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Understanding *Rafflesia zollingeriana*: A Comprehensive Study of Bud Development, Growth, Mortality, and Life Cycle

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ABSTRACT

Rafflesia zollingeriana is one of the endemic species in the eastern Java Region of Indonesia that has gained much attention from researchers. *R. zollingeriana* has not been studied for its flower bud development, mortality, and population dynamics. The present study investigated the flower growth, mortality, flowering success, sex ratio, and life cycle of *R. zollingeriana* in the Papring Forest, Kalipuro Banyuwangi, East Java, Indonesia. Five populations of *R. zollingeriana* with 412 individuals were observed visually every two weeks for 12 months. Each bud was observed to determine the growth dynamics, growth rate, life cycle, distribution size, bud sustainability, mortality, and sex ratio of *R. zollingeriana*. The bud phase development was recorded to determine its population structure and life cycle. The results showed *that R. zollingeriana* required between two and three years to complete its life cycle. The smaller buds grew more slowly than the larger buds. The bud mortality rate was quite high at 73.54% and occurred during the cupule and bract transition phase. The blooming success rate of its buds was only 17.71%, with a higher proportion of female flowers than male flowers. *R. zollingeriana* in Papring Forest was flowering throughout the year, with the most frequent flowering incidents occurring during the high rainfall months of January, February, March, and June. There is a relationship between the number of flowering incidents and environmental

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factors such as rainfall, temperature, and length of irradiation. This study underscores the species' vulnerability, low blooming success, and high mortality, which inform conservation strategies for *R. zollingeriana* in Papring Forest, Banyuwangi.

Keywords: Growth dynamics, phenology, *Rafflesia zollingeriana*, sex ratio

INTRODUCTION

Rafflesia is a genus of parasitic plants with no leaves, stems, or true roots and only has flowers. *Rafflesia* flowers are known as the largest single flower in the plant kingdom. This unique appearance of *Rafflesia* attracts significant attention among biologists. These plants are only found in Southeast Asia, from Southern Thailand, Peninsular Malaysia, Sumatra, Java, Kalimantan, and several islands of the Philippines (Maezulpah et al., 2019). Unfortunately, not all *Rafflesia* species have their conservation status recorded by the International Union for Conservation of Nature (IUCN) (Janra, 2019). The IUCN considers only *Rafflesia magnifica* as Critically Endangered (CR) (Malabrigo et al., 2023). Researchers in Southeast Asia have developed a conservation status classification based on IUCN criteria from 2001 to 2024. Nine species of *Rafflesia* were classified in the CR category (Nais, 2001), with only one species listed in the Vulnerable category (Susatya, 2011). Some endemic *Rafflesia* species in Gunung Lauser National Park, Sumatra, Indonesia, including *R. lawangensis*, are classified as CR, and *R. micropylora* is classified as Endangered (Mahyuni et al., 2024). Renjana et al. (2022) categorize all Indonesian *Rafflesia* as CR, except for *Rafflesia arnoldii*, which is in the vulnerable category. Kusuma et al. (2022) showed that all Java-endemic *Rafflesia,* consisting of *Rafflesia rochussenii*, *Rafflesia patma*, and *Rafflesia zollingeriana*, experienced higher extinction risks compared to the others due to global warming and climate change, and the high pressure of human activities. According to the classification of Nais (2001), three types of *Rafflesia* endemic to the island of Java are included in the vulnerable category. Furthermore, according to the 2011 criteria, it is included in the critically endangered category (Susatya, 2011).

More research related to *Rafflesia*'s life history is necessary to provide complete information regarding its mortality according to the flower development phase (Wicaksono et al., 2021a). *Rafflesia bengkuluensis*, *Rafflesia conrueloae,* and *Rafflesia patma* have a mortality rate of 67%–100%, 77.3%, and 75%, with a flowering success of 7.9%, 19.7%, and 6.7%–12.5%, respectively (Mohd-Elias et al., 2021). Another study has reported the mortality of *R. zollingeriana* in Meru Betiri National Park, which is one of five known geographical sites of this species. The mortality of *R. zollingeriana* was 43.5% in 2003, 49.1% in 2006, and 28.95%–57.14% in 2014 (Hikmat, 2006). More information on mortality and population dynamics of *R. zollingeriana* at other sites, such as Papring forest, Banyuwangi, is crucial to provide a better understanding and

comprehensive ecology of the species *R. zollingeriana*, endemic to the East Java region, was first discovered in 1918 in Puger Jember by Kooders. It has since been confirmed in several areas, including Meru Betiri National Park, Pasirian and Tempursari Lumajang, and most recently in the Papring Forest area in northern Banyuwangi. Several studies have assessed its population profile. In 2012, the distribution and population structure of *R. zollingeriana* in Meru Betiri National Park were assessed (Kusuma et al., 2023). In 2019, the population structure development of *R. zollingeriana* in Meru Betiri National Park was studied (Maezulpah et al., 2019), including the morphological comparisons of *R. zollingeriana* from Meru Betiri National Park and Lumajang, as well as morphological variations in the Papring Forest area (Lestari & Susatya, 2022). Life history is important for understanding the interaction between the *Rafflesia* and its environment to ensure maximum fitness. The fitness results from the interaction between growth and mortality at various growth and development phases (Susatya, 2020). Not many life history studies have been conducted for *Rafflesia* species. Hidayati et al. (2000) initiated a life history study for *R. patma*. A more detailed study was then carried out by Susatya (2020) for *R. arnoldii* and Wee et al. (2024) for *R. cantleyi*.

The study of *R. zollingeriana* life history is important because it has been considered an endemic *Rafflesia* in eastern Java Island, including Watang Nature Conservation Area, Meru Betiri National Park, Jember, Pasirian and Tempursari, Lumajang, and Papring, Northern Banyuwangi (Lestari & Susatya, 2022). All these locations are isolated and fragmented habitats. The life history study results will help find a proper alternative conservation scheme for *R. zollingeriana*. Therefore, the present study aimed to investigate the flower growth, mortality, flowering success, sex ratio, and life history of *R. zollingeriana* in the Papring Forest, Kalipuro Banyuwangi, East Java, Indonesia.

MATERIALS AND METHODS

Study Site

This research was conducted in the forest area of North Banyuwangi Forest Management Unit (KPH), located at Papring Village, Kalipuro sub-district, Banyuwangi. The research site was a hilly terrain covered by mixed teak and pine plantation forests with canopy coverage ranging from 62.57% to 98.35% (Table 1). The percentage of canopy was measured using the hemispherical photography method, which uses the front of a cell phone camera directed perpendicular to the sky. The trick of taking photos is between trees with several takes. Furthermore, it was analyzed using ImageJ software. This area was covered with bamboo sprouts, which sometimes became a dominant vegetation in the open area of the site. Five populations of *Rafflesia zollingeriana* were selected with latitude and longitude of S 08°06’34.52” E 114°21’31.42” (location 1), S 08°06’33.71” E 114°21’29.43” (location 2), S 08°06’33.55” E 114°21’29.90” (location 3), S 08°06’33.98” E

114°21’34.13” (location 4) and S 08°09’34.83” E 114°21’30.52” (location 5). Each location was observed every two weeks from January to December 2023 (Figure 1). The habitat has an elevation ranging from 283–436 m above sea level (ASL) and various slopes ranging from mild slope (18°) to moderate heavy slope (30°). The nearest and farthest distances of the habitat to the river were 10 m and 200 m, respectively (Table 1).

