Received: October 05, 2024. Accepted: January 10, 2025.
https://doi.org/10.4322/2359-6643.15288

Original Article

Revista
Ciência, Tecnologia & Ambiente

Patterns of fecundity and abortion in *Canavalia ensiformis* (L.) D.C.

Padrões de fecundidade e aborto em *Canavalia ensiformis* (L.) D.C.

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Como citar: POLIZELLI-RICCI, N.A.; AGOSTINI, K., 2025. Patterns of fecundity and abortion in *Canavalia ensiformes* (L.) D.C. *Revista Ciência, Tecnologia & Ambiente*, vol. 15, e15288. https://doi.org/10.4322/2359-6643.15288

ABSTRACT

Studies were conducted on patterns of fruit and seed sets to assess the potential factors causing high fruit and seed abortions in *Canavalia ensiformis* (L.) D.C., as the available literature is reduced to Papilionoideae species. The analyzes were performed comparing the flower position, in the inflorescence, that fruits with complete development were obtained, in addition to the fruit and seed abortions. The study was conducted in an agricultural crop at UFSCar, from august 2013 to july 2014. The percentage of developed fruits was 9.73% (194 fruits in 1,992 flowers). A total of 148 fruits was developed in the basal position (76.29%), 40 in the median (20.62%) and six in the apical (3.09%). There was a higher abortion of seeds in the basal position (410 developed seeds, 26.99%), in median (532, 35.02%) and apical (577, 37.99%). Since significant differences were found in relation to the position of fruit set, the hypothesis that relates abortion by fruits to the order of floral opening in the inflorescence is the most likely. Regarding fruit abortion, selection according to the cost of fruiting and seed maturation seemed to be the most likely hypothesis. It follows the importance of maternal resources for fruit set is highlighted, due to the fact of the development of more fruits close to the mother-plant, but for the seed set, it was observed that the ovules closest to the stigma have an advantage in capturing maternal resources and successful development.
Keywords: agricultural crop, fruit set, jack bean, reproductive success, seed set.

RESUMO

Foram conduzidos estudos sobre padrões de frutificação e produção de sementes para avaliar os potenciais fatores causadores de altos abortos de frutos e sementes em *Canavalia ensiformis* (L.) D.C., uma vez que a literatura disponível é reduzida a espécies de Papilionoideae. As análises foram realizadas por comparação da posição da flor, na inflorescência, em que frutos com desenvolvimento completo foram obtidos, além dos abortos de frutos e sementes. O estudo foi conduzido em uma parcela de área rural, na UFSCar, entre agosto de 2013 e julho de 2014. A porcentagem de frutos desenvolvidos foi de 9,73% (194 frutos em 1992 flores). Foram desenvolvidos 148 frutos na posição basal (76,29%), 40 na mediana (20,62%) e seis na apical (3,09%). Houve maior aborto de sementes na posição basal (410 sementes desenvolvidas, 26,99%), na mediana (532, 35,09%) e na apical (577, 37,99%). Como foram encontradas diferenças significativas em relação à posição de frutificação dentro de uma inflorescência, a hipótese que relaciona o aborto por frutos à ordem de abertura floral na inflorescência é a mais provável. Em relação ao aborto de frutos, a seleção segundo o custo de frutificação e maturação das sementes pareceu ser a hipótese mais provável. Conclui-se que a importância dos recursos

maternos para a frutificação é destacada, devido ao fato do desenvolvimento de mais frutos próximos à planta-mãe, mas para a frutificação, foi visto que os óvulos mais próximos do estigma têm vantagem na captura de recursos maternos e no desenvolvimento bem-sucedido.
Palavras-chave: cultura agrícola, frutificação, feijão-de-porco, sucesso reprodutivo, formação de sementes.

INTRODUCTION

Leguminosae Lindl. is one of the largest families among angiosperms, consists of 770 genera and approximately 19,500 species, and is distributed in six subfamilies (Azani et al., 2017), with the subfamily Papilionoideae having the highest number of described species. Papilionoideae comprises 486 genera and about 14,000 species (Azani et al., 2017), occurring in a lot of biomes, predominantly in the Brazilian Atlantic Forest. In tropical regions, available information on the reproductive ecology of Papilionoideae is included in community-level studies (Losapio et al., 2019).

