

Anatomical traits and economic potential of *Amorphophallus variabilis* and conservation implications in Selo Arjuno Forest, Central Java, Indonesia

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Abstract. Wahidah BF, Khasanah R, Husain F. 2026. Anatomical traits and economic potential of *Amorphophallus variabilis* and conservation implications in Selo Arjuno Forest, Central Java, Indonesia. *Biodiversitas* 27 (2): d270213. <https://doi.org/10.13057/biodiv/d270213>. *Amorphophallus variabilis* is rarely utilized or studied despite its ecological and economic value. This study aimed to identify its anatomical characteristics, secretory structure, and the distribution of ergastic substances in its organs, including assessing their implications for conservation and local economic development. The study was conducted in Selo Arjuno Forest, Kendal District, Central Java, Indonesia. Anatomical slides from six mature individuals were prepared with paraffin methods and examined under a light microscope. Socio-economic data were collected through in-depth interviews. All data were analysed descriptively. The results showed that tubers are the primary storage organs, with a very high starch granule content ($\pm 8400/\text{mm}^2$), far exceeding those in petioles ($\pm 25/\text{mm}^2$) and leaf blades ($\pm 71/\text{mm}^2$). Sand and druse calcium oxalate crystals dominate tubers, contributing to stress tolerance. Tannin distribution is organ-specific, namely schizogenous cavities are more abundant in petioles, while idioblasts occur more frequently in tubers. Interviews indicate that *A. variabilis* is rarely cultivated, although its glucomannan-rich tubers have strong potential for functional food and health products. These findings highlight the importance of functional anatomy for conservation planning. In situ conservation and community-based ex situ cultivation can support sustainable management while creating utilization opportunities that enhance local livelihoods.

Keywords: *Amorphophallus variabilis*, ergastic substances, glucomannan, Selo Arjuno Forest, utilization-based conservation

INTRODUCTION

Amorphophallus, a genus in the family Araceae, is notable for its distinctive morphology and ecological adaptations. Some species of this genus have large tubers and flowers with a putrid odor due to sulfur compounds, particularly dimethyl trisulfide, which produces a carrion-like odor (Kang et al. 2023; Liu et al. 2023). They are distributed across Africa, Madagascar, Asia, and Australia, with the highest centers of diversity in Southeast Asia, mainly West Malaysia Region (Rambey et al. 2025). In Indonesia, around 25 species have been recorded, some of which are used as food or traditional medicine (Faristy and Vauzia 2024). In India, *Amorphophallus paeoniifolius*, for example, is used in Ayurvedic practices to treat various ailments, including tumors, inflammation, hemorrhoids, asthma, and anemia (Islam et al. 2023).

Amorphophallus variabilis, known locally in Indonesia as iles-iles, is a lesser-known species despite its abundance in Java. This species is often found around settlements and secondary forests, including in Selo Arjuno Forest, Limbangan Sub-district, Kendal District, Central Java (Wahidah et al. 2022). Its utilization by local communities is still very limited. Some even consider it a weed and a food source for snakes (Pambudi et al. 2020; Wahidah et al. 2022), although Chairiyah et al. (2011) and Makiyah and

Tresnayanti (2017) have reported that *A. variabilis* tubers are safe for consumption as they do not cause toxic reactions in test animals.

The tubers of this species are known to contain relatively high levels of glucomannan, giving them considerable potential to be developed as functional food ingredients as well as economically valuable health products. The presence of glucomannan is closely associated with various ergastic substances found in plant tissues, such as calcium oxalate crystals, starch granules, and tannins. These components play important roles in the physiological processes of the plant, including serving as energy reserves, supporting adaptation to environmental stress, and functioning as natural defense mechanisms against herbivores and other external disturbances (Ceretto and Nacca 2018; Miyamoto et al. 2021). The secretory structure and distribution of ergastic substances are also important in phytochemical analysis to identify bioactive compounds and determine pharmacological potential (Simon and Nayagam 2018). However, to date, information on the distribution of ergastic substances in *A. variabilis* organs and studies of the socio-economic value of this species in rural communities are still very limited. This situation has resulted in *A. variabilis* receiving little attention, despite its potential to support food security and sustainable local development.

