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Soil fertility and rainfall during specific phenological phases affect seed trait variation in a widely distributed Neotropical tree, *Copaifera langsdorffii*

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PREMISE: Knowledge of intra-specific variation in seed traits and its environmental determinants is important for predicting plant responses to environmental changes. Here, we tested the hypothesis that differences in soil fertility and rainfall during specific phenological phases drive variation in seed traits in a widely distributed tree, *Copaifera langsdorffii*. We also tested the hypothesis that climatic heterogeneity increases within-plant variation in seed traits.

METHODS: Inter- and intra-population and within-plant variation in seed mass, number, and seed size/seed number were evaluated for 50 individuals from five populations distributed along a rainfall gradient and occurring on varying soil types. Using multivariate approaches, we tested the effects of soil fertility characteristics and rainfall in five reproductive phenological phases on seed traits.

RESULTS: The seed traits varied greatly both among populations and within plants. Inter-population variation in seed mass was driven by total rainfall during fruit development, and variation in seed number was influenced by total rainfall during the dry season before the reproductive phase. Phosphorus levels and potential acidity of the soil also explained the variations in seed mass and seed mass/seed number, respectively. A positive association between intra-annual variation in rainfall and within-plant variation in seed mass and seed number was found.

CONCLUSION: Both rainfall during specific reproductive phases and soil conditions shape the variation in the seed mass and number of *C. langsdorffii*. Environment-driven seed trait variation may contribute to this species' broad niche breadth, which in turn may determine the species' persistence under future climatic conditions.

KEY WORDS Climate change; environmental unpredictability; Fabaceae; masting species; reproductive phenology; resource availability; seed mass/number trade-off.

Understanding intraspecific variation in functional traits of plant species has been a challenge for many scientists (Reich et al., 2003; Díaz et al., 2015; Souza et al., 2018). The quality and quantity of seeds produced by plant populations are key functional traits that determine the natural distribution of plant species (Valladares and Sánchez-Gómez, 2006; Skalova et al., 2012). Intraspecific variation in the seed set of plants is widely recognized (Baskin and Baskin, 1998) and can occur both within (Dolan, 1984; Valencia-Díaz and Montaña, 2005; Souza et al., 2015b) and among populations (Thompson, 1981; Goulart et al., 2006; Sales et al., 2013).

Seed size and number are important attributes of plant life histories (Smith and Fretwell, 1974; Lloyd, 1987) and can vary by several orders of magnitude (Moles and Westoby, 2006; Souza et al., 2015b). This variation has been attributed to resource availability and genetic factors (Wulff, 1986; Gnan et al., 2014). In mass-flowering species (masting species), seed production is often attributed to a combination of weather cues and internal plant-resource dynamics because of the interactions with flower production, pollination success, and seed maturation (Pearse et al., 2016). The effects of weather conditions on the seed traits of plant species, such as temperature and precipitation, vary according to the phenological phase of the mother plant (Korte et al., 1983; Abel and Boelt, 2018), and these effects can be evident not only in the year of seed production but also after one or more years in perennial plants (Kelly et al., 2013; Gallego-Zamorano et al., 2018). Despite the importance of establishing how weather during different phenological phases can affect seed traits, especially in the face of ongoing climatic change, there are no studies that directly assess this in wild Neotropical tree species.

Investment in seed size or seed number is habitat dependent and affects both seed germination and plant recruitment (Guariguata and Ostertag, 2001; Souza and Fagundes, 2014). Even though production of high numbers of seeds can translate directly to reproductive success (Westoby et al., 1992; Leishman et al., 2000), plants may invest in large seeds, with the trade-off of decreased seed number, under specific environmental conditions (Westoby et al., 1996). In general, plants produce larger seeds in stressed habitats (Halpern, 2005; Lázaro and Traveset, 2009; Kołodziejek, 2017), but contradictory results have been found (Fenner, 1992). Large seeds are more likely to germinate and produce more vigorous seedlings, which is crucial for survival in stressful environments (Baker, 1972; Hanley et al., 2007). However, small seeds produced in greater quantity favor the attraction of dispersers and increase the probability of dispersion and colonization of new habitats; besides, they germinate faster (Baskin and Baskin, 1998; Souza and Fagundes, 2014). Therefore, the trade-off between seed size and number optimizes the reproductive success of plants in different habitats (Venable, 1992; Paul-Victor and Turnbull, 2009).

Differential investment in seed size or number can increase the resilience of plant species during initial seedling recruitment, especially for populations that occur in environments with large intra-annual variations in temperature and rainfall (Baker, 1972; Westoby, 1998). Variation in seed traits under unstable environmental conditions (i.e., greater climate unpredictability) is poorly understood, and its importance in the context of global climate change is often ignored (Cochrane et al., 2015). Climate change is expected to increase the average global temperature, rainfall variation, and frequency of extreme events, thereby generating drier environments in many already arid regions (Pachauri and Mayer, 2014). Species with wide geographic distributions generally encounter great variations in climate and soil conditions, which makes them excellent models for evaluating the effects of environmental conditions on functional traits of natural populations (Gianoli and González-Teuber, 2005; Lázaro-Nogal et al., 2015). Soil fertility and climatic conditions are key factors that determine intraspecific variation in the functional traits of plant species (Lovato et al., 1994; Ribeiro et al., 2016; Souza et al., 2018), including the ratio between seed size and number (Ramírez-Valiente et al., 2009; Yuan et al., 2016). One of the most important sources of intra-population variation in plant organs, such as seeds, is the variation that occurs within individuals (Herrera et al., 2015). This variation is rarely considered, despite increasing evidence of its ecological and evolutionary importance (i.e., improving species' exploitation of resources and broadening species' ecological niches; Alonso et al., 2018).

