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Patterns of Intrafruit Seed Abortion and Variation in Seed Mass of the Guanacaste Tree (*Enterolobium cyclocarpum*, Fabaceae) in Populations From Mexico and Costa Rica

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ABSTRACT

Analyses of the variation in the abortion rate and mass of seeds of tropical trees are scarce, despite their importance in modulating seed production, plant recruitment, and herbivore foraging patterns. We studied these reproductive processes in a tropical dry forest tree species. We studied the patterns of intrafruit abortion and seed mass in fruits of the Guanacaste tree, *Enterolobium cyclocarpum*, in samples of trees from 5 populations in Mexico and Costa Rica. We analyzed the effects of developmental phase, fruit and maternal tree effects, and seed position within the fruit on the abortion rate and mass of seeds from mature and immature fruits. Naturally pollinated flowers were studied to determine the patterns of ovule fertilization within the ovaries. Overdispersion of the abortion rate per fruit within trees and a higher frequency of abortions in the extreme positions of the fruit were common patterns in all populations. These patterns were observed from the beginning of fruit formation. Ovules in the stylar position do not have higher survival rates, despite their precedence in fertilization. A negative relationship was found between abortion events and seed mass. Fruit-specific fertilization and developmental conditions seem to be the main factors driving the fruit abortion rate and seed mass, causing high variability in seed survival and mass within maternal trees. The correlation between the fruit abortion rate and seed mass may be related to the capacity of the fruit to drain maternal resources. These patterns are common to all studied Guanacaste tree populations.

1 | Introduction

Fruit and seed inputs in ecosystems are crucial for the maintenance of plant populations and the availability of resources for herbivores, especially seed and fruit eaters. The number and size of seeds affect seed dispersal and seedling recruitment, as well as the patterns of foraging of fruits and seeds by herbivores (Janzen 1971, 1982; Dylewski et al. 2020). Abortion of seeds is one of the most important mechanisms regulating the production of seeds in plants (Stephenson 1981).

The loss of potential seeds has multiple causes, including failure of fertilization, the expression of genetic load, and/or predation and parasitism by natural enemies. However, these factors fail to explain all potential progeny loss in plants. Selective abortion by maternal plants is a well-recognized mechanism for the

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early abscission of flowers and fruits, and the failure of immature seeds to mature (Stephenson 1981). To explain abortion patterns in plants, it has been proposed that abortion evolves (i) as an adaptive trait to respond to oscillations in pollination levels and maternal resources for different reproductive events, (ii) as a mechanism to allow maternal selection of the quality of the progeny, or (iii) as a result of the maternal-progeny conflict and sibling competition among developing seeds (Stephenson 1981; Lee 1988; Shaanker, Ganeshaiah, and Bawa 1988). Experimental manipulations of maternal resources, as well as the quantity and genetic diversity of pollen loads, have shown that both the variation in maternal resources and the quantity and quality of pollen tubes affect the rate of seed abortion (Stephenson 1981; Lee 1988; Shaanker, Ganeshaiah, and Bawa 1988; Rocha and Stephenson 1991a; Quesada, Winsor, and Stephenson 1996; Shen et al. 2018; Cardel and Koptur 2022).

After or parallel to the abortion of flowers and immature fruits, the abortion of seeds within fruits further reduces the number of progeny produced by plants. The regulation of this phase of abortion and the consequent filling of the surviving seeds have been explained by the same mechanisms and evolutionary explanations proposed for the abortion of whole flowers or fruits (Lee 1988). In species where the mature fruit is the unit of seed dispersal, a reduction in the number of seeds can favor the dispersal of fruits, particularly in species dispersed by wind (Bawa and Webb 1984; Ganeshaiah and Shaanker 1988) but also in those dispersed by animals (Shaanker, Ganeshaiah, and Bawa 1988). Furthermore, nonrandom abortion of seeds based on the ovule position within the ovary is a common process in many plant species, especially in families that produce fruits with a linear sequence of ovules, such as Fabaceae. In this plant group, position effects on the probability of seed maturation have been related to factors such as pollination precedence or gradients in the access of developing seeds to maternal resources within fruits (Nakamura 1988; Rocha and Stephenson 1991a; Akhalkatsi, Pfauth, and Calvin 1999; Mena-Alí and Rocha 2005; Susko 2006; Arathi 2011).

The number of seeds within fruits, and the fruit mass per seed, can affect the fruit abortion rate and the fruit mean seed mass, as they influence the intensity of the competition for maternal resources (Nakamura 1988; Shaanker, Ganeshaiah, and Bawa 1988). These variables (abortion and seed mass) are physiologically related since seed growth is mediated by the production of phytohormones and growth inhibitors by the seeds, as well as by the translocation of maternal resources (Lee 1988; Stephenson 1981; Shen et al. 2018).

The study of patterns of seed abortion and variation in seed mass within and among individuals can reveal factors that influence the regulation of abortion and seed growth processes (Shaanker, Ganeshaiah, and Bawa 1988). This analysis is particularly useful in tropical trees, where the size of the individuals and their slow growth prevent experimental manipulations. Little studied in this context is the geographic variation within a species in terms of abortion rate and seed mass and the repeatability of abortion patterns and mass distribution in different populations of a species. As different populations within the geographic range of a species may experience different pollination conditions, resource availability (Quesada et al. 2004; Pérez-Barrales, Arroyo, and Armbruster 2007), seed dispersal strategies, or germination conditions (Tamura and Hayashi 2008; Snell et al. 2019), abortion patterns and seed size could be expected to vary within species (Kärkkäinen, Koski, and Savolainen 1996; García et al. 2000). In contrast, stabilizing selection and the absence of variation in environmental conditions that affect seed development would promote the same abortion and seed-filling patterns among populations.

The Guanacaste tree (*Enterolobium cyclocarpum* (Jacq.) Griseb) presents an interesting case for the study of seed abortion and seed development. It is a large Neotropical dry forest species that has a fruit development strategy defined by Frankie, Baker, and Opler (1974) as a "dry season fruiter," where pollination occurs at the end of the dry season or the beginning of the moist season, but the ovaries develop into very small immature fruits that stop ripening until the beginning of the next dry season, when they rapidly expand into large pods shortly before the new flowering. Thus, the abortion and seed-filling processes can occur progressively in different phases of the slow development of fruits or be concentrated only in the final phase of exponential growth before dispersal. Janzen (1982) presented the general aspects of reproduction and variation in the abortion rate and seed mass of this species, relating this variation to different strategies of seed dispersal by large extinct or extant vertebrates. However, his observations were restricted to the mature fruits phase of a single tree.