Table 1
Physical attributes of the habitat of R. zollingeriana *at Papring Forest, Banyuwangi Regency*

Site Location	Site Characteristic			
	Elevation (above sea level/asl)	Slope	Distance from River (m)	Percentage of Canopy Cover (%)
Location 1	357	18°	50	71.36
Location 2	376	28°	10	62.47
Location 3	379	21°	25	95.38
Location 4	436	30°	200	70.81
Location 5	283	23°	50	84.57

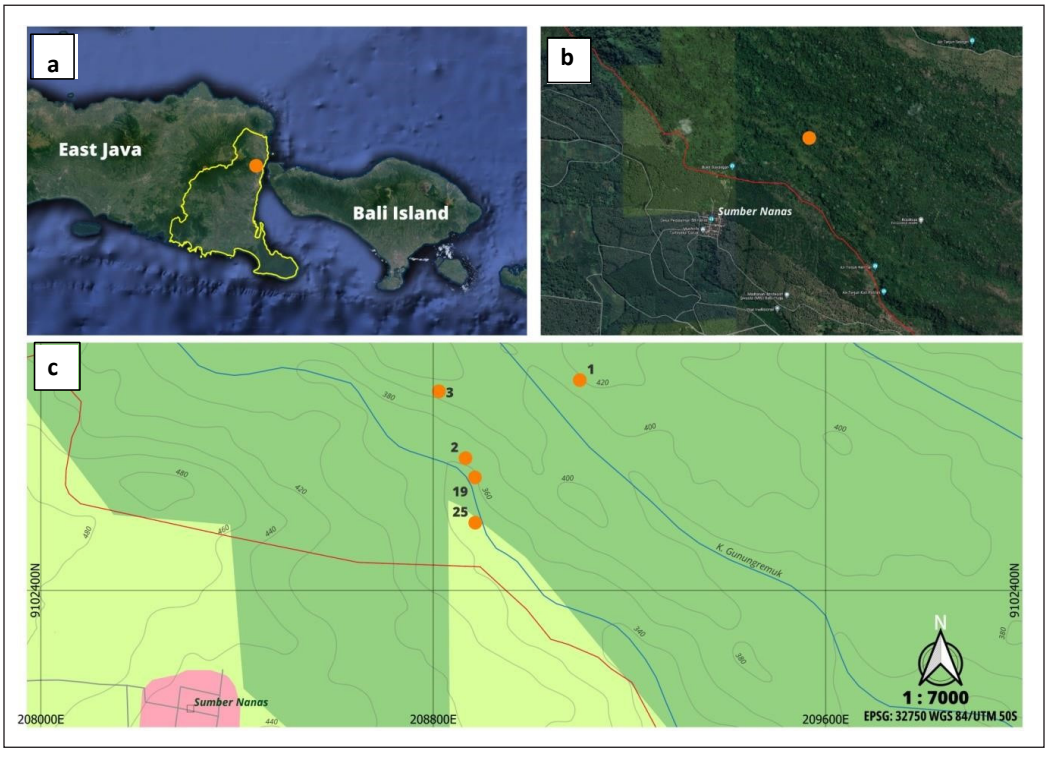

Figure 1. Map of the research location: (a) Papring Forest area, which is part of Kalipuro Subdistrict located in Banyuwangi regency, East Java, Indonesia; (b) Focus of Papring Forest Area, which is in the Forest area adjacent to the Sumber Nanas area; (c) Observation location of *R. zollingeriana* life history is shown with orange circles. Five locations are marked 1, 2, 3, 19, and 25

Morphological Identification of *R. zollingeriana*

The species of *Rafflesia* in Papring Forest was determined as *R. zollingeriana* based on the identification of morphological characteristics according to Susatya et al. (2023). The identification results show that the diameter of the fully bloomed flower is only 24–34 cm. Its perigone consists of five lobes with whitish orange or creamy white warts, numerous, small in size, close to the edge and become larger towards the center of the lobes, denser towards the diaphragm, and large, rectangular or circular warts. The diaphragm is convex towards the aperture with many creamy white, irregularly shaped warts, surrounded by orange color. Wart with discontinuous concentric apertures meeting has a thin ring of solid dark orange and white with no windows. It has ramenta from the rim of the lower surface of the diaphragm to the base of the perigone tube. The upper ramenta are tuberculate and have several variations from the top to the inside of the diaphragm. In the center, the type is swallowed lobes ramenta; in the lower diaphragm, the type is branched ramenta; in the lower part of the perigone tube, the type is simple tubercle ramenta. Processus truncated cone-shaped with various blunt spikes at its top, light orange at its base, and darker at its top. The processus forms four rings from the outside to the center of 20, 17, 8, and 4 processus, respectively. It has a well-developed interior annulus and a poorly developed exterior annulus. These characteristics correspond to the morphological characteristics of *R. zollingeriana*.

Growth Dynamics of *R. zollingeriana*

The study collected 412 flower buds from five populations of *R. zollingeriana*. Buds of *R. zollingeriana* were located on the soil surface and identified by visual observation. Observation was conducted every two weeks from January to December 2023 at all five populations. Each bud in each population was labeled, mapped, and photographed for every observation. The diameters were measured using vernier calipers for diameters less than 10 cm and a tape measure for diameters greater than 10 cm. The growth dynamics of *R. zollingeriana* were determined by observing the flower development stage, the blooming process, and the development stage of fruit formation. The development of *R. zollingeriana* flowers was determined by observing bud changes from the swollen host to the anthesis stage.

Flowering Pattern and Phenological Stage of *R. zollingeriana*

The flowering pattern of *R. zollingeriana* was determined by counting the flowers that successfully bloomed in all plots and associated with environmental factors. The fruit formation stage was observed from when the flower bloomed until it decayed and lost its perigone, and only the disk containing the fruit ovule remained. Phenological stage observations were made to see the type of perigone opening during the blossoming process. These observations were made on fully covered perigones that were ready to bloom, and

then observed every two days to see the process of opening perigones one by one until they opened completely.

The phenological stages of *R. zollingeriana* flowering were analyzed using multiple linear regression to assess the significant effects of environmental factors such as rainfall, air temperature, and duration of irradiation. Multiple linear regression was carried out with R software. The regression model used the mathematical form Y = a + b1X1 + b2X2 + b3X3, where Y represents the predicted value, a is a constant, b1 to b3 are regression coefficients, and X1 to X3 are the environmental variables. The notation X1 is rainfall, X2 is air temperature, and X3 is the duration of irradiation.

The Growth rate of *R. zollingeriana*

The growth rate of *R. zollingeriana* was observed based on the results of measuring the diameter of the bud every two weeks, recording the size of the smallest and largest diameters in each phase. The flower's diameter growth rate was determined by subtracting two consecutive measurements. Growth rates were computed by comparing the diameter at each developmental stage over the observation period. The formula for determining growth rates is as follows:

$$\text{Growth Rate} = \frac{\text{Average}}{\text{length of each observation period}} = \frac{\frac{\sum_{i=1}^{n} x_i}{n}}{14} \qquad [1]$$

Life History Reconstruction

The largest and smallest diameter sizes for each phase were also used to determine the life cycle of *R. zollingeriana*. The life history reconstruction of *R. zollingeriana* buds utilized an exponential growth model, similar to models used for *R. patma* and *R. arnoldii* (Hidayati et al., 2000; Susatya, 2020). The exponential equation $Yt = c\ e^{kX}$ was applied, where Yt represents bud diameter at time t, c is a constant, e is the base of the natural logarithm (~2.719), k denotes the growth rate constant, and X signifies the time required for buds to reach a specific diameter during development. Constants c and k were derived by transforming the exponential equation into a linear form and conducting regression analysis (Susatya, 2020). The regression model was built using bud diameters observed biweekly, encompassing the entire developmental span from initial stages to just before blooming. Based on empirical observation data, this approach aimed to provide a comprehensive life history reconstruction of *R. zollingeriana* at each developmental stage.

