

Morphological and Phenological Study of Flowers and Fruits of Wild-Type Raspberries (*Rubus* spp.)

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Abstract

Wild-type raspberries are part of forest succession and could be cultivated owing to their benefits and economic value. The development of cultivated plants depends on the quality of the genetic material used for propagation. Phenological studies are the first step in assessing the quality of genetic material and in determining the overall developmental process. This research aims to study the development and morphology of flowers, fruits, and seeds. This research was conducted at Cibodas Botanical Garden from September 2022 to March 2023. The experiment used wild-type raspberry species as a factor in a randomized complete block design. The results showed differences in the developmental phases and morphology of flowers, fruits, and seeds, as well as in stigma receptivity, among *R. fraxinifolius*, *R. rosifolius*, and *R. ellipticus*. Flowers take 11–15 days from initiation to anthesis, and the receptivity of the stigmas of the three species reaches a peak one day after anthesis in the morning. The fruit is ripe at 39–46 days after anthesis with a different color.

Keywords: diversity, flowering time, fruit development, generative phase, stigma receptivity

Introduction

Raspberries have been domesticated and have become a commercially valuable fruit in a few countries, such as the United

States of America, Russia, China, and Japan. In Indonesia, wild-type raspberries have been domesticated as commercial plants. These plants not only offer aesthetic appeal but also possess various health benefits and applications in traditional medicine (Gao et al., 2024). *Rubus fraxinifolius*, for example, has vitamin C content and anthocyanin up to 88.68 mg/100 g and 452.44 mg/100 g, respectively (Setiyadi et al., 2018). *Rubus rosifolius* has been utilized for cosmetic ingredients, such as lotion and lipstick in Indonesia. It's an antioxidant that helps delay skin aging and reduce wrinkles (Santoso et al., 2024). Wild-type raspberries were found in some area in Indonesia, such as West Java, Kalimantan, and Sulawesi forest-mountain areas. *Rubus fraxinifolius* is a *Rubus* dispersed in West Java, and natives called it 'Arben' (Ismaini et al., 2017; Surya et al., 2018).

The domestication of raspberries relies on genetic propagation (Normasiwi et al., 2021). Contemporary *Rubus* breeding initiatives produce enhanced genotypes through controlled hybridization and genomic-assisted selection. However, once these superior genotypes are developed, they need to be clonally propagated to maintain genetic fidelity, uniformity, and stability in commercial production. Clonal propagation is essential to prevent the segregation of important domestication traits such as fruit quality, flavor, firmness, yield, and disease resistance, which would otherwise be lost through sexual reproduction. Reviews of *Rubus* breeding emphasize that the commercial raspberry industry relies on asexual propagation to preserve cultivar identity derived from complex

hybrid backgrounds (Foster et al., 2019).

Seeds are the primary material for developing raspberry plants; therefore, understanding of their reproductive biology is crucial for successful domestication and high-quality seed production. This understanding encompassing pollination mechanisms, fruit growth patterns, and germination requirements is most effectively achieved through detailed phenological observations (Masny et al., 2022). Phenological observation is vital not only for determining optimal harvest periods and facilitating automated yield estimation (Fagundes et al., 2024), but also for evaluating plants adaptability. While past studies have largely focused on the morphological traits, nutritional profiles, and genetic diversity of wild *Rubus* species in Indonesia (Normasiwi et al., 2021; Setiyadi et al., 2018), or the phenology of commercial cultivars in other regions (Fagundes et al., 2024), a significant research gap remains. Specifically, there is very limited comprehensive research on the comparative flowering phenology, stigma receptivity phases, and fruit developmental timelines of Indonesian wild-type raspberries grown in a shared environment. Addressing this gap is critical for establishing effective artificial pollination strategies and securing high-quality genetic material for future breeding. Furthermore, because environmental factors such as temperature and humidity strongly influence floral development, precise phenological monitoring is essential (Peng et al., 2024). Ultimately, these baseline studies provide the essential data needed for adaptive agricultural management and for predicting how reproductive cycles will respond to broader climate shifts (Czinege, 2024).

