Annual Research & Review in Biology

Volume 39, Issue 8, Page 39-45, 2024; Article no.ARRB.121168
ISSN: 2347-565X, NLM ID: 101632869
(Past name: Annual Review & Research in Biology, Past ISSN: 2231-4776)

Nature's Precision: The Intricate Pollen Dispersal Mechanisms of Papilionaceous Crops

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

Article Information

DOI: https://doi.org/10.9734/arrb/2024/v39i82107

Open Peer Review History:
This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: https://www.sdiarticle5.com/review-history/121168

Review Article

Received: 29/05/2024
Accepted: 02/08/2024
Published: 06/08/2024

ABSTRACT

Pollination, a fascinating natural process, is crucial for the reproduction of flowering plants. It involves the transfer of pollen from the male reproductive part to the female reproductive part, enabling successful fertilization. Papilionaceous crops, belonging to the Fabaceae family, exhibit highly specialized pollen dispersal mechanisms that ensure effective pollination and genetic diversity. These mechanisms involve intricate interactions between floral structures and pollinators,

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***Cite as:** R, Nirmalaruban., R. Suvitha, Jai Prakash Prasad, Kanshouwa Modunshim Maring, Rajasekar, and P. Anantharaju. 2024. "Nature's Precision: The Intricate Pollen Dispersal Mechanisms of Papilionaceous Crops". Annual Research & Review in Biology 39 (8):39-45. https://doi.org/10.9734/arrb/2024/v39i82107.*

primarily bees. By integrating findings from various studies, this review provides a comprehensive understanding of the intricate pollen dispersal mechanisms in papilionaceous crops such as piston/pump mechanism, explosive type mechanism, brush type mechanism and valvular mechanism. It also provides information about the role of different floral parts in pollen dispersal among the flowers. This review will be helpful in gaining insights about pollen dispersal mechanism and it contribution in improving crop yields and breeding programs.

Keywords: Pollen dispersal mechanism; valvular; piston; brush; explosive.

1. INTRODUCTION

Pollination is one of nature's most captivating processes, essential for the reproduction of flowering plants. Pollination is referred as the process by which pollen is transferred from male reproductive part to the female reproductive part in order to effect successful fertilization. For many plants, this pollen transfer relies on the help of pollinators. Plants and their pollinators share a mutualistic relationship, where both parties benefit. Pollinators, such as insects, feed on nectar and pollen provided by the flowers. In return, as they move from flower to flower in search of these food rewards, they transfer pollen, enabling the plants to reproduce and exchange genetic information. Most flowering plants depend on these pollinator relationships to successfully reproduce.

Pollination can be accomplished by cross-pollination or by self-pollination. Self-pollination also titled as *autogamy* involves transfer of pollen within the same flower. The architecture of flowers is devised in such a way that aids in transfer of pollens from anther to stigma of the same flower. It is considered to be the closest form of inbreeding and it is thought to be evolved as adaptation in the absence of pollinators for the successful advancement of generations. The bisexual flowers, *homogamy, cleistogamous flowers*, *chasmogamy* and appropriate position of anthers in order to supply pollen to stigma were the mechanisms promoting autogamy. Autogamy leads to increase in homozygosity among the population. Wyatt [1] put forward that delayed autonomous selfing is an adaptive pollination mechanism in plants. It assures seed set during the absence of pollinators in the flowers, which readily agrees to outcrossing, if done on hand. It is likely to occur at the later stage of anthesis as a result of delayed curvature of stylar branches with stigma towards anthers. Klips and Snow [2] reported the presence of delayed autonomous self-pollination in *Hibiscus laevis* belonging to the family Malvaceae. They concluded that these stylar movements as a mechanism bequeathing first preference to outcrossing, but facilitating selfing if out- crossing fails. Cross-pollination is also called as *allogamy*. Cross-pollination is the most prevalent mode of pollination in both cultivated as well as uncultivated plant species. Floral architecture such as *dicliny, heterostyly, herkogamy, self-incompatibility, male sterility* and *dichogamy* are mechanisms which promotes cross-pollination [3].