From a conservation perspective, the global status of *A. variabilis* has not been evaluated on the IUCN Red List, indicating a data gap regarding population trends and its international extinction risk. At the national level, several threats, such as habitat degradation, forest fragmentation, and land-use change continue to persist and threaten the sustainability of wild populations (Gaveau et al. 2021). This lack of data on anatomy, ergastic substance distribution, and economic potential has led to poorly formulated conservation strategies for this species. Therefore, this study aimed to identify and analyze the types and distribution of ergastic structures on *A. variabilis* from Selo Arjuno Forest, describe the characteristics of secretory structures, and understand its potential utilization. This study offers an integrative anatomical and socio-economic analysis of *A. variabilis*, filling a key knowledge gap by linking internal plant traits with its underutilized value in rural communities. The results of this study are expected to provide a scientific basis for conservation efforts and local economic development, as well as support the conservation through utilization strategy that links biodiversity protection with improving community well-being (Rakatama and Pandit 2020). This approach emphasizes the importance of sustainable utilization of biological resources so that ecological and social benefits can be achieved in a balanced manner.

MATERIALS AND METHODS

Study area

This research was conducted in Selo Arjuno Forest, Kedungboto Village, Limbangan Sub-district, Kendal District, Central Java, Indonesia (Figure 1). The forest is

located on the slopes of Mount Ungaran, with mixed land cover of trees, shrubs, and agricultural fields, and a tropical climate with temperatures ranging from 20–27°C and high humidity throughout the year. Selo Arjuno Forest is a natural habitat for *A. variabilis*, allowing observation of plants in their natural environment and analysis of their potential for community-based conservation. Anatomical preparation and microscopic analyses of *A. variabilis* were carried out in the Microtechnique Laboratory, Faculty of Science and Technology, Universitas Islam Negeri Walisongo, Semarang, Central Java, Indonesia.

Plant materials

Sampling was conducted using the cruise method, following existing natural paths within the forest. During path exploration, several *A. variabilis* individuals were encountered, and six mature plants were randomly selected based on the criteria of being healthy, pest/disease-free, and having relatively uniform morphological dimensions (Dowling and Blaesing 2022). Six individuals were deemed sufficient to represent the anatomical variation within a natural *A. variabilis* population, while also considering conservation ethics to avoid disrupting the population's sustainability.

The samples used consisted of three main organs, i.e., leaves, petioles, and tubers. The selection of these three organs aimed to obtain a comprehensive picture of the anatomical structure and distribution of ergastic substances throughout the plant. All samples from six individuals were collected, with leaf and petiole samples processed immediately during the rainy season when vegetative growth is most active (September–April). Meanwhile, tuber samples were taken during the dry season, coinciding with the optimal harvest time (May–August). All samples were then preserved using standard fixation techniques before further analysis in the laboratory.

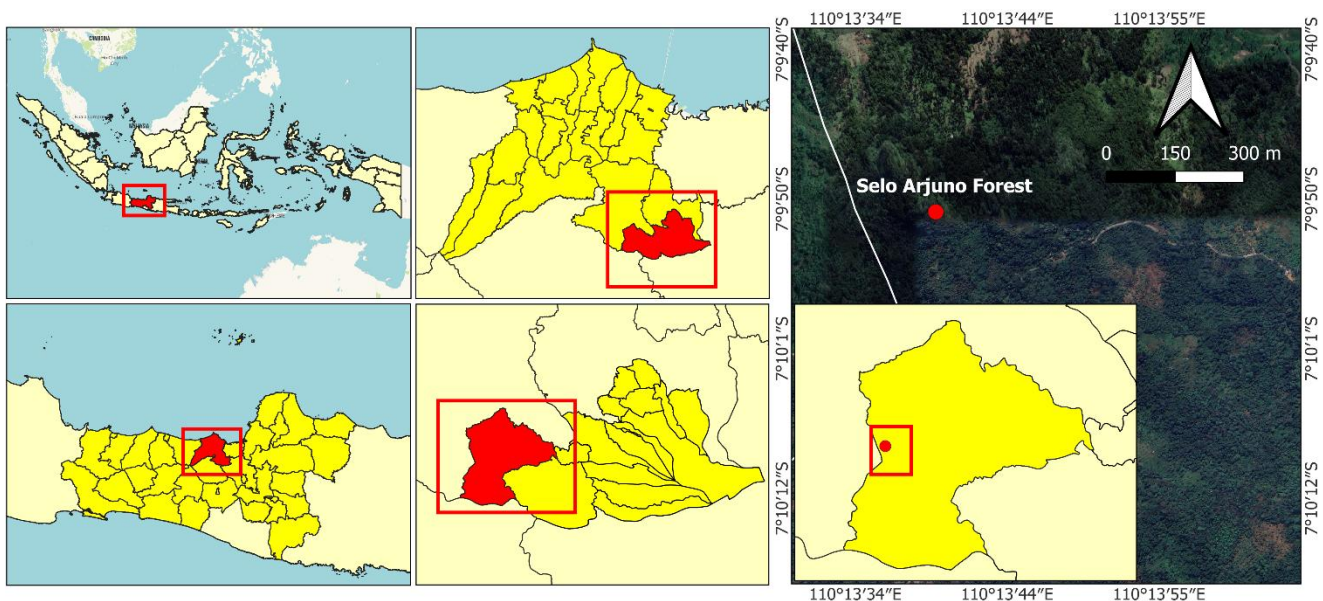


Figure 1. The sampling site in Selo Arjuno Forest, Kedungboto Village, Limbangan Sub-district, Kendal District, Central Java, Indonesia, where six mature and healthy *Amorphophallus variabilis* individuals were selected along natural forest paths