Flowering phenology marks the beginning of a plant's reproductive phase and is a vital aspect of its life cycle. Phenological research is valuable for breeders as it helps identify floral traits, enabling them to understand the fertilization process and determine the necessary steps for cultivating wild-type plants (Hiregoudar et al., 2019; Normasiwi et al., 2021). These studies often reveal that flowering and fruiting patterns vary significantly among

species, spanning stages from the emergence of flower buds to fruit ripening (Normasiwi et al., 2021). Stigma receptivity is a critical parameter that directly influences natural pollination rates, successful fertilization, and gametophyte selection (Heslop-Harrison, 2000; Makwana & Akarsh, 2017). While various methodologies are available for assessing receptivity, enzymatic activity-based approaches remain the most prevalent (Makwana & Akarsh, 2017; Souza et al., 2004). Beyond agricultural optimization, morphological and phenological evaluations are crucial for comprehending climate resilience. For example, environmental changes can disrupt the visual signals plants provide to pollinators, such as seasonal alterations in background colors that modify visual contrast and affect pollinator detection rates (Martins et al., 2021). To address these interconnected factors and bridge existing research gaps, this study investigated the development and morphology of flowers, fruits, and seeds through a comprehensive phenological analysis of three wildtype *Rubus* species: *R. fraxinifolius*, *R. rosifolius*, and *R. ellipticus*.

Materials and Methods

Observations were made at the Cibodas Botanical Garden (CBG), Cianjur, West Java, Indonesia, from September 2022 to March 2023. CBG is located at 1200-1400 m a.s.l. with an average temperature of 21 ± 0.6 °C, relative humidity up to $88\% \pm 3.3\%$, and precipitation reaching 20.48 mm per day (National Aeronautics and Space Administration, 2023). Three species of wild-type raspberries were collected: *R. fraxinifolius*, *R. rosifolius*, and *R. ellipticus*. The observations consisted of flowering phenology, fruit, and seed development. The phenological study started with flower bud initiation at 1 mm diameter, continued through flower development until anthesis, and through fruit development until the fruit ripened.

Flower Morphology and Development

The study was designed in a randomized

complete block design. The three wild-type raspberry species were divided into five groups based on tagging times. Five flowers were selected from each group, resulting in a total of 75 observation units. Flower development was observed daily for diameter and the day to anthesis. A vernier caliper was used to measure flower size. Morphological characteristics observed were the structure, size, and color of the flowers at anthesis. The Royal Horticultural Society (RHS) color chart was used to identify the flower color. The flower structure was observed by using a Microdirect 1080P HDMI Handheld digital microscope.

Stigma Receptivity Test

Stigma receptivity was observed during three phases of flower development: flower bud, anthesis, and after anthesis (start to wither). Flower samples were collected five days before (D-5) anthesis and up to three days after (D+3) anthesis every morning at 8 am and afternoon at 1 pm (Hiregoudar et al., 2019). Receptive stigma was observed by collecting the stigma, placing it on an object glass one by one, and then dripping 3% hydrogen peroxide (H_2O_2) onto it. The reaction was observed under an Olympus CX21i microscope at 10× magnification. The number of bubbles was scored into six levels from 0 to 5: (0) no reactivity, (1) very low reactivity, (2) less reactivity, (3) moderate reactivity, (4) high reactivity, and (5) very high reactivity (Makwana & Akarsh, 2017).

Fruit Morphology and Development

The three wild-type raspberry species were divided into five groups based on tagging times. Five flowers were selected from each group, resulting in a total of 75 observation units, and the study began by tagging the anthesis flowers. The fruit set was calculated as the ratio of the total number of ripe fruits to the total number of flowers in anthesis (Kumar et al., 2014). The fruit development phase was observed every two days until the fruit was ripe. A vernier caliper was used to measure the fruit length and diameter.

A destructive fruit sample was collected and weighed on a digital scale. Its structure was observed by cutting it longitudinally. The seed size was measured using a tool in the Olympus CX21i microscope. The Royal Horticultural Society (RHS) color chart was used to identify fruit color.

Data Analysis

Qualitative data were analyzed descriptively, and the identification score data for stigma receptivity were analyzed with the Wilcoxon Mann-Whitney test ($\alpha = 5\%$). ANOVA was used to analyze quantitative data, and Duncan's multiple range test (DMRT) at $\alpha = 5\%$ was applied to detect significant differences when detected. DMRT using the Agricolae package on R-Studio (de Mendiburu, 2023).