In this study, we incorporate observations of seed production and seed mass in fruits from various populations in Mexico and Costa Rica to study the patterns of intrafruit seed abortion and seed mass in this species. The position of pollen tubes at their entrance to the ovaries was studied to verify the precedence of the fertilization of ovules at different positions from the style. In addition, to understand the dynamics of ovule/embryo abortions within fruits during their development, a comparison was also made of the contents of fruit during their annual development cycle in one of the studied populations. In mature fruits, we tested the following hypotheses: (i) seed loss rates (including abortion) and seed mass have an overdispersed distribution (higher variance than expected by chance) among fruits within trees as a result of differences between fruits in terms of the quality of pollen load or availability of maternal resources; (ii) low seed number in the fruit (due in part to a higher abortion rate) increases the mass of the remaining seeds due to fewer seeds competing for maternal resources; and (iii) the position of the developing ovule can increase the probability of seed abortion and decrease seed mass if it is in an extreme position within the fruit (basal or stylar) due to poor access to limited maternal resources or delayed fertilization. A comparison of the patterns between populations allowed us to verify the generality of the effects studied.

2 | Materials and Methods

2.1 | Study Species

Enterolobium cyclocarpum (Jacq.) Griseb. (Mimosoideae: Fabaceae) is a tree species that grows in deciduous dry forests of low regions of Mexico and Central America, reaching the center of Brazil (https://www.gbif.org/species/2961150). It has white, tubular, hermaphrodite flowers organized in spherical-headed inflorescences, which open at dusk and wither the next morning. Flowering occurs in the dry season during the months of February and March in the studied locations. Its pollination is attributed to moths and nocturnal butterflies (Janzen 1982). However, in one of the populations under study (El Rodeo, ROD), the only floral visitors observed were bees (*Apis mellifera*), which visited the flowers at dawn. Pollen is dispersed as polyads contain 32 pollen grains (monads), enough to fertilize the ovules of an individual flower (6–22 ovules per flower, see the Results section). Typically, only one fruit develops per inflorescence. The immature tiny fruits stop growing at the onset of the rainy season (May in the Costa Rican sites), remaining 4–8 mm in size during the rest of the rainy season and the onset of the next dry season; then, they rapidly expand to their normal size during the middle and end of the dry season (March–April in Costa Rican sites) before the next flowering season. Approximately the same annual cycle occurs in Mexican localities.

Ripe fruits are dry, brown, indehiscent, ear-shaped, and 4–12 cm long and have a variable number of seeds (2–22) (Janzen 1982). The ovary is divided into locules separated by partial septa, which are flexible in mature fruits. Each locule contains one ovule. When the ovule aborts, the corresponding locule is empty or contains a very small and deformed seed. The walls of the fruit become weaker with the first rains, allowing the seeds to germinate as the seed cover is gradually degraded. The fruits can also be ingested by large herbivores, or the seeds can be predated upon by small rodents. Past and present seed dispersal has been attributed mainly to the consumption of fruits and the defecation of seeds by large herbivores, extant or extinct (Janzen 1982). A very important factor in the mortality of flowers and fruits is gall formation attributed to the fly *Hemiasphondylia enterolobii* of the Cecidomyiidae family, which remains within a small gall during the entire dormant phase of the fruits until hatching simultaneously with the ripening of the fruits (Janzen 1982). The galls are abundant, many times more abundant than the fruits, and there may be trees where almost all the flowers develop into galls rather than mature fruits. The predation of green fruits by parrots (*Amazona ochrocephala*) is also an important factor in fruit loss (Janzen 1982).

Genetic analyses using isozymes have shown that, in a population from the province of Guanacaste, Costa Rica, each fruit is fertilized by a single pollen donor, and a high number of pollen donors fertilize the ovules of each maternal tree (Apsit, Hamrick, and Nason 2001). The same type of genetic marker has shown that outcrossing is predominant in this tree species, although with low levels of selfing in some reproductive years and populations (Rocha and Aguilar 2001).

2.2 | Sampled Populations

Five populations were sampled: three in Mexico (San Lucas (SL), Chamela-Cuixmala (CEC) and Veracruz (VER)) and two in Costa Rica, Central America (El Rodeo (ROD) and Santa Rosa (SR)). While the Mexican populations SL, CEC, and SR from Costa Rica occur in habitats classified as dry deciduous forest, with a strong and defined dry season, the VER and RO populations occur in areas with a more humid and less seasonal climate. Table 1 summarizes the main characteristics of each locality studied and the sample sizes obtained at each site.

2.3 | Collection of Ripe Fruits

To study the variation in the abortion rate, mass of seeds within and among fruits, trees, and populations, we collected fruits from the ground under tree canopies during the fruiting season (February–May) in 2021 at the mentioned locations. An average of 10 trees was sampled at each location, with 10–14 fruits collected per tree. The fruits were taken to the laboratory, where they were opened, the seeds were individually weighed, and their positions within the fruit were recorded. The positions of the aborted and mature seeds were noted. An abortion event was recorded when the locule was empty or contained a small, deformed seed (wrinkled at the edges and very flat); most aborted seeds weighed less than 0.2 g, although some slightly heavier seeds were classified as abortions due to their shape (see Results). Normally filled seeds and abortion events were classified by their position in the fruit into three categories: stylar position (closest to the style position), basal (closest to the flower pedicel) or intermediate (any position between these two extreme positions). The total number of locules (empty and with abortions) and the total number of filled seeds per fruit were counted. Mature seeds were weighed to the nearest 0.001 g.

In the population of Santa Rosa, a comparison was also made between the mass of the mature fruit and the mass of the individual seeds of the fruit to verify the positive correlation between the fruit/seed mass ratio and seed mass proposed by Janzen (1982). After collecting ripe fruits in 2021, we weighed the dry fruits once the seeds had been extracted from a subsample of 104 fruits.

2.4 | Germination Tests

Some small seeds had a shape and mass close to those of the aborted seeds. For this reason, we performed a seed germination test to sample all the observed mass variation and to test small seeds of different shapes (deformed and normally oval). In this way, while the minimum germination mass was verified, the germination capacity of deformed seeds with a mass close to 0.2 g could be verified. Three hundred aborted and filled seeds from the Santa Rosa population, ranging in mass from 0.15 to 1.2 g, were germinated in a greenhouse on a ground coconut fiber substrate and moistened every two days. Germination (complete opening of the cotyledons and radicle growth up to 5 mm in the substrate) was recorded up to 2 months after sowing.

2.5 | Collection of Immature Fruits

A more detailed study of the evolution of the number of locules and the abortion rate during their annual development was carried out for the Santa Rosa population. To this end, during the flowering period (March–April) of the trees in the study population, we collected flowers six hours after nocturnal anthesis to verify the number of ovules per ovary. The flowers were fixed in 70% alcohol, treated with 1 M NaOH, and colored with aniline

TABLE 1 | Populations of *E. cyclocarpum* sampled in the present study.

