Reproductive strategy of *Copaifera langsdorffii* (Fabaceae): more seeds or better seeds?

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Abstract: The trade-off seed size/number is a recognized phenomenon capable of shaping ecological processes of colonization and establishment of plant species. Studies that describe trade-offs size/number of seeds in supra-annual fruiting species are still rare. In this study, two predictions for trade-off size/number hypothesis were tested: (i) on a population scale, seeds produced during years of greater reproductive investment showed reduced size, and (ii) on individual scale there is an inverse relationship between size and number of seeds produced by individual plant. To test these predictions, 102 *Copaifera langsdorffii* adult plants were monitored monthly from January to September during four consecutive years (2008 to 2011) in order to study the reproductive investment of plants. *C. langsdorffii* plants exhibited reproductive activity only during years 2008 and 2011. The mean number of seeds per branch was 26.4 % greater in 2008 comparatively to 2011. It was also observed that seed size was greater in the year of 2008, when plants produced greater number of fruits. Thus, the data did not support the first prediction of seed size/number hypothesis. In both reproductive years, there was a negative relationship between seed size and number of seeds, supporting the second prediction of the seed size/number hypothesis. The interaction term with the reproductive year suggests that the trade-off size/number of seeds was indeed stronger in 2011, when the plants produced lower seed number. Finally, this study calls the attention to supra-annual fruiting pattern in *C. langsdoffii*, and suggests that the phenological patterns contribute to explain the wide variation in their seed size and geographical distribution. Rev. Biol. Trop. 63 (4): 1161-1167. Epub 2015 December 01.

Key words: plant phenology, reproductive investment, resource allocation, supra-annual fruiting, trade-off size/number of seeds.

Variations in seed size and number affect key ecological processes of colonization and establishment of plant species within and across different habitats (Silvertown & Bullock, 2003; Guariguata & Ostertag, 2001; Moles & Westoby, 2006). In fact, smaller seeds germinate faster (Dolan, 1984; Souza & Fagundes, 2014), contributing with a greater competitive advantage to the plant, especially in early successional stages (Baskin & Baskin, 1998). Contrarily, larger seeds, while germinating more slowly, often have higher rates of germination than smaller seeds, being favoured in predictable habitats (Harper, 1977; Geritz, 1995; Ferreira & Borghetti, 2004). In addition, broad variations in seed size allow the species to be able to colonize different habitats and expand their geographic distribution ranges (Leishman, 2001; Souza & Fagundes, 2014). Therefore, the seed size can affect the distribution and abundance of plants in natural communities (Jakobsson & Eriksson, 2000; Leishman, 2001).

The relationship seed number *versus* seed biomass is a recognized trade-off capable of shaping seed size (Westoby, Leishman, Lord, Poorter, & Schoen, 1996; Leishman, 2001; Moles & Westoby, 2006). There is strong empirical evidence for a negative relationship between seed mass and seed crop, both per individual per year and per square meter of canopy, or per gram of plant biomass, per year (Leishman, 2001; Moles & Westoby, 2006). However, several ecological (e.g. resource availability for the plant and interactions with pollinators and seed predators) and evolutionary (e.g. plant life form and phenological patterns) factors can change the result of the trade-off size/ number of seeds (Westoby, Leishman, Lord, Poorter, & Schoen, 1996). These ecological and evolutionary interactions generate large variations in size and number of seeds produced by plants among and within species (Leishman, Westoby, & Jurado, 1995; Silvertown & Bullock, 2003; Moles & Westoby, 2006).

Trade-off size/ number of seeds occupy a central core in plant ecology because it reflects ecological and evolutionary aspects of plant species (Sadras, 2007; Souza & Fagundes, 2014). Studies that describe trade-offs size/ number of seeds are relatively common (see Moles & Westoby, 2006 and references). However, studies of this nature that focus on supra-annual fruiting species are still rare, especially when comparing the trade-off size/number of seeds between years of low and high reproductive investment. Supra-annual reproduction in plants is characterized by the alternating fruit production cycles in plant species, with years of intense fruit production and years of little or no fruiting (Kelly, 1994; Koenig & Knops, 2005; Souza & Fagundes, 2014). These cycles have an enormous potential to affect the trade off size/number of seeds. Theoretically, it is expected that in years of intense reproductive activity the resource available for seed production would have to be distributed to a large number of seeds (Silvertown, 1980). Therefore, supra-annual plants should produce larger fruits and seeds during years of low reproductive activity (Souza & Fagundes, 2014).

However, in these supra-annual species, the expected trade-off size/number of seed can be masked because resource available for plant reproduction can change among cycles of reproductive events (Koenig & Knops, 2005). Thus, the objective of this study was to test the hypothesis of trade-off size/number of seeds among and within years of high and low reproductive investment in *Copaifera langsdorffii*, an arboreal tropical species with supra-annual fruiting. Hence, two predictions for trade-off size/number hypothesis were tested: (i) on a populational scale, seeds produced during years of greater reproductive investment showed reduced size and (ii) on individual scale (within same event reproductive) there is an inverse relationship between size and number of seeds produced by individual plant.