Results and Discussion

The raspberry flower is a complete flower that forms in the leaf axils of *R. rosifolius*, whereas *R. fraxinifolius* and *R. ellipticus* form clusters at the end of the branches. The buds of *R. fraxinifolius* have smooth and shiny surfaces, while *R. rosifolius* and *R. ellipticus* have fine hairs on the surface of their buds. Each species had a distinct flower characteristic, either morphological or phenological (Table 1). *R. rosifolius* had the largest diameter and length, as well as the pedicle length, which was 2.36 cm, 1.01 cm, and 2.61 cm. *R. ellipticus* had the smallest petal size, namely 2.32 cm in diameter, 0.61 cm in length, and 1.14 cm in pedicle length. All three species had five white corollas, except for *R. fraxinifolius*, which is a pale yellow-green group based on the RHS color chart, and green petals with the same surface as the flower buds. Raspberry has many stamens consisting of anthers and filaments and many separate carpels consisting of stigma, stylus, and ovary attached to a conical receptacle modified into a torus (Fuentes et al., 2019; Hiregoudar et al., 2019) (Figure 1).

The fruits of *R. fraxinifolius*, *R. rosifolius*, and *R. ellipticus* are aggregates of small drupelets

attached to a receptacle called a torus (Figure 2). Significant differences among the three species were observed in the morphological characteristics of fruits (Table 2). *R. rosifolius* had the same fruit diameter as *R. fraxinifolius*, which is 1.83 cm. Still, the fruit lengths were different, namely 1.38 cm and 1.88 cm. *R. rosifolius* had the greatest fruit weight (2.63 g). *R. ellipticus* had the smallest diameter, length, and fruit weight, which are 1.13 cm, 0.87 cm, and 0.56 g. Each drupelet consists of a mesocarp that becomes the fruit flesh. The endocarp becomes hard and forms a small pit that encloses a single seed (Figure 3). The number of seeds per aggregate and the size and weight of seeds among the three species were significantly different (Table 3). *Rubus fraxinifolius*, had a large fruit size followed by a large number of seeds, which was similar to *R. rosifolius*. *Rubus fraxinifolius*, which had the highest number of seeds per fruit, had the smallest size (1.27 mm in diameter and 1.93 cm in length) and 100-seed weight (28.4 mg). *Rubus ellipticus* had the smallest number

of seeds per fruit (59.76) but had the largest diameter, length, and 100-seed weight, namely 1.67 cm, 2.67 cm, and 66.4 mg. Based on the classification of wild-type raspberry seeds by Surya et al. (2021), the seeds of *R. fraxinifolius* were included in the group of seeds with the least prominent sculpture and blunt backs. In contrast, *R. rosifolius* and *R. ellipticus* were included in the group with prominent reticulate sculptures and sharp protruding backs.

Each species had different developmental flower and maturation fruit periods (Table 4). Based on the phenology, bud development continued until anthesis at different times in each species (Figure 4). *Rubus rosifolius* required the longest anthesis time, approximately 15 days after initiation (DAI), whereas *R. fraxinifolius* and *R. ellipticus* required approximately 12 and 11 DAI, respectively. This observation differs from that of Normasiwi et al. (2021), who observed an anthesis time of 11–12 DAI. This difference can be influenced by observation periods. These observations began in September, which is the

Table 1

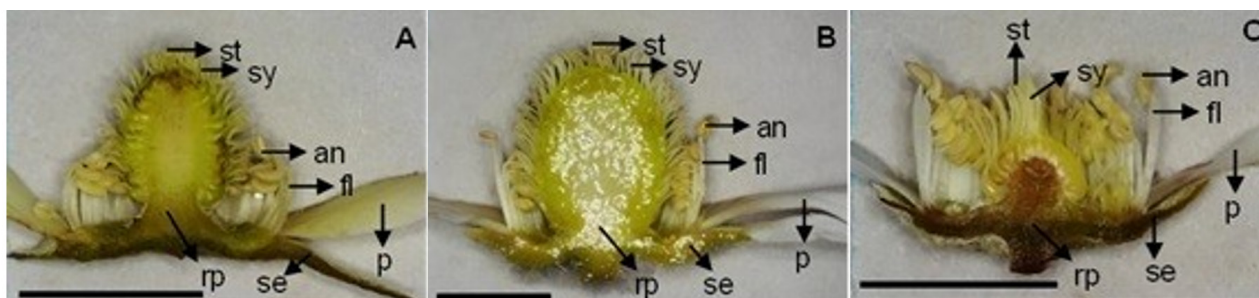
Flower Characters of Wild-Type Raspberries