Country/locality/State or province	Coordinates	Average annual rainfall/number of dry months	Average annual temperature	Land use	Sample size (number of trees/fruits/seeds)
Mexico					
San Lucas (SL) Michoacán	18º 35' N 100º 46' W	900 mm (6 months, Dec-May)	27.5°C	Trees in cattling areas	10/81/1048
Chamela-Cuixmala (CEC), Jalisco	19º 32' N 105º 02' W	700 mm (6 months, Dec-May)	25.0°C	Protected area, mostly large old forest remnants	10/98/1193
Veracruz (VER)	19º 30' N 96º 22' W	1300 mm, (5 months, Dec-Apr)	24.0°C	Forest fragment (50 ha) surrounded by mangrove and pastures	10/98/1217
Costa Rica					
El Rodeo (ROD), San José	9º 54' N 84º 14' W	1950 mm, (4 months, Jan-Mar)	22.0°C	Trees in coffee plantations, near a forest reserve (~ 800 ha)	9/78/874
Santa Rosa (SR), Guanacaste	10º 50' N 85º 37' W	1500 mm (6 months, late Dec to late May)	28.0°C	Protected area, mostly secondary forest in regeneration with old forest remnants	11/112/1404
Total					50/467/5736

blue to observe longitudinal sections of the ovaries with epifluorescence (Martin 1959). The ovules can be easily observed with this technique due to the presence of highly fluorescent polysaccharides. To study the growth of pollen tubes during different time periods, we observed pollen tubes in styles and ovaries fixed at 12 and 24 h after collection. We observed the ovules and pollen tubes of 100 flowers from 3 trees, but only a fraction of the preparations were flowers that produced clear longitudinal images of pollen tubes growing inside the ovary (Figure 1). One month after flowering (June 2022), we collected small green immature fruits directly from the branches with extension pruners. Nine months after flowering (December 2022), we collected a new set of immature fruits. In each collection, 100 fruits were obtained from 5 different maternal trees, from which ripe fruits were also obtained. The small immature fruits were sectioned longitudinally with a razor to count the number of aborted seeds, the positions of the aborted seeds, and the number of seeds and locules within the fruit. Aborted seeds in immature fruits were detected by their smaller appearance and characteristic brownish color (Figure 1). Developing galls were also obtained from the same branches from which immature fruits were collected (Figure 1).

2.6 | Data Analysis

To study the distribution of the number of seeds lost by fruit, the logit of the probability of a seed abortion was analyzed with a generalized linear mixed model (Bolker et al. 2009) with a binomial distribution of seed abortion, where the fixed effects were the number of locules of the fruit and the position of the locule within the fruit. Fruit (nested in tree), tree (nested in population) and population were considered random effects. The number of locules of the fruit was used as an approximation of the initial number of ovules or immature seeds developing in fruits in each developmental phase, representing a variable that measures the strength of intrafruit competition between embryos.

To study the effects of the fruit abortion rate, fruit size (number of seeds), and position within the fruit on seed mass, we analyzed the mass of individual seeds with a mixed linear model (Bolker et al. 2009) with a normal distribution of seed mass, with fixed effects being the number of filled seeds, the number of abortions in the fruit, and the position of the seed within the fruit. Fruit, tree, and population were included as random effects.

In both analyses (abortion rate and seed mass), the use of random effects (fruit, tree, and population) allowed us to estimate the degree of intraindividual and intrapopulation variation in the two variables studied. In addition, this analysis strategy allows for the study of the abortion rate and mass at the individual seed level, avoiding the use of average statistics per fruit, which would lead to the loss of information on the variation within fruits. Random effects allow the correction of correlated measurements, such as those that occur between individual

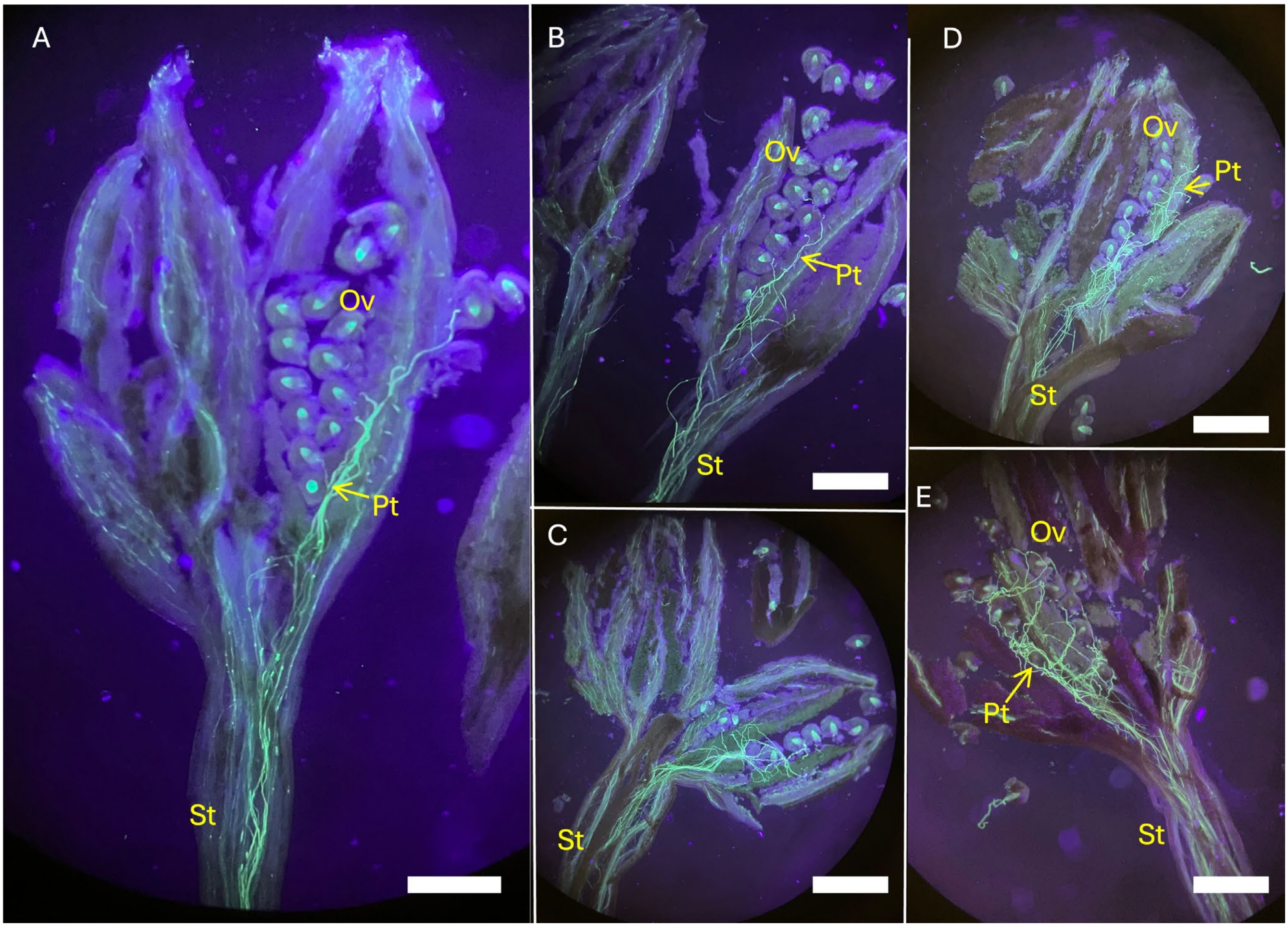

FIGURE 1 | Epifluorescence images of ovaries of naturally pollinated *E. cyclocarpum* flowers stained with aniline blue. The flowers were fixed for 12 h (A–C) or 24 h (D–E) after collection. White bars are the scale (0.5 mm). Pt: Pollen tubes, Ov: Ovaries, St: Styles.

measurements of seeds or locules of the same fruit, tree, or locality (Bolker et al. 2009).