In the present study, we evaluated the variation in seed mass and number in populations of *Copaifera langsdorffii*, a widely distributed masting tree species, along a rainfall gradient and under different soil conditions. We tested the hypothesis that differences in soil fertility and rainfall during specific phenological phases drive variation in seed traits by using a multivariate approach. We also investigated whether plants from resource-limited environments would have a trade-off between seed size and number, with larger and fewer seeds than those from environments with more resources. Finally, we investigated the effects of climatic heterogeneity (intra-annual variation in rainfall) on within-plant variation in seed traits.

MATERIALS AND METHODS

Study species, sampling area, and climate

Copaifera langsdorffii Desf. (Fabaceae) is a tropical tree species widely distributed in South America (Carvalho, 2003). In Brazil, it occurs in Caatinga, Cerrado, Atlantic Forest, and Amazon biomes (Fagundes, 2014). Adult *C. langsdorffii* trees reach a height of 2–35 m, depending on the environmental conditions (Costa et al., 2012, 2015). The species exhibits supra-annual reproduction alternating years of high reproductive activity, followed by 2–3 yr of low or no fruit production (Souza et al., 2015b). Flowering occurs in the rainy season, with seed dispersion during the dry season (Pedroni et al., 2002; Costa et al., 2016). The fruits have a single ellipsoid black seed that is partially wrapped in a yellow-orange aril (Carvalho, 2003; Fagundes et al., 2013). Birds are the main dispersers (Rabello et al., 2010), but seeds that fall on the ground can also have their arils removed by ants (Leal and Oliveira, 1998; Fagundes et al., 2013). The seeds of *C. langsdorffii* are orthodox, and their germination is greatly affected by seed size and aril presence (Souza and Fagundes, 2014; Souza et al., 2015a).

In the present study, five *C. langsdorffii* populations distributed among Brazil's three distinct biomes (Caatinga, Cerrado, and Atlantic Forest; Table 1) were selected; the distances between them ranged from 90 to 600 km. The Japonvar population (JAP) is located in a seasonally dry forest in the Caatinga biome. In this forest, trees of some species can exceed 25 m, and the foliar abscission of the trees is >90% during the dry season (Pezzini et al., 2014). In general, the soils of dry forests are rich in nutrients, and leaf fall contributes to soil fertility (Rizzini, 1997). The Montes Claros population (MOC) is located in Cerrado *sensu stricto*, a savanna vegetation compounded by small and tortuous trees, where soils are frequently deep, acidic, and nutrient poor (Rizzini, 1997). The Paraopeba population (PAR) is located in Cerradão, a forest formation in the Cerrado biome that includes larger trees with a closed canopy, in deep, slightly acidic soils with medium organic matter content mainly derived from leaves that fall during the dry season (Rizzini, 1997; Sano et al., 2008). The Canga population (CAG) is located in a ferruginous rock field. This vegetation, which is characterized by predominantly herbaceous-shrub species, occurs on mountaintops at altitudes above 900 m in the Cerrado-Atlantic Forest transition zone and in very shallow, iron-rich soils (Jacobi et al., 2007). The Lavras population (LAV) is located in a semi-deciduous montane forest in the Atlantic Forest, with large trees that form a continuous canopy in deep soils.

Climatic data for 54 yr (1961–2014) for each location were obtained from the Brazilian National Institute of Meteorology (INMET, 2015). The meteorological stations are near the study sites, at a maximum distance of ~20 km. The selected study sites follow a gradient of dryness. The more northern locations are more xeric (average annual rainfall 858–1029 mm) and receive most of the rainfall over a few months, whereas the more southern populations receive greater average annual rainfall (1490–1511 mm) that is more evenly distributed across the year (Table 1; Fig. 1). To quantify the intra-annual

TABLE 1. Environmental characterization and soil fertility variables of locations of *Copaifera langsdorffii* populations.