Species	Petal diameter (cm)	Petal length (cm)	Pedicle length (cm)
<i>R. fraxinifolius</i>	2.36 ± 0.04 b	0.78 ± 0.03 b	1.80 ± 0.23 b
<i>R. rosifolius</i>	3.16 ± 0.28 a	1.01 ± 0.07 a	2.61 ± 0.56 a
<i>R. ellipticus</i>	2.32 ± 0.12 b	0.61 ± 0.10 c	1.14 ± 0.17 c

Notes. DAI= Days After Initiation. The values followed by the same letter in the same column show no significant difference according to the DMRT at $\alpha = 5\%$. n = 5. Values are means followed by standard deviation.

Figure 1

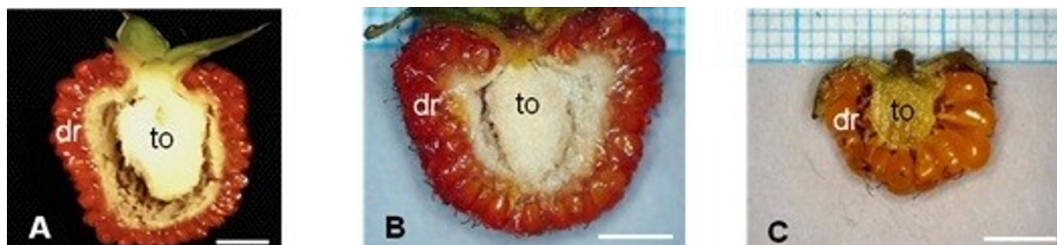
Flower Structure of Wild-Type Raspberry (A) R. fraxinifolius, (B) R. rosifolius, (C) R. ellipticus



Note. se= sepal, pt= petal, rp= receptacle, an= anther, fl= filament, st= stigma, sy= stylus, bar = 0.5 cm.

Figure 2

Fruit Aggregate Structure (A) R. fraxinifolius, (B) R. rosifolius, (C) R. ellipticus



Note. to = torus, dr = drupelet, bar = 0.5 cm.

Figure 3

Seed Morphology (A) R. fraxinifolius, (B) R. rosifolius, (C) R. ellipticus



Note. bar= 0.5 cm.

Table 2

Fruit Characters of Wild-Type Raspberries

Species	Fruit diameter (cm)	Fruit length (cm)	Fruit weight (g)
<i>R. fraxinifolius</i>	1.82 ± 0.07 a	1.88 ± 0.08 a	2.03 ± 0.08 b
<i>R. rosifolius</i>	1.83 ± 0.21 a	1.38 ± 0.30 b	2.63 ± 0.27 a
<i>R. ellipticus</i>	1.13 ± 0.11 b	0.87 ± 0.12 c	0.56 ± 0.13 c

Notes. DAA= days after anthesis. The values followed by the same letter in the same column show no significant difference according to the DMRT at $\alpha = 5\%$. n = 5. Values are means followed by standard deviation.

Table 3

Seed Characters of Wild-Type Raspberries

Species	Number seeds per fruit	Seed diameter (mm)	Seed length (mm)	100-Seed weight (mg)
<i>R. fraxinifolius</i>	362.31 ± 33.57 a	1.27 ± 0.04 c	1.93 ± 0.03 c	28.4 ± 0.62 c
<i>R. rosifolius</i>	352.60 ± 33.27 a	1.52 ± 0.03 b	2.36 ± 0.04 b	39.8 ± 1.03 b
<i>R. ellipticus</i>	59.76 ± 11.18 b	1.67 ± 0.02 a	2.67 ± 0.06 a	66.4 ± 1.23 a

Notes. The values followed by the same letter in the same column show no significant difference according to the DMRT at $\alpha = 5\%$. n = 5. Values are means followed by standard deviation.

beginning of the rainy season in Indonesia. The onset and duration of flower and fruit development stages are influenced by endogenous plant factors and climatic conditions especially temperature and precipitation (Normasiwi et al., 2021; Włodarczyk et al., 2023). Wild fruit tree species are highly susceptible to climatic factors and sudden changes in the weather can lead to a delay the phenophase (Cosmulescu et al., 2022).