Procedures

Anatomical observation

Anatomical preparation was performed using the paraffin embedding technique following a systematic procedure as described by Ruzin (1999). Fresh samples were fixed in FAA solution (formalin-acetic acid-alcohol, 1:1:18) for 24-48 hours to arrest physiological activity, prevent autolysis, and enhance tissue dye uptake. Dehydration was performed through a graded ethanol series, i.e., 30%, 50%, 70%, 85%, 95%, and absolute ethanol, each for 30-60 minutes, to gradually remove water from the tissue. This was followed by clarification using xylene to remove residual alcohol before paraffin infiltration began. The tissue was then infiltrated and embedded in a paraffin block at 58-60°C and then sectioned at a thickness of 8-12 µm using a rotary microtome. The sections were mounted on mounted on albumin-glycerol adhesive slides. Deparaffinization was performed using xylene, followed by rehydration through a graded ethanol series and distilled water. Safranin (1% in 50% ethanol) was applied for 12-24 hours to stain cell walls, secretory structures, and ergastic substances, and excess dye was then removed by ethanol differentiation. The slides were finally covered with glycerin to maintain tissue integrity and ensure long-term stability during microscopic observation.

The anatomical structures of leaves, petioles, and tubers were observed using a binocular microscope (CX23 Olympus), with a primary focus on the secretory structures that produce Ca oxalate crystals, starch granules, and tannins. Further analysis included calculating the average number of Ca oxalate crystals in each preparation to understand the distribution pattern of ergastic substances in each plant organ. The data obtained were presented in the form of textual descriptions supported by visual images of anatomical structures to provide a more comprehensive understanding of the anatomical and physiological potential of *A. variabilis*.

Socio-economic data

Socio-economic data were collected through semi-structured interviews with five local farmers living around Selo Arjuno Forest. The five farmers were selected based on the criteria of living near the forest, having farming experience, knowledge of *Amorphophallus muelleri* Blume, and willingness to participate in the interviews. Interview questions focused on four main aspects: (i) their knowledge of the presence of *A. variabilis* around their cultivated land, (ii) their experience in cultivating or utilizing *A. muelleri*, (iii) their perception of the potential utilization of *A. variabilis*, and (iv) the obstacles or barriers they might face in cultivation. Although they have not yet utilized *A. variabilis*, their experience cultivating *A. muelleri* is expected to provide a relevant picture. The interview results were analyzed thematically, by grouping responses into categories, such as species knowledge, cultivation experience, utilization potential, and cultivation obstacles, allowing qualitative conclusions to be drawn regarding farmers' perceptions and expectations of *A. variabilis*.

Data analysis

Data analysis was conducted qualitatively using a descriptive approach. The anatomical data were analyzed to identify tissue types and characterize secretory structures and ergastic substances, supported by textual descriptions and microscopic documentation to provide a comprehensive overview of their role in enhancing the pharmacological potential and economic value of *A. variabilis*. Socio-economic data from interviews were analyzed descriptively to illustrate farmers' knowledge, experiences, and perspectives regarding the presence and potential utilization of *A. variabilis* in the Selo Arjuno Forest area.

RESULTS AND DISCUSSION

Characteristics of secretory structures

Amorphophallus variabilis possesses a variety of secretory structures, which ensure the synthesis and accumulation of ergastic substances, including Ca oxalate crystals, starch granules, and tannins. The results revealed that the most common secretory structures are found in leaf and tuber organs, suggesting an adaptive strategy for storing bioactive substances. Secretory structures normally serve as sites for the accumulation of secondary metabolites that have an important role in plant defense and a nutrient reserve in the wild (Paiva 2019). Starch in *A. variabilis* is found in all organs with variations in shape and distribution. Microscopy reveals that starch granules exhibit varied shapes, such as circular, elliptical, oval, and polygonal (Figure 2). The variation of starch shapes in *A. variabilis* tubers can be presented as single structures, such as round/circular, semi-circular, or polygonal granules or as compound formations consisting of two or three granules.