In most angiosperms, few ovules result in viable seeds. Some ovules do not develop due to lack of fertilization, and for those that are fertilized, the embryos may be aborted during embryogenesis. The occurrence of ovule abortion is not exclusive to the Leguminosae, however, this family offers convenience for abortion studies, to the detriment of the linear arrangement of ovules in the ovary, which allows the study of seed set gradients in fruits. A myriad of factors can lead to abortion of flowers and fruits (Lamonica et al., 2020). Among them are the amount of pollen grains that are deposited on the stigma and the competition of ovules for essential resources for seed set. This competition added to the limited resources can trigger ovule-selective abortion and affect plant reproductive success (Gardarin et al., 2018).

In Leguminosae species, abortion of embryos that lie farther from the stigma is the most common pattern observed (Gibbs, 1998). In that case, the ovules furthest from the stigma may be the last to be fertilized, because of their position. Despite the genetic variables and the ability of the pollen grains that fertilize the female structure of a flower to be similar, the fertilized ovule will have an advantage over the others in obtaining maternal resources. Thus, this ovule becomes the dominant embryo, resulting in the abortion of other ovules with few maternal resources available, or even without sufficient resources to develop into seeds. If basal ovules have a spatial advantage (Zwolak et al., 2022), stigmatic ovules may have a similar advantage of being the first to be fertilized and establish a more efficient resource pool. Such strong resource pool in first fertilized ovule at the stigmatic end leading to a high frequency of pods with stigmatic seeds has been shown in many different species (Teixeira et al., 2006; Nottebrock et al., 2016; Bogdziewicz et al., 2018; Polizelli-Ricci and Agostini, 2023).

Even so, there is a reduced number of reproductive approaches, isolated in Papilionoideae (Gibbs, 1998), mainly in agricultural landscapes, where many representatives can be used for different purposes, including green manuring technique. Among the green manure species, *Canavalia ensiformis* (L.) D.C. is widely used in crop rotation systems and can incorporate significant amounts of nitrogen into agricultural production systems. It can also be used in direct planting systems or intercropping. The formation of a large amount of straw favors the protection of the physical, chemical and biological characteristics of the soil and makes it difficult the establishment of invasive plants.

Jack bean (*C. ensiformis*) is an annual and rustic species, with herbaceous habit, originating in the neotropical region, and is resistant to high temperatures and periods of drought (Baltasar, 1993). It does not have a good palatability; therefore, it is rarely used as pasture and can be toxic to animals. Also, can be used as green manure and to stimulate the population of mycorrhizal fungi, microorganisms that increase the absorption of water and nutrients through the root system.

Yet, the species has alternate leaves, trifoliate, large elliptical-oval leaflets, bright dark-green in color, with prominent veins, axillary inflorescences in large racemes. Inflorescences are violet or purple in color, the pods are flattened, wide and long (0.25 m or more), coriaceous, containing from four to 18 seeds (pers. obs., N.A.Polizelli-Ricci, 2014). Seeds are large, rounded-oval in shape, white or pink in color, oblong hilum in brown color, surrounded by a brown zone. It has erected and non-creeping herbaceous growth, reaching between 1.2 m and 1.5 m in height. It has a productivity between 20 and 40 tons of green matter and from four to eight tons of dry matter per hectare (Baltasar, 1993).

Therefore, when studying the effects of the components of fecundity and abortion on the reproductive success of a given plant species, it is possible to verify the existence of reproductive problems, in addition to those related to embryo nutrition by maternal resources and competition of pollen grains. Preliminary observations showed that fruiting and seed set were low in spite of the production of numerous flowers. Moreover, many fruit and seed were aborted.

Based on this, to test these arguments, a neotropical species *C. ensiformis* was used as a study model, and it was examined the potential factors causing high fruiting and seed abortions processes in its representatives. Thus, the following goals were addressed: (1) to verify the fruiting rate; (2) verify the rate of seed set; (3) to evaluate the pattern of fruit and seed set in the reproductive processes of this species. Thus, it was intended to answer the following questions: (a) Were there differences in the development of fruits in certain positions in the inflorescence? (b) Was there a difference in the development of seeds at certain positions in the ovary/fruit? (c) Can we infer that the differences reflect favoring maternal resources or the competitive ability of the pollen grains?

MATERIAL AND METHODS

The study was carried out at the Federal University of São Carlos (UFSCar), *Campus* Araras, São Paulo, Brazil (22°18'27.4"S, 47°22'45.5"W), from august 2013 to july 2014. Annual average temperature is around 23°C. From december to february is the period responsible for about 50% of the annual precipitation, which is between 1,400 and 1,500 mm. UFSCar has an extension of 226.50 hectares with 69.61 hectares of built area, 144.12 hectares of agricultural crop areas and only 12.77 hectares of remnants of native vegetation. In an attempt to recover natural areas and increase the forestry of the *Campus*, in march 2009, reforestation began with heterogeneous planting of seedlings located in a permanent preservation area.