All three species experienced a rapid change in fruit color from unripe to ripe six days before the fruit was fully ripe. The fruits of *R. fraxinifolius* and *R. rosifolius* were formed and developed by attaching to the open oval-

shaped receptacle. In contrast, the ovules of *R. ellipticus* developed and were protected by the flower sepal. The sepals of *R. ellipticus* closed again after pollination and opened during fruit development until they were fully open when the fruit was fully ripe and yellow. In contrast to *R. ellipticus*, the *R. fraxinifolius* and *R. rosifolius* fruits were red when fully ripe (Figure 5). Ripe fruit is characterized by soft and watery drupelets that easily fall off the fruit stalk. *R. fraxinifolius* had the highest fruit set value, up to 89.07%, whereas *R. ellipticus* had the lowest fruit set. *R. ellipticus* ripened the longest, 46 days after anthesis (DAA), whereas the other two species ripened at 40 DAA (Table 4).

Table 4

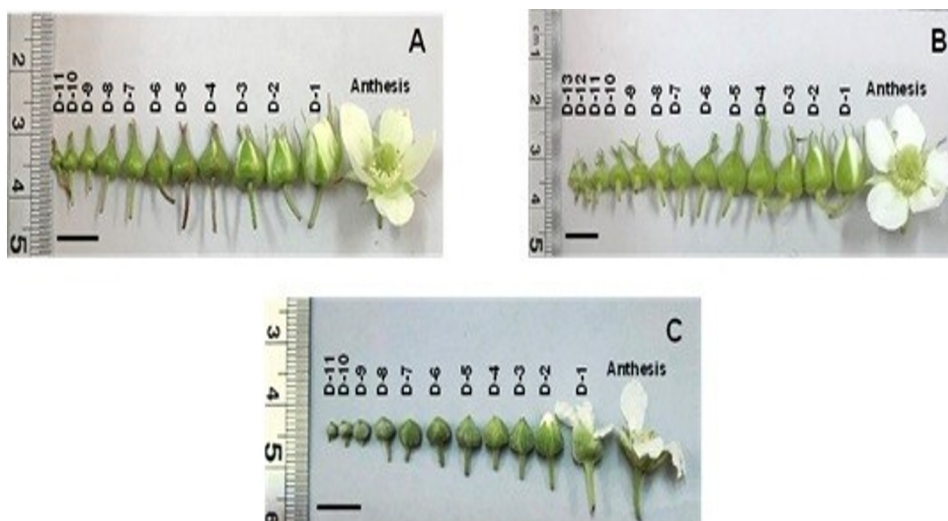
Flower and Fruit Phenology Of Wild-Type Raspberries

Species	Day of anthesis (DAI)	Fruit set (%)	Fruit ripening time (DAA)
<i>R. fraxinifolius</i>	12.12 ± 0.23 b	89.07 ± 5.53 ^a	40.52 ± 0.11 ^b
<i>R. rosifolius</i>	14.84 ± 0.17 a	87.67 ± 2.72 ^a	39.80 ± 0.20 ^c
<i>R. ellipticus</i>	11.24 ± 0.09 c	64.17 ± 9.13 ^b	46.16 ± 0.17 ^a

Notes. DAA= days after anthesis, DAI = days after initiation. The values followed by the same letter in the same column show no significant difference according to the DMRT at α = 5%. n = 5. Values are means followed by standard deviation.