MATERIALS AND METHODS

Studied system: *Copaifera langsdorffii* (Fabaceae: Caesalpiniaceae) is a tropical, deciduous, heliophytic, selective xerophytic tree species with 7-30 m height. The species have a wide distribution from Northeast Argentina to Southern Bolivia and can be found throughout Brazil (Fagundes, 2014). The plants show complete deciduousness in the dry season (July to September) and new leaves begin to appear immediately after the drop of leaves produced in the previous growing season (Fagundes, Maia, Queiroz, Fernandes, & Costa, 2013). *C. langsdorffii* exhibits supra-annual mass fruiting (Pedroni, Sanchez, & Santos 2002). Flowering is concentrated from November to January and fruit ripening occurs from August to October, with producing flowers and fruits in the terminal portion of the branch (Fagundes et al., 2013). Upon opening, each fruit exposes a single ellipsoid seed, which is black and shiny and is partially covered by a yellow-orange aril (Carvalho, 2003).

Study area: Fieldwork was conducted in a Cerrado (Savanna) area located in the municipality of Montes Claros (16°40’26” S - 43°48’44” W), Northern Minas Gerais State, Brazil. This region is located between the domains of the Cerrado and Caatinga (Rizzini, 1997), with a semi-arid climate characterized by well-defined dry and rainy seasons. The soil of the study area is dystrophic with a developed herbaceous sub-shrub layer, generally affected by fire (Costa, Siqueira, Oliveira, & Fagundes, 2011; Fagundes, Camargos, & Costa, 2011). The historical average annual temperature is approximately 23 °C, and the average precipitation is about 1 100 mm/year, with the rainy season concentrated between November and February (Costa et al., 2011). While annual average temperature has not changed significantly during the study years, the rainfall ranged from 1 360, 1 139, 1 058 and 1 073 mm/year during 2008, 2009, 2010 and 2011, respectively (INMET, 2014).

Data collection: In December 2007, a total of 102 *C. langsdorffii* plants were selected in the study area and properly identified with metal platelets. All trees were with a fully developed crown and in a good phytosanitary state (e.g. without lianas, parasitic plants or evidence of pathogens attack). The plants selected for the study were monitored monthly from January to September during four consecutive years (2008 to 2011) to characterize occurrence of flowers and fruits. Additionally, during the month of April of each reproductive year (2008 and 2011), ten terminal branches (30 cm long) were collected from each plant in different points of the tree canopies to minimize the possible effects of microclimate variations on fruit development (Costa et al., 2011). These branches were taken to the Conservation Biology Laboratory of the State University of Montes Claros in order to determine average number of fruits per plant. All the marked trees produced fruits in 2008, none produced fruits in 2009 or 2010, and only 47 individuals (46 %) were fruiting in 2011. Plants that produced seeds in 2008 and 2011 (n= 65) were categorized in two groups: g1= plant fruiting in 2008 (n= 33) and g2 = plant fruiting in 2011, and not already selected in g1 (n= 30). The exclusion of plants belonging to treatment g1 from treatment g2 was necessary to avoid temporal pseudoreplication.

During September of 2008 and 2011 (period of fruit maturation), 100 fruits were collected from each plant belonging to group g1 e g2 in order to determinate seed size. All fruits were manually processed, eliminating malformed seeds and seeds exhibiting symptoms of attacks by predators or pathogens. The volume of the seeds was used as indicative of seed size. The seed volume was determined using the formula for cone volume [$V= (\pi.r^2.l)/3$], where "r" is the radius and "l" is seed length (Souza & Fagundes 2014).

The data were analyzed using R software (R Core Team, 2014). Regression tests were performed by constructing generalized linear models (GLM) to test hypotheses predictions proposed in this study. Variations in seed number and size between reproductive events were tested using mean of seed number or volume per plant as response variables and reproductive years (2008 and 2011) as explanatory variable. The analysis of trade-off size/number of seeds within reproductive event was tested using the number of seeds/branch and years as explanatory variable and the average size of seed produced by each plants as response variables. All minimal adequate models were created with the removal of non-significant terms and compared with null model. All models were built using the appropriate error distribution considering the nature of each response variable, following by model criticism via residual analysis (Crawley, 2007).