The number of flowers in n=30 specimens of *C. ensiformis* was estimated throughout the flowering period. The ovule count per ovary was performed on n=10 flowers per plant and the number of seeds per fruit on n=194 fruits. In each fruit, the total number of viable seeds (number of ovules that developed) and the total number of aborted seeds (number of unviable ovules) were counted. It was also measured the fruiting rate of each specimen (i.e. number of fruits of the specimen / total number of flowers of the specimen), the fruiting rate of the species (i.e. number of fruits total / number of flowers total) and the percentage of viable seeds (i.e. number of viable seeds / total number of seeds).

Differences in the development of fruits (pods) were analyzed in basal, median and apical positions of the inflorescence, in n=30 specimens, sampling all the developing fruits of each plant and counting the number of fruits per position. Basal position is closest to the stem axis, median/intermediate position is between the base and the apex, and the apical position is the extremity of the inflorescence farthest from the stem axis (Teixeira et al., 2006; Polizelli-Ricci and Agostini, 2023). A total of n=30 specimens with immature fruits was dissected to determine the spatial distribution of aborted and developing seeds. Aborted seeds were classified into two categories: basal, located nearest to the pedicel, and apical, situated closest to the floral stigma. Specimens of *C. ensiformis* were observed, weekly, throughout the species' fruiting months (from january to march 2014). The data were submitted to the Shapiro-Wilk normality-test and the Kruskal-Wallis non-parametric statistical-test, using the software R® version 4.1.1 (R Core Team, 2021).

RESULTS

In n=30 specimens, a total of n=1,992 flowers and n=194 fruits were quantified, thus the number of fruits developed in the specimens was smaller than the number of flowers produced, corroborating the literature data (Teixeira et al., 2006; Polizelli-Ricci and Agostini, 2023). Regarding the fruiting rate of specimens of *C. ensiformis* analyzed in the field, it was verified that the results obtained varied between 2% and 30%. As for the fruiting rate of the species, there was a percentage of 9.7%.

Of the 194 fruits developed in 30 specimens, n=148 developed in the basal position (76.29%), n=40 in the middle position (20.62%) and n=6 in the apical position (3.09%) (Table 1). With the Shapiro-Wilk normality-test, it was verified that the data do not follow a normal distribution (p<0.05). Therefore, Kruskal-Wallis non-parametric-test was used, and a statistical difference was obtained between the number of fruits developed, in the different positions of the inflorescences (H=56.234, df*=2, p=6.151^{-13}, p<0.05, *df=degrees of freedom). Furthermore, the statistical differences were plotted through boxplot (Figure 1).

Regarding the percentage of viable seeds, it was observed that 71.42% of the seeds were viable (n=1,519) and 28.58% of the seeds aborted (n=608). Selective seed abortions occurred in greater numbers in the basal region of pods, with a percentage of 26.99% of seed development (n=410), while in the median position it was equal to 35.02% (n=532), and, in the apical position, 37.99% (n=577) (Table 2). It is worth noting that, the apical position had the highest value of development seeds, corroborating the data in the literature.

DISCUSSION

It was expected that *C. ensiformis* would have low fruit and seed set, as it is a common scenario in several families of angiosperms, where viable seeds are formed from a small proportion of ovules. Furthermore, it was also expected that seed abortions would occur in the ovary positions farthest from the stigma, a result previously evidenced within Leguminosae (Teixeira et al., 2006). In this case, basal ovules would be fertilized by pollen tubes with slower growth or less competitive capacity, resulting in less vigorous progeny and, therefore, more likely to be aborted.

Since significant differences were found in relation to the position of fruit set within an inflorescence in *C. ensiformis*, the hypothesis that relates abortion by fruits to the order of floral opening in the inflorescence (Stephenson, 1981) is the most likely. This hypothesis predicted that, in the case of acropetal opening (i.e. from the base to the apex of the inflorescence), which is found in most Leguminosae, including *C. ensiformis*, the basally located flowers would be pollinated first and the fruits would be more able to develop. In this way, they would acquire the available resources before the fruits with later development (Laughlin et al., 2020).