Figure 4

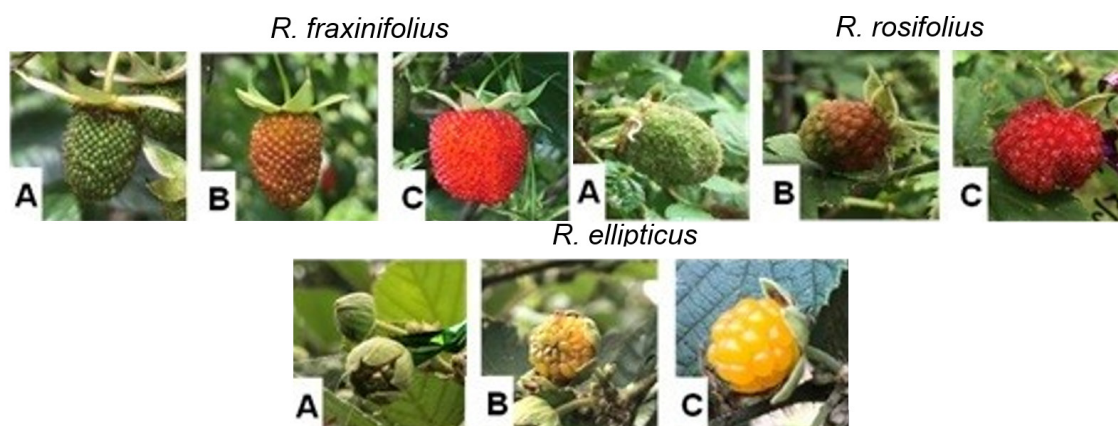
Flower Development from Bud to Anthesis Phase (A) R. fraxinifolius; (B) R. rosifolius; (C) R. ellipticus



Note. scale = 1 cm. D-: refers to days before anthesis; D+: refers to days after anthesis; D: refers to the anthesis day.

Figure 5

Fruit Development in the Field (A) Unripe, (B) Semi-Ripe, (C) Ripe



Three species of wild raspberry anthesis in the morning for a whole day looked fresh and slowly withered. Some flowers appeared to have been pollinated because the anthers appeared withered. On the second day, the flower appears withered, and the corolla begins to fall off one by one. The entire corolla fell off on the third day after the anthesis. The fall of the corolla indicates that pollination occurred in all three species. The bubbles that appeared on the stigmas of *R. fraxinifolius*, *R. rosifolius*, and *R. ellipticus* differed in number and phase at different observation times (Figure 6).

The bubbles were visible on the stigmas of *R. fraxinifolius*, *R. rosifolius*, and *R. ellipticus* during the bud phase, anthesis, and after anthesis. Stigma receptivity was low during the flower bud phases of all three species. *Rubus fraxinifolius* and *Rubus ellipticus* at D-5 anthesis did not show a receptive stigma, either in the morning or during the day, while *R. rosifolius* already showed a receptive stigma with a score of 0.5 in the morning observations. Stigma receptivity in the three species increased from the budding phase to the peak and decreased after reaching the peak. The peak occurred on D+1 anthesis in the morning, resulting in a score of 4–4.5. During the wilted flower phase (D+2 and D+3 anthesis), many bubbles remained in all three species (Figure 7).

Observations of stigma receptivity conducted in the morning and during the day

showed significantly different results on several days of observation. Observations in the morning revealed that the three species showed more bubbles than in the afternoon. The non-parametric Wilcoxon Mann-Whitney test results showed a difference in the significance level between morning and afternoon observations. A significant difference was visible between the morning and afternoon observations at the peak of stigma receptivity (D+1 anthesis) in the three species. So, the peak of receptivity in all three species was at the D+1 anthesis stage in the morning. An increase in relative humidity increases peroxidase activity, indicating increased stigma receptivity (Sage et al., 2015).

The notably higher bubble counts observed in the morning suggest that elevated humidity and cooler temperatures promote optimal enzymatic activity, ensuring peak receptivity during the early hours when pollinators are most active. This timing is vital because environmental stressors, such as intense afternoon heat, can have adverse effects. High ambient temperatures, generally exceeding 30 °C, accelerate the aging of stigmatic papillae, drastically reducing the effective pollination period from several days to just one or two days. This swift decline often results in a phenological mismatch where the stigma desiccates before adequate pollinator visits occur (Hedhly, 2011; Hiregoudar et al., 2019). Extensive studies across various species provide comparative evidence that fluctuations