To test the significance of each parameter, we use the Akaike information criterion (AIC) to select the best statistical model (Richards 2005; Burnham and Anderson 2007). The parameters included in the model with the minimum AIC were considered significant (Bolker et al. 2009). We applied this procedure to the analysis of each population of the whole sample and the samples of immature fruits. These analyses were performed using the commands glmer (for seed loss rate) or lmer (for seed mass) within the lme4 package in R (De Boeck et al. 2011; Bates et al. 2015).

To analyze the effects of fruit mass on individual seed mass, fruit mass was added as an additional fixed effect to a subset of the data from Santa Rosa (97 fruits, 1029 seeds), and the same modeling procedure described above was used. The relationship between the seed number and the proportion of fruit mass/seed was examined through their respective coefficients in the model.

To calculate the germination rate, we divided the seeds into six categories based on mass (0.2–0.39, 0.4–0.59, 0.6–0.79, 0.8–0.99, 1–1.19 and 1.2–1.4 g). The germination rate was calculated for each category to determine the minimum mass of the seeds that could germinate.

3 | Results

3.1 | Pollen Tubes in the Ovary

Only 40% of the collected flowers had numerous pollen tubes growing along the style and ovary. In these samples, fifteen 12-h preparations and twelve 24-h preparations resulted in longitudinal images of the ovary that clearly showed the position of the pollen tubes. Figure 1 (A–C) shows the growth pattern of pollen tubes in 12-h fixed ovaries, while Figure 1 (D–E) shows examples of 24-h fixed flowers. At 12 h, it is possible to see how the stylar (distal) ovules of flowers are fertilized first. Later (24 h), a mesh of pollen tubes is formed enveloping all the ovules.

3.2 | Fruit and Gall Growth

The immature fruits collected in April (1 month after flowering) had an average size of 4.1 mm, while the immature fruits collected in December (9 months of development) had grown to an average of 8.8 mm (Figure 2B). Both in the postflowering phase

FIGURE 2 | Time course of fruit development and abortion in *E. cyclocarpum*. A. Development of galls produced by the fly *Hemiasphondylia enterolobii* (Cecidomyiidae) after 1 month (left) and 9 months (right) of development. B. Immature fruits at 1 month (left) and 9 months (right) of development. C. Immature fruit at 1 month of development, showing several seeds in the process of abortion (solid arrows) and viable seeds (dashed arrows). D. Immature fruit at 9 months of development, showing a case where almost all the seeds are viable (dashed arrows). E. Two examples of mature fruits, one with 11 locules and all seeds aborted (left, three cases of abortion indicated by white arrows) and another large fruit with 16 locules with all viable seeds (right). The scale of A and B is in mm, the thick lines in C and D indicate 2 mm, and the scale in E is shown in cm.

and after 9 months, smaller brown seeds that were most likely abortions were observed within the fruits (Figure 2C), while the viable seeds in the development phase were white and larger (Figure 2D). In the populations of El Rodeo and Santa Rosa, the incidence of galls produced by the cecidomyiid fly was very high. In some trees, the number of galls seems to be greater than the number of developing immature fruits in the tree, indicating the importance of cecidomyiid attack in fruit production in these populations. However, these galls were not observed in any of the Mexican populations. Galls appeared from the first month of fruit development and grew from an average of 2.5 mm in diameter in the first month to an average of 4.04 mm in diameter in the ninth month (Figure 2A). Both structures, fruits and galls, doubled in size after 9 months.

In the interval between January and March–April (i.e., the fruit ripening period), the immature fruits grow very quickly until they develop into a pod with a typical ear shape that can measure up to 12 cm long by 10 cm wide for fruits with many filled seeds. However, small mature fruits with many aborted seeds are also possible, with a minimum size of 7 cm long by 5 cm wide (Figure 1E).

3.3 | Germination Rate and Seed Mass

Germination tests of seeds collected from fruits of the Guanacaste population showed that seeds weighing less than 0.2 g did not germinate, seeds with mass ranging from 0.2 to 0.4 g had a 25% germination rate, seeds with mass between 0.4 and 0.8 g had a 44% germination rate, and seeds with mass greater than 0.8 g had a germination rate of 60%, with maximum values of 83% in the heaviest seeds (1–1.2 g). The smallest seeds that germinated had an oval and filled shape, which confirms that both seed mass and seed shape should be considered when classifying the smallest seeds as abortions. Taking these data into