Distribution Size, Mortality, Bud Sustainability, and Sex Ratio Determination

The distribution size of *R. zollingeriana* was observed by counting the number of buds at each study site every two weeks. Furthermore, the population size difference was

accumulated every three months to determine the population structure. The population structure was seen from the changes in the number of buds found alive. The population structure illustrates the sustainability of buds, as indicated by changes in buds due to bud death and the emergence of new buds. The population's structure was constructed according to its flower development phases and consists of (a) swollen host; (b) cupule; (c) cupule bract transition (CBT); (d) bract; (e) bract perigone transition with witish (BPT Witish); (f) bract perigone transition with pinkish (BPT pinkish); (g) perigone full covered; and (h) anthesis stage. All photographed buds were accordingly assigned to their flower growth phase.

The mortality of each bud was recorded during observation and calculated using the formula:

$$\text{Mortality Rate} = \frac{\text{Total number of Dead Bud}}{\text{Total number of Bud}} \times 100\% \qquad [2]$$

Observations of mortality were also included on the cause of death. The observations also recorded the bite marks, damage, and other signs of rot to assess the causes of the bud mortality. Each bud found was also categorized based on size: < 2 cm, 2–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, and > 20 cm. The < 2 cm size class indicates the swollen host and cupule phase size, and the 5–10 cm size class corresponds to CBT and bract. Size class 10–15 cm corresponds to bract to perigone. Class 15–20 cm corresponds to BPT until the perigone and a small part of the anthesis. The >20 cm class corresponds to buds that have fully bloomed and entered the ovule formation stage. Bud sustainability was also observed by calculating the percentage of buds that survived, those that died before blooming, those that successfully bloomed, and those that died after passing through the decay process. The sex ratios between male and female flowers were determined based on the presence of anthers at the disc of flowering *Rafflesia* by palpating the underside of the disk. The male and female flowers found are counted, and the ratio is calculated.

Environmental Factors Measurement

Environmental factors were measured based on weather factors, including air temperature, air humidity, length of irradiation, and rainfall. Air temperature and humidity were measured using a thermohydrometer. Measurements were taken every two weeks. Rainfall and length of irradiation data were obtained from Meteorology, Climatology, and Geophysical Agency for one year of observation. The weather data were then averaged every month.

RESULTS AND DISCUSSION

Growth Dynamics of *R. zollingeriana* Bud

Bud growth is divided into two stages: flower and fruit development. The flower development stage begins with the appearance of buds from *Tetrastigma* and continues

until the blooming phase. The fruit development stage begins with the aging of flowers until the formation of fruit and seeds. This stage includes the rotten stage and the formation of mature fruit containing seeds.

Flower Development Stage

The flower development stage of *R. zollingeriana* begins with the appearance of swelling on the *Tetrastigma* root called a swollen host (Figure 2a). The swollen host was measured from 1.06 to 1.98 cm high. The second stage is the cupule stage, where the true *Rafflesi*a body is still completely covered by *Tetrastigma* bark (Figure 2b). The size of the cupule ranges from 1.53 to 4.97 cm in diameter. The next stage is characterized by an increase in the diameter of the *Rafflesia* body, which causes the *Tetrasigma* bark to crack and gives rise to a visible whitish bract of *Rafflesia*. This condition indicates the bud enters the transition phase from cupule to bract or cupule-bract transition (CBT) (Figure 2c). The diameter of the CBT of *R. zollingerian*um in Papring Forest varies from 3.56 cm to 7.91cm.

The bract phase is marked by a whitish bract covering the whole surface of the flower bud (Figure 2d). The flower bud is 3.56 to 12.65 cm in diameter at this phase. The whitish Bract Perigone Transition (BPT) phase is indicated by emerging whitish perigone lobes, which slowly replace bracts (Figure 2e) and are 4.51 to 17 cm in diameter. The next phase is the Pinkish BPT phase, characterized by changing the color of perigone lobes from white to pinkish (Figure 2f). It ranges from 7.26 to 8.76 cm in diameter. Bract is still seen in these two last phases. When the perigone lobes completely cover the upper surface of the bud,

Figure 2. Stage of flower development of *R. zollingeriana*: (a) swollen host; (b) cupule; (c) Cupule Bract Transition (CBT); (d) bract; (e) bract perigone transition with whitish (BPT whitish); (f) Bract Perigone Transition with pinkish (BPT Pinkish); (g) perigone full covered; and (h) anthesis stage

then it becomes a perigone-fully covered phase with a diameter ranging from 15.09 to 20.9 cm. This phase also indicates that the flower bud will be flowering soon. The flowering or anthesis phase occurs at buds with a 24.43 to 36.42 cm diameter.

Blossoming Process and Phenology. The blossoming process of *Rafflesia* shows a certain pattern, which can be observed at the perigone phase bud. Two types of *Rafflesia* bud blooming process patterns exist, including spiral and flap types (Tolod et al., 2020). The flowering pattern of *R. zollingeriana* also follows these two processes. The first flowering was the spiral type, indicated by the simultaneous opening of the perigone lobes. The second type of flowering pattern of *R. zollingeriana* was the flap type. The blooming process in the type one-by-one perigone lobe will open from the outermost to the innermost lobes (Figure 3).

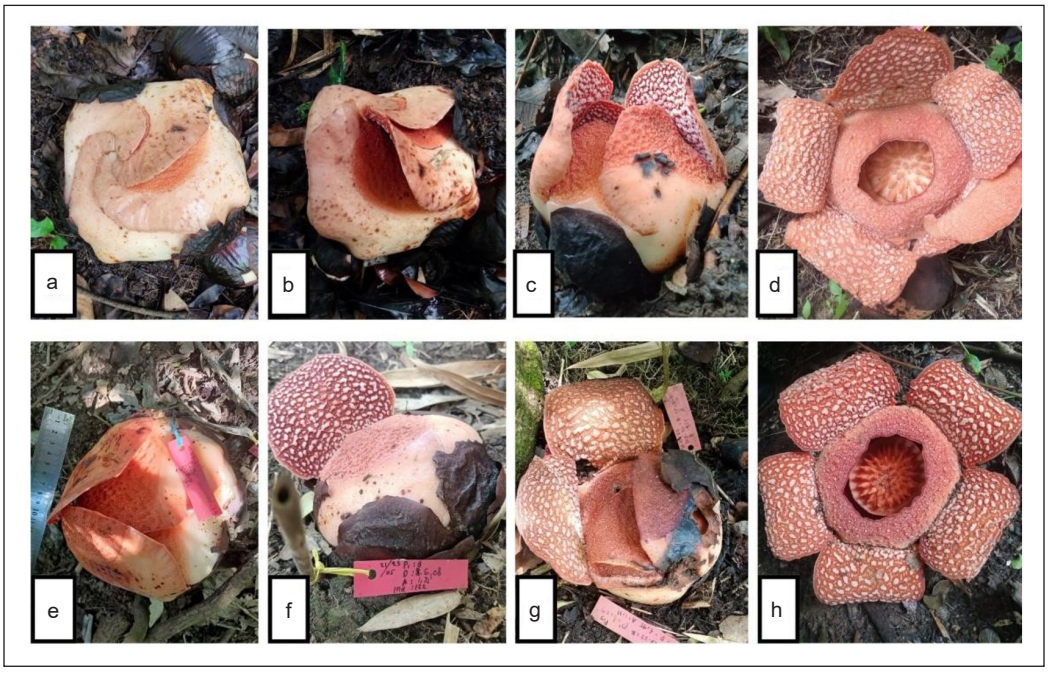

Figure 3. The flowering pattern in *R. zollingeriana*: (a–d) spiral type flowering pattern; (e–h) flap

Flowering Pattern. The observations for 12 months revealed variations in the number of flowers that successfully bloomed each month. During the 12 months of observation, 73 *R. zollingeriana* in the Papring Forest have bloomed. The study obtained the multiple regression model of $Y=-96.11916 + 0.45501X_1 + 3.10024X_2 + 1.40725X_3$. The results of multiple linear regression showed that rainfall, air temperature, and length of irradiation significantly influenced the success of *R. zollingeriana* flower blooms. There is a relationship between

the rainfall, air temperature, and length of irradiation variable and the number of blooming *R. zollingeriana* flowers. Every 1-unit increase in air temperature leads to a rise in the number of *R. zollingeriana* blooming flowers by 3.10. Also, every 1-unit change in the duration of irradiation causes the number of blooming flowers to increase by 1.41. The variables of rainfall, air temperature, and length of irradiation also have significant effects ($p<0.05$) on the number of blooming flowers. Figure 4 shows a linear pattern, indicating that the number of blooming flowers was influenced by rainfall, temperature, and length of irradiation.