Population	JAP	MOC	PAR	CAG	LAV
Environmental characterization					
Coordinates	15°58′S, 44°16′W	16°40′S, 43°48′W	19°20′S, 44°24′W	20°04′S, 43°59′W	21°15′S, 45°02′W
Biomes	Caatinga	Cerrado	Cerrado	Cerrado	Atlantic Forest
Habitat	Seasonally dry forest	Cerrado strictu sensu	Cerrado strictu sensu	Ferruginous rock field	Semideciduous montana forest
Altitude (m)	804	645	763	1423	948
Mean annual rainfall (mm)	858.03	1029.27	1295.27	1490.12	1511.51
Intra-annual rainfall variation (%)	100.68	101.99	94.69	91.15	83.69
Mean annual temperature (°C)	24.23	22.97	21.29	20.74	20.02
Soil fertility					
pH (in H_2O)	5.57 (0.25)^b	5.30 (0.26)^b	5.33 (0.21)^b	4.50 (0.20)^a	5.10 (0.35)^b
H+Al ($mmol_c.dm^{-3}$)	3.42 (0.67)^a	5.63 (1.10)^a	7.56 (1.94)^a	20.31 (4.74)^b	7.20 (2.11)^a
Al ($mmol_c.dm^{-3}$)	0.39 (0.38)^a	1.43 (0.50)^a	1.17 (0.80)^a	1.55 (0.67)^a	0.84 (0.66)^a
Ca ($mmol_c.dm^{-3}$)	1.72 (0.49)^a	1.29 (0.36)^a	2.46 (1.54)^a	1.70 (0.29)^a	2.05 (1.23)^a
Mg ($mmol_c.dm^{-3}$)	0.91 (0.24)^a	0.68 (0.08)^a	1.22 (0.54)^b	0.33 (0.03)^a	0.63 (0.43)^a
P ($mg.dm^{-3}$)	1.97 (0.31)^a	1.33 (0.35)^a	2.60 (0.61)^a	4.43 (0.55)^b	3.33 (1.50)^b
K ($mg.dm^{-3}$)	86.33 (13.05)^a	166.00 (22.27)^b	182.67 (20.53)^b	76.33 (14.29)^a	109.00 (41.61)^a
SB ($mmol_c.dm^{-3}$)	2.85 (0.54)^a	2.40 (0.37)^a	5.47 (1.33)^a	2.22 (0.27)^a	2.96 (1.75)^a
T	6.39 (1.15)^a	8.02 (0.84)^a	11.80 (0.18)^a	22.50 (4.51)^b	10.16 (1.05)^a
t	3.24 (0.57)^a	3.83 (0.23)^a	5.47 (1.33)^a	3.77 (0.41)^a	3.8 (1.19)^a
M	11.52 (11.07)^a	22.07 (15.84)^a	26.63 (21.50)^a	40.13 (12.9)^a	26.91 (23.57)^a
V	45.57 (3.36)^b	30.26 (6.52)^b	35.46 (17.35)^b	10.28 (3.23)^a	29.37 (18.73)^b

Notes: Values of intra-annual variation in annual rainfall are coefficients of variation (CV = SD mean^{-1}) expressed as percentage. Data were obtained from the Brazilian National Meteorology Institute (http://www.inmet.gov.br) for the period 1961–2014. H+Al = potential acidity; SB = sum of bases; T = cation exchange capacity; t = effective capacity of cation exchange; M = aluminum saturation index; V = base saturation. Mean values and standard deviation (in brackets) for soil variables are shown. Different letters after mean and standard deviation indicate significant differences among populations in contrast analysis in generalized linear models ($P < 0.05$).

variation in rainfall at each location, we calculated the coefficient of variation among months ($CV_{\%}$ = SD/mean × 100). The variation in intra-annual rainfall was negatively correlated with annual rainfall ($r = -0.88$, $P < 0.05$), indicating that the more xeric environments are characterized by greater annual heterogeneity in rainfall.

To characterize soil fertility, three soil samples (~500 g each) were collected from each location at depths of 0–10 cm. Soil analyses were conducted at the Instituto Mineiro de Agropecuária by using the methodology described by EMBRAPA (1997). The soil fertility of the locations were then compared using generalized linear models (GLMs), with Gaussian error distribution (Crawley, 2000). The soil fertility varied among the locations, especially CAG population, which occurs in more acidic soil (lower pH and higher potential acidity, H+Al) and low base saturation (Table 1). The soils of all the study sites were deep, except that of CAG, in which the plants occur in depressions between iron-rich rock outcrops (where there is soil accumulation; Jacobi et al., 2007).

Sampling seed traits across populations

The seed traits of 50 individual *C. langsdorffii* (10 from each population) were evaluated. The data were collected during 2013, a year in which *C. langsdorffii* exhibited mass reproduction (i.e., ~75% of the trees exhibited high-intensity reproductive efforts). The selected trees had fully developed crowns and were in a good phytosanitary state (i.e., without lianas, parasitic plants, or evidence of disease). For each selected tree, 10 terminal branches of 30 cm in length were collected from different parts of the crown (Souza et al., 2015b) to determine the average number of seeds produced per branch (N_s). To estimate average seed mass, mature fruits were randomly collected from the crown of each individual and then manually processed to eliminate malformed, diseased, and damaged seeds. We considered only seeds that had no obvious sign of predation. The number of non-filled seeds was visually low (i.e., ≤5% in the evaluated trees), and these were discarded. However, the seed fill was not completely assessed, so the data presented here can account for both filled and non-filled seeds. After processing, 20 seeds per individual were randomly chosen and individually weighed to calculate average seed mass (M_s, in grams). The seed traits of each sampled tree are provided in Appendix S1.

Effects of rainfall during specific phenological phases on seed traits

To determine the effects of rainfall during different phenological phases on the seed traits of the populations, we evaluated the reproductive phenology of each *C. langsdorffii* population during the year of masting reproduction (2013). The periods of flowering, fruit development, and seed dispersion of each population were recorded. The populations showed differences in the periods of flowering and fruit development. The individuals in mesic environments produced flowers early, and the fruits had a longer development time than those of individuals in xeric environments (Appendix S2). Taking into account the reproductive phenology of each population, we generated five rainfall datasets: RDS = total rainfall during the dry season, before the reproductive phase (June–August 2012, for all populations); RFW = total rainfall during flowering of each population; RFR = total rainfall during fruit development of each population; RPR = total rainfall during the reproductive period of each population, flower production to seed dispersion period; and RPM = accumulated rainfall from the beginning of the reproductive season of the previous year (January 2012) until the end of the masting reproductive period of each population (July–September 2013, depending on the population).