RESULTS

The population of *C. langsdorffii* exhibited reproductive activity only during 2008 and 2011. It was also found that seed production per plant varied between the two reproductive years (χ^2 = 16.82, $p < 0.001$, Fig. 1A). In fact, the mean number of seeds per branch was approximately 26.4 % greater in 2008, when compared to 2011 (Fig. 1A). In addition, it is worth stating that most plants belonging to studied population (all marked plants) produced fruits in 2008, while only few individuals did in 2011. Seed volume resulted greater in

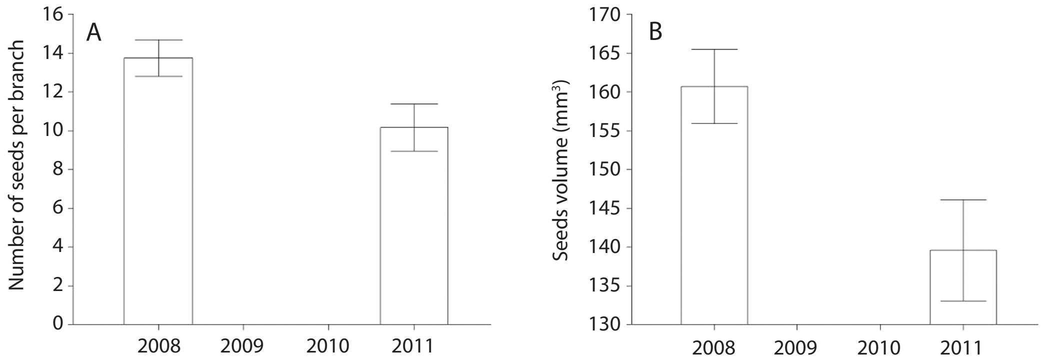

Fig. 1. Variation in the number of seed per branch (A) and volume of seeds (B) produced by *Copaifera langsdorffii* during four consecutive years (2008-2011).

TABLE 1
Analysis of deviance of complete models to evaluate the trade-off size/number of seeds in *Copaifera langsdorffii*

Response Variable	Explanatory variable	Deviance	Residual Df.	Residual deviance	F	P
Seed number	Year	1.037	60	7.201	10.118	< 0.05
	Seed volume	1.073	59	6.469	7.135	< 0.01
	Year x Seed volume	1.052	58	5.949	5.075	< 0.05

2008, when plants produced higher number of fruits ($F= 6.32$, $p < 0.05$, Fig. 1B).

For both reproductive years (2008 and 2011), there was a negative relationship between seed volume and number of seeds produced per branch of *C. langsdorffii*, and the interaction term with the reproductive year was significant. The interaction suggests that the trade-off size/number of seeds was indeed stronger in 2011, when plants producing lower seed number (Table 1, Fig 2).

DISCUSSION

The result of this study indicates seed crop produced by *Copaifera langsdorffii* population was significantly greater in 2008 comparatively to 2011. The data is especially relevant if we consider that most plants were fruiting in 2008 while only a few individuals did so in 2011. Moreover, plants produced bigger seeds in 2008, suggesting greater resource availability for seed development in this year of higher reproductive investment. Our data therefore do not support the first prediction of the trade-off seed size/ number hypothesis in populational scale.

In this scenario it is important to stress that *C. langsdorffii* have supra-annual phenology with fruiting intervals of at least two to three years. Moreover, years of intense fruiting can be followed by years where fruit production

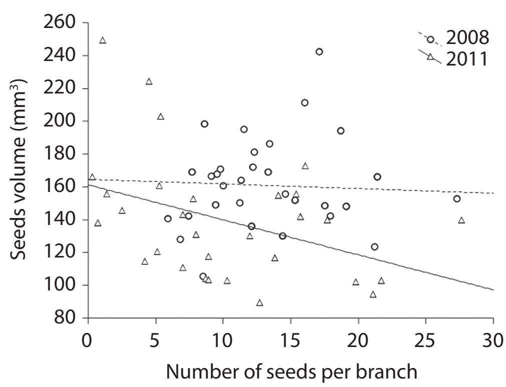

Fig. 2. Trade off size/number of seeds in *Copaifera langsdorffii* during years of high (2008) and low (2011) reproductive investment.

is reduced to less than 10 % (Pedroni et al., 2002; Fagundes, 2014; Souza & Fagundes, 2014). The main evolutionary advantages of supra-annual fruiting for plants are to increase in pollination efficiency and seed survival, due to seed predator satiation in years of mass production (Silvertown, 1980; Kelly & Sork, 2002; Schauber et al., 2002; Kolb, Ehrlén, & Eriksson, 2007). In addition, some authors have proposed that resource availability is a key factor for supra-annual species to display their reproductive activity and intensity of fruit production. Limited resource availability is probably a factor that inhibits fruit production in years of low reproductive activity (Sork, 1993; Koenig & Knops, 2005). While temperature has not significantly varied between years in the studied area, total rainfall was 21.2 % higher in 2008 comparatively to 2011. Thereby, the lower rainfall resource available in 2011 may explain the lower number of seeds, as well as the smaller seed volume produced by *C. Langsdorffi* during the year 2011.