Schrire [4] detailed the complex floral architecture of plants belonging to Fabaceae. The plants within the sub-family Papilionoidea consists mostly of zygomorphic flowers [5,6] and are habitually entomophily (bee pollinated). Ornithophily and chiropterophily have also been reported in leguminous flowers. Studies on pollination biology and mating system of *Vigna caracalla* Verdcourt (Fabaceae: Papilionoideae) by Etcheverry et al. [7] showed off that self-fertilization may evolve in the peripheral population. The results of the study with five different treatments of pollination such as free pollination, autonomous self-pollination, hand self-pollination, apomixis and outcrossing revealed the absence of fruit set in apomixis treatment, which discarded the chance of asexual reproduction. Outcomes of autonomous self-pollination showed the entire dependence of reproductive success on the pollinators. *Bombus morio* and *Xylocopa eximia* were the most frequent visitors and effective pollinators of *Vigna Caracalla.* These insects carried pollens on the pronotum. Index of self-incompatibility (ISI) showed that all the five populations were self-compatible in nature but depends on pollinators for successful seed set.

Stirton [8] spelled out that the specific role of each part of the flower in serving pollination. The standard petal was specialized for attraction of pollinators towards the flowers, wing petals served as the landing platform for the insects to rest and keel petals encloses the androecium and gynoecium inside it (Figs. 1, 2). The floral architecture plays a significant role in deciding the type of pollination and the pollinators visiting

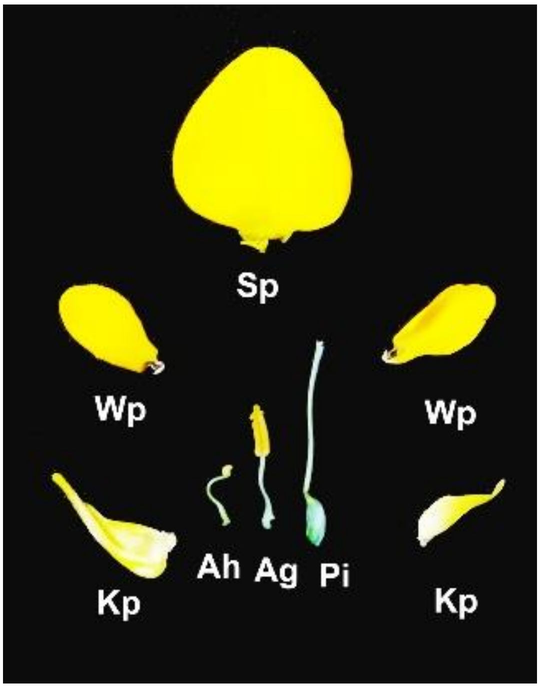

Fig. 1. Leguminous flower-Sunnhemp (C. juncea) Foral parts. Sp- Standard petal (Vexillum), Wp- Wing petal, Kp- Keel petal, Ah& Ag- Androecium, Pi- Pistil (Gynoecium) [9]

Fig. 2. Pollination vectors*: a) Xylocopa latipes b) Xylocopa pubescens c) Megachile lanata* [10]

the flowers which resulted in crops with improved yield. Pollen dispersal in papilionaceous plants occurs through various mechanisms, each contributing to successful fruit set and yield improvement. In this review, we explore in depth the various pollen dispersal mechanisms present in papilionaceous flowers and the way it contributes to the reproductive success of the crop.

2. POLLEN DISPERSAL MECHANISMS

There are four primary types of pollen dispersal mechanisms in these plants [11]:

1. Piston mechanism
2. Explosive type mechanism
3. Brush type mechanism
4. Valvular mechanism

These mechanisms ensure effective pollen transfer and enhance reproductive success. Fig. 3 illustrates the floral architecture appropriate for all four mechanisms.