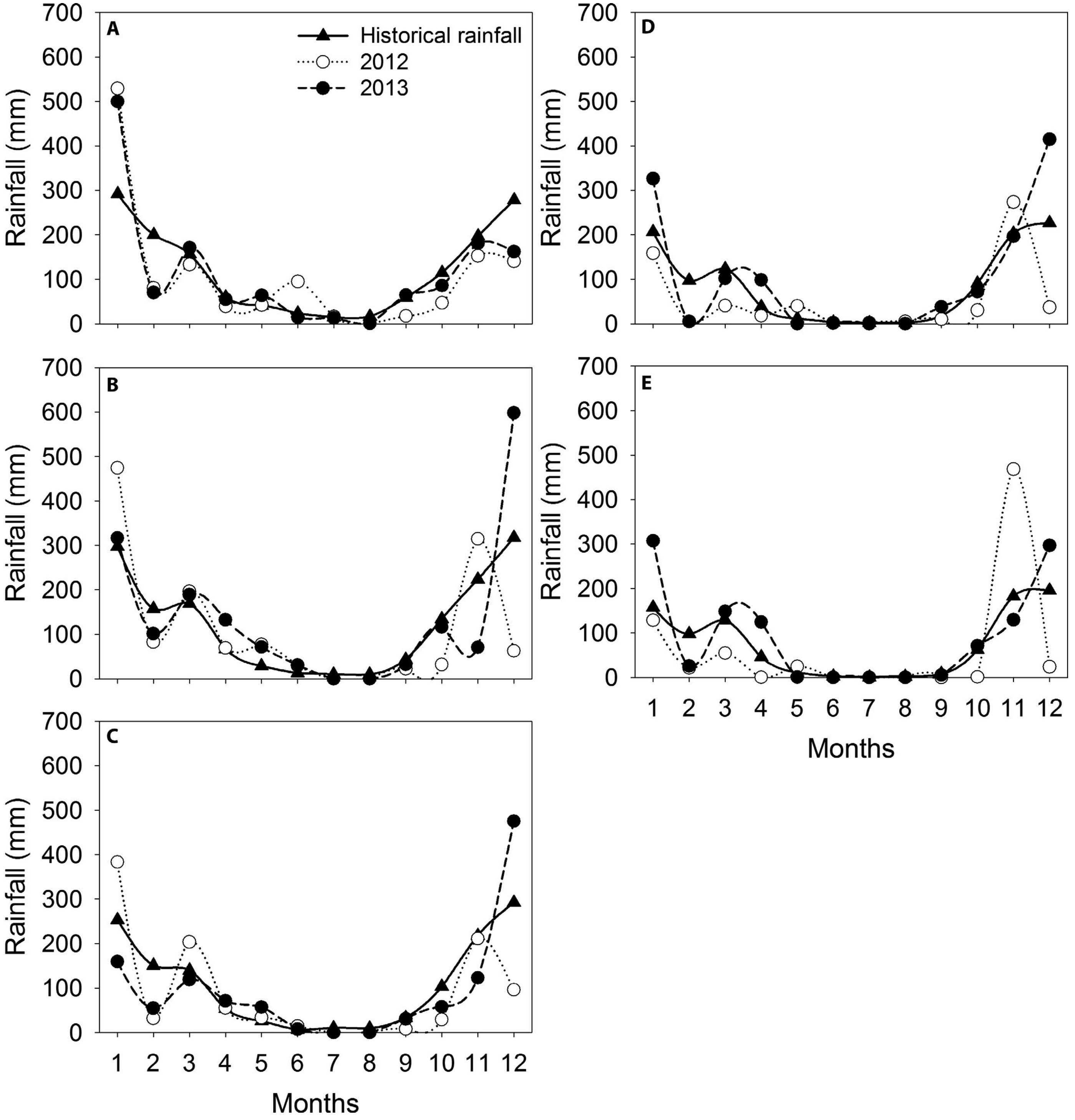

FIGURE 1. Average monthly rainfall for five *Copaifera langsdorffii* populations: (A) LAV, (B) CAG, (C) PAR, (D) MOC, and (E) JAP. Values were calculated using data for a 54 yr period (1961–2014) from the Instituto Nacional de Meteorologia (INMET, 2015).

Statistical analysis

Variation in the seed traits (seed number, seed mass, and seed mass/seed number ratio) among the five *C. langsdorffii* populations was investigated using GLMs. In this case, seed number, seed mass, and seed mass/seed number of each individual were used as the response variables, whereas population site was used as the explanatory variable. Gaussian error distribution was used for all GLMs. The models were compared using *F*-test, and contrast analysis was used to group the populations (Crawley, 2000).

To test the occurrence of seed mass/number trade-off in each population, we constructed GLMs to assess the relationship between seed mass (M_s) and number of seeds (N_s) produced within each individual by using seed number as the explanatory variable and average seed mass as the response variable.

The associations between seed traits and environmental factors (soil fertility and rainfall) were investigated using multiple regression analyses. The soil fertility variables (Table 1) and rainfall in specific phenological phases (RDS, RFW, RFR, RPR, and RPM) were used as the explanatory variables, and seed number, seed mass, and seed mass/seed number of each individual were used as the response variables. Using Spearman's rank correlation coefficient ($r < 0.6$), collinearity was evaluated separately between the predictor variables. Thus, two correlated rainfall or soil variables were not used together in any of the elaborated models. To determine the most explicative variables in each model, we used an approach based on the second-order Akaike information criterion (AIC), where the best model is indicated by the lowest AIC value (Burnham et al., 2011; Niinemets, 2015). These analyses were performed using functions implemented in the "AICcmodavg" and "psych" packages.

