001	0
		I_s	0	0	0	0.000	0.018	0.009
		A	0	0.001	0.004	0.000	0.009	0.936*

Stages ontogenetic stages, λ annual population growth rate, *CI* confidence interval for λ, S_l seedlings, Y_r young ramets, I_r immature ramets, Y_s young seedlings, I_s immature seedlings, *A* adult

An asterisk (*) indicates the rates that most influenced λ

seedling growth) can be indicative of vegetative regeneration via sprouting in *C. americana.* This result corroborates a suggestion by Hewitt (2004), which proposed that regions colonized after glacial periods have reduced the levels of genetic variation. In contrast, in the Cerrado of central Brazil and in the Amazon, seed dispersal efficiency and the favorable climatic conditions actually enhance the genetic diversity of *C. americana* (Canuto 2011).

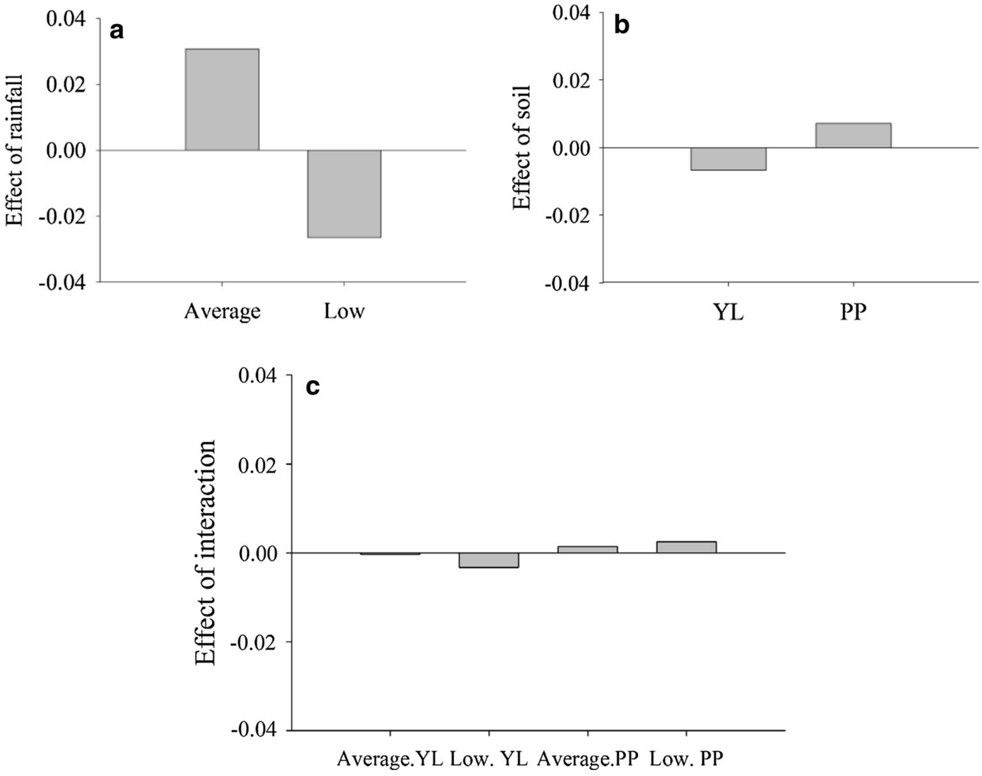
When ramets have higher densities and higher survival rates than those of seedlings, a population's dependence on seeds may decrease (Bond and Midgley 2001). In this context, sprouting not only promotes species persistence (Bond and Midgley 2001; Witte and Stöcklin 2010) but also produces offspring that will make greater contributions to population growth than those originating from sexual reproduction.

As noted for forest trees (Bond and Midgley 2001), *C. americana* produces ramets continuously, even in the absence of severe disturbances, such as prolonged drought or fire. This continuous production of ramets suggests that sprouting is the ancestral state of woody angiosperms (Wells 1969).

Although more ramets were produced than seedlings, basal sprouting was nevertheless constrained by decreased soil fertility and low rainfall. Despite favorable environmental conditions (i.e., average rainfall and PP soil, in this study), ramets were still produced at higher numbers than seedlings. Although this finding contradicts the theory that sprouting plants are more common at low resource sites (Hoffmann et al. 2012), it supports an alternative idea that ramets are produced in better environmental conditions (Oborny and Englert 2012).

