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Seed abortion and the individual weight of castor seed (*Ricinus communis* L.)

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ABSTRACT

The weight of each individual seed plays an important but often neglected role in the determination of castor (*Ricinus communis* L.) seed yield. Studies were made under field and greenhouse conditions to assess how seed abortion and the weight of individual castor seeds are influenced by: (i) water availability, (ii) position in the raceme, (iii) manipulation of source-sink ratio, and (iv) competition among seeds in the same capsule. Samples of 150 seeds were obtained from a field experiment in Lubbock, TX, USA with six cultivars under seven irrigation treatments. The seeds were individually weighed. Some racemes with mature fruits were harvested and kept with attached fruits for taking data on the position and weight of each seed. In a greenhouse experiment, castor plants of two cultivars were subjected to sink reduction (clipping of racemes) and source reduction (partial defoliation). The histogram of seed weight was not a bell-shape curve because there was a relatively high frequency of light (aborted) seeds. When more water was available, the plant increased the maximum seed weight and reduced the seed abortion rate. The lowest seed abortion rate was observed in the cv. BRS Nordestina (7.4%) and the highest in the cv. Hale (18.1%). The seed weight and the probability of seed abortion were not associated with the position in the raceme. No evidence was found that seeds in the same capsule compete for assimilates. The seed abortion rate increased in response to defoliation after flowering (source reduction), but it did not decrease in response to the racemes clipping (sink reduction). The sink reduction did not increase the number of seeds in the first raceme and the maximum and mean seed weight. Seed abortion was found to play an important role in adjustments of sink according to source capacity.

1. Introduction

Each individual seed has a large influence on its own fate, in opposition to the idea that they simply result from the assimilate supply from the mother plant (Egli, 2006). The variability in the individual seed weight has a potentially high impact on final seed production, but usually only the mean seed weight is considered. The mean seed weight is determined predominantly by the plant's genetic potential (Egli et al., 1987), but variability in seed weight can be caused by many physiological processes that are sensitive to environmental conditions. Variability in seed weight is inevitable even under controlled growing conditions (Hay et al., 2010).

In cross-pollinated species, the diploid origin of the embryo and the triploid nature of the endosperm is a potential source of variability in seed weight as observed in caucasian clover (*Trifolium ambiguum* Bieb.) (Hay et al., 2010). Environment is an important source of variability because seeds develop at different times and experience different conditions of temperature, light, moisture, etc.

Two phases of seed development are particularly sensitive to environmental factors: the phases of cell division (phase I) and dry matter accumulation (phase II). Phase I begins with the ovule fertilization and ends with the beginning of phase II (without overlapping) (Egli, 1998). Seeds are more sensitive to environment during the cell division phase because the number of cells formed in this phase will later define the rate of accumulation of reserves (seed growth rate) and ultimately the final seed weight (Munier-Jolain and Ney, 1998). There have not been many detailed studies on castor seed development, but the general characteristics of seed growth are remarkably uniform across species (Egli, 2006), and the studies performed with this oilseed confirm that it is similar to most species regarding seed development (Carvalho et al., 2010; Greenwood and Bewley, 1982; Kermode and Bewley, 1985; Lucena

Abbreviations: DAP, days after planting; MSW, maximum seed weight; RSW, relative seed weight.

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et al., 2010; Moshkin and Alekseev, 1986; Vallejos et al., 2011; Velasco et al., 2005).

Because phase I does not occur at the same time for all seeds in an indeterminate plant such as castor, high variability in seed characteristics is expected due to the environmental effect. Environmental factors can also create additional variability to seed weight by acting directly on the seed (like the temperature influencing seed metabolism rate) or indirectly when a change in the photosynthesis rate influences assimilates supply.

Seed abortion is another factor influencing final seed yield because it plays an important role in the determination of the sink size. Because of seed abortion, many fertilized ovules do not develop into fruits and seeds. Seed abortion only occurs before the beginning of dry matter accumulation (Duthion and Pigeaire, 1991; Ney et al., 1994; Egli, 1998). Many seeds are aborted after they expand to a full size, but no reserves have been accumulated yet. Those light seeds are rarely accounted for because they are usually lost during harvesting and dehulling, and because they have little impact on seed yield (Egli et al., 1987).

Another source of variability is the position in the inflorescence, fruit, ear, or pod because seed weight is rarely independent of this factor. Seed position is more likely to influence seed weight when the ovules are lined inside the ovary. Heavier seeds are usually found closer to the assimilate supply. Some hypotheses that explain the influence of the position on seed characteristics include: (i) competition for resources, (ii) non-uniform pollination, and (iii) architectural limitations. Seeds in the same raceme can also begin development at different times and experience different environmental conditions (Gutiérrez et al., 1996; Medrano et al., 2000; Navarro, 1998; Rocha and Stephenson, 1990; Severino and Auld, 2013).