The effect of intra-annual variation in rainfall on within-plant variation (WPV) of both seed size and number was also investigated using GLMs. WPV = (SD/x) × 100, where SD and x are the standard deviation and mean, respectively, of each trait in each individual.

All data were analyzed using R version 2.15.3 (R Core Team, 2013). All models were built using the appropriate error distribution and considering the nature of each response variable, followed by an assessment of the model. All the created models were compared with null models (Crawley, 2000).

RESULTS

Variation in seed traits

All seed traits varied significantly among populations (Table 2). The CAG population produced heavy seeds ($M_s = 0.75$ g) that were ~75% larger than those produced by the MOC and JAP populations, which yielded the smallest seeds ($M_s = 0.42$ and 0.44 g, respectively). The LAV population produced the greatest number of seeds per branch ($N_s = 8.29$). The seed number of LAV ($N_s = 8.29$) was about two times greater than the number of seeds produced by CAG and JAP populations ($N_s = 3.0$ and 4.16, respectively), which produced the fewest seeds per branch (Table 2).

By contrast, the seed mass/seed number did not vary among populations, except for the CAG population, which yielded a ratio that was two to three times greater than the others (Table 2). The CAG population exhibited a significant and negative relationship between the size and number of seeds produced ($F_{1,8} = 16.18$, $P < 0.001$, $R^2 = 0.67$), thereby indicating a trade-off between seed mass and number (Fig. 2). Other populations did not show any association between seed number and seed mass.

Effects of rainfall and soil fertility on seed traits

The multiple regression analysis detected an association between the seed traits and rainfall in specific phenological phases and soil fertility (Table 3). Seed mass was the trait more strongly explained by the analyzed environmental variables ($R^2 = 0.60$, $P < 0.001$). Specifically, seed mass variation was positively determined by rainfall during fruit development (Fig. 3A) and soil phosphorus availability (Fig. 3B). A weak positive association ($R^2 = 0.08$, $P < 0.05$) was observed between seed number and rainfall during the dry season before the reproductive period (Fig. 3C). A positive relationship ($R^2 = 0.18$, $P < 0.001$) was also observed between the seed mass/seed number and potential acidity of the soil (Fig. 3D).

Within-plant variation vs. intra-annual variation in rainfall

The populations exhibited high WPV in the seed traits, mainly seed number. The within-plant variation in seed mass ranged from 15% (CAG) to 25% (JAP), whereas the within-plant variation in seed number per branch varied from 113% (LAV) to 172% (MOC; Fig. 4). The within-plant variations in seed mass ($F_{1,48} = 9.05$, $P < 0.01$; $R^2 = 0.94$; Fig. 4A) and number of seeds per branch ($F_{1,48} = 8.46$, $P < 0.05$; $R^2 = 0.91$; Fig. 4B) were positively correlated with the intra-annual variation in rainfall.

DISCUSSION

Our results indicate that the seed traits of *C. langsdorffii* vary among populations and within individual plants, and this variation is shaped by rainfall in specific phenological phases and soil fertility characteristics. Rainfall during fruit development and soil phosphorus availability determined the variation in seed mass. The rainfall occurred during the dry season, before the reproductive phase influenced the variation in seed number, whereas soil potential acidity affected seed mass/seed number.

The fruiting pattern of *C. langsdorffii* is marked by years of high seed production, followed by years in which production is drastically reduced (Silvertown, 1980; Souza et al., 2015b). Although the causes of masting events have not yet been determined for this species, it has been suggested that masting in general is caused by a combination of weather cues (temperature, precipitation and wind, inter-annual variation) and internal plant resource dynamics that affect flower production, pollination success, and seed maturation (Pearse et al., 2016). In seed masting episodes, internal resources, such as non-structural carbohydrates, nitrogen, phosphorus, and water, would be depleted, affecting the amount of resources required for other processes, including maintenance, growth, and defense (Pearse et al., 2016). The data from our present study indicate that environment resource availability can mediate among-population variation in the seed traits of a widely distributed leguminous tree during masting events. The observed effect of rainfall during

TABLE 2. Analysis of deviance of complete models to evaluate the differences in seed traits among populations of *Copaifera langsdorffii*.

Seed trait	JAP	MOC	PAR	CAG	LAV
Seed mass (g)	0.44 (0.11)^a	0.42 (0.09)^a	0.54 (0.08)^b	0.75 (0.11)^c	0.56 (0.10)^b
Seed number	4.16 (3.06)^a	5.65 (4.05)^b	6.87 (3.50)^b	3.00 (1.90)^a	8.29 (6.57)^c
Seed mass/number ratio	0.18 (0.15)^a	0.14 (0.16)^a	0.10 (0.05)^a	0.36 (0.24)^b	0.17 (0.19)^a

Notes: Mean values and standard deviation (in brackets) are shown. Different letters after mean and standard deviation indicate significant differences among populations in contrast analysis in generalized linear models ($P < 0.05$).