Previous studies on *C. americana* indicate that there is flexibility in this species' resource use efficiency. *C. americana* is tolerant to droughts in the Cerrado and floodings in the Pantanal, surviving in habitats with widely contrasting hydrology (Dalmagro et al. 2014). However, this species' CO_2 assimilation and photosynthetic capacity

Fig. 5 Results of the life table response experiment analysis (LTRE). The effects (*y* values) of **a** rainfall (average vs. low), **b** soil [Petric Plinthosol (PP) vs. Yellow Latosol (YL)] and **c** their interaction on the population growth rate of *C. americana*



decrease with flooding (Dalmagro et al. 2013). Additionally, as shown in this study, adult survival rate decreases and the regression rates of I_s, I_r and adults increase during periods of low rainfall.

Although water availability was similar in PP and YL soils, sandier soils are the first to experience reductions in water availability (Baruch 2011); this was our original prediction for YL soils. Our results suggest that there is a range of rainfall levels that may limit the survival, growth and the spatial and temporal distributions of this species. In addition to soil water availability, the physiological performance of *C. americana* is affected by the soil phosphorus concentration (Dalmagro et al. 2013). For example, *C. americana* leaf physiology is influenced by only small amounts of this macronutrient (Baruch 2011). In this study, YL soil contained less phosphorus than PP soil, which may have also contributed to the lower densities and vital rates exhibited by A and I_s individuals.

For the remaining life stages, survival, growth and regression rates were similar. These similarities may be due to the morphological plasticity of *C. americana* in response to variation in nutrient and water availability. *C. americana* displays a horizontally and vertically extensive root system, which can be 4 times larger than its aerial system under certain environmental conditions (Foldats and Rutkis 1975). Consequently, greater resource allocation to the root system contributes to the survival of young and immature individuals in a similar manner. Our findings agree with optimal resource partitioning theory, in which plants respond to environmental variability by differentially allocating resources between aerial and subterranean biomass (Chapin et al. 1987). The population growth rate (λ) was limited by low rainfall in sandy and YL soils. Plants are considered to be more sensitive to environmental variations when $\lambda < 1.5$ (Menges 1998). In savannas, where environmental conditions tend to be more stressful in terms of nutrient and water availability and fire occurrence, λ is close to 1 (Curth et al. 2012).

When rainfall levels were low, adult survival rate explained approximately 90 % of λ. For perennial plants with long life cycles (Franco and Silvertown 2004), including tropical species (Guedje et al. 2003; Portela et al. 2010), the vital rates of the adult stage are the most crucial. Adult *C. americana* have water-storing leaves (Medina and Francisco 1994) and a deep root system (Foldats and Rutkis 1975), which promote adult survival during the dry season. When rainfall levels were average, adult survival rate became less important to λ, and I_r survival rate (which formerly accounted for approximately 10 % of λ) became more important. This finding confirms the positive influence of ramets on *C. americana* population dynamics in favorable environmental conditions.

Vegetative growth contributed more than sexual reproduction to λ, especially in PP soil when rainfall levels were average. This result corroborates a study conducted by Madujano et al. (2001), in which the relative contribution of genets and ramets varied as a function of environmental conditions. The abundance and wide geographic distribution of *C. americana* may, therefore, be explained in part by the high survival rates of A and I_s and the higher contribution of ramets than of seedlings. This result contrasts with reports from the Amazon, in which sexual reproduction was found to have greater importance (Canuto 2011).

Flexible investment into seedling production according to environmental conditions may have important effects on population dynamics and growth (Mandujano et al. 2001; Clark-Tapia et al. 2005; Marcante et al. 2009). For example, this study demonstrated that *C. americana* populations experienced a decrease in sexual reproduction that corresponds to low-rainfall and nutrient-poor soil conditions. Variations in *C. americana* population dynamics are strongly linked to rainfall level and soil type, as also noted for this species in the Venezuelan savannah (Baruch 2011).

Conclusion

Low rainfall and low soil fertility limited seedling and ramet densities, seedling growth, ramet survival rate, ramet regression rate, and adult survival rate in an abundant and widely distributed woody species, *C. americana*. Under favorable conditions (i.e., average rainfall and fertile soil), ramet production increased. Regeneration via basal sprouting permitted this species to persist, despite a lack of seedling recruitment at annual intervals. I_r survival rate also affected population growth. The results of this study contradict the hypothesis that sprouting plants are more common in low resource environments. Basal sprouting not only ensures persistence of this species but also promotes population growth in heterogeneous environments. Therefore, basal sprouting plays an important role in the establishment of woody species in heterogeneous environments.

Author contribution statement I. C. Lucena designed the study, conducted the experiment, performed the analysis and wrote the paper. R. S. S. Amorim and F. A. Lobo co-supervised this study, conducted the experiment, assisted with manuscript preparation, and reviewed drafts of the manuscript. R. B. Silva conducted the experiment and wrote the paper. T. A. Sampaio-e-Silva performed the analysis and wrote the paper. D. M. S. Matos was the principal supervisor of this study, designed the study and reviewed drafts of the manuscript.

