

Comparative analysis of pollen morphology at three flowering stages of *Trimezia martinicensis* (Jacq.) Herb. (Iridaceae), an invasive species in Indonesia

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ABSTRAK

Morfologi serbuk sari menyediakan wawasan penting mengenai reproduksi, taksonomi, dan hubungan evolusi tumbuhan. Penelitian ini mengkaji perkembangan serbuk sari pada *Trimezia martinicensis* (Iridaceae), jenis asing invasif di Indonesia, pada tiga tahap pembungaan: kuncup tertutup, kuncup berkembang, dan bunga mekar. Karakter vegetatif dan morfologi bunga didokumentasikan bersamaan dengan analisis palinologi spesifik tahap. Serbuk sari diamati menggunakan mikroskop cahaya untuk menilai perubahan orientasi, bentuk, apertur, serta arsitektur eksin. Hasil penelitian menunjukkan adanya transisi morfologi yang jelas, termasuk butiran berbentuk sferoidal dengan apertur monokolpat pada tahap awal, yang berkembang menjadi bentuk lebih membulat dengan struktur dinding yang lebih halus pada bunga mekar. Temuan ini menegaskan dinamika morfologi serbuk sari selama proses antesis dan menyoroti relevansinya bagi biologi reproduksi, taksonomi, serta pengelolaan jenis IAS di Indonesia.

Kata kunci: Antesis, apertur, jenis IAS, kuncup bunga, ornamentasi, reproduksi

ABSTRACT

Pollen morphology provides critical insights into plant reproduction, taxonomy, and evolutionary relationships. This study investigates pollen development in *Trimezia martinicensis* (Iridaceae), an invasive alien species in Indonesia, across three flowering stages: closed bud, developed bud, and mature flower. Vegetative and floral traits were documented alongside stage-specific palynological analyses. Pollen grains were examined under light microscopy to assess changes in orientation, shape, aperture, and exine architecture. Results revealed distinct morphological transitions, including spheroidal grains with monocolpate apertures at early stages, progressing to more rounded forms with refined wall structures in mature flowers. These findings highlight the dynamic nature of pollen morphology during anthesis and underscore its relevance for reproductive biology, taxonomy, and management of IAS in Indonesia.

Keywords: Anthesis, aperture, flower bud, IAS, ornamentation, reproduction

INTRODUCTION

Pollen is a male generative organ in flowering plants (angiosperms) found in anthers, with primary function in reproduction, the pollination. This organ is evolutionary important as variation in pollen morphology is a known driver of evolutionary changes

in flowering plants (Bahadur et al., 2022). During reproductive function, pollen undergoes a developmental phase before pollination occurs. Pollination is a process in plants in which pollen is transferred from the male to the female reproductive organs of seed plants (Agashe & Caulton, 2009; Hesse et al., 2009). Pollen development is a critical step in plant sexual reproduction, in which male gametophytes develop from microspores into mature structures capable of generating male gametes (Hafidh et al., 2016). Pollen development in flowering plants involves orderly cell differentiation, wall development, and interaction with the tapetum, the innermost layer of the anther that supplies nutrients and wall material to the developing pollen (Song et al., 2022). The pollen wall of angiosperms consists of two main layers: intine and exine. The intine is the inner layer and is composed of pectin and cellulose, while the exine is the outer layer, composed mainly of sporopollenin, acetolysis-resistant biopolymers (Hesse et al., 2009). These characters in pollen morphology play significant role in taxonomy as they serve as a good descriptive character on family or even lower levels, such as the species level. Several pollen morphological characteristics, which are usually used to identify plants, are polarity and symmetry, dispersal units, size, form, wall structure, ornamentation (sculpture), and gaps or apertures of the pollen (Hesse et al., 2009).