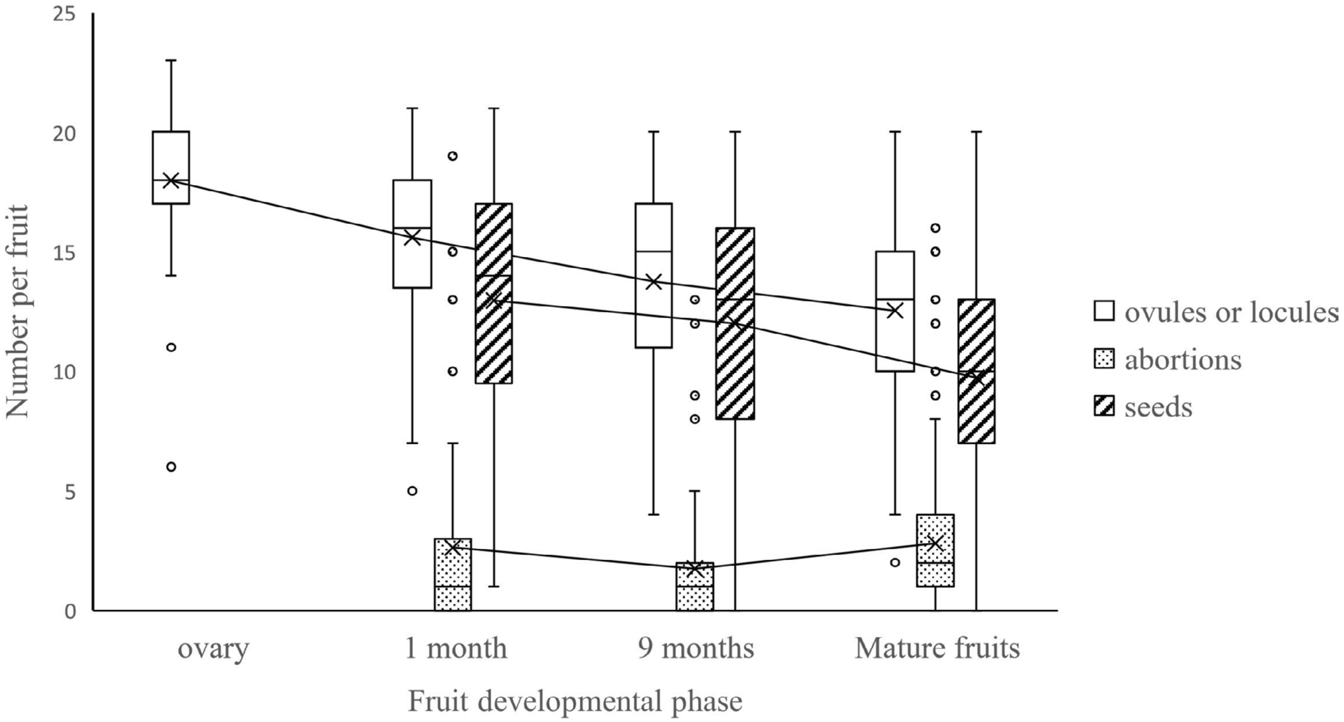

FIGURE 3 | Boxplots of the numbers of ovules, locules, seeds, and abortions for each stage of development (ovaries, immature fruits and mature fruits) in a population of *E. cyclocarpum* in Santa Rosa, Guanacaste, Costa Rica. The lines intersect the averages of each phase of development. The boxes cover the interquartile range (IQR), the lines extend to 1.5 IQRs above and below the 1st or 3rd quartiles, respectively, and the points are outliers.

consideration, the criteria for categorizing abortions within mature fruits were their mass ≤ (0.2 g) and shape (thin, flattened or deformed).

3.4 | Abortion Rate During Fruit Ripening

Since the first month and throughout fruit development, the abortion of ovules, embryos, and immature seeds, as well as a reduction in the number of locules, occurred progressively within the fruits of *E. cyclocarpum* in the Santa Rosa population (Figure 3). Ovaries began with an average of 18 ovules (IQR, interquartile range = 17–20). Mature fruits had an average of 12.5 locules per fruit (IQR = 10–15) and an average of 10 filled seeds per fruit (IQR = 12.5–7.5). We observed that in one-month-old fruits, 15% of the immature seeds were aborted, 12.8% were aborted in eight-month-old fruits, and 21.9% were aborted in immature fruits just prior to fruit maturation. Therefore, the final number of seeds in mature fruits depends both on the initial number of ovules in the ovary and the intensity of the abortion that occurs progressively during the long developmental process.

The progressive reduction in the number of locules in fruits may be a result of the fusion of the empty locules with nearby ones. In this way, the empty spaces in the fruit, left by early abortion events, are later occupied by neighboring seeds or by fruit tissue. Outlier values in the number of abortions per fruit, that is, fruits with several abortions that exceeded the whisker value (1.5 IQR below the first quartile or above the third quartile), were observed at 1 month, at 9 months, and especially during the ripe fruit phase (Figure 3). Many of these cases involve fruits with all or almost all seeds aborted.

The analysis of the probability of abortion during fruit development (Appendix S1; see Supplemental Data with this article) showed that the number of abortions does not follow a simple binomial distribution among fruits in all phases of development; rather, the effect of the random components, especially the fruit component, is required to fit the data to the model. The tree component was significant only in mature fruits. The number of locules of the fruit, immature or mature, does not affect the rate of seed loss. Both extreme positions in the fruit (stylar and basal) increased the probability of seed loss, and this effect was stronger in immature fruits than in mature fruits (Appendix S1, Figure 4).

3.5 | Seed Abortion in Mature Fruits

Figure 5 shows the distribution of the number of locules per fruit, the number of abortions, and the number of seeds per fruit per population. The maximum number of locules per fruit was 20, while the maximum number of filled seeds per fruit ranged from 16 to 20, depending on the population. There is greater variation in the number of viable seeds per fruit than in the number of locules per fruit, which is an effect of the variation in the seed abortion rate per fruit. Abortion was lower in the CEC population (0.103), intermediate in the ROD, SL, and SR populations (0.228, 0.201 and 0.216, respectively) and highest in the VER population (0.519). In all populations except Veracruz, an asymmetric distribution of the abortion rate per fruit was observed, with a median of approximately 0–2 abortions/fruit, but with several fruits showing an excess of abortions, with outlier-type values of 6 or more abortions per fruit. Most of the seeds aborted in these fruits. In the ROD and VER populations, fruits with abortions in all locules were observed at low frequencies (0.02–0.04). The abortion rate of the VER population did not have outliers but did have an average that was much greater than that of the other populations.

The variance components and fixed effects on the probability of seed loss from mature fruits in all populations (Appendix S2) showed the same patterns observed in immature fruits: a higher value of the fruit variance components than of the tree or population components. The variation due to the fruit effect was approximately 2–3 times greater than that produced by the tree effect. Overall, the effect of population was less than the effect of fruit or maternal trees within the population.

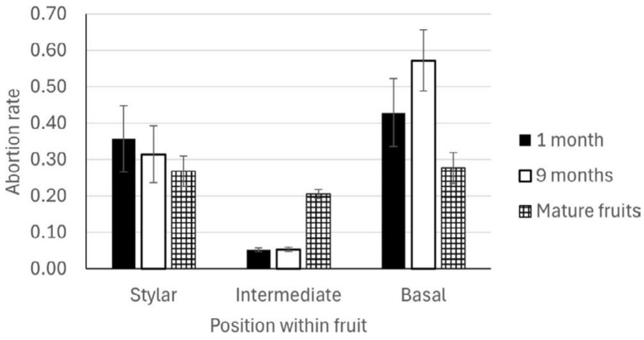

FIGURE 4 | Abortion rates observed in the SR population during fruit development. The rates are separated by the position of the abort in the fruit. Lines indicate standard errors of binomial proportions.

The effect of the number of locules on the abortion rate showed a negative trend of reduced magnitude for two populations (CEC and SL), while for the others, this effect was not included in the best model (Appendix S2). On the other hand, the effect of position within the fruit was significant in all populations, showing a similar trend: an increase in the probability of abortion in the two extreme positions. The average abortion rate of seeds in nonextreme positions of the fruit was 0.21, while the abortion rate in locules in the stylar position was 0.25 and that in locules in the basal position was 0.27.