Limited resource availability generates a stronger trade-off in the allocation of energy among the different plant drains, so an optimal investment in growth, storage and reproduction will not be generally satisfied simultaneously by plants (Chapin, 1991). Trade-offs can be also observed within each of these metabolic routes (Leishman, 2001), as for example, the strategy of producing few large seeds *versus* numerous small seeds, that represents a key trade-off in resource allocation for many plant species (Leishman, 2001; Moles & Westoby, 2006). On an individual scale, the results of this study support the prediction of the trade-off seed size/number hypothesis, as it was observed a negative relationship between seed size and number of seeds produced per plant in both two reproductive years of *C. langsdorffii*. The trade-off in seed size/number of seeds has a solid theoretical basis (Smith & Fretwell, 1974; Lloyd, 1987) and several studies have demonstrated this pattern for several plant species (Werner & Platt, 1976; Shipley & Dion, 1992; Turnbull, Rees, & Crawley, 1999; Jakobsson & Eriksson, 2000; Henry & Westoby, 2001; Leishman, 2001). However, it is important to emphasize that this relation was stronger in 2011, when plants produced fewer fruits. Again, it should be clear that the resource availability may play a central role to justify this variation. Therefore, resource (rainfall) was more limited during 2011, accentuating the trade-off size/number of seed observed in this study.

Finally, the study calls the attention to supra-annual fruiting pattern in *C. langsdoffii,* and suggests that the phenological patterns contribute to explain the wide variation in their seed size and geographical distribution. Indeed, variations in seed size represent an important attribute of plant life history (Smith & Fretwell, 1974; Lloyd, 1987) and influences important ecological processes of colonization and establishment of species across habitats (Guariguata & Ostertag, 2001). Larger seeds produce more vigorous seedlings (Dan, Mello, Wetzel, Popinigis, & Zonta, 1987) allowing greater competitive ability in predictable habitats (Geritz, 1995). In contrast, smaller seeds germinate faster and colonize transient habitats easily (Aniszewski, 2001). Thus, supra annual fruiting could be favouring the colonization of different habitats by *C. langsdorffii*, facilitating its extended geographic distribution (see also Souza & Fagundes, 2014). This study suggests that the resource availability affects the size/number of seeds trade-off in in *C. langsdorffii*. However, predicting the effect of ecological (e.g. resource available, ecological interaction) and evolutionary forces on supra-annual reproduction in plants will be essential to understanding this phenological pattern, a subject that remains unsolved.

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RESUMEN

Estrategia reproductiva de *Copaifera langsdorffii* (Fabaceae): ¿Más semillas o mejores semillas? El *compromiso o balance adaptativo de las semillas en tamaño/número* (trade-off seed size/number) es un reconocido fenómeno capaz de dar forma a los procesos ecológicos de la colonización y el establecimiento de especies de plantas. Los estudios que describen el compromiso adaptativo de las semillas en tamaño/número en especies con fructificación supra-anual siguen siendo raros. En este estudio, se probaron dos hipótesis predictivas para compromiso adaptativo de las semillas en tamaño/número: (i) una a escala poblacional, semillas producidas durante el año de mayor inversión reproductiva mostraran un tamaño reducido, y (ii) otra a escala individual que se dará una relación inversa entre el tamaño y número de semillas producidas por la planta individual. Para probar estas predicciones, 102 plantas adultas de *Copaifera langsdorffii* fueron monitoreadas mensualmente entre enero y septiembre, durante cuatro años consecutivos (2008-2011) con el fin de estudiar la inversión reproductiva de las plantas. Plantas *langsdorffii C.* exhibieron actividad reproductiva sólo durante el 2008 y 2011. El número promedio de semillas por rama fue 26.4 % mayor en 2008 en comparación con 2011. También se observó que el tamaño de la semilla fue mayor en 2008, cuando las plantas producen mayor número de frutos. Por lo tanto, los datos no apoyan la primera hipótesis de predicción de tamaño/número. En ambos años reproductivos, existía una relación negativa entre el tamaño de la semilla y el número de semillas, comprobando la segunda hipótesis de predicción del tamaño/número de semillas. El periodo de interacción con el año reproductivo sugiere que el compromiso adaptativo de las semillas en tamaño/número fue de hecho más fuerte en 2011, cuando las plantas produjeron baja cantidad de semillas. Por último, este estudio llama la atención por el patrón de fructificación supra-anual en *C. langsdoffii*, y sugiere que los patrones fenológicos contribuyen a explicar la amplia variación en el tamaño de la semilla y la distribución geográfica.

Palabras clave: fenología de la planta, inversión reproductiva, asignación de recursos, fructificación supra-anual, compromiso adaptativo de semillas en tamaño/número.

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