Regarding fruit abortion, selection according to the cost of fruiting and seed maturation seemed to be the most likely hypothesis, to the detriment of the high number of aborted fruits at the beginning of development, before the substantial increase in fruit and seed masses. According to Nakamura and Stanton (1987), aborted fruits (or seeds) could contain little of the maternal resources allocated for reproductive success. This makes us think that the costs of fruits and seeds are high in *C. ensiformis*: the seeds and pods are large, the pods hold a large number of seeds, reaching 18 seeds (pers. obs., N.A.Polizelli-Ricci, 2014), the cotyledons are well developed and

Table 1. Fruits developed in different positions of the inflorescence of *Canavalia ensiformis* (L.) D.C. The positions considered were: basal (nearly mother-plant), median (intermediate position between the base and apex of the inflorescence) and apical (apex of the inflorescence). The total amount of fruits developed, by position, are represented in percentages in parentheses.

Fruits developed per position (inflorescence)		
Basal	**Median**	**Apical**
148 (76.29%)**a**	40 (20.62%)**b**	6 (3.09%)**c**

Different letters indicate that the positions of fruit development showed statistical difference (p<0.05).

Table 2. Seeds developed in different positions of the pod/fruit of *Canavalia ensiformis* (L.) D.C. The positions considered were: basal (nearly maternal resource), median (intermediate position between the base and apex of the fruit) and apical (nearly stigma). The total amount of seeds, by position, are represented in percentages in parentheses.

Seeds developed per position (pod/fruit)		
Basal	**Median**	**Apical**
410 (26.99%)	532 (35.02%)	577 (37.99%)

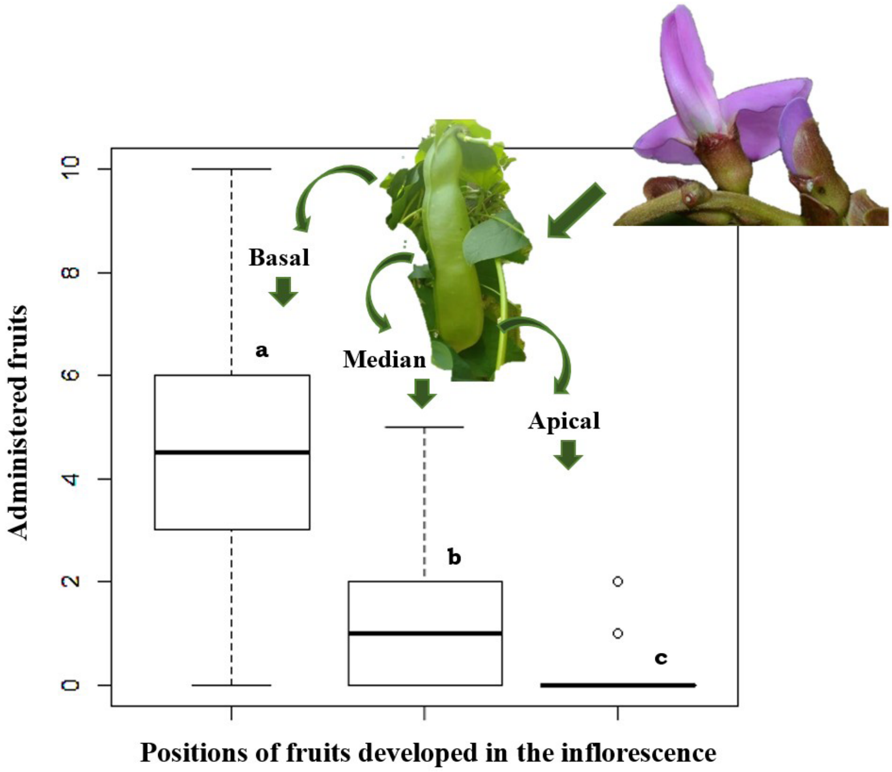

Figure 1. Boxplots showing fruit development, by position, in sampled Canavalia ensiformis (L.) D.C. inflorescences. Different letters indicate that the positions of fruit development showed statistical difference ($p<0.05$). Box on the left 'a' (basal position), box in the middle 'b' (median position) and box on the right 'c' (apical position). The black horizontal bands in the boxplots represent the medians. The corresponding lines represent the upper and lower limits. White circles represent outliers. The X axis represents the positions of the fruit: the apical position of the inflorescences corresponds to the furthest from the stem axis. The median position corresponds to the protected portion between the apical and basal position. The basal position corresponds to the one closest to the stem axis. The Y axis represents the administered fruits.

photosynthetic rate and seed germination requires the embryo to break the integument (Qiu et al., 2022).