3.6 | Variation in Seed Mass

The average mass of the viable seeds from all the samples was 0.842 g, with a standard deviation of 0.228 and a coefficient of variation of 0.27. The seed mass distribution reasonably fit a normal distribution (skewness = 0.174, kurtosis = 3.102). Except for a slight decrease in mass in the SR population, the averages and distributions of mass variation were very similar among populations, resulting in a nonsignificant population random effect (Appendix S3). For all the samples, the best random effects model, selected based on the AIC values, was the one that considered only the tree and fruit effects. Fruit and tree effects

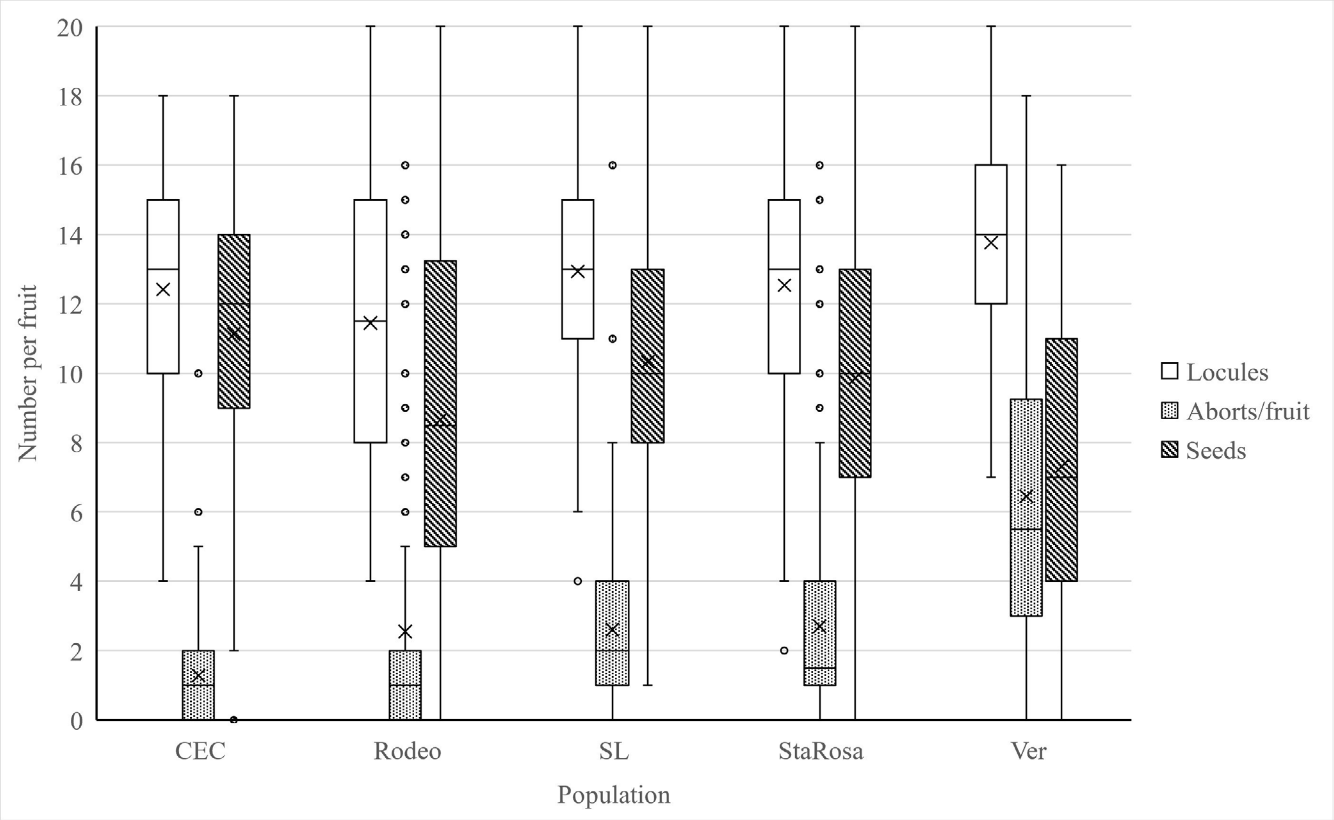

FIGURE 5 | Boxplots of the distribution of the number of locules, number of abortions, and number of full seeds per fruit in mature fruits of *E. cyclocarpum* in five populations of Mexico and Costa Rica.

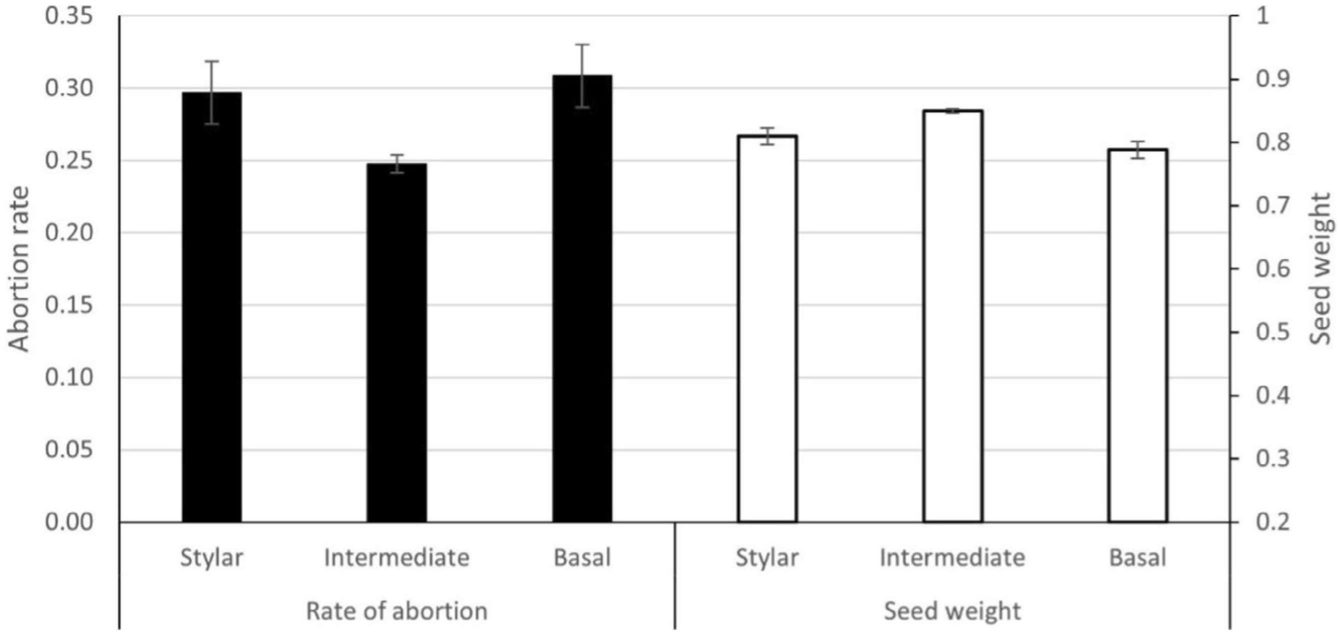

FIGURE 6 | Abortion rates and mean seed mass by position within the fruit in the whole sample of Guanacaste fruits.

were similar, a different result than that obtained for the seed abortion rate.

The number of seeds in the fruit had a slight effect (a decrease of 0.003–0.007 g per seed, which was not significant in the CEC, SL and VER populations), but the effect of the number of abortions in the fruit was negative and of greater magnitude (−0.012 to −0.044 g per abortion, in all populations, Appendix S3). The effect of style or basal position was significant in all populations, and it was the most important of all the variables (decreases of −0.050 and − 0.074 g, respectively, in the total sample). There was a tendency toward a greater effect of extreme positions in populations with higher abortion rates (VER, SR and ROD). The average mass of the seeds in the stylar position was 0.810 g (sd = 0.235), with 0.850 g (sd = 0.227) for the intermediate position and 0.788 g (sd = 0.232) for the basal position. Not only are embryos or seeds in the stylar or basal position more likely to be lost, but the final mass of the seeds in these positions that survive the abortion phase is also affected (Figure 6).