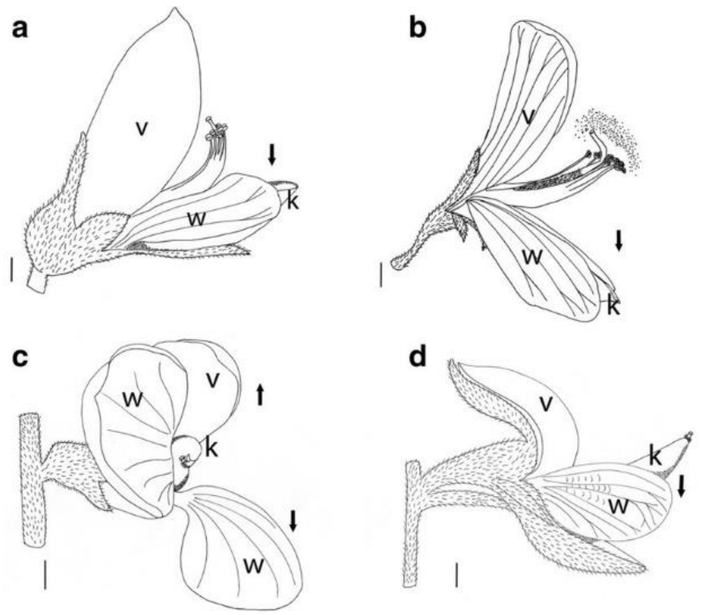

Fig. 3. Schematic representation of the pollination mechanisms in Papilionoidea. a) valvular; b) explosive; c) Brush; d) pump (k- keel, *v* -vexillum, *w* -wings, arrows indicate the movement of the floral pieces during the activation of the mechanisms) Source: Adopted and modified from Alemán et al. [12]

2.1 Piston Mechanism

Arroyo [13] explained the piston mechanism of pollen dispersal as when the pollinator visits the flower, the stigma and anthers retain their positions, while the tip of keel moves under the pressure of the pollinator. Pollen gets released and pushed towards the tip of keel petal. Pollens can be released quite a lot number of times through the hole at the tip of the keel petals during the visit of pollinators. Flowers having piston mechanism of pollen presentation have high Pollen/Ovule ratio compared with flowers having explosive mechanism. During the visit of pollinators, the piston mechanism operating inside keel pushes the released pollens through the tip and it gets attached to the pollinators and dispersed. The pump mechanism is reversible and dispenses pollen in doses [14,15,16].

2.2 Explosive Type Mechanism

The explosive type of mechanism is also popularly called as tripping mechanism. In flowers devising this kind of mechanism, the staminal column is seized under pressure inside the keel petal. On liberating the tension, all the pollens get released instantaneously as the staminal column cracks against the standard petal. The position of staminal column will not be reversed as former, once after the explosion. Tripping not only occurs, when the tension is released by the visiting insects, it also occurs due to high temperature or heavy rain as they weaken the turgidity of the keel petals. The low Pollen/Ovule ratio shows off the highly specialized mechanism, which allows only one effective exchange of pollen with pollinators [17].

Raju and Rao [18] studied the pollination mechanism in *Rhynchosia beddomei* Baker belonging to Fabaceae. The results of the study showed that the staminal column was held in pressure inside the keel petal. Tripping or explosive type of mechanism happened when insect pollinators landed on the flowers, which released the reproductive column from keel boat. The stigma got pollinated with cross-pollen from other flowers, when it touched the ventral side of the insect if it had previously visited some other flowers. If it was first visit for the insect to the flower, then the stigma got pollinated with self-pollen. The staminal column and pistil of flowers remained unexposed, if the flowers remained untouched by the insects. Such flowers might fell off without fruit set.

The process of pollen transfer is irreversible in explosive type of mechanism, the keel and the hidden reproductive organs push in opposite directions, creating a spring-like tension [19].

When a pollinator makes contact, this tension is released all at once, transferring a cloud of pollen to the pollinator [20]. This explosive mechanism allows for only a single opportunity for pollen exchange [21,22,23].