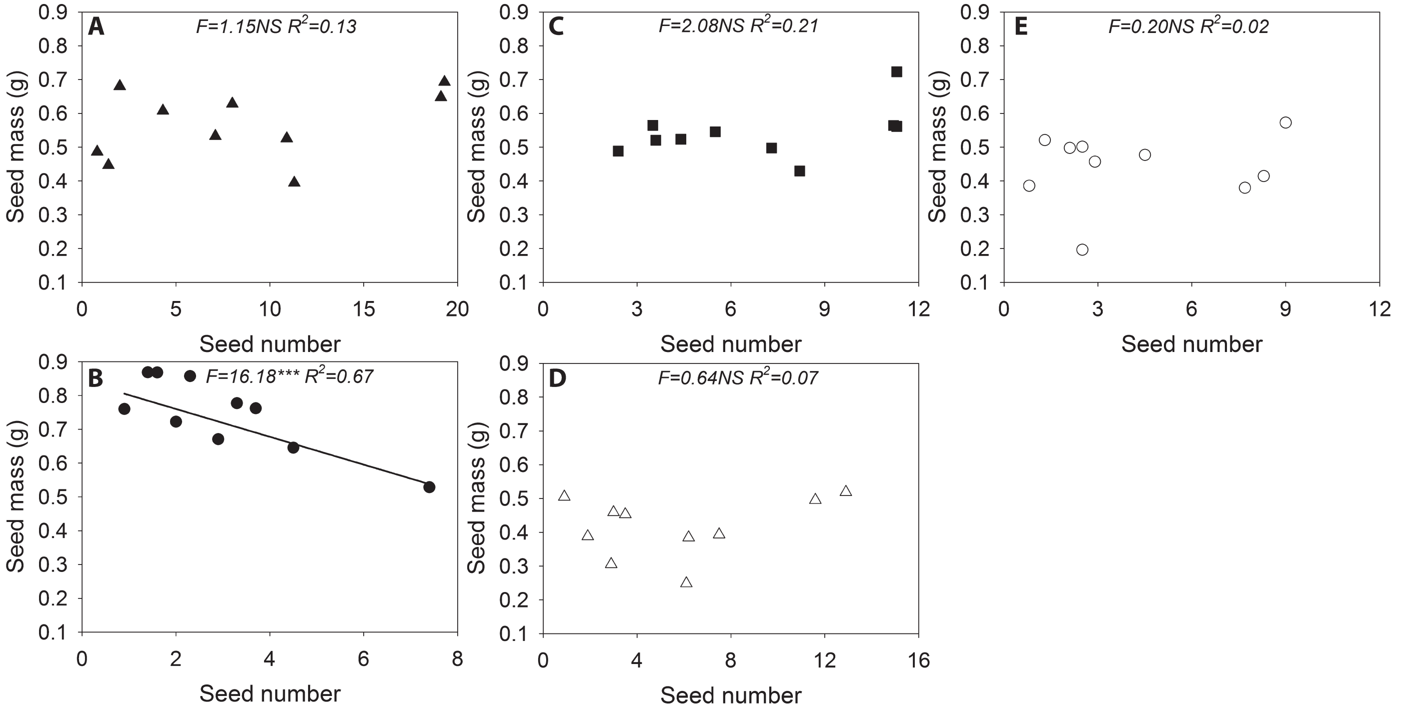

FIGURE 2. Relationship between seed size and number for plants (N = 10) from five *Copaifera langsdorffii* populations: (A) LAV, (B) CAG, (C) PAR, (D) MOC, and (E) JAP (signifiance: *** $P < 0.001$; NS $P > 0.05$; generalized linear models).

TABLE 3. Results of multiple regression analyses for seed traits of *Copaifera langsdorffii* with climate and soil variables.

Regression	N	AIC	R^2	F	P
Seed mass = 0.22 + 4.93^{-4} RFR + 0.06 P	50	−85.53	0.60	34.35	<0.001
Seed number = 4.60 + 0.03 RDS	50	292.11	0.08	4.19	<0.05
Seed mass/number ratio = 0.03 + 0.01 H+Al	50	−30.51	0.18	10.53	<0.001

Notes: RDS = rainfall during the dry season, before the reproductive phase (rainfall data of June–August 2012); RFR = rainfall during fruits development in each population; H+Al = potential acidity in the soil; P = phosphorus in the soil.

the dry season before the pre-reproductive phase on seed number suggests that pre-flowering water availability affects seed yield in *C. langsdorffii* populations. Seed mass was positively determined by the amount of rainfall received during fruit formation and soil phosphorus availability. The greater availability of water and phosphorus in the soil probably allowed greater accumulation of internal resources in the trees. Populations with greater water resources usually have higher productivity (Llorens et al., 2004; Lázaro-Nogal et al., 2015) and may allocate more resources to reproduction and produce more and larger seeds (Yuan et al., 2016). Besides water availability, phosphorus has been indicated as a determinant for seed yield in masting species (Pearse et al., 2016).

Our hypothesis that plants in resource-limited environments (i.e., low rainfall and low soil fertility) would have a trade-off between seed size and number, with larger and fewer seeds than those from environments with more resources, was confirmed. A seed size/number trade-off was found in only the CAG population (i.e., trees in this population that had fewer seeds presented larger ones (Fig. 2). The CAG population trees had larger seeds (78% larger than those of the MOC population) and fewer seeds than the other populations. Our data showed that potential acidity (H+Al) of the soil was the factor most strongly correlated with seed mass/number (Fig. 3D). Although the CAG population had more soil phosphorus availability and more rainfall during fruit development, it had significantly higher potential acidity than the other populations. High potential acidity, high aluminum, and low base saturation as found in the CAG population (Table 1) are characteristics of infertile soils. In addition, it is important to note that ferruginous rock grassland soils, like those at the CAG site, are very shallow, exhibiting low water-storage capacity. Seed number was associated positively with rainfall during the dry-season pre-reproduction period (Fig. 3C); although CAG did not receive lower rainfall than the other populations in this period, low soil water storage can be a strong limiting factor in the dry season (Jacobi et al., 2007). The trade-off between seed size and number has a solid theoretical basis (Smith and Fretwell, 1974; Lloyd, 1987), and it has been reported in several plant species (Shipley and Dion, 1992; Leishman, 2001; Sadras, 2007). Limited resource availability generally generates a trade-off, usually shifting to production of large seeds (Baker, 1972; Stromberg and Patten, 1990; Murray et al., 2004; Ramírez-Valiente et al., 2009). Seed size is directly related to the amount of nutritional reserves allocated to initial seedling growth (Primack, 1987), and large seeds produce more vigorous seedlings than small seeds (Gross and Werner, 1983; Gross, 1984; Souza and Fagundes, 2014). Greater amounts of stored reserves increase the probability of seedling establishment at sites with lower resource availability (Baker, 1972; Moles and Westoby, 2004). However, further studies are necessary to understand the role of seed size on germination and seedling establishment in *C. langsdorffii*.