Furthermore, as a result of the high rates of ovules and seed abortion, the hypothesis that fruits with more seeds would be selected over others was rejected (Walter et al., 2022). Also, seed abortion occurred randomly in *C. ensiformis*. Yet, the observed pattern in *C. ensiformis* cannot be explained by the advantage in seed dispersal distance, since *C. ensiformis* has indehiscent fruits (Rüger et al., 2018; Pagel et al., 2020). No animals were found dispersing seeds during field observations, nor ripe fruits that had fallen to the ground. Another point to be mentioned is predation as a factor involved in fruit abortion (Arista et al., 1999). Although stingless bees of the genus *Trigona* (Jurine, 1807) (Apidae, Meliponini) were observed around the floral calyx and keel-blossom, with some floral parts pierced, these lesions did not prevent the foraging of large bees of the species *Xylocopa* (*Neoxylocopa*) *frontalis* (Olivier, 1789) (Apidae: Xylocopini), nor fruit development. Also, point out that no injuries were observed in any fruits.

Random abortions related to the ovule and seed development position occurred randomly in *C. ensiformis*, and the apical position showed greater development of ovules in seeds. The apical ovules (stigmatic position) did not define greater chances of seed development than the other positions, despite being fertilized first. Yet, embryo sac viability, in Leguminosae, tends to be high (Teixeira et al., 2006), as *C. ensiformis* flowers can last two or more days on the plant. Thus, basally positioned ovules also have a chance of being fertilized, and have the same probability of development as ovules from other positions. The results differed from those found by Horovitz et al. (1976) within genera *Lupinus* L. and *Medicago* L. (Leguminosae). According to these authors, basal eggs, which are closer to maternal nutrition, have a greater probability of complete development.

Alternatively, the high rates of ovule and seed abortion occurring randomly in *C. ensiformis* could be explained by the hypothesis of (a) limited resources coming from the parent plant; (b) genetic conflicts between endosperm, maternal tissues and embryos within a fruit (kin selection) and/or (c) high inbreeding depression. In Queller's proposition (Queller, 1983) about kin selection, the conflict between endosperm, maternal tissues and embryos occurs because maternal tissue and endosperm (double fertilization) share more genes with the maternal plant, controlling the amount of resources provided for embryonic development. Natural selection favored maternal control over resources to maximize their *fitness*, restricting resources to individual embryos and aborting certain embryos. This control is possible, because maternal tissues (teguments) control the resources allocated to each embryo (Korbecka et al., 2002).

Finally, it is observed in the literature that the influence of the environment on seed development is mainly translated by variations in size, weight and physiological potential. However, the rate of seed development is relatively stable in different environments, since adjustments in the number of seeds produced by the plant or plant community can maintain a relatively constant supply of photoassimilates for them (Marcos Filho, 2005). In any case, knowledge of the biometric variation of fruits and seeds is important for improving these characteristics in number or uniformity, allowing the maintenance of the production of more vigorous plants or contributing to the selection of the best matrices (Santos et al., 2017).

It is believed that further studies focusing on genetics, embryology, demographic rates and plant community with interaction networks at multiple life stages (Yang et al., 2018; Kattge et al., 2020; Kinlock, 2020) would be important to assess the limitation of maternal resources, pollinator's behavior, pollen release dynamics, and the genetic load due to recessive lethal genes are acting in *C. ensiformis*.

CONCLUSIONS

The number of fruits developed in the inflorescences was lower than the number of flowers produced. Furthermore, it was important demonstrate that maternal resources are necessary for fruit development (more fruit set in the basal position of the inflorescences). However, for seed set, it is noted that proximity to the style and, consequently, the contact with the first pollen tubes is more advantageous than be close to the base of the ovary (more seed set in the apical position of the fruit). In this case, genetically better pollen grains produce pollen tubes more quickly and fertilize the first ovules (apical region), while the genetically worse ones are slower and fertilize the last (basal region). In this way, selective abortions would be directed to the basal region of the pod.

ACKNOWLEDGMENTS

The authors thank the funding source (National Council for Scientific and Technological Development - CNPq), grant number 155978/2013-6, and the Federal University of São Carlos (UFSCar) - *Campus* Araras, São Paulo, Brazil. Also, thank the technicians of the Biology Laboratory at UFSCar, and to the researchers M.Sc. Jéssyca Danieli Barros and Dra. Natalia Sêneda Martarello, for their contribution in data collection in the field and revision of the writing of this manuscript, respectively.

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