Starch granules in *A. variabilis* tubers are predominantly irregular/granular/composite in shape, with a significantly higher abundance than in other organs (Table 1). The large standard deviation indicates high variation between samples or cross sections, emphasizing the role of tubers as the primary organ for storing energy reserves. This pattern is consistent with findings in other tuber plants, where granule morphology correlates with storage function. This suggests that starch accumulation may occur in distinct phases associated with the plant's growth stage and environmental conditions (Dereje 2021; Rashwan et al. 2024). This result is also supported by molecular studies on *A. muelleri*, which show that key genes involved in starch biosynthesis, such as AmAGP, are actively expressed in tuber tissues to enhance starch accumulation (Shi et al. 2020). Starch granules were also found in leaves, but in much lower quantities than in tubers. This is consistent with studies showing that leaves function primarily as photosynthetic organs, producing starch transiently during the day before exporting it to storage tissues. Meanwhile, starch granules in petioles were found in very small quantities or sporadically. For example, polygonal granules were observed only once in all preparations, indicating localized starch accumulation in specific tissues. This sporadic pattern indicates that energy storage in petioles is transient and not physiologically significant (Zavala-García et al. 2018).

The plant's adaptation to storing carbohydrates as a backup energy source is reflected in this variety of shapes. Similar phenomenon is also occurred in Fagaceae that starch granules can be oval, sub-circular, droplet, rounded triangular, polygonal, and other shapes (Yu et al. 2022). In addition, differences in the size of starch play a crucial role in determining the potential use of the starch (Sari and Putra 2019). The starch granule size in the tuber organ of *A. variabilis* falls into the large-size category, with an average range between 55 μm^2 and 182 μm^2 (Table 2), in line with the criteria for large granules as reported by Lindeboom et al. (2004). Large-sized starch has a high water absorption capacity, expands easily, and produces high viscosity, making it ideal for use as a staple food source (Sari et al. 2017; Xie et al. 2024).

The size of starch granules in petioles and leaves shows variation but generally remains relatively large, with granules in leaves tending to be slightly larger than those in petioles. This variation indicates that although the quantities are limited, granules in vegetative organs can reach sizes above the functional threshold, suggesting their physiological role as local, short-term energy reserves. A pattern also reported in *Arabidopsis thaliana*. leaves, where granule size increases with leaf aging to support transitory storage (Liu et al. 2021).

The diversity of granule shapes, including circular, semi-circular, elliptical, oval, polyhedral, and irregular/compound forms represents a morphological adaptation strategy. The dominance of complex and irregularly structured granules in the tuber reflects an active starch accumulation process, which aligns with the tuber's role as the primary energy reserve in a fluctuating semi-seasonal tropical environment. Ca oxalate crystals in *A. variabilis* are found in various forms, such as raphides, druses, prisms, sand, and rhombohedral (Figure 3). These crystals can be found solitary or, more commonly, in bundles, where several crystals cluster to form a specific structure.

The formation of Ca oxalate crystal types in plants is influenced by the intravacuolar matrix, which is a macromolecular structure that plays a role in determining the shape and growth of crystals (Lawrie et al. 2023). The result showed that sand-like crystals were the most abundant type, particularly in tubers, with decreasing abundance in petioles and leaves (Table 3). In contrast, raphides were found consistently in all organs, albeit in relatively small numbers, with leaves showing the highest abundance. The size of raphides were generally the largest in petioles, while druse crystals showed a significant size dominance in tubers (Table 4).

Table 1. Average number of starch grains in *Amorphophallus variabilis*

Organ	Round/Circular	Semi-circular	Elliptical	Oval	Polyhedral	Irregular/Granular/Compound
Tuber (mm^2)	153 \pm 97	131 \pm 100	28 \pm 17	13 \pm 10	21 \pm 30	8021 \pm 8944
Petiole (mm^2)	6 \pm 8	0 \pm 0	1 \pm 1	0 \pm 0	0.2 \pm 0.4	18 \pm 23
Leaf (mm^2)	33 \pm 23	7 \pm 7	2 \pm 2	3 \pm 4	0 \pm 0	26 \pm 31

Table 2. Average starch granule size in *Amorphophallus variabilis*

Organ	Round/Circular	Semi-circular	Elliptical	Oval	Polyhedral	Irregular/Granular/Compound
Tuber (μm^2)	55.91 \pm 42.56	56.13 \pm 19.31	38.91 \pm 26.83	76.13 \pm 35.36	69.71 \pm 29.41	182.29 \pm 84.61
Petiole (μm^2)	45.96 \pm 10.69	-	72.90 \pm 25.66	-	54.08 \pm 0.00	49.37 \pm 12.44
Leaf (μm^2)	53.50 \pm 26.71	15.06 \pm 3.02	47.63 \pm 24.39	84.08 \pm 9.29	-	81.67 \pm 24.51