During flower development, pollen varies at every stage of pollen development include polar axis length, equatorial diameter, exine thickness, and the number of longitudinal ribs/flanges (Suratman et al., 2022). These morphological characteristics of pollen grains are essential for understanding plant evolution, adaptation, diversity, and taxonomic discrimination (Taia et al., 2023). Understanding pollen development will also reveal evolutionary states of pollen morphology maintained by selection (Albert et al., 2011; Kant, 2019; Taia, 2022). Thus, examining the developmental stages of pollen provides a vital framework for understanding character evolution, offering a clearer taxonomic perspective within the family.

Trimezia martinicensis (Jacq.) Herb. is an invasive alien species, or IAS (Rahmawati & Rosleine, 2023) from Central and South America, with Brazil hosting the most species diversity of the genus (Lovo et al., 2018). In Indonesia, *T. martinicensis* was abundant in communities with high humidity, suggesting that moist conditions favor its growth (Rahmawati & Rosleine, 2023). While it has potential as a blood depurative (Moraes Carlesso et al., 2025) and occasionally cultivated as an ornamental plant (Setyawati et al., 2015), it is included as IAS for Indonesia (Nofitasari et al., 2025; Rahmawati & Rosleine, 2023). As an IAS, this species has a high survival rate and may reproduce quickly and readily (Rahmawati & Rosleine, 2023). That is why studying the reproduction aspect of this species is important for the conservation of native plant in Indonesia. Consequently, the observation of pollen morphological characteristics of *T. martinicensis* is essential for identifying the developmental phase of this species, thus contributing in the understanding the reproduction aspect of this IAS.

In terms of reproductive timing, *Trimezia* exhibits a highly coordinated, restricted, short-lived anthesis. This period of floral activity is concentrated into a few hours. Flower development of the flower of *T. martinicensis* consists of a closed bud, a developed bud, and a mature flower. The early stage of flower development is when the bud is closed by the sepal and petal primordia, which are starting to form. It will develop into a developed

bud or an open flower. The more detailed flower will be found in the mature flower stage (Lovo et al., 2021). Observing pollen development in *T. martinicensis* will provide valuable insights into *Trimezia* taxonomy and will contribute to efforts to regulate its reproduction as IAS in Indonesia.

METHODOLOGY

Plant material

The sample was obtained from the lowland region of Banyumas Regency, Central Java, at a mean elevation of approximately 108 m above sea level (asl). Geographically, the sampling area lies between 7°15'05"–7°37'10" S and 108°39'17"–109°27'15" E, climatically categorized as tropical rainforest climate, with mean annual precipitation exceeding 2,500 mm and an annual humidity exceeding 80% (BPS-Statistics Indonesia Jawa Tengah Province, 2022). These humid conditions are optimal for the naturalization and reproductive success of *T. martinicensis*, ensuring the availability of all required developmental stages (budded, nearly blooming, and fully bloomed flowers) for this study. The sampling method was purposive sampling.

The analysis of *T. martinicensis* was conducted across three distinct developmental stages, from early bud to full anthesis, to ensure their development. A variety of field-collected floral specimens was collected to provide a broad representation of these phases. Multiple samples from the same developmental category were combined into a single representative cohort. This approach allowed for a focused, stage-specific characterization of the pollen morphology as it transitioned through each identified phase of maturity.

Plant and pollen observation

This study was based on observations of morphological characteristics and pollen characteristics of *T. martinicensis*. Initial observations were centred on a qualitative morphological assessment of the collected specimens. Detailed descriptions were recorded for the vegetative organs, including the rhizome and foliar arrangement, to ensure correct species identification. This was followed by examination of the reproductive organs, with particular emphasis placed on the floral traits and their development.

For the characterization of pollen characteristics, specimens were categorized into three developmental stages: closed buds, developed buds (near-anthesis), and mature open flowers, following the framework established by Lovo et al. (2021). Pollen grains were harvested by dissecting the anthers of *T. martinicensis* directly onto glass slides. The samples were mounted in distilled water and secured with a cover glass for observation under a light microscope (Olympus CH20).