2.3 Brush Type Mechanism

Lavin and Delgado S [24] studied the pollen brush of eight species of Papilionoidea and recorded the following fallouts. The flowers with brush type pollination mechanism were provided with pistil longer than the stamens, which prevented the occurrence of self-pollination. The trichomes at the upper part of the style acting as pollen brush and collected the released pollen grains. At the time of pollination, the sufficient pressure exerted by the pollinators made the pistil protrude out the tip of the keel petal, the stigma made primary contact with insect and received pollens (if present), whereas the trichomes brushed the pollen on the pollinator. The stigma and style reverted back to their original position at the departure of pollinator as the pressure exerted on flower was released [7,24].

2.4 Valvular Mechanism

In the valvular mechanism, staminal column is not seized under pressure. The tip of the keel petals opens along its length, when the pollinator takes a pew and closes when they leave the flower. In this mechanism, pollen grains can be released repeatedly to numerous visitors. The flowers with this mechanism have highest P/O ratio, which perhaps explains the association with less efficiency of pollen transfer mechanisms [20]. There presence a school of thoughts that all the other three methods of pollen dispersal get derived from the valvular mechanism.

Studies on floral biology and pollination mechanism in *Coronilla emerus* L. belonging to Fabaceae by Aronne et al. [25] revealed that the staminal column was held inside the keel without any pressure. Insect visits exposed the stamens and pistil out of the keel, they remain unexposed, if they were left untouched. Insects approached flowers both from front and back. The insects approaching the flowers from front landed on the wing petals which pulled the keel petals. This repeated backward and forward action pushed the anthers and pistil towards the acute end of keel petal. After the dehiscence of anther, the pollen grains were pushed towards the tip of keel petal. Sufficient pressure exerted by the visit of pollinators squeezed the pollen grains and stigma through the tip of keel petal. Pollen grains which squeezed out through the tip of keel got adhered to the body of pollinators and got transferred to other flowers. The stigma, which protruded through the tip of keel during insect visit got dusted with pollen grains from the body of insect pollinators, which got adhered to its body while visiting some other flowers. Stigma returned to its original position, when the insects took off from the flower. Table 1 provides a list of leguminous crops that utilize various pollen dispersal mechanisms.

Table 1. List of crops with their respective pollen dispersal mechanism

Pollen Dispersal Mechanism	Common Name	Scientific name	References
Valvular	Pigeon Pea	*Cajanus cajan* (L.) Millsp.	Aronne et al. (2012) [25]
	Scorpion senna	*Coronilla emerus* L.	
Explosive	Graham's tick-clover	*Desmodium grahamii* A. Gray	Miguel-Peñaloza et al. (2019) [26]
	Spanish broom or rush broom	*Spartium junceum* L.	Galloni et al. (2007) [22]
	Alfalfa	*Medicago sativa* L.	
Brush	Lathyrus	*Lathyrus sativus* L.	Lavin and Delgado S (1990) [24]
	Pisum	*Pisum sativum* L.	
	Vicia	*Vicia faba* L.	
	Common Bean	*Phaseolus vulgaris* L.	
Pump/piston	Lupinus	*Lupinus albus* L.	Arroyo (1981) [13]
	Crotalaria	*Crotalaria juncea* L.	Nirmalaruban et al. (2020) [9]

3. CONCLUSION

The intricate pollen dispersal mechanisms of papilionaceous crops underscore the importance of plant-pollinator interactions in agricultural ecosystems. This review concludes that the specialized floral structures and pollinator behaviours are crucial for effective pollination and genetic diversity. From the available literature, it is obvious that different pollination mechanism prevailing in different crops aids not only plants in achieving higher yield, in parallel it serves as food resources for pollinators in a mutualistic manner. This mutualistic sharing encourages the ecological balance among the beings present in the environment. Future research should focus on the impact of environmental changes on these mechanisms and explore ways to enhance pollination efficiency in agricultural practices in order to achieve improved yield with limited resources.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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Peer-review history:
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