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Conflict of interest The authors declare that they have no conflict of interest.

References

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorol Z 22:711–728

Arruda MB, Proença CEB, Rodrigues SC, Campos RN, Martins RC, Martins ES (2008) Ecorregiões, Unidades de Conservação e Representatividade Ecológica do Bioma Cerrado. In: Sano M, Almeida SP, Ribeiro JF (eds) Cerrado: Ecologia e flora, 2nd edn. Embrapa Cerrados, Brasília, pp 231–272

Baruch Z (2011) Leaf trait variation of a dominant neotropical savanna tree across rainfall and fertility gradients. Acta Oecol 37:455–461

Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. Oikos 89:409–416

Bond JB, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. Trends Ecol Evol 16:45–51

Brys R, Jacquemyn H, Endels P et al (2005) Effect of Habitat Deterioration on Population Dynamics and Extinction Risks in a Previously Common Perennial. Conserv Biol 19:1633–1643

Canuto JZ (2011) Filogeografia de *Curatella americana* L. (Dilleniaceae): uma espécie arbórea das savanas da Amazônia e Brasil Central. Dissertation, Instituto nacional de Pesquisa da Amazônia

Carter R, Kim JA, Chambers WB, Teixeira P, Girard P (2004) Interlinkages Approach for Wetland Management: The case of the Pantanal Wetland. United Nations University Institute of Advanced Studies, Yokohama

Caswell H (2001) Matrix population models: construction, analysis, and interpretation, 2nd edn. Sinauer Associates, Sunderland

Chapin FS, Bloom AJ, Field CB et al (1987) Plant responses to multiple environmental factors. Bioscience 37:49–57

Clarke PJ, Lawes MJ, Midgley JJ et al (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytol 197:19–35

Clark-Tapia R, Mandujano MC, Valverde T et al (2005) How important is clonal recruitment for population maintenance in rare plant species? The case of the narrow endemic cactus, *Stenocereus eruca*, in Baja California, Mexico. Biol Conserv 124:123–132

Curth MIT, Ghermandi L, Biscayart C (2012) Are *Fabiana imbricata* shrublands advancing over northwestern Patagonian grasslands? A population dynamics study involving fire and precipitation. J Arid Environ 83:78–85

Dahlgren JP, Ehrlén J (2009) Linking environmental variation to population dynamics of a forest herb. J Ecol 97:666–674

Dalmagro HJ, Lobo FA, Vourlits GL et al (2013) Photosynthetic parameters of two invasive tree species of the Brazilian Pantanal in response to seasonal flooding. Photosynthetica 51:281–294

Dalmagro HJ, Lobo FA, Vourlits GL et al (2014) The physiological light response of two tree species across a hydrologic gradient in Brazilian savanna (Cerrado). Photosynthetica 52:22–35

Davidson EA, Carvalho CJR, Vieira ICG et al (2004) Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. Ecol Appl 14:150–163

De Kroon H, Van Groenendael J, Ehrlen J (2000) Elasticities: a review of methods and model limitations. Ecology 81:607–618

Del Tredici P (2001) Sprouting in temperate trees: a morphological and ecological review. Bot Rev 67:121–140

Devillers P, Devillers-Terschuren J (1996) A classification of South American habitats. Report. Institute of Terrestrial Ecology, Institute Royal des Sciences Naturelles de Belgique

Diniz GL, Fonseca M, Campelo JH Jr (2008) Análise harmonica do regime de precipitação em duas localidades da baixada cuiabana. Biomat 18:37–48

Dodd RS, Mayer W, Nettel A et al (2013) Clonal growth and fine-scale genetic structure in Tanoak (*Notholithocarpus densiflorus*: Fagaceae). J Hered 104:105–114

Empresa Brasileira de Pesquisa Agropecuária (2006) Sistema brasileiro de classificação de solos. Embrapa Solos, Rio de Janeiro

Foldats E, Rutkis E (1975) Ecological studies of Chaparro (*Curatella americana* L.) and Manteco (*Byrsonima crassifolia* H.B.K.) in Venezuela. J Biogeogr 2:159–178

Franco M, Silvertown J (2004) A comparative demography of plants based upon elasticities of vital rates. Ecology 85:531–538

Garwood NC (1983) Seed germination on a seasonal tropical forest in Panama: a community study. Ecol Monogr 53:159–181

Gatsuk LE, Smirnova OV, Vorontzova LI et al (1980) Age states of plants of various growth forms: a review. J Ecol 68:675–696

Grady JM, Hoffmann WA (2012) Caught in a fire trap: recurring fire creates stable size equilibria in woody resprouters. Ecology 93:2052–2060