To ensure the reliability of the qualitative data, observations were replicated within each developmental cohort to confirm morphological consistency. While the study utilized a stage-specific sampling design, we performed multiple technical replicates on each slide. This involved examining a single anther across various fields of view to capture different pollen orientations such as proximal, distal, and equatorial views. Thereby strengthening the descriptive analysis of the grains within that specific stage.

The resulting pollen morphology was described qualitatively, focusing on diagnostic characters including pollen unit, shape, size class, and exine architecture. The palynological terminology used for these descriptions was standardized according to the established frameworks of Halbritter et al. (2018) and Hesse et al. (2009).

RESULTS AND DISCUSSION

Plant observation and identification

From the field observations, *T. martinicensis* grows as a perennial, rhizomatous herb that typically forms dense, organized clumps. This plant arises from a short, thick rhizome. The foliage is arranged in a distinct fan-like (distichous) pattern, consisting of flat, ensiform (strap-like) leaves. Its inflorescence is borne on an elongated, wingless peduncle that emerges from the basal rosette (Figure 1a). When it's mature, the flowers are notably ephemeral, featuring three large, triangular yellow tepals accented by intricate brown banding at the centre.



FIGURE 1. (A) Habitus of *T. martinicensis*; (B) *T. martinicensis* flower arranged by its development phase, (C) *T. martinicensis* anther arranged by its development stage. From left to right, the categories consist of closed bud, developed bud, and mature flower. One scale bar indicates 1 cm.

Throughout the observations, the anthers showed significant changes in both size and texture as they matured (**FIGURE 1.B-C**). In the early bud (closed bud) stage, the anthers are small, pale, and juvenile. As the flower nears its anthesis (developed bud), the anthers swell and turn a vibrant yellow. Interestingly, as the flower fully blossoms (mature flower), the water content in the anthers drops sharply. This causes the tissue to dry out and darken to a blackish hue. This desiccation is a critical step; it allows the anther to eventually split (dehisce) and release the dried pollen for dispersal.

Taxonomically, these specimens align with the established descriptions for *T. martinicensis*. The species is characterized by short stem internodes and a corm-like rhizomatous base (Acevedo-Rodríguez & Strong, 2005). Furthermore, our measurements of the flowering stem confirmed that the peduncle is significantly longer than the rhipidium at the first proximal node, a key morphological marker for this species (Lovo et al., 2018).

Pollen observation

The pollen morphological observations show that *T. martinicensis* exhibits distinct characteristics across different stages of flower development. The morphology of *T. martinicensis* pollen taken from budding flowers (closed bud) observed at 400x magnification (Figure 2) shows an elliptical or prolate spheroidal shape, where the length of the pollen is greater than its width. Microscopic observations at proximal, distal, and

equatorial views show that the pollen exhibits a smooth surface with psilate-type ornamentation, meaning there are no conspicuous protruding structures. The monocolpate ornamentation is visible as a slit at the centre of the pollen, giving it a shape resembling a coffee bean. The structure of this aperture is visible, with the colour appearing greyish yellow almost transparent.

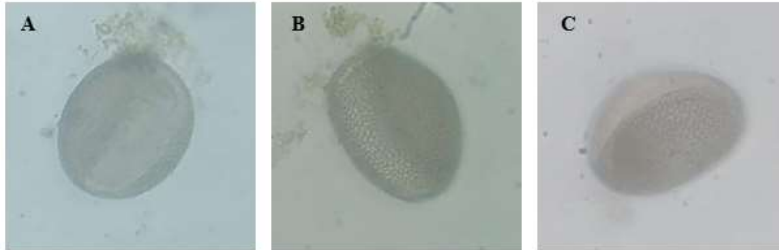


FIGURE 2. *Trimezia martinicensis* *T. martinicensis* pollen taken from closed bud flowers was observed from (A) proximal view, (B) distal view, and (C) equatorial view with a microscope at 400x magnification.