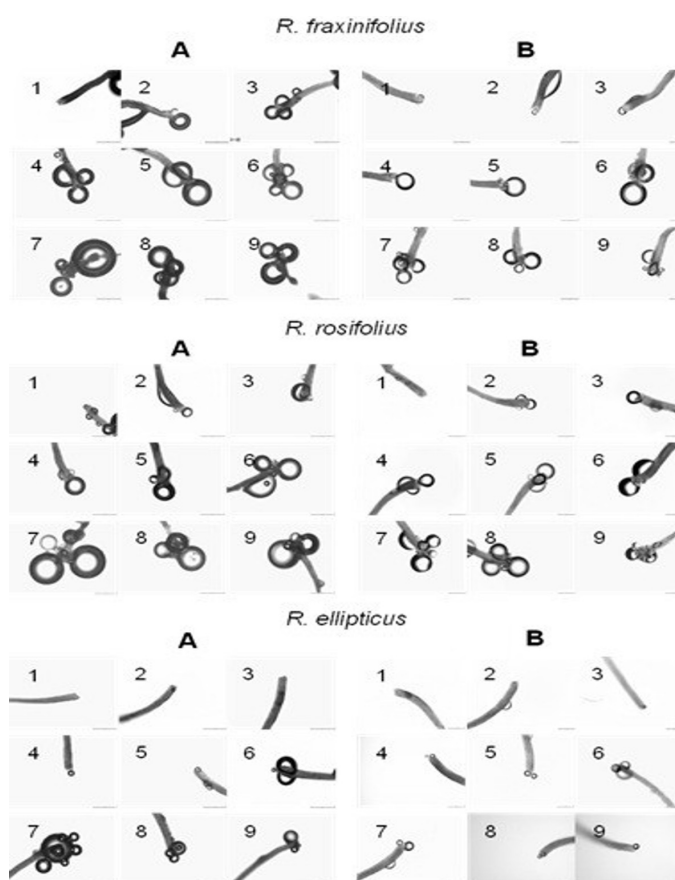
in several abiotic factors, such as average temperature, aridity index, and solar radiation, correlate with differences in floral longevity. Among these factors, temperature is the most significant predictor, with flowers generally having longer lifespans in cooler climates (Song et al., 2022). At higher altitudes, the environmental temperature drops, leading to reduced metabolic activity and consequently lower pollination rates (Zambon et al., 2018).

The number of bubbles in the stigma cavity after dropping H_2O_2 indicates the peroxidase activity which plays a role in the pollination process (Zambon et al., 2018). Stigma receptivity is related to the activity of enzymes, such as peroxidase, esterase, and dehydrogenase (Souza et al., 2004). Enzymes play roles in

pollen germination, pollen tube penetration of the stigma, and the pollen incompatibility response to the stigma (Nasrallah, 2023). The greater the quantity of bubbles, the more receptive the observed stigma identified. Peroxidase on the stigma surface facilitates pollen-carpel association by loosening the stigmatic cell wall, allowing pollen tube entry to fertilize the ovule (Gupta et al., 2015). In the wilted-flower phase, the cells may have died, leading to an accumulation of H_2O_2 ; therefore, the bubbles were still quite visible (Makwana & Akarsh, 2017). Stigma receptivity was used to identify the optimum flower age for artificial pollination; therefore, pollen use is efficient and effective for successful pollination.

Figure 6

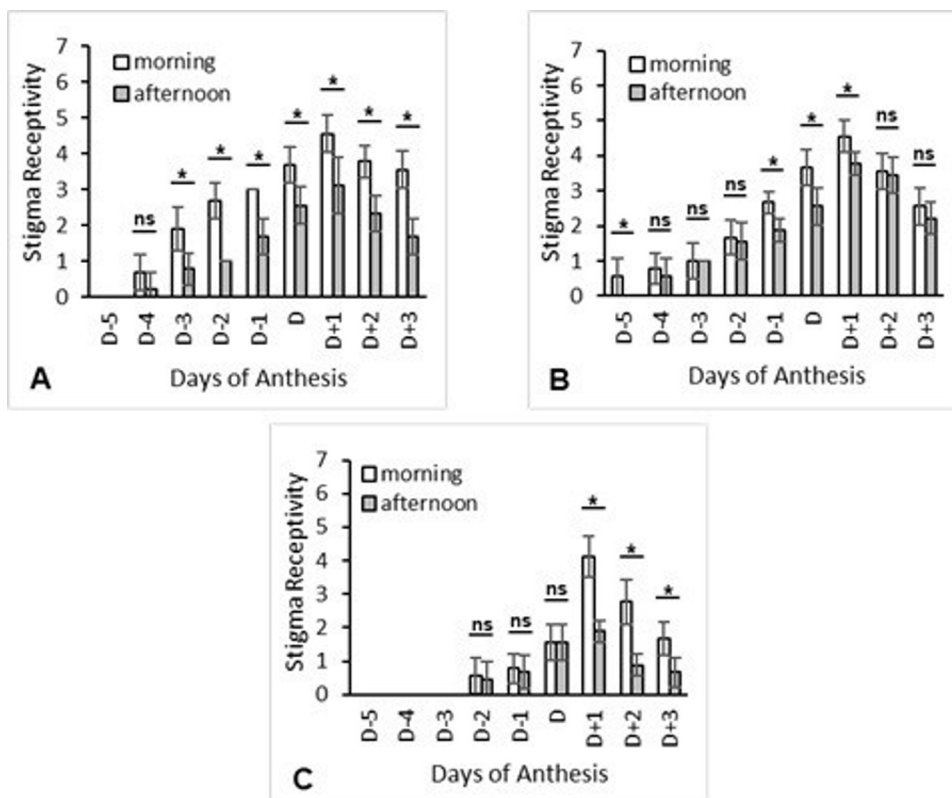
Bubbles on the Stigma After Being Treated with 3% H_2O_2 ; 10× Magnification, (A) Morning, (B) Afternoon Observation