Guedje NM, Lejoly J, Nkongmeneck B et al (2003) Population dynamics of *Garcinialucida* (Clusiaceae) in Cameroonian Atlantic forests Forest. Ecol Manag 177:231–241

Gurevitch J, Scheiner SM, Fox GA (2009) Ecologia Vegetal. Artmed, Porto Alegre

Hallé F, Oldeman RAA, Tomlinson PB (1978) Tropical trees and forests: an architectural analysis. Springer-Verlag, New York

Herben T, Nováková Z, Klimešová J (2014) Clonal growth and plant species abundance. Ann Bot. doi:10.1093/aob/mct308

Hewitt GM (2004) Genetic consequences of climatic oscillations in the quartenary. Phil Trans R Soc Lond 359:183–195

Hoffman WA, Geiger EL, Gotsch SG et al (2012) Ecological thresholds at the savannah-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecol Lett 15:759–768

Hoffmann WA (1999) Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. Ecology 80:1354–1369

Jeník J (1994) Clonal growth in woody plants: a review. Folia Geobot Phytotx 29:291–306

Loehle C (2000) Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. Am Nat 156:14–33

Lucena IC, Amorim RSS, Lobo FA et al (2014) Spatial heterogeneity of soils of the Cerrado-Pantanal ecotone. Rev Cienc Agron 45:673–682

Mandujano MC, Montana C, Franco M et al (2001) Integration of demographic annual variability in a clonal desert cactus. Ecology 82:344–359

Manly BFJ (2007) Randomization. bootstrap and monte carlo methods in biology, 3rd edn. Chapman & Hall, CRC, Boca Raton

Marcante S, Winkler E, Erschbamer B (2009) Population dynamics along a primary succession gradient: do alpine species fit into demographic succession theory? Ann Bot 103:1129–1143

Matsuchita M, Tomaru N, Hoshino D et al (2012) Factors affecting the production, growth, and survival of sprouting stems in the multi-stemmed understory shrub *Lindera triloba*. Botany 88:174–184

McCarthy-Neumann S, Ibáñez I (2012) Tree range expansion may be enhanced by escape from negative plant–soil feedbacks. Ecology 93:2637–2649

Medina E, Francisco M (1994) Photosynthesis and water relations of savanna tree species differing in leaf phenology. Tree Physiol 14:1367–1381

Menges ES (1998) Evaluating extinction risks in plant populations. In: Fiedler PL, Kareiva PM (eds) Conservation Biology for the Coming Decade. Chapman & Hall, New York, pp 49–65

Muñoz-Costa A, Calleja-Alarcon JA (2013) Plant size and local abiotic factors determine the intra-specific variation in the multi-stemmed architecture of *Prunus lusitanica* at the Northeast limit of its global distribution. Forest Sys 22:423–432

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 203:853–858

Nepstad DC, Tohver IV, Ray D et al (2007) Mortality of large trees and lianas following experimental drought in an amazon forest. Ecology 88:2259–2269

Oborny B, Englert P (2012) Plant growth and foraging for a patchy resource: a credit model. Ecol Model 234:20–30

Portela RCQ, Bruna EM, Santos AM (2010) Demography of palm species in Brazil's Atlantic forest: a comparison of harvested and unharvested species using matrix models. Biodivers Conserv 19:2389–2403

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Sardans J, Rodà F, Peñuelas J (2006) Effects of a nutrient pulse supply on nutrient status of the Mediterranean trees *Quercus ilex* subsp. *ballota* and *Pinushalepensis* on different soils and under different competitive pressure. Trees 20:619–632

Sarukhan J (1974) Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. Reproductive strategies and seed population dynamics. J Ecol 62:151–177

Silvertown J (2008) The evolutionary maintenance of sexual reproduction: evidence from the ecological distribution of asexual reproduction in clonal plants. Int J Plant Sci 169:157–168

Silvertown J, Franco M, Mendoza IPA (1993) Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. J Ecol 81:465–476

Soliveres S, De Soto L, Maestre FT et al (2010) Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. Perspect Plant Ecol 12:227–234

Villlellas J, Ehrlén J, Olesen JM et al (2013) Plant performance in central and northern peripheral populations of the widespread *Plantago coronopus*. Ecography 36:136–145

Wells PV (1969) The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23:264–267

Witte LC, Stöcklin J (2010) Longevity of clonal plants: why it matters and how to measure it. Ann Bot 106:859–870

Xiao Y, Tang J, Qing H et al (2011) Trade-offs among growth, clonal, and sexual reproduction in an invasive plant *Spartina alterniflora* responding to inundation and clonal integration. Hydrobiologia 658:353–363

Zuidema PA, Jongejans E, Chien PD, During HJ, Schieving F (2010) Integral Projection Models for trees: a new parameterization method and a validation of model output. J Ecol 98:345–355