The morphology of *T. martinicensis* pollen in later-developed buds or nearly blooming flowers differs slightly from bud flowers, particularly in the structure of the aperture and a few other characteristics (Figure 3). Pollen from later-developed buds or nearly blooming flowers typically have pollen with a more oblong or prolate spheroidal form, with the length being more noticeable than the breadth. The pollen of blossoming flowers has a more enlarged curve on the side and a deeper cleft, whereas this pollen has a sharper curve at the aperture and a shallower slit. In terms of decoration, the pollen from nearly blooming flowers maintains a psilate texture, meaning it is smooth and devoid of noticeable ornamentation. It is often greyish yellow in tone with a hint of transparency.

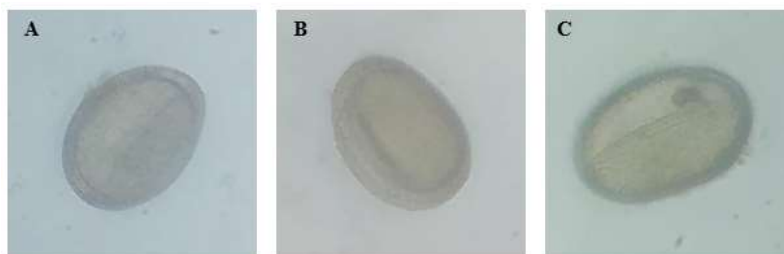


FIGURE 3. *T. martinicensis* pollen taken from almost blooming flowers (developed bud) was observed from (A) proximal view, (B) equatorial view, and (C) distal view with a microscope at 400x magnification.

Pollen from *T. martinicensis* fully bloomed flowers (mature flowers) revealed a range of morphologies, from nearly round ovals to precisely spherical, seen from different views (Figure 4). The exine was seen as psilate sculpture and the intine-designated middle layer was also plainly evident. These pollens are often clear with yellow-brown undertones. While pollen from developing flowers displays a more open, visible slit, pollen from blooming flowers has a monocolpate aperture with a less noticeable slit than pollen from budding or near-blooming flowers. Even while this aperture shift is visible, the pollen's fundamental morphology, such as its form and colour, remains consistent throughout these flower development phases.



FIGURE 4. *T. martinicensis* pollen taken from fully bloomed flowers (mature flower) was observed from (A) proximal view, (B) distal view, and (C) equatorial view with a microscope at 400x magnification.

To summarize, the difference pollen morphological characteristics from the three different flowering stages was described as **TABLE 1**. Despite the detailed morphological data available for *T. martinicensis*, specific records of formal micrometric characterization of the pollen size were beyond the scope of this initial observation.

TABLE 1. The differences of pollen morphological characteristics of *T. martinicensis*

Characters	Closed Bud	Developed Bud	Mature Flower
Exine ornamentation	Psilate	Psilate	Psilate
Aperture	Monocolpate, visible as a slit at the center	Monocolpate, enlarged curve in the side, deeper cleft, but shallower slit	Monocolpate, almost unnoticeable slit
Shape	Spheroid to round oval	Oblong spheroid	Oval to spheroid
Color (intine)	Greyish yellow to transparency	Greyish yellow	Yellow brown

The morphological analysis of *T. martinicensis* pollen across three developmental stages reveals a coordinated transition in shape, aperture visibility, and pigmentation (**TABLE 1**). While some features, such as the psilate (smooth) exine surface, remained constant throughout all stages, other characters showed clear modifications as the flower approached anthesis. The persistence of the psilate exine suggests that the fundamental architecture of the pollen is established early in the bud stage and does not undergo significant structural reorganization during later maturation. However, in some study related to pollen development, in the early stages of pollen formation, the surface of the pollen looks simple (Haas et al., 2017), but the mature pollen is basically coated with thin exine, complex exine, and a coat (tryphine) that is deposited in the exine's pores (Ariizumi & Toriyama, 2011; Shi et al., 2015; Song et al., 2022). Exine development necessitates a synergy of complicated metabolic events. A mature pollen grain with a perfect exine will have an elaborate, more defined ornamentation aperture structure (Haas et al., 2017).

