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Study on the effect of air temperature on seed development and determination of the base temperature for seed growth in castor (*Ricinus communis* L.)

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Abstract

Castor (*Ricinus communis* L.) is an industrial oilseed crop that is tropical by origin but cultivated in temperate regions. There are reports that castor seed yield is significantly reduced by exposure to cool temperatures during the seed filling stage. The aim of this study was to measure the effect of the air temperature on the growth rate of castor seed and to determine the base temperature for this critical physiological process. Racemes of castor cv. Brigham initiated at different days were tagged after pollination, and fruits were harvested in five days increments during the 2012 growing season at Lubbock, TX, USA (latitude 33°36' N).The air temperature was recorded at 5-minutes intervals from tagging the first raceme until the end of the growing season. The seed water content and seed dry weight were used for the calculation of the influence of air temperature in the seed growth rate and to determine the base temperature of this physiological process. It was found that the seed growth rate was reduced as the air temperature became cooler. The seed growth rate was 13.8 mg day^{-1} in the racemes initiated on 31 July (28 °C, on average), compared with 4.3 mg day^{-1} in the racemes initiated on 20 August (20 °C, on average). The base temperature (used for calculation of degree-days) for castor seed growth was estimated to be 15 ˚C, and a castor seed required 464 degree-days to reach physiological maturity.

Keywords: degree-days, environmental influence, oilseed crop, physiological maturity, seed filling duration, seed growth rate.
Abbreviations: DAP_days after planting; MSW_maximum seed weight; RSW_relative seed weight; SGR_seed growth rate.

Introduction

Castor (*Ricinus communis* L.) is a tropical oilseed crop that probably originated in Ethiopia. Currently, global castor seed annual production is around 1.5 million metric tons with four countries (India, China, Brazil, and Mozambique) accounting for 96% of total production. Although the main producing regions are in the tropics, this crop has been grown commercially on large areas in temperate countries such as the United States and the former USSR (Russia and Ukraine). Castor is still being considered for cultivation in regions that experience cool temperatures (10 to 20 ˚C) that prevail in temperate climates and high elevations during the phase of seed filling (Moshkin, 1986; Weiss, 2000; Falasca et al., 2012; Severino et al., 2012). Due to its tropical origin, castor is a heat-loving plant, and cool temperatures during seed filling have been reported to reduce seed yield. According to Moshkin (1986, p. 57), 48˚30' N was the furthest North latitude suitable for castor cultivation in the former USSR due to low temperatures and short growing season. Only early-ripening varieties were adapted for cultivation at 53˚ N latitude. Castor seed yields were reduced by 32% due to incomplete ripening in 1977 in which the temperatures were below average. Testing dates of termination in the State of Nebraska, USA, Kittock and Williams (1967) found that the weekly increments of seed yield were greater when air temperatures were higher (August and early September) than in cooler periods of early-Fall (mid-September through October). Severino and Auld (2013b) found that 74% of the seeds reached maturity during 42-days of warmer air temperature (from 88 to 130 days after planting), while only 8% of the seeds reached maturity during 44 days of cooler air temperature. Many seeds (accounting for18% of the seed yield) were still immature when the killing frost occurred. An agroclimatic zoning for castor producing regions in Argentina considered 15 ˚C as the minimum temperature for castor plant growth. A portion of the country was considered unsuitable for castor due to the occurrence of low temperatures (Falasca et al., 2012). Temperature is an important environmental factor influencing the rate of plant growth and development. For that reason, plant growth and development are more associated to the thermal time than to chronological time. The degree-days approach is a method widely used for quantification of thermal time. It is based on the assumptions that the growth ceases below a given temperature (base temperature, T_b), and that growth increases linearly in response to incremental increases in the temperature (Yang et al., 1995). The T_b can assume a different value for each physiological process, and an adequate calculation of the degree-days depends on an accurate determination of the T_b. The development of castor seed is similar to most species and occurs in three phases: cell division, seed filling, and desiccation (Severino and Auld, 2013a). The phase of cell division (Phase I) begins with ovule fertilization and ends when the seed has the maximum number of cells. During this phase, there is negligible accumulation of reserves (oil, protein, carbohydrates, and minerals), the seed grows close to its final size, and the water content is around 900 g kg^{-1}. The phase of seed filling (Phase II) is characterised by a linear increase in the dry weight due to accumulation of reserves. Usually, the Phase II does not overlap the cell division phase and it ends when the seed reaches the physiological maturity. In the desiccation phase (Phase III) the seed loses vascular connection with the mother-plant and passively loses water at a rate dependent upon environmental conditions (Egli, 1998; Munier-Jolain and Ney, 1998). The physiological conditions of the mother-plant influences the number of seeds and the seed characteristics that are defined during the Phase I. However, once the Phase II begins, the mother-plant plays the important role of supplying the seed with assimilates, but it has little control on the seed growth rate. For instance, during Phase I the mother-plant controls the abortion rate and the number of cells in the seed, which are determined by sucrose availability. Nevertheless, during the Phase II, there is no abortion, and seed growth is primarily controlled by the number of cells that was previously differentiated during Phase I (Munier-Jolain and Ney, 1998). Thus, the seed growth during Phase II is influenced by environmental condition rather than by the mother-plant (Egli, 1998). Only under extreme conditions, such as severe drought, high temperatures, or pests attack, can seed growth during Phase II be significantly influenced by the physiological condition of the mother-plant. The impact of air temperature on seed growth rate and the limited influence of the plant's physiological condition is well documented in the literature for crops such as maize (*Zea mays*), wheat (*Triticum aestivum*), soybean (*Glycine max* L.), and rice (*Oryza sativa* L.) (Soffield et al., 1977; Yoshida and Hara, 1977; Egli and Wardlaw, 1980; Tollenaar and Bruulsema, 1988; Egli, 1998, p. 45; Tacarindua et al., 2012). The objective of this study was to measure the effect of the air temperature on the growth rate of castor seed and to determine the base temperature for this physiological process. Determination of the impact of air temperature on castor seed growth is essential for the efficient management of this crop in regions suffering with cool temperatures during seed maturation.