The *C. langsdorffii* populations expressed high within-plant variation in seed mass and seed number. Substantial within-plant

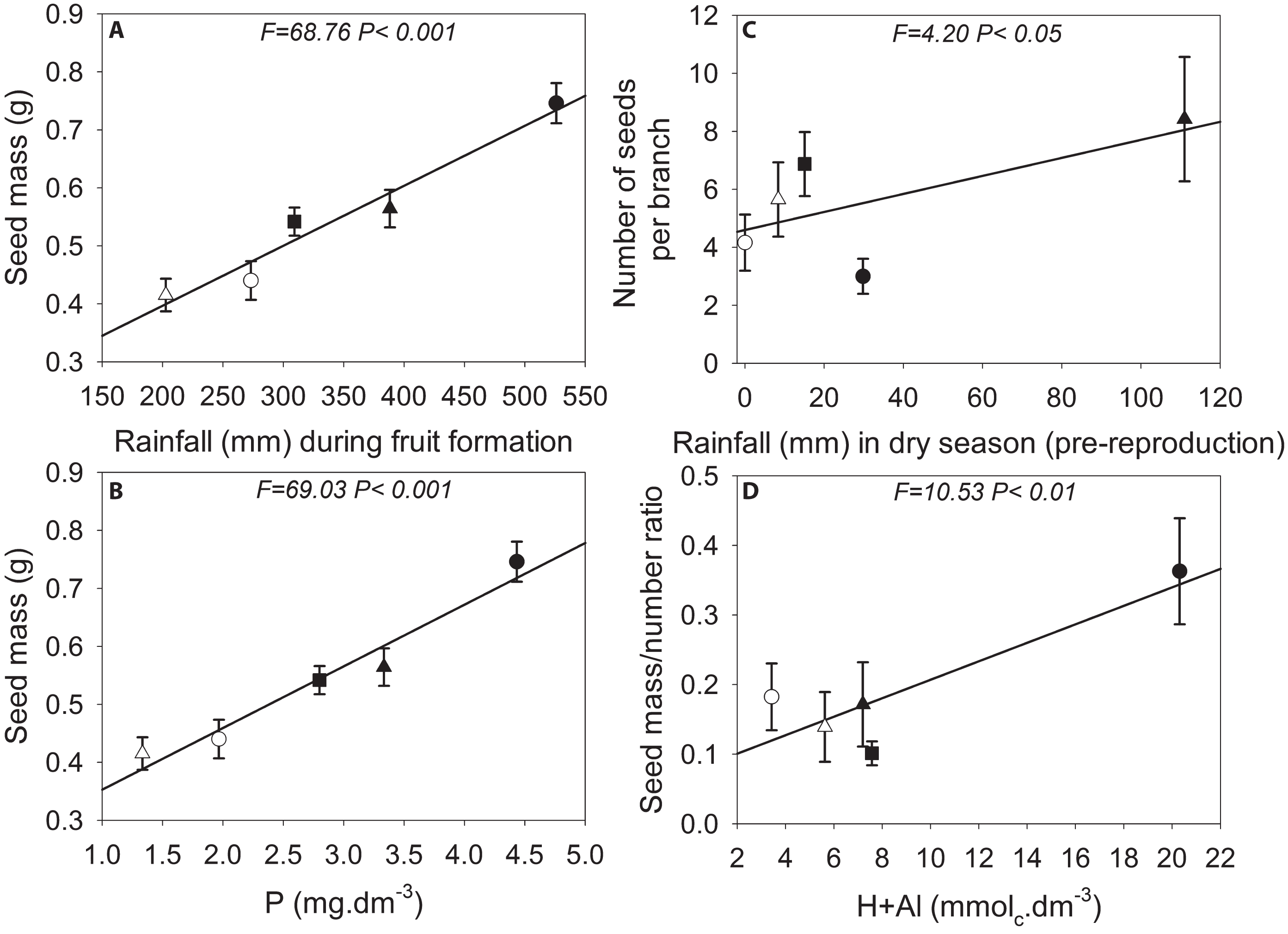

FIGURE 3. Effects of rainfall and soil fertility on seed traits of five *Copaifera langsdorffii* populations: (A, B) seed mass (g); (C) number of seeds per branch; (D) seed mass/number ratio. Values and error bars indicate means ± SE for each population (closed triangles = LAV; closed circles = CAG; closed squares = PAR; open triangles = MOC; open circles = JAP).