As for the aperture, the three stages of pollen have the same monocolpate aperture, but the "slit" showed the dynamic changes. In the early bud stage, the aperture is a simple, visible slit. However, as the flower nears blooming (developed bud), the cleft appears to deepen and curve. Interestingly, in the fully bloomed flower, this slit becomes almost unnoticeable under light microscopy. According to Haas et al. (2017), the aperture, the slit or opening in the pollen wall, starts to become more distinct, while ornamentation, the decorative pattern on the surface, becomes more defined. However, in this observation, while the aperture of the pollen becomes more distinct, the ornamentation shows a characteristic of persistence.

Furthermore, observations of several pollen development stages of *T. martinicensis* show that pollen development can be distinguished by changes in pollen shape and the distinction of the aperture. In this observation, the pollen shape of *T. martinicensis* shifts from round-oval in the bud to an oblong spheroid in the developed bud. Finally, it returns to a spherical/oval form in the mature flower. The suggested reason for these changes is likely to reflect changes in the grain's hydration state and internal pressure, in response to the desiccation of the anther tissue observed in this study.

In addition, the transition in pigmentation from a greyish yellow/transparent hue to a deeper yellow brown in the mature flower indicates the accumulation of cytoplasmic contents or the maturation of the intine and sporopollenin layers. The presence of the intine layer, which became more evident as the colour deepened, underscores the completion of the pollen wall development prior to the opening of the flower. These developmental nuances suggest that *T. martinicensis* prioritizes internal gametophyte readiness and aperture modification over external exine ornamentation to ensure successful reproduction within its brief temporal niche.

Overall, these characteristics are found to be similar to the description of Abbas & Sukarsa (2022), which said that *T. martinicensis* pollen exhibits the morphology of a monadic unit, which means that it does not stand in groups but instead stands alone, with the polar axis size $27.2 \pm 33.6 \mu\text{m}$ and the equatorial diameter $24.3 \pm 31.3 \mu\text{m}$. The pollen type is prolate spheroidal, which has a slightly oval form and a long axis diameter greater than the short axis diameter. The pollen size is medium, as indicated by the size falling into the medium group. This pollen's aperture is monocolpate, meaning it has a single longitudinal groove or slit. The pollen's surface or ornamentation is called psilate, which means it is smooth and devoid of noticeable decorations or extra structures. This description is similar to the pollen from a mature flower observed.

All things considered, these findings demonstrate that the shifts in pollen geometry and aperture structure are representative of specialized reproductive adaptations in *T. martinicensis*. By establishing this qualitative baseline, the study contributes a significant taxonomic marker for the genus. In addition, understanding these developmental nuances is a pivotal step toward mastering the regulation of its reproductive cycle, which is essential for developing strategies to regulate its reproduction in future conservation of Indonesian flora, as a mean of control of an IAS in general.

CONCLUSIONS

Pollen development in *Trimezia martinicensis* exhibits clear morphological shifts in aperture, shape, and intine colour across successive flowering stages, while the exine surface remains consistently psilate. Early-stage pollen shows a distinct monocolpate aperture with a central slit and spheroid to oval form, progressing to oblong spheroid grains in developed buds, and finally to rounded pollen with a faint aperture and yellow-brown intine in mature flowers. These stage-specific variations provide a valuable morphological baseline for taxonomic classification and reproductive regulation of *T. martinicensis*, supporting efforts to understand and manage its invasive potential.

SUGGESTION

We advise on the use of *Scanning Electron Microscopy* (SEM) and *Transmission Electron Microscopy* (TEM) for future investigations for a definitive characterization of the exine's surfaces and to elucidate the ultrastructural layers of the pollen, particularly the distinction between the endexine and the intine during the final stages of maturation.

AUTHOR CONTRIBUTIONS

A.W.P.A., I.N.A., H.D.K., S.L., R.D.A.: project conception; I.N.A., S.L., R.D.A.: methodology; H.D.K., A.W.P.A.: data analyses; I.N.A.: original manuscript draft; H.D.K., A.W.P.A.: manuscript review and editing.

CONFLICTS OF INTEREST STATEMENT

There are no conflicts to declare.

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