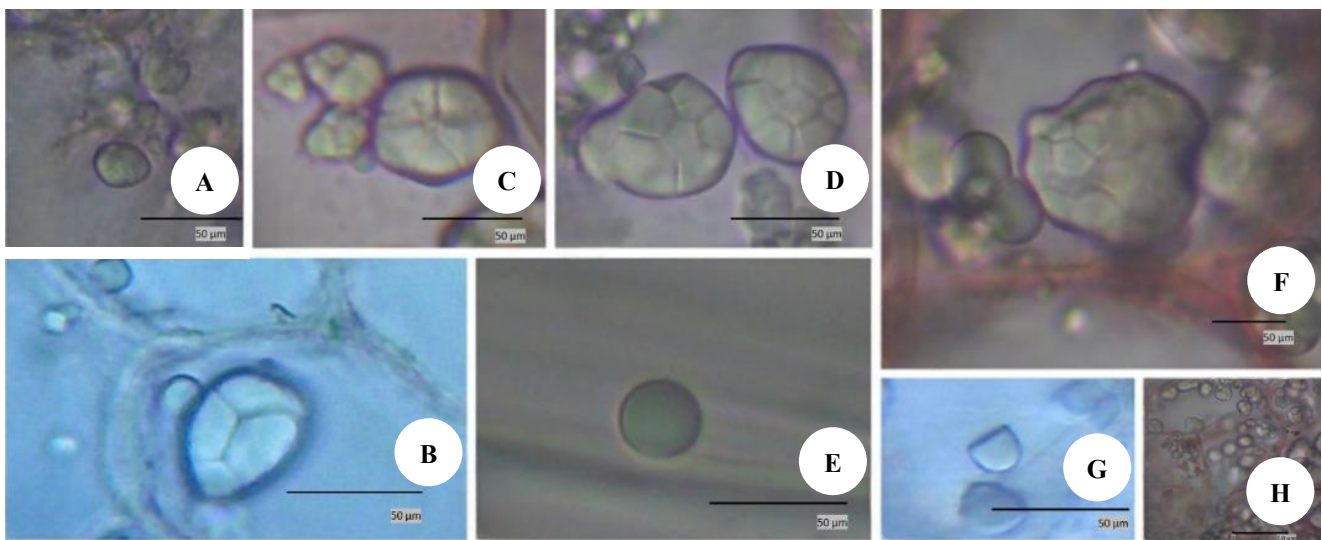


Figure 2. Starch granule types in *Amorphophallus variabilis*: A, B, C, D, F, H: Compound starch granules, E, G: Single starch granules

Li et al. (2023) presented that the formed Ca oxalate crystals in *Mammillaria schumannii* have a close relationship with an organic matrix consisting of polysaccharides, flavones, or lipids, as confirmed by Raman spectroscopy analysis. In some cases, the crystals are trapped in a cell wall material or layered sheath, which is thought to regulate crystal development by restricting the rate of supply of calcium and oxalate into the chamber of crystallization. Calcium and oxalate concentrations have also been shown to affect crystal form, implying sophisticated regulation in their formation. The updated isolation methods allow the separation of small crystals that tend to be attached to plant tissues or suspended in solution. The study also found that although genes specifically encoding proteins controlling the crystal formation process have not been reported, transcripts related to lipid, polysaccharide, and cell wall metabolism were highly expressed during biomineralization. These results further strengthen the hypothesis that biomineralization in plants functions in calcium regulation and as an adaptation mechanism to extreme environmental stresses such as high sunlight intensity and drought conditions (Liu et al. 2018; Cerritos-Castro et al. 2022; Khan et al. 2023; Li et al. 2023).

Raphide crystals are classified into two types based on their number and arrangement of needles, i.e., single raphide crystals with pointed tips and raphide bundles configured in differing patterns, such as straight to parallel, conical, interlocking, or similar to straw bundles. These crystals are

typically contained within idioblasts. Variations in the form of these crystals suggest distinctions in function and role in the plant cell. For instance, the raphide-shaped crystals have a long needle-like shape that provides a physical defense against herbivores (Jaume et al. 2025). When plant tissue is bitten or damaged, these crystals can irritate an animal’s mouth or digestive system, reducing the risk of the plant being eaten (Prychid et al. 2008; Siroka 2023). Interestingly, the largest raphide crystals were found in the petiole, indicating an additional role in reinforcing structural tissue. Their significantly larger size compared to