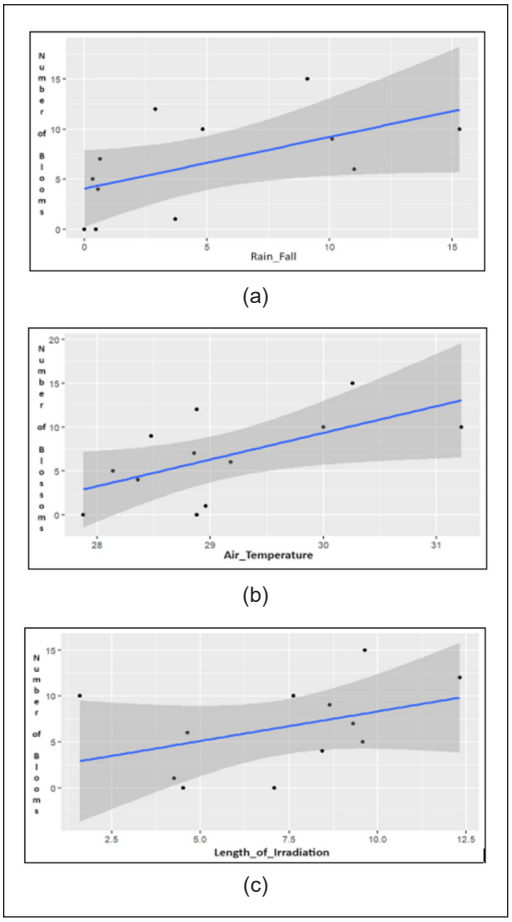

Figure 4. Graph of the relationship between the number of blooming flowers and environmental factors: (a) the relationship between the number of blooming flowers and rainfall (R^2 0.45501); (b) the relationship between blooming flowers and air temperature (R^2 3.10024); and (c) the relationship between blooming flowers and the length of exposure ($R^2$1.40725)

Flowering is generally influenced by temperature, water, and light availability (Tolod et al., 2020). The results revealed optimum rainfall conditions, air temperature, and length of irradiation support the flowering of *R. zollingeriana*. *R. zollingeriana* buds that successfully bloomed in Papring Forest occurred throughout the year. However, flowering occurs more frequently in months with rainfall and temperatures above average monthly values. This study found that the optimum air temperature to support the blooming of *R. zollingeriana* buds in Papring Forest ranged from 28°C to 31°C. The average temperature at the study site was 29.1°C. Flowering frequently occurred in months with higher temperatures than the average, including January, March, April, and July (Figure 5a). In those months, 6, 20, 15, 10, and 9 flowering incidences were recorded. High temperatures facilitate enzyme activity to support the bud development into flowers. A similar pattern is also found in *R. consueloae*, whose flowering occurs in the hottest period of the year, including January to June (Tolod et al., 2020).

Susatya (2020) stated that the optimum temperature for the development and blooming of *Rafflesia* is about 25–30°C. The blooming of the *Rafflesia* flower is a complex process

influenced by light and the availability of nutrients. The average monthly rainfall was 4.91 mm^{3,} and flowering often occurred in months with rainfall above the monthly average (Figure 5c). The most frequent flowering incidence was recorded in February. Rainfall becomes an important factor that triggers the flowering process of tropical species (Satake et al., 2021). The high flowering pattern of *R. cantleyi* was recorded at higher rainfall (Wee et al., 2024). The duration of irradiation is also an important factor in the flowering of *Rafflesia.* Related to the duration of irradiation, flowering of *R. zollingeriana*

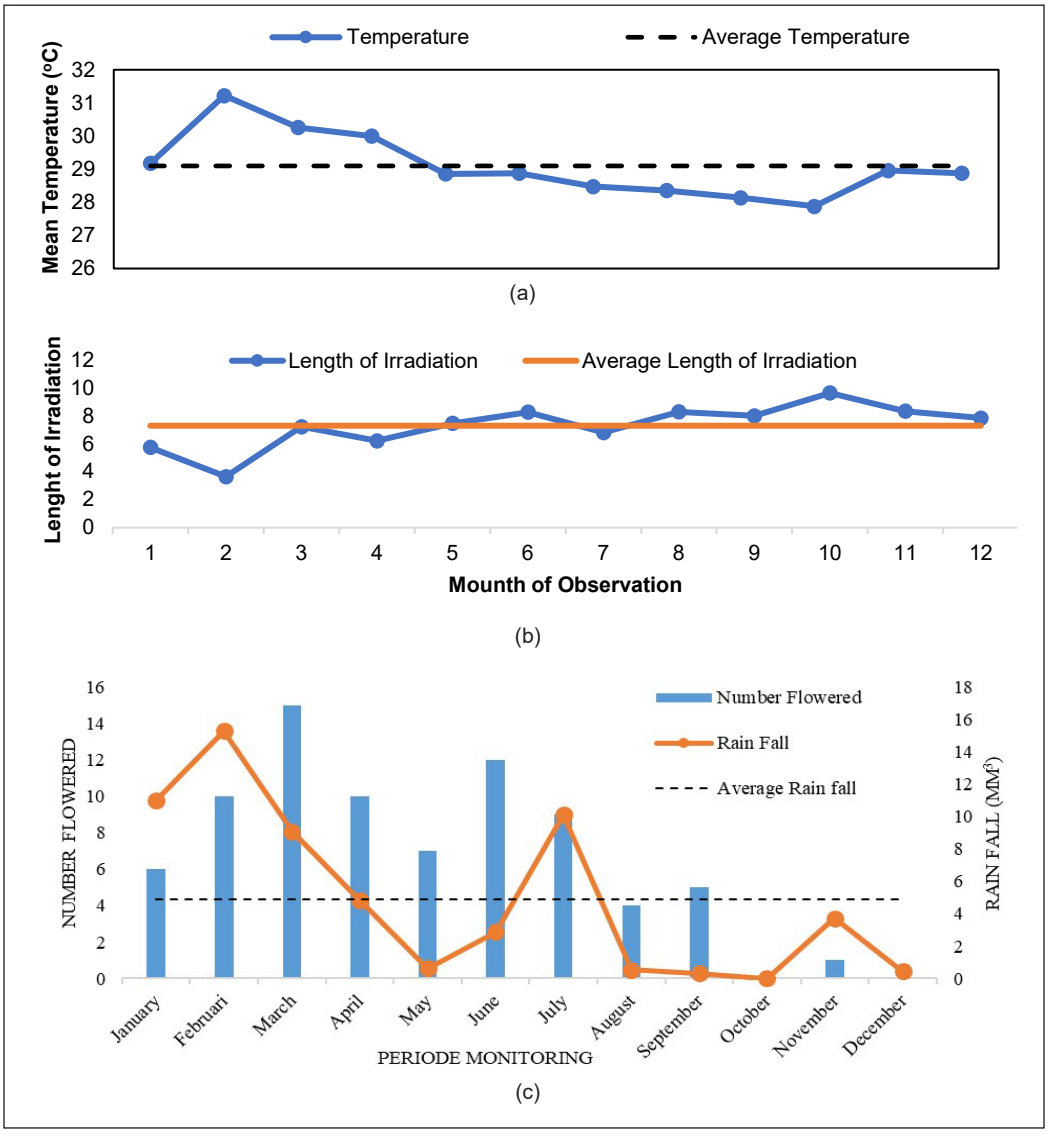

Figure 5. Flowering phenology of *R. zollingeriana* is shown as the total number of flowers blooming each month, in relation to: (a) average temperature; (b) length of irradiation; and (c) monthly rainfall