Results

Methods for calculating accumulated degree-days

The calculation of accumulated degree-days using both the daily mean temperature and the mean amplitude methods resulted in values fairly close to those calculated using 5-min intervals (Fig. 1). Both alternative methods resulted in only 0.3 degree-days below the accumulated value during the experimental period and were slightly different only on the days when temperatures changed quickly. Because there were positive and negative deviations, the accumulated error during the experimental period was negligible.

Tolerance to freezing temperature

Castor tolerated a light freezing temperature (90 minutes at -0.6 ˚C) and an extended period with temperatures below 4 ˚C without any apparent chilling damage. Leaves and seeds were not damaged and resumed growth after temperatures warmed.

Determination of base temperature for seed growth

At the end of the experiment, 957 seeds were collected, but 213 seed were rejected as aborted, 29 as early developing, and 63 as late developing. The abortion rate (22.1%) was higher than what was observed for other cultivars in previous

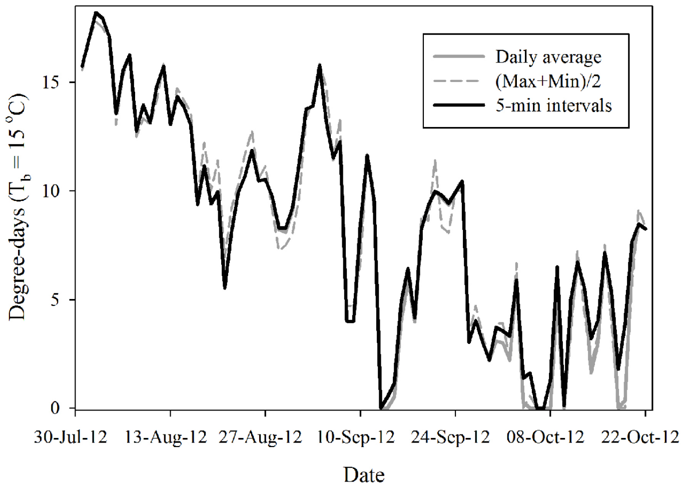

Fig 1. Degree-days calculated for the 2012 growing season at Lubbock, TX, USA with the base temperature of 15 ˚C using the methods of daily average, mean amplitude, and 5-min intervals.