3.7 | Effect of Fruit Mass on Seed Mass

The mass of the mature dry fruits varied between 4.83 and 26.69 g, with an average of 14.00 g. The mass of the fruit increased with the number of locules and the number of filled seeds at approximately the same rate (b = 0.40 g/seed or locule). However, the fruit/seed mass ratio decreased with the number of filled seeds in the fruit (b = −0.030 g/seed). In fruits with 2–8 seeds, the fruit/seed mass ratio was 1.15 g/seed, while in fruits with 13–20 seeds, the ratio was 0.96 g/seed.

The analysis of the seed mass in the subsample of SR fruits shows that the number of seeds of the fruit has a slightly negative effect on seed mass (−0.003), and it was not included in the best model (Appendix S4). The abortion ratio of the fruit and position of the seed had significant negative effects on seed mass, with the same order of magnitude as the whole sample estimates (Appendix S4). The ratio of fruit mass/seed increased the seed mass (coefficient = 0.051). Seeds in heavy fruits with few seeds (1.19–2.19 g of fruit/seed) weighed on average 0.865 g, while seeds in light fruits with many seeds (0.36–0.90 g of fruit/seed) weighed on average 0.554 g. However, the ratio of fruit pericarp per seed is not the only factor influencing seed mass; it also depended on the seed abortion rate of the fruit. Fruits with few seeds but a high number of empty locules produced by a high abortion had lighter seeds than expected based only on the ratio of fruit mass/seed.

4 | Discussion

4.1 | Fruit Effect on Abortion Rate

We proposed that the distribution of abortion rates among fruits from the same maternal tree would depart from a binomial random distribution. As expected, an important random effect of fruit on the probability of abortion was observed in all the analyses. This effect produces an overdispersion of the number of abortions per fruit within trees, where fruits with all or almost all aborted seeds and those without abortions occur at frequencies higher than expected by a binomial random distribution of abortions per fruit. Factors inherent to pollination and the development of each fruit could generate this variation (Stephenson 1981; Casper 1984; Lee 1988; Shen et al. 2018), including the possibility of mechanisms that promote the contagion of abortions within fruits, such as a reduction in the ability to attract maternal resources that produce the first abortions (Stephenson 1981) or abortions of healthy seeds within fruits attacked by herbivores (Meyer et al. 2014). Variation in the quality of pollen loads between flowers can also be a factor that determines differences in the sink capacity of developing fruits. A greater diversity of pollen donors can increase seed number and reduce seed abortion (Kron and Husband 2006).

Variation in pollen quality between fruits is enhanced by the fact that Guanacaste trees receive pollen from many donors, and the ovules from each flower are pollinated by a polyad from a single donor (Apsit, Hamrick, and Nason 2001), as seems to be the mating pattern in other mimosoid trees (Lassen et al. 2014). Pollination with pollen from more distant trees may produce fruits with lower rates of abortion than fruits resulting from geitonogamy or crossing with more related nearby trees, as observed by Koptur (1984) in several species of *Inga*.

4.2 | Abortions During Fruit Growth

Observations of the immature fruits showed that seed abortions occurred during the first weeks of development and that these abortions were already overdispersed from that stage onward. This indicates that the dispersion of the abortion rate is triggered in the initial process of fruit development, during the initial growth of the embryos, when high cell division rates predominate (Marshall and Ludlam 1989; Duthion and Pigeaire 1991; Ney, Duthion, and Fontaine 1993). It is possible that these early abortions are unpollinated embryos or deaths due to genetic defects and inbreeding (by geitonogamy or biparental inbreeding). However, as shown by the continuous reduction in the number of locules and the increase in the number of abortions per fruit during development, abortions occurred successively until the final ripening of the fruit. The immature fruit could absorb some of the empty locules originating from previous abortions, and late abortions increased the overdispersion of their distribution in the final phase of ripening. These findings confirm that immature fruits are not in a state of absolute "dormancy" during the rainy season. Slow growth also occurred in the galls of the cecidomyiid fly, which showed a growth rate similar to that of immature fruits during this period.

4.3 | Effect of Progeny Number Within Fruits

Neither the number of locules in immature and mature fruits nor the number of filled seeds was included in the most parsimonious models of abortion rate and seed mass. A positive effect on the abortion rate and a negative effect on seed mass are expected if more progeny increases competition for resources (Harper, Lovell, and Moore 1970; Schaal 1980; Sadras 2007) or accentuate rivalry between sister seeds and the release of seed growth inhibitors (Shaanker, Ganeshaiah, and Bawa 1988; Krishnamurthy, Shaanker, and Ganeshaiah 1997). A negative correlation between the mass of the seeds and the number of seeds in a fruit has been observed in various studies (Wulff 1986; Ganeshaiah and Shaanker 1988; Akhalkatsi, Pfauth, and Calvin 1999; Chen et al. 2009; Cardel and Koptur 2022), but others have reported a positive correlation or no correlation (Schaal 1980; Hendrix and Sun 1989; Severino and Auld 2013). It seems that in the Guanacaste tree, the progeny number within a fruit interacts in a complex way with other fruit variables (such as fruit mass and the number of abortions) to determine the individual seed mass within the fruit. As shown in the analysis of fruit mass in the SR population, the number of filled seeds can have a slight negative effect on seed mass when this effect is estimated in conjunction with fruit mass. The analysis of the fruit mass/seed ratio also showed that fruits with a higher number of seeds have a lower cost of seed packaging for the mother tree, as the investment in fruit pericarp per seed decreases in these fruits. The increase in the sink capacity of fruits with respect to the number of seeds (Stephenson 1981; Lee 1988) or the increase in the fruit mass with respect to the number of seeds could compensate for the increase in the resources required in fruits with more ovules or seeds.

4.4 | Nonrandom Abortion Within Fruits

As expected, abortions and seed mass are not distributed randomly within the fruits of the Guanacaste tree. This pattern has been described in different species of Fabaceae (Janzen 1982; Bawa and Webb 1984; Nakamura 1988; Rocha and Stephenson 1991b; Mena-Alí and Rocha 2005). However, while in other Fabaceae species, the basal position is the one with the highest probability of abortion (Bawa and Webb 1984), in Guanacaste, as already observed by Villalobos and Bianchi (2000), this effect occurs in both terminal (stylar and basal) positions of the ovary. This pattern was also observed in *Pisum sativum* by Linck (1961) and in some varieties of *Phaseolus vulgaris* by Nakamura (1988). However, contrary to what is observed in other species, the higher abortion rate in terminal positions does not mean that aborted seeds concentrate mainly in these positions. The mean abortion rates in terminal and intermediate locules are approximately 30% and 25%, respectively.