in Papring forest often occurs when the irradiation is below the average daily irradiation length that occurs every month, which was 7.3 hours (Figure 5b). This result shows that *R. zollingeriana* has low adaptation to light conditions, like other types of *Rafflesia*. The duration of irradiation indirectly affects temperature, humidity, and host health by providing nutrients for the flowering process (Nurchayati et al., 2024).

Fruit Development Stage

The fruit development stage in *R. zollingeriana* starts immediately after the flower enters the senescence stage. This stage was characterized by a change in color from red to blackish. The perigone lobes slowly turn blackish, decay, and eventually enter the rotten phase. The female flower has a disc and column that does not undergo a decay process and turns into fruit (Figure 6D). However, the male flower has both its disc and column undergo. All female flowers are assumed to produce ripe fruits if no decay occurs (Mohd-Elias et al., 2021).

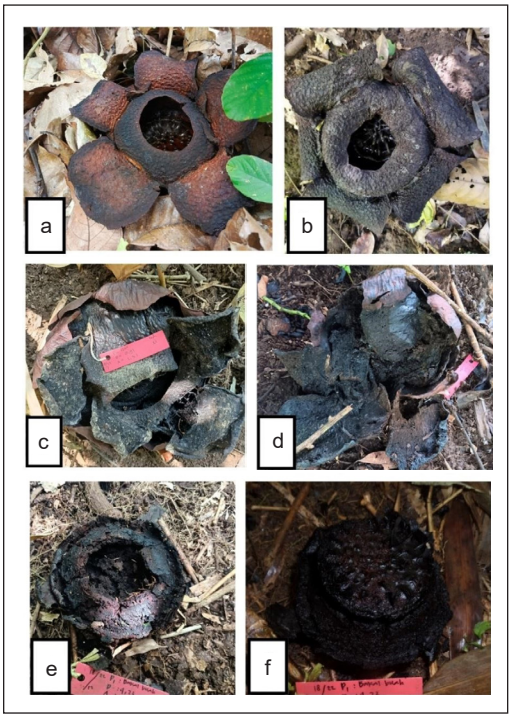

Figure 6. Stage of fruit development: (a) flower begins to turn blackish red after 2 to 3 days of blooming; (b) flower begins to enter the stage of decay or rotten stage after 5 to 7 days of blooming; (c) perigon dries up and begins to shed after 7 to 14 days of blooming; (d) perigon is fully decay after 14 to 20 days of blooming; (e) remain parts of the diaphragm and disc after 20 to 40 days of blooming; (f) leaves the discus and the fruit after 45 to 70 days of blooming

Growth Rate of *R. zollingeriana*

The growth of *R. zollingeriana* in Papring Forest was analyzed based on data on its diameter and size. The average bud growth rate reflects the variation of growth at different flower bud phases. Figure 7 shows that the growth pattern follows the exponential growth models and fits the growth model of *R. arnoldii* (Susatya, 2020), *R. patma* (Mursidawati et al., 2019; Mursidawati & Wicaksono, 2020), and both *R. cantley* and *R. azlanii* (Kamal et al., 2022). The bud growth model is expressed as Y (diameter)= $3.897e^{(0.0067x)}$, where Y represents the bud diameter and X represents the time (R^2=0.984). The model shows that the smaller buds have a slower growth rate, while the larger ones have faster rates. The cupule phase had the slowest growth rate (0.0099 cm/day). Meanwhile, the fastest was the perigone phase (1.1971 cm/day). The growth rate value showed the lowest value relative to the other stages. The developmental stage with

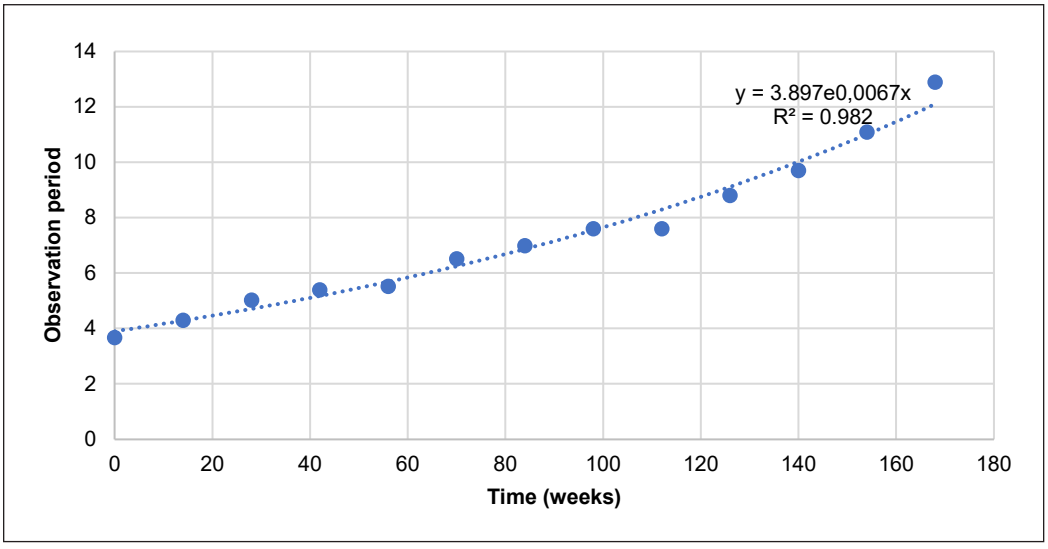

Figure 7. Growth Rate of *R. zollingeriana* based on time and observation period

Table 2
Growth rate and coefficient of variation of bud diameter by growth stage

Flower Development Stage of *R. zollingeriana* (Diameter Range in cm)	Growth Rate (cm day^{-1})	Standard Deviation (cm day^{-1})	Variation Coefficient (%)
Swollen Host (1.06–1.98)	-		
Cupule (1.53–4.97)	0.0099	0.0100	101.4239
Cupule Bract Transition (3.56–7.91)	0.0291	0.0319	91.3867
Bract (3.56–12.65)	0.0292	0.0278	105.3223
BPT with Witish (4.51–17)	0.0668	0.0557	119.9845
BPT with Pinkish (7.26–18.76)	0.0866	0.0706	122.5660
Perigon (15.09–20.19)	0.1971	0.1079	9.0113

the highest growth rate is the perigone stage, which was 1.1971 cm/day (Table 2 and Figure 7). The perigone phase is 19 times faster than the cupule phase.