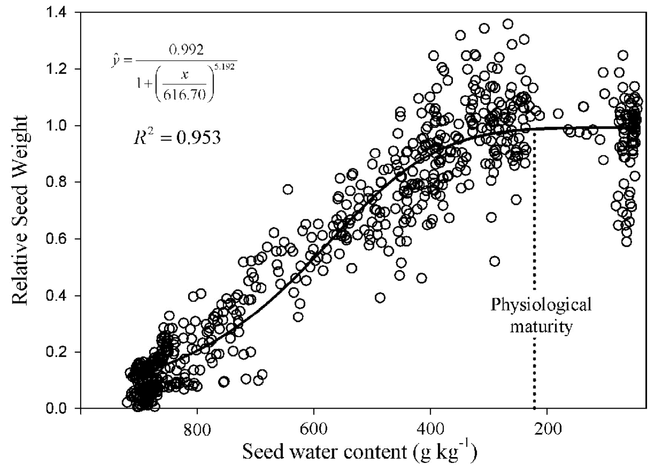

Fig 2. Relative Seed Weight of castor seeds shown as a function of the moisture content from pollination to physiological maturity (n=652).

studies (varying from 7.4 to 18.1%), but this rate is acceptable, and previous studies found that the aborted seeds do not impact the growth of the regular seeds (Severino and Auld, 2013c). The high abortion rate could also be a characteristic of the cultivar Brigham. After rejecting atypical seeds, the Logistic Equation showed a good fitness (R^2=0.953) between castor seed growth and seed water content (Fig. 2). The Maximum Seed Weight (MSW) varied among plants from 235.03 to 342.52 mg. The largest R^2 (0.855) between the accumulated degree-days and the seed moisture content was observed with the T_b = 15 ˚C (Fig. 3). Consequently, this value was assumed to provide the best estimate of the base temperature for castor seed growth. Using this T_b, a castor seed would require 464 accumulated degree-days beginning at pollination to reach physiological maturity. Therefore, it was estimated that a castor seed would reach physiological maturity within 93 days after pollination at mean air temperature of 20 ˚C, while it may require only 31 days at a mean air temperature of 30 ˚C.

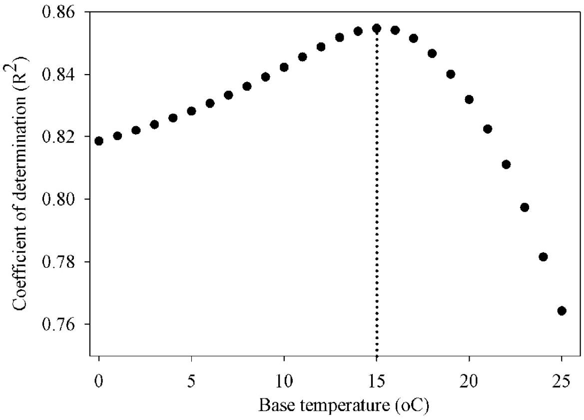

Fig 3. Coefficient of determination (R^2) between the castor seed moisture content and the accumulated degree-days calculated with base temperatures varying from 0 to 25 °C (n=563).