In addition to the overdispersion of abortion rates among fruits, the slight increase in the probability of abortion in terminal positions is initiated from the first weeks of development. Differences in the timing of fertilization between ovules, or gradients in the distribution of maternal resources within fruits, have been suggested to explain the greater abortion rate in the basal positions of the fruit in Fabaceae (Lee 1988; Nakamura 1988; Mena-Alí and Rocha 2005). We observed that ovules in the stylar position became the first fertilized ovules, a pattern described in other Fabaceae (Hossaert and Valéro 1988; Rocha and Stephenson 1991b). However, this precedence in terms of fertilization order does not increase survival rates. Lee (1988) and Hossaert and Valéro (1988) stated that the abortion rate can increase in terminal positions, such as in the Guanacaste tree, if the fertilization order is favorable for ovules in stylar positions, but the proximity of maternal resources is favorable for ovules in basal positions. Intermediate seeds are not affected by low maternal resources or delayed fertilization. Another possible cause of more abortions in terminal positions of the fruit is "architectural effects" (Diggle 1995), that is, sources of variation inherent in plant axes. In this case, the locules located in extreme positions may have space limitations for the growth of seeds, causing early abortion or defective development.

4.5 | Abortion and Seed Mass Relationship

This study confirms that the positional effect of the seed on the fruit, described above for the abortion rate of seeds, is also present in the mass of the seeds. This may be because seeds in terminal positions, although they escape abortion, remain in unfavorable conditions that cause greater local abortion. If these conditions reduce the flow of resources for seed filling, these seeds compete at a disadvantage with seeds of the same fruit, creating similar positional effects on the abortion rate and seed mass. Although embryonic growth and seed filling occur at different times during development, a correlation between the probability of abortion and seed mass has been found in various experiments and in fruit samples from plants (Lee 1988; Nakamura 1988; Rocha and Stephenson 1991a; Susko 2006; Shen et al. 2018).

The relationship between the probability of abortion and seed mass also seems to manifest at the fruit level since we found a slight negative effect of the number of abortions in the fruit on seed mass. This trend contrasts with the proposal of Janzen (1982) that fruits that undergo more abortions have heavier seeds due to greater fruit/seed mass. Contrary to this proposal, negative factors at the fruit level that increase the probability of seed abortion can also affect the individual mass of the remaining filled seeds. Shen et al. (2018) proposed that mass and abortion are related to mechanisms that regulate the activity of invertases in the cell wall and the amount of sucrose in the seed. A smaller number of seeds can also reduce the sink capacity of the fruit due to the lower release of hormones that mobilize resources toward the developing fruits (Stephenson 1981).

We verified that the ratio of the mass of fruit tissue to seed mass is greater in fruits with fewer seeds, and a high ratio has a positive effect on seed mass, as proposed by Janzen (1982). Since the fruit is green until ripening, the flux of photosynthates from the fruit may be important during the seed-filling phase. However, this variable alone does not explain all the variation in seed mass between fruits. It is necessary to add negative effects originating from the same forces that promote abortion within fruits.

4.6 | Patterns of Variation in the Content of the Fruit Among and Within Populations

Mature Guanacaste fruit had a similar number of locules across the surveyed populations. The greatest interpopulation variation was observed in the abortion rate and, consequently, in the number of filled seeds per fruit. The variation in the number of seeds per fruit among populations seems to be primarily a function of the population abortion rate and secondarily of the variation in the number of ovules per fruit.

Natural variation in seed abortion rates among plant populations has been little studied. In commercial crops (Tischner et al. 2003) and in conifers (Kärkkäinen, Koski, and Savolainen 1996; García et al. 2000), variation in the abortion rate among populations has been associated with differences in the genetic load among populations. Pollen limitation has also been mentioned as a cause of high abortion rates in populations of endemic rare plants (Fernández et al. 2012). In our study, a high rate of seed abortion was observed in the population of Veracruz (VER). The population of trees in the La Mancha Biological Reserve in Veracruz is characterized by having few trees and being isolated in a fragment of forest covering just 50 ha, which may cause a reduction in the quantity and quality of pollen loads. Interestingly, the absence of cecidomyiid galls in Mexico did not reduce the abortion rate of seeds within fruits or increase the seed mass in these populations, as would be expected if cecidomyiid galls drain maternal resources from developing fruits. It is possible that cecidomyiid galls simply reduce fruit production in Costa Rican populations, replacing many potential fruits with galls without changing the net competition for maternal resources in developing fruits in comparison with fruits in trees without gall parasitism.

4.7 | Geographical Stability and Intraindividual Plasticity of Seed Mass

The effect of geographical origin on seed mass was not significant, indicating a general tendency for wild plants to show greater variation in seed mass within individuals and within populations than among populations (Wulff 1986; Silvertown 1989; Hendrix and Sun 1989; Halpern 2005). It must be noted that the coefficients of the fixed effects estimated for seed mass (number of seeds, number of abortions, and position within the fruit) were small in all the populations. A seed in the “worst of all worlds,” pertaining to a fruit that suffers 5 aborts, located in the basal position, would weight 0.165 g less (the sum of the respective negative coefficients in Table 4) than a seed in an intermediate position in a fruit without abortions. This difference was only half of the standard deviation of the seed mass for the whole sample (0.27 g). Again, an interesting case is that of the Veracruz population, where despite being a population with a high abortion rate, the average and variance of the seed mass were very similar to those of other populations. It seems that seeds that have escaped the abortion phase show little differentiation between populations but flexibility in size within and between fruits, a variation that is only partially explained by the fruit and seed variables analyzed in this study. Stabilizing selection on seed mass, high plasticity of seed mass within populations, or selection forces channeled to change the number rather than the mass of seeds have been proposed to explain these patterns of variation (Wulff 1986; Silvertown 1989; Sadras 2007; Arathi 2011).

4.8 | Future Studies on the Patterns of Variation in Seed Mass

The great variation among fruits in abortion rate and seed mass points to future studies on the factors that lead to this variability in tropical trees, particularly in mimosoid species. The importance of the time of flowering and the spatial variability in the density of flowers and fruits that compete for local resources are some of the environmental factors that could be studied. Pollination by polyads can reduce the variation in pollen loads among pollinated stigmas and the genetic diversity of pollen within fruits to levels that occur in plant species that are pollinated by pollen loads composed of individual pollen grains. Genetic analysis of full seeds and abortions could elucidate possible paternal effects among the factors that explain the variation in the abortion rate and seed mass within the large progeny of Guanacaste trees.

4.9 | Conclusions

In this tree species, the variation among fruits within trees is the most important component of variation in the abortion rate. This pattern begins in the initial phases of fruit development and influences the mass of surviving seeds through a slight negative effect of the fruit abortion rate on seed mass. The two terminal positions in the fruit are detrimental to the survival and mass of the seeds, although this effect is gradual and not extreme, as observed in other plant species. The pollination precedence of stylar ovules is not as important for their survival and vigor as that of other legume plants. Despite the broad geographical range of the sampled trees, the abortion and seed mass patterns of the populations were very similar.

Author Contributions

J.A.L., M.Q., and E.J.C. designed the study. All authors collected the samples and prepared the databases. J.A.L. analyzed the data and wrote the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All scripts and data generated by this study are available from the following Dryad Digital Repository: https://doi.org/10.5061/dryad.0rxwdbs8v.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.