Life Cycle of *R. zollingeriana*

The life history of *Rafflesia* is very important to investigate because it is both an invisible and a visible stage. The invisible stage is hard to study and starts from seeds infecting the cambium tissues of the host plant, *Tetrastigma*. The seed then grows its endophytes and radially spreads into the host's vascular tissues. It later develops into the expansion of the tissue network toward the xylem and phloem, which leads to the formation of new *Rafflesia* shoot protrusions or flower buds (De Rybel et al., 2016; Wicaksono et al., 2020; Wicaksono et al., 2021b). This intricate development process contributes to the formation

of new shoot protrusions, which play a vital role in the reproductive cycle of *Rafflesia*. This part is the beginning of the generative stage, which is part of the visible stage of *Rafflesia* (Kamal et al., 2021; Mursidawati et al., 2019; Wicaksono et al., 2020).

The vegetative development during the invisible stage is hard to observe due to the whole invisible stage taking approximately 2 to 3 years (Lestari & Susatya, 2022; Nurchayati et al., 2024). The visible stage was observable and divided into eight developmental phases: swollen host, cupule, CBT, bract, BPT with whitish, BPT with pinkish, perigone, and anthesis. The fruit development stage encompasses the stages of rotting and ripening fruit. The swollen host phase is the first sign of the emergence of the *Rafflesia* and takes 36 days to reach the CBT stage. From the CBT stage, a bud needs 21 to 70 days to enter the Bract stage (Figure 8).

The time required for buds in the bract phase to turn to the Bract Perigone Transition with whitish (BPT Whitish) phase is 21 to 43 days. The total time needed from the first stage to the BPT whitish stage is 219 days. The next stage is BPT pinkish. The analysis results show that the time required to reach the BPT Pinkish stage is 234 days. The time required for development from BPT whitish to BPT pinkish is approximately 15 to 71 days. The change from the BPT pinkish phase to the perigone stage takes 11 to 30 days (Figure 8). The time required for the perigone to develop to the anthesis stage is 28 to 118 days.

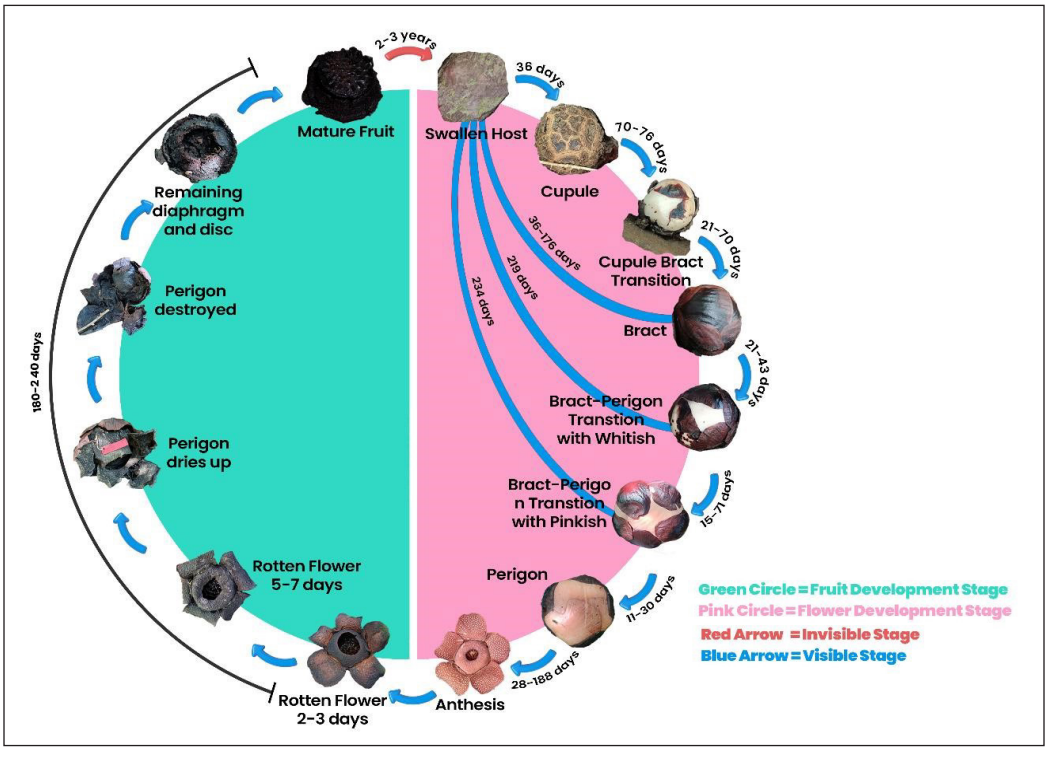

Figure 8. Life cycle reconstruction of *R. zollingeriana*

The anthesis phase or flower stage of *R. zollingeriana* bloomed perfectly for only 5 to 7 days and then blackened and entered the rotten stage. During the rotten stage, it takes 180 to 240 days to shed all the perigones and leave the ripe fruit (Figure 8).

Distribution Size, Bud Sustainability, Mortality, and Sex Ratio

The observation was made on five populations, with 9 to 171 buds in each. This condition changed as the observation time increased over 12 months (Table 3). During the 12 months, differences in mortality and bud emergence were observed. The buds that managed to stay alive and successfully bloom to form mature fruit without decaying until the end of the observation varied from different populations. The change in the population structure of the number of buds at each stage of development is shown in Figure 9.

Table 3
Condition of R. zollingeriana *buds during all observation periods in Papring Forest, Kalipuri Subdistrict, Banyuwangi, East Java, Indonesia*

Monitoring Period	Location	Total Buds Founded	Total dead Buds (%)	Blossom			Still in Buds Condition (%)
				Anthesis (%)	Rotten (%)	Mature Fruit (%)	
January–March 2023	1	86	24.42	1.16	5.81	4.65	63.95
	2	5	0.00	0.00	11.11	0.00	100.00
	3	11	72.73	0.00	0.00	0.00	27.27
	4	59	18.64	3.39	15.25	0.00	62.71
	5	67	16.42	1.49	14.93	1.49	65.67
Mean		45.50	26.38	1.21	9.42	1.23	63.92
April–June 2023	1	103	53.40	0.00	8.47	0.00	37.86
	2	9	100.00	0.00	0.00	0.00	0.00
	3	9	88.89	0.00	0.00	0.00	11.11
	4	58	77.59	0.00	3.45	0.00	18.97
	5	74	67.57	0.00	6.76	0.00	25.68
Mean		50.60	77.49	0.00	3.74	0.00	18.92
July–September 2023	1	83	54.22	2.41	10.84	0.00	32.53
	2	0	0.00	0.00	0.00	0.00	0.00
	3	12	16.67	0.00	0.00	0.00	83.33
	4	24	62.50	0.00	0.00	0.00	37.50
	5	34	67.65	2.94	11.76	0.00	17.65
Mean		30.60	40.21	1.07	4.52	0.00	34.20
October–December 2023	1	49	59.18	0.00	0.00	0.00	40.82
	2	0	0.00	0.00	0.00	0.00	0.00
	3	25	52.00	0.00	4.00	0.00	44.00
	4	11	45.45	0.00	0.00	0.00	54.55
	5	21	66.67	0.00	0.00	0.00	33.33
Mean		21.20	44.66	0.00	0.80	0.00	34.54