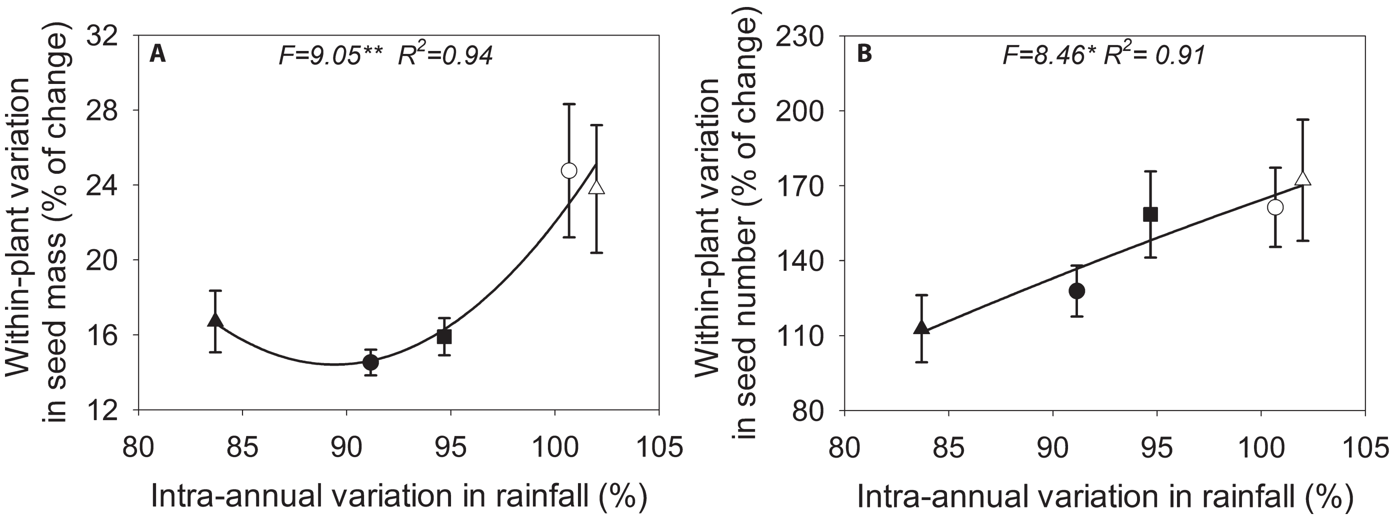

FIGURE 4. Relationship between within-plant seed trait variation and intra-annual rainfall variation (coefficient of variation = SD/mean) for plants from five *Copaifera langsdorffii* populations: (A) seed mass; (B) number of seeds per branch. Values and error bars indicate mean ± SE for each population (closed triangles = LAV; closed circles = CAG; closed squares = PAR; open triangles = MOC; open circles = JAP; ** $P < 0.01$; * $P < 0.05$; generalized linear models).

variation in seed traits has frequently been found in several species (Thompson, 1984; Obeso, 1993; Vaughton and Ramsey, 1998; Herrera, 2000). In the present study, we found a positive association between within-plant variation of seeds traits and temporal climate heterogeneity. Populations in environments with higher intra-annual variation in rainfall exhibited greater within-plant variation in both seed mass and number. This association can be attributed to environmental unpredictability due to climate seasonality. In unpredictable environments, plants can develop morphological and physiological adaptations in their seed production that increase survival under uncertain environmental conditions (Harper and Ogden, 1970; Wang et al., 2008). Within-plant variation in seed mass has been suggested to allow plants to decrease temporal variation in offspring success (Venable et al., 1987). Small seeds, which germinate more quickly, produce seedlings that can colonize the environment more quickly (Baskin and Baskin, 1998; Souza and Fagundes, 2014), thereby making better use of temporary resource availability. By contrast, large seeds produce more vigorous seedlings that are more likely to survive, especially under stressful conditions (Baker, 1972; Hanley et al., 2007). Therefore, variation in seed size allows species to cope with a relatively wide range of environmental conditions, thereby buffering the negative influence of unpredictable resources, such as rainfall.

CONCLUSIONS

The great variation in seed traits found among *C. langsdorffii* populations may contribute to explain the broad geographic range and niche breadth of the species. Although other (non-tested) factors can also contribute to seed trait variation along gradients of rainfall and soil condition, we found that both rainfall during fruit development and rainfall during the dry season prior to the reproductive phase contributed significantly to variation in seed mass and seed number, respectively. Additionally, soil phosphorus availability contributed to determining seed mass variation, while potential acidity influenced the seed mass/number. The high within-plant variation in seed traits observed in sites with great intra-annual variation in rainfall likely increases the ability of the species to cope with environmental unpredictability. The high variation in seed traits of *C. langsdorffii*, especially in environments with high variability in rainfall, may be important for ensuring the long-term persistence of the species under ongoing climate changes.

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AUTHOR CONTRIBUTIONS

M.L.S., M.F., F.V., and J.P.L.-F. conceived the study and designed the experiments. M.L.S. collected and analyzed the data. M.L.S., M.B.L., and J.P.L.-F. interpreted the data and led the writing of the manuscript. All the authors contributed critically to the drafts and approved the final version of the manuscript for publication.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Mean values and standard deviation (in brackets) of seed traits of each individual of *Copaifera langsdorffii* populations.

APPENDIX S2. Rainfall data in different phases of reproductive phenology in the locations of *Copaifera langsdorffii* populations. RDS = total rainfall during the dry season, before the reproductive phase (June–August 2012, for all populations); RFW = total rainfall during flowering; RFR = total rainfall during fruit development; RPR = total rainfall during the reproductive period (flower production to seed dispersion period); RPM = accumulated rainfall from the beginning of the reproductive season of the previous year (January 2012) until the end of the masting reproductive period.

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