Notes. (1) D-5, (2) D-4, (3) D-3, (4) D-2, (5) D-1, (6) D, (7) D+1, (8) D+2, (9) D+3 anthesis. D-: refers to days before anthesis, D+: refers to days after anthesis, D: refers to the anthesis day.

Figure 7

Stigma Receptivity from D-5 to D+3 Anthesis (A) *R. fraxinifolius*, (B) *R. rosifolius*, (C) *R. ellipticus*



Note. D-: refers to days before anthesis, D+: refers to days after anthesis, D: refers to the anthesis day.

There is a notable positive relationship between the length of stigma receptivity and the success rate of pollination, as the receptive period determines the effective timeframe for pollen germination and tube development in wild raspberry species (*Rubus* spp.). Stigma receptivity in *Rubus paniculatus* usually peaks at anthesis and remains effective for several days. This extended period is crucial, as it increases the likelihood that insect pollinators deliver compatible pollen, thereby directly boosting the percentage of fruit set (Hiregoudar et al., 2019). Additionally, high receptivity physically indicated by a glossy, sticky stigmatic surface and chemically by optimal enzymatic activity ensures that enough ovules are fertilized to form the aggregate fruit structure. If receptivity declines before sufficient pollen is deposited, this results in partial fertilization, leading to malformed fruit with fewer drupelets, thereby diminishing the

plant's overall reproductive yield (Hiregoudar et al., 2019).

Environmental factors, especially temperature and relative humidity, play a crucial role in regulating the duration and intensity of stigma receptivity in *Rubus* species. On the other hand, moderate relative humidity preserves stigmatic secretions, maintaining the sticky, enzymatic surface necessary for pollen adhesion and germination. When these environmental conditions fluctuate, such as during heat stress combined with low humidity, stigma receptivity ends prematurely, directly causing incomplete fertilization. This physiological failure is evident morphologically as "crumbly fruit," where only a portion of the aggregate drupelets develop, significantly affecting the berry's structural integrity and marketability (Heide & Sønsteby, 2008).

Conclusions

The comprehensive findings of this study offer direct practical benefits for the future cultivation and commercial production of wild-type raspberries. By precisely determining the timeline from flower initiation to anthesis and identifying that peak stigma receptivity occurs one day after anthesis in the morning, cultivators and breeders can optimize artificial pollination schedules to maximize fruit set and quality. Furthermore, understanding the distinct fruit ripening timelines and seed morphological differences among *R. fraxinifolius*, *R. rosifolius*, and *R. ellipticus* provides a scientific basis for highly synchronized harvest planning. Ultimately, these phenological baselines will assist in the targeted selection of superior propagation materials and the development of specialized cultivation protocols that ensure genetic fidelity and uniformity in commercial raspberry production. The three observed species had different stages in flower, fruit, and seed development, as well as in morphology. Flowers take 11-15 days from initiation to anthesis, and the receptivity of the stigmas of the three species reaches a peak on D+1 of anthesis flowers in the morning. The fruit is ripe at 39–46 days after anthesis with a different color.

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