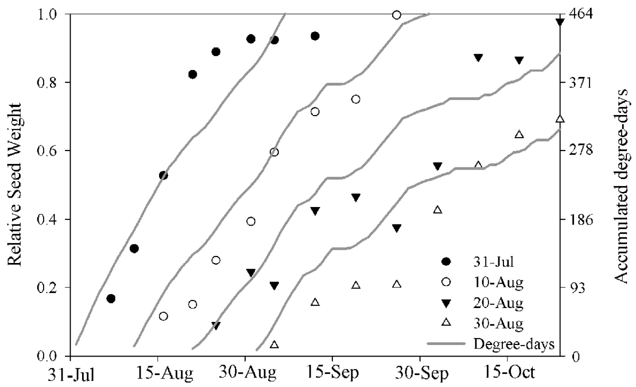

Fig 4. Changes in the Seed Growth Rate of castor along the 2012 growing season at Lubbock, TX, USA and the accumulated degree-days of each raceme according to the initiation day**.**

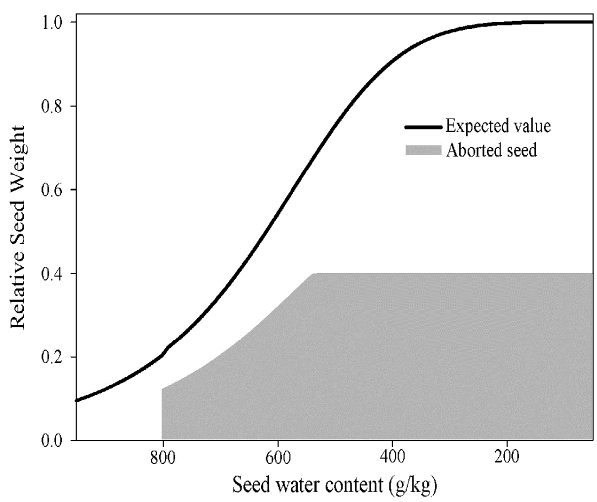

Fig 5. Criterion for discarding data from castor seeds due to abortion based on the expected relative seed weight and moisture content.

Seed growth rate at different air temperatures

The seed growth rate (SGR) changed during the growing season (Fig. 4) because the seeds grew slower when the air temperature was reduced. The SGR was 13.8, 7.2, 4.3, and 5.5 mg day^{-1} in the racemes which were initiated in 31 July, 10 August, 20 August, and 30 August, respectively. The progress of seed growth in each raceme was consistent with the accumulated degree-days calculated for the respective day of initiation (Fig. 4).

Discussion

Base temperature and temperature affecting castor seed growth

A T_b of 15 ˚C is higher than usually observed in temperate-adapted crops, and it is consistent with the tropical origin of castor. The T_b for seedling emergence of castor (12.5 ˚C) compares with other tropical crops such as sesame (*Sesamum indicum*) (15.9 ˚C) and guar (*Cyamopsis tetragonoloba*) (14.7 ˚C), but not with temperate crops such as lentil (*Lens culinaris*) (1.4 ˚C) and wheat (2.6 ˚C) (Angus et al., 1981).
Slow seed growth has been reported in castor at the end of the cropping season in temperate climates (Kittock and Williams, 1967; Severino and Auld, 2013b) and in subtropical climate where cold temperatures occur at the end of the growing season when seeds are being filled (Nagabhushanam and Raghavaiah, 2005; Zuchi et al., 2010; Falasca et al., 2012; Severino et al., 2012). The same problem was observed in other crops such as pearl millet (*Pennisetum americanum*), soybean, and wheat (Soffield et al., 1977; Egli and Wardlaw, 1980; Fussel et al., 1980; Tacarindua et al., 2012). Yoshida and Hara (1977) observed that the seed filling duration in rice was 18 days with a daily mean temperature of 28 ˚C compared with 43 days when the air temperature was 16 ˚C. Zheng et al. (2009) observed that higher soybean yields were obtained in the years with higher mean air temperature during seed filling stage and that the mean air temperature accounted for 22% of the year-to-year variation in seed yield. In temperate regions, low temperatures are frequent at the end of the growing season, but occasional unseasonable cold temperatures can reduce the crop yield. Therefore, the potential effect of temperature on seed filling must be considered when developing a breeding program or crop management for castor seed production.

Linearity of the phase of reserves accumulation

Seed growth is traditionally assumed to be linear during Phase II (reserves accumulation), but it was observed that it deviated from linearity due to the influence of air temperature (Fig. 4). Thus, linearity in Phase II is expected only under constant temperature or if it is plotted against thermal rather that chronological time.