We conducted several experiments in castor at field conditions and in greenhouse to investigate seed abortion and the variability in individual seed weight in response to irrigation treatments, manipulation of the source and sink, position in the raceme, and competition among seeds in the same capsule.

2. Materials and methods

2.1. Individual seed weight influenced by water availability

A field experiment was run in the Texas Tech University Experimental Farm at Lubbock, TX (33°35′ N; 101°54′W, 990 m a.s.l.) in 2009. Six castor cultivars with highly divergent seed size and plant architecture (AL Guarany, BRS Energia, BRS Nordestina, Campinas, Divela, and Hale) were subjected to seven irrigation treatments varying from 0 to 6 mm d^{-1} (with 1 mm d^{-1} increments between treatments) in a randomized block design with four replications. Water was delivered by subsurface drip irrigation. The cultivars AL Guarany, BRS Energia, BRS Nordestina, and Campinas were developed in Brazil (Freire et al., 2001; Milani et al., 2007), Hale was developed by USDA/ARS and Texas A&M University (Brigham, 1970), and Divela is the PI 183078 introduced from India. Plant spacing was 0.9 m × 0.9 m resulting in 12,346 plant ha^{-1}.

The experiment was planted on 28 May 2009. The irrigation was applied daily for 106 d beginning at 10 d after planting (DAP). Total water applied through irrigation ranged from 0 to 646 mm. Total precipitation was 188 mm from planting to harvesting. A precipitation of 15 mm at 65 DAP was followed by 39 d in which only a 3.3 mm precipitation occurred. Precipitation that occurred after 150 DAP was not considered due to low air temperatures (5–15 °C) and the short time before killing frost. The soil had pH 8.6, 11 g kg^{-1} of organic matter, 45 mg kg^{-1} of P, and 520 mg kg^{-1} of K. An application of 67 kg ha^{-1} of nitrogen was made at 30 DAP. Weeds were controlled by hand hoeing, and no disease or pest requiring control was observed during the study.

Racemes were individually harvested in one plant randomly selected in each plot. Racemes were considered matured when all the capsules had hard spines and brownish color (up to two green capsules were tolerated). The capsules were separated from the rachis, placed in paper bags, and oven dried (75 °C, for at least 7 d). The seeds were manually threshed. A 150-seeds sample was obtained from each plant. In this sample, each raceme was represented proportionally to its total number of seeds. Seventeen plants (out of 168) produced less than 150 seeds because of water deficit. Special caution was taken to prevent bias related to seed weight when handling the samples.

The seeds were individually weighed in a scale with precision of 0.01 g. Seeds weighing <0.02 g were excluded. The weight of the five heaviest seeds in each sample was averaged to obtain the maximum seed weight (MSW). The relative seed weight (RSW) was calculated as the weight of each seed divided by the MSW.

The MSW was analyzed by linear regression ($y = ax + b$) in function of the total water. The slope significance was tested with the t test, and the significance was presented. The regression equations were used to estimate the MSW at 188 and 834 mm of water. The RSW was presented in histograms of frequency. The values of RSW were grouped in 20 classes of 0.05 increments. The hypothesis that the frequency of seeds in each class is influenced by the total water was tested with regression analysis (linear model, $p < 0.10$). Seeds with RSW < 0.40 were assumed as aborted. The point of 0.40 was determined based on the histograms of seed weight. The frequency of aborted seeds among genotypes was compared by protected t test ($p < 0.10$) (the normality was tested with Shapiro–Wilk test at $p < 0.01$).

2.2. Seed weight influenced by the position in the raceme and in the capsule

Racemes were harvested in an experiment run in 2010 similar to that previously described and run in 2009. Four mature primary racemes were harvested from two cultivars (BRS Energia and AL Guarany) cultivated at the extreme levels of total applied water (rainfed = 294 and maximum irrigation = 897 mm). Those two cultivars were chosen because they have racemes with the highest number of seeds. The racemes were oven dried (4 d, 40 °C) with special care to avoid shattering of capsules. Data on capsule position in the raceme was taken as follow. The height of 1 cm was assigned to the lowest capsule in the raceme, and from that point, the height of each capsule was measured. The relative position of each capsule was calculated dividing its height by the highest capsule in the raceme. The seeds were dehulled by hand and individually weighed. The RSW was calculated as described in the Section 2.1.

The RSW was analyzed by linear regression having the relative height as the independent variable. The slope significance was tested by t test ($p < 0.10$). Logistic regression was used to test the probability of occurrence of a capsule with one, two, or three aborted seeds in function of the relative position in the raceme. Contrasts and t test ($p < 0.10$) were used to test the hypotheses that: (i) a castor seed was heavier when the other seeds in the same capsule aborted; (ii) capsules that contained only one or two seeds developed heavier seeds compared to the average of regular three-seeded capsules; (iii) the water availability and the cultivar influenced the frequency of capsules with at least one aborted seed. The normality of distribution was tested in all data set with Shapiro–Wilk test ($p < 0.01$).