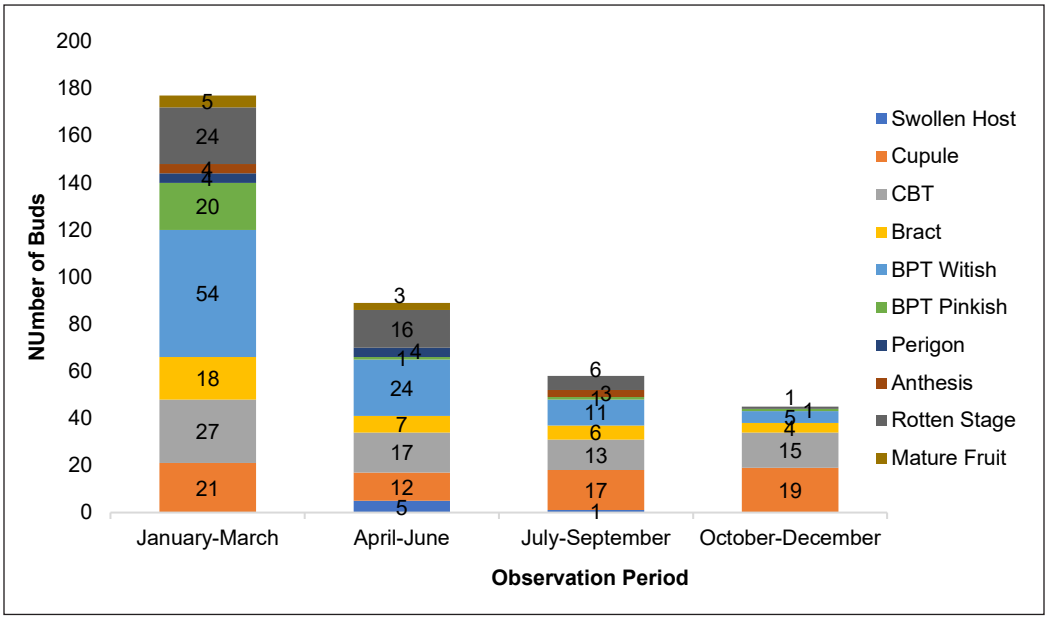

Figure 9. Population structure of *R. zollingeriana* buds in each phase after three months (January–March), six months (April–June), nine months (July–September), and 12 months (October–December)

The population size of *R. zollingeriana* in Papring Forest, Banyuwangi, has undergone varied dynamic changes across five populations. Initially, at the start of the observation, there were 148 individuals, predominantly in the bract phase, with 44 individuals, 38 in the CBT phase, and 23 each in the cupule and BPT whitish phases. Other phases, such as BPT pinkish (8 individuals), perigone (2), anthesis (2), rotten stage (6), and mature fruit (2), were present in smaller numbers. This initial phase series in Papring Forest was more comprehensive than the one found in Meru Betiri National Park, which only consisted of cupule, CBT, and bract phases (Lestari et al., 2014).

Over the following three months, the population structure of *R. zollingeriana* changed with the incoming 29 new buds, buds in growth development from a certain phase to the next growth stages, and bud mortality. Some buds in the cupule, CBT, bract, and BPT whitish phases died, while others progressed to the next phases. By the end of the three months in January to March, the number of buds in the BPT whitish phase increased to 54 individuals, whereas there were decreases in the cupule (21), CBT (27), and bract phases (18). There was an increase in the percentage of buds in the BPT pinkish (20), perigone (4), anthesis (4), rotten stage (24), and mature fruit phases (5). The observed mortality after three months was 51 buds, approximately 22.57% of the total observed (Figure 9).

Subsequent observations after six months, from April to June, revealed further changes in population size. New buds emerged, starting at the swollen host stage with five individuals. There were 89 live buds, including those in bloom or post-bloom stages.

Increases were noted in the cupule (12), CBT (17), perigon (4), and rotten stage conditions (16). The number of BPT whitish buds decreased as some transitioned to the rotten stage, resulting in 24 remaining individuals. BPT pinkish was represented by only one individual, and mature fruit by three. The observed mortality after six months rose to 167 buds, approximately 53.6% of the total buds.

From July to September, nine-month observations indicated a reduction in buds, leaving 58 individuals alive in stages such as anthesis, the rotten stage, and mature fruit. Increases were observed in the cupule stage (17), while decreases occurred in the swollen host stage (1), CBT (13), bract (6), and anthesis (3). The number of BPT whitish buds remained stable, with only one individual. Notably, perigon and mature fruit phases were absent at this stage due to either progression to subsequent phases or mortality, which claimed 85 buds, approximately 55.56% of the total.

Significant changes were evident by the end of twelve months, from October to December, with only 45 live buds remaining, mostly in the rotten stage. The swollen host stage disappeared as buds progressed, resulting in increased cupules (19) and CBT (15). Decreases were noted in the bract (4), BPT whitish (5), and rotten stage phases (1). One individual represented BPT pinkish, while the perigon, anthesis, and mature fruit phases were absent. The observed mortality after twelve months amounted to 51 buds, approximately 52.96% of the total observed during the entire period.

The total population size within one year of observation substantially varies among the five populations. The average population size, flowering success rate, and date rate were 82.13% and 78%, respectively (Table 4). The second population was recorded as the smallest population size, with nine buds, and also experienced the highest mortality within one year. All its buds had died. The first population has 171 flower buds, with a success rate of 16.4%, or 28 flowering buds. Flowering success was considered to vary from 0 to 28% and is not influenced by the population size. Similar to the success rate, the death rate does not seem to be influenced by population size. However, the death rate is considered high and ranges from 72.1% to 100%.

Table 4
Percentage of successful blooms versus percentage of deaths that occurred during the 12 months of observation

Location	Total Buds found	Number of Blooms	% Success Blooming	Number of dead	% Mortality
Plot 1	171	28	16.4%	124	72.5%
Plot 2	9	0	0	9	100%
Plot 3	43	1	2.3%	31	72.1%
Plot 19	82	14	17.1%	62	75.6
Plot 25	107	30	28%	77	72%
Average	82	15	13	61	78

Figure 10 shows that mortality was observed at various stages. The highest mortality was found in the CBT stage (27%), then followed by the rotten stage (21%), bract (16%), and cupule stages (15%). The rotten stage is dead when the bud has passed the blooming period and dies when no mature fruit has formed. So, its death was the end of the phase. The greatest mortality before blooming occurs in the CBT, bract, and cupule phases (1.53–4.97 cm, 3.56–4.97 cm, and 3.56–12.65 cm, respectively). All this high mortality was observed in small bud sizes. Susatya et al. (2017) revealed that buds smaller than 9 cm have high mortality. The buds with more than 15 cm exhibited zero mortality, leading to the blooming or flowering stage. The small bud sizes have a greater susceptibility to death. However, larger buds survived the conditions that caused death (Figure 11).

The high mortality rate of *R. zollingeriana* and the unbalanced ratio of male and female flowers pose significant challenges to the existence of *R. zollingeriana* populations in the future (Hidayati et al., 2000). Studies have shown that the mortality rates of *R. patma* and *R. bengkuluensis* buds are notably high at 44% and 49%, respectively (Mohd-Elias et al., 2021; Pelser et al., 2016). Additionally, *Rafflesia* bud mortality always occurs in various endemic areas. This high mortality is often considered a form of natural population control, linked to the host plant's ability to meet the nutritional needs of *Rafflesia* (Teppabut et al., 2018). The flowering success of *R. zollingeriana* has been observed to be relatively low, with a cumulative success rate of 17,71%. Female flowers tend to dominate the blooming flowers, with a ratio of 55% female flowers to 45% male flowers. This unbalanced ratio of male and female flowers is a natural phenomenon that has also been observed in *R. cantleyi*, where female flowers are more dominant than male flowers. However, the exact mechanism behind this imbalance in the ratio of male and female flowers remains unclear