Fruit`s heat budget

When considering the air temperature to study seed growth, it should be understood that the actual seed temperature could be considerably different from the surrounding environment. An increase by a few degrees in the seed temperature could have significant effect on castor seed filling, especially if the air temperature is close to the T_b. Sunlight radiation is potentially the most important component of the heat budget

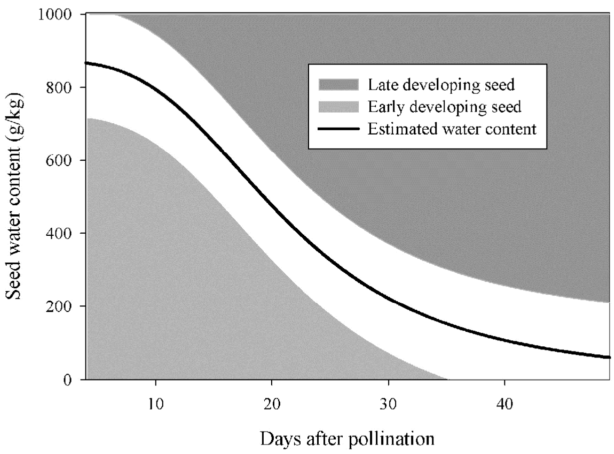

Fig 6. Criterion for discarding data from castor seeds due to growth ahead or behind the majority of seed in the same raceme.

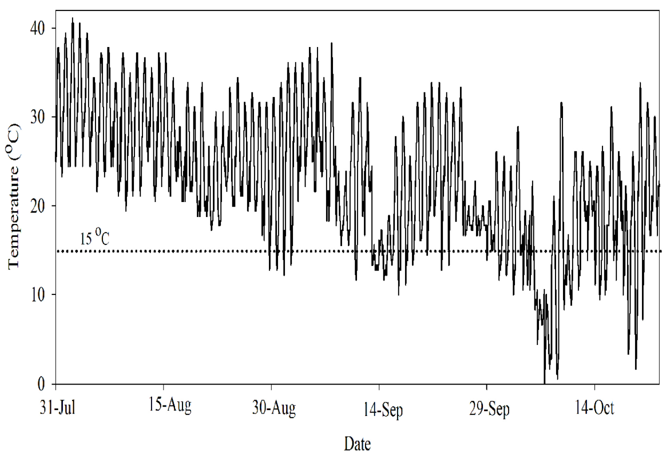

Fig 7. Plot of air temperatures at 5-min intervals during the experimental period in Lubbock, TX, USA during the 2012 growing season.

of a castor fruit. A raceme directly exposed to sunlight will probably be warmer than a raceme shaded inside the canopy. Similarly, one side of the fruit can also be exposed to the light while the opposite side is shaded. Such uneven heat distribution could potentially cause a difference in the growth rate among seeds in the same fruit or in opposite sides of the same raceme. In this experiment, it was observed that there was considerable difference in the weight of seeds in the same fruit. It was hypothesised that the uneven heat distribution was responsible for the differential growth. Additional characteristics that can impact the fruit's heat budget are the pigmentation and cuticle wax properties related to radiation absorbance (Richardson et al., 2003; González et al., 2012), the density of spines covering the fruit, the thickness and heat conductivity of the fruit shell, and the heat generated by the seed metabolism.

The importance of temperature and base temperature for the determination of yield

Castor breeding should take advantage of the variability of T_b found in many cultivated species. For instance, tropical varieties of rice were sensitive to low temperatures while temperate varieties were more sensitive to high temperatures (Yoshida and Hara, 1977). There are limited reports on the effect of temperature on seed filling and its impact on selection of plants being considered in castor breeding programs. However, castor seed yield can be positively impacted by selecting varieties with reduced T_b for seed filling or increased SGR under chilling temperatures. In this experiment, the T_b was determined for the combination of Phases I and II. However, it is possible that those two phases have different T_b's because they are distinct physiological processes. The initial phase consists of cell division and expansion, while the following phase consists in the metabolism of assimilates and nutrients into storage compounds. A better understanding of the effect of temperature on each phase is essential for a deeper knowledge on the development of castor seed and ultimately seed yield.

Materials and methods

Plant material and field conditions

This study was conducted in 2012 at the Experimental Farm of Texas Tech University in Lubbock, TX, USA (33°36' N; 101°54'W, 990 m of elevation). The plant material was castor cv. Brigham, which was the first commercial variety with reduced ricin content (Auld et al., 2001). The field was planted 12 June 2012 at a spacing of 0.9 m between rows and 0.75 m between plants. Irrigation was applied with a subsurface drip irrigation system with tapes buried 30 cm below the soil surface. Irrigation was applied at a rate of 5 mm day^{-1} from planting until 9 September 2012. After irrigation was withheld, precipitation totaled 69 mm, which was considered enough to sustain a regular seed growth. The soil had a pH of 8.6, 11 g kg^{-1} of organic matter, 45 mg kg^{-1} of P, and 520 mg kg^{-1} of K. Nitrogen was applied through irrigation water at the rate of 67 kg ha^{-1} 30 days after planting (DAP). Weeds were controlled by hand, and no disease or pest requiring control was observed. A row with 20 plants was randomly selected in a large field planted for seed production. Racemes were randomly tagged at intervals of approximately 10 days beginning at 49 DAP (31 July 2012) and ending at 83 DAP (3 September 2012). Racemes were tagged when they had three quarters of the female flowers recently open (visual analysis). Two fruits were harvested in each tagged raceme at 5-days intervals until the fruits turned brown. Immediately after harvest, the fruits were packed in plastic bags, and kept under refrigeration. Later, the seeds were manually extracted, weighed, oven dried at 80 °C for 24 h, and weighed again. Seed moisture content was calculated based on fresh and dry weights. Data on tagging and harvesting dates, fresh and dry weights, and moisture content was recorded for each individual seed.

Measured and calculated seed characteristics

The seed water content was used to track the progress of seed growth toward maturity (Severino and Auld, 2013a). The Relative Seed Weight (RSW) was calculated as a normalization procedure to avoid the variability in the mean seed weight among plants. Calculations were made using the software Sigma Plot. The Logistic Model was chosen for this study because it fits the slow seed growth during Phase I, the quasi-linear growth during Phase II, and no growth during Phase III. A Logistic Equation was assumed as

{ $y=a/(1+\left(\frac{x}{x_0}\right)^b)$ }, in which y is the seed dry weight (mg), x is the seed water content (g kg^{-1}), and a, b, and x_0 are the regression coefficients. Using this equation, the maximum seed weight of each plant was estimated as the seed dry weight when the seed water content was 100 g kg^{-1}. Then, the relative seed weight was calculated as *RSW = Seed Dry Weight / Maximum Seed Weight*. The RSW varied from 0.006 to 1.357. The RSW of mature seeds varied across a wide range, but the average was equal to one because by definition the MSW was equal to the Seed Dry Weight when the seed was at physiological maturity.

Rejection of aborted and underdeveloped seeds

Seeds that were considered aborted were eliminated to reduce variability. According to Severino and Auld (2013c), castor seed aborts only during Phase I of seed development and before the seed accumulates 40% of the MSW. In order to identify aborted seeds, the values of RSW of each plant were plotted against the seed water content, and a Logistic Equation was estimated. Seeds were considered to have been aborted when three conditions were met (Fig. 5): 1) the water content was smaller than 800 g kg^{-1} (i.e., the seed was not in Phase I), ii) the observed RSW was smaller than 0.60 of the predicted RSW (i.e., the seed was not growing as expected), and iii) the RSW was smaller than 0.4 (i.e., the seed was not heavier than the threshold for abortion). After the data on aborted seeds were discarded, a new Logistic Equation was calculated, and the same analysis was repeated until no aborted seed was found. Because castor racemes initiate female flowers during an extended period, some fruits can begin growing considerably ahead or behind the majority of fruits in the same raceme (Vallejos et al., 2011; Severino and Auld, 2013a). In order to reduce the error associated with this early and late growing seeds, the water content of seeds in each raceme was plotted against the number of days after tagging the raceme, a Logistic Equation was calculated, and the seeds falling out of the range ± 15% of the estimated value of water content were also discarded (Fig. 6).

Acquisition of data on temperature and calculations on degree-days and base temperature

Temperature was assumed to be the only factor controlling seed growth rate for this study. As previously discussed, if the mother-plant is not severely stressed, the seed growth rate is not influenced by factors such as current photosynthesis, respiration rate, plant nutrition status, and soil water availability (Egli, 1998; Munier-Jolain and Ney, 1998). Data on air temperature was collected at 5-min intervals beginning on the date of tagging the first raceme until the last fruit was harvested. The air temperature was measured at a height of 1.8 m using an automated meteorological station located 500 m from the experimental field. Between 31 July 2012 and 22 October 2012, the temperature varied between -0.6 and 41.1 ˚C (Fig. 7). The mean temperature was 27.3 ˚C in August and 22.5 ˚C in September. A cold period occurred from 5 to 8 October 2012 with a mean temperature of 9.3 ˚C, but the temperature increased to an average of 19.1 ˚C from 9 October to 22 October 2012 (Fig. 7). The accumulated degree-days were calculated considering the interval from tagging to harvesting the seed. For each seed, sets of accumulated degree-days were calculated, considering T_b's varying from 0 to 25 ˚C with 1 ˚C increments. The accumulated degree-days was calculated considering all the 5-min periods in which the temperature was above the T_b. The formula was $DD=\sum_{t}^{h}(T-T_b)/288$, in which DD is the accumulated degree-days, t and h are the time of tagging and harvesting the raceme, T is the air temperature, T_b is the base temperature, and 288 is the number of 5-min intervals in a day. For comparison of accuracy, the degree-days was also calculated using the daily mean temperature ($T_m=\sum T/288$), and the average of the daily maximum and minimum temperatures (called mean amplitude). For determination of the T_b, the method of the least standard deviation (Durand et al., 1982; Yang et al., 1995) was used with some adaptation for its use in the analysis of seed growth. Physiologically mature seeds (i.e., when the seed water content was smaller than 220 g kg^{-1}) were not included because the effect of temperature on the desiccation is different of its effect on enzyme-based processes occurring in Phases I and II. Thus, the analysis to determine the T_b was made with the data from 563 seeds. The data on seed water content were plotted against the accumulated degree-days calculated for each T_b, a Logistic Equation was calculated, and the R^2 of the regression analysis was used as the measurement of the fitness. The highest R^2 among T_b's was chosen as the one that explained with the minimum error the progress of seed growth using the linear degree-days approach.

Calculations on seed growth rate

In order to investigate the influence of air temperature on the Seed Growth Rate (SGR), the data on RSW of the racemes tagged on 31 July, 10 August, 20 August, and 30 August were plotted against the chronological time (days), and Logistic Equations were calculated for each of them. The SGR was calculated using the time that the seed needed to grow from 0.3 to 0.7 of its RSW (i.e., the core of the phase of linear growth). This interval was estimated using the Logistic Equation of RSW plotted against the harvesting date. The mean seed weight of all the mature seeds in this study was found to be 285 mg. The calculation was made with the equation SGR = 114 mg / ($t_{0.7} - t_{0.3}$), in which $t_{0.7}$ and $t_{0.3}$ are the time in which the RSW was respectively 0.7 and 0.3, and 114 mg is the increment in the seed dry weight in that period ((0.7-0.3) x 285 mg = 114 mg).

Conclusions

Castor seed growth rate was highly influenced by air temperature. Growth rates were higher in the racemes that grew during the warmer periods and were consistently reduced following the decrease in air temperatures at the end of the growing season. The base temperature for castor seed growth was found to be 15 ˚C, and a castor seed required 464 degree-days after pollination to reach physiological maturity.

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