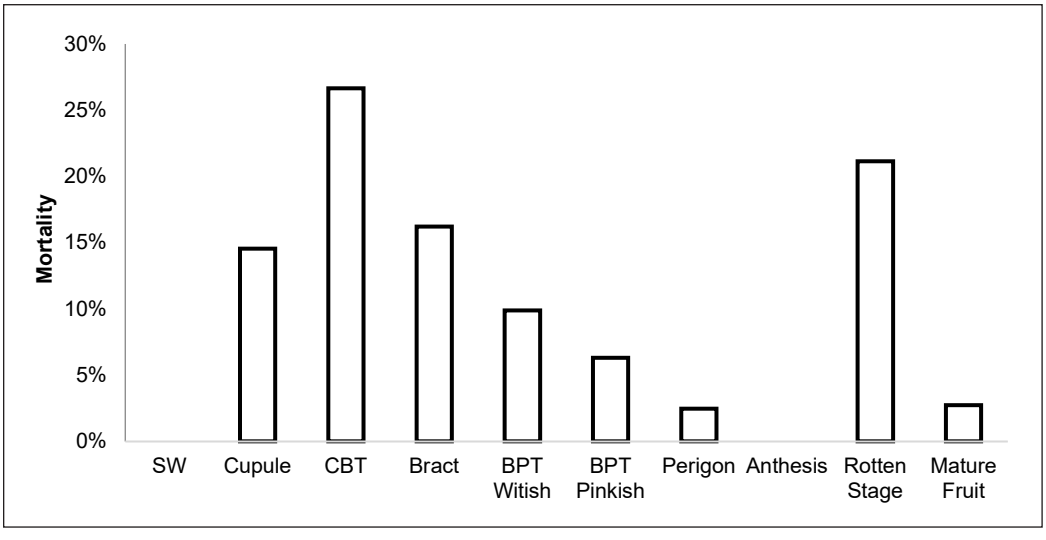

Figure 10. Mortality percentage at each time point during the 12 months of observation

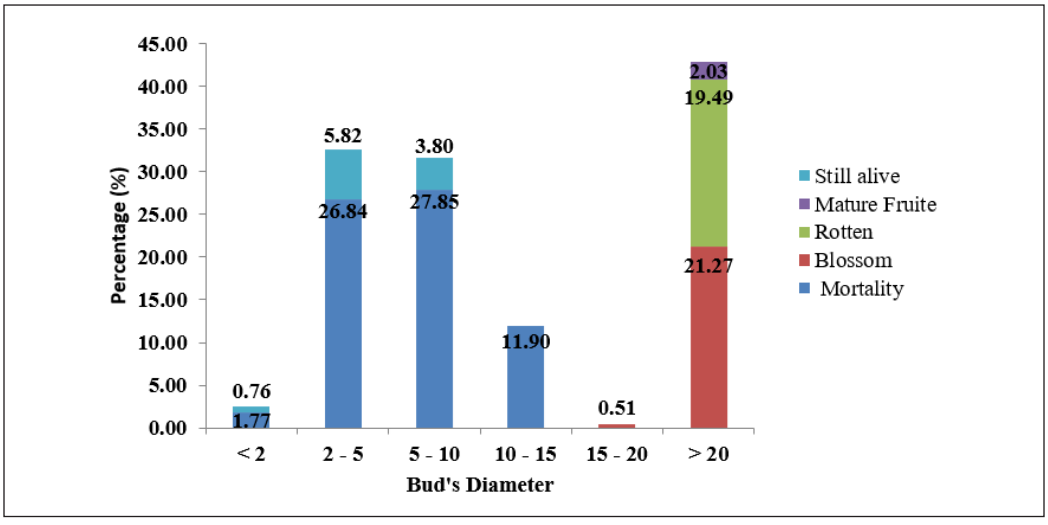

Figure 11. Condition of *R. zollingeriana* based on the distribution of bud size categories during the 12-month observation period in Papring Forest, Kalipuro subdistrict, Banyuwangi

due to limited research on the life history of *Rafflesia* (Hidayati et al., 2000). Future research is crucial to conduct a more comprehensive study of bud growth in relation to environmental factors to gain a clearer understanding of the impact of environmental conditions on bud development. DNA-based research is also needed to elucidate the mechanism behind the unbalanced sex ratio in *R. zollingeriana*. This information is vital for the *in situ* conservation of *R. zollingeriana* species in the Papring Forest, Banyuwangi Regency (Susatya, 2020).

Death of the buds was observed at different phases with different causes (Figure 12). The cause of death occurs due to environmental factors, such as drought or excessive water, and biological factors. In general, drought conditions cause the buds to dry out and disintegrate. Death was also found in the swollen host phase, as well as root damage to the host. Damage to the roots in the form of openings on the surface of the swollen host causes the cessation of its growth. This also happens to buds at the cupule and CBT phase (Figure 12b). The death of buds during the phase of CBT is probably a result of submerging buds in rainwater during the rainy season (Figure 12e). Submerging in excessive water will increase the infection of pathogenic organisms, which leads to the acceleration of the decay process (Figure 12c). Interestingly, the death caused by animal predation is also recorded at the site. Animal bites generally occur at large bud sizes or in BPT and Perigone stages (Figure 12g). Suspected animals were monkeys, wild boar, and rats. Dry conditions caused the CBT to dry and disintegrate (Figure 12d).

The condition of dead bracts in the Papring Forest often occurs because they are submerged in water and rot (Figure 12e). Excess water in *Rafflesia* buds can inhibit oxygen access to plant tissues, causing tissue death. Some BPT whitish phases were dead with holes

in the center due to being eaten by animals (Figure 12f). Injury to the bud surface can also cause death when the buds have entered the BPT with a pinkish phase (Figure 12g). The condition is similar to *R. cantleyi,* which died due to herbivory activity. Perigone phase *R. zollingeriana* buds that died due to dry conditions showed clear damage (Figure 12h).

The bract that protects the bud starts to dry out and lose its moisture. The thick and fleshy part of the perigone turns wrinkled and blackened. The inner part, the candidate flower part, decomposes and dries so that the bud can no longer open. In *Rafflesia*, normal death is at the end of the phase, namely after the flower blooms and enters the rotten stage (Figure 12i).

After blooming, *Rafflesia* flowers undergo a natural decay process essential for the ecosystem. This decay stage is marked by changes in the flower's appearance and smell. The previously large, fleshy, and reddish perigone transitions to a dark brown-to-black

Figure 12. Various cases of death in *R. zollingeriana*: (a) Cupule that dies blackened because the *Tetrastigma* roots of its host are broken and damaged so that the supply of food intake is stopped; (b) CBT that rot because they are submerged in water during rain; (c) CBT that is destroyed due to drought conditions; (d) Bract that dies due to rotting submerged in water; (e) BPT Whitish that dies because monkeys eat it; (f) BPT Pinkish that died due to drought; (g) Perigon that died because of bite marks on its surface; (h) Perigon that dies due to drought; (i) Dead condition in flowers that have bloomed because they have entered the rotten stage phase

color, losing its thick texture. The flower's surface becomes slimy and watery, leading to the disintegration of the flower structure. This decay process is crucial as it contributes to the restoration of soil nutrients and supports the surrounding ecosystem (Mohd-Elias et al., 2021). The decay of *Rafflesia* flowers is part of their life cycle, where they play a role in nutrient recycling and ecosystem functioning. The decay process aids in returning organic matter and nutrients to the soil, enriching it and supporting the growth of other plants in the ecosystem. Additionally, the decay of *Rafflesia* flowers contributes to the overall biodiversity and functioning of the ecosystem by providing resources for various organisms (Pelser et al., 2016). Furthermore, the decay of *Rafflesia* flowers is a natural phenomenon that has been observed in other plant species as well. Studies on other flowers, such as Oenothera, have shown changes in petal color and chemical components during senescence, highlighting the natural progression of flower decay in different plant species (Teppabut et al., 2018). This senescence process is common in flowers and essential for nutrient recycling and ecosystem sustainability.

CONCLUSION

These findings underscore the species' vulnerability, low blooming success, and high mortality, which inform conservation strategies for *R. zollingeriana* in Papring Forest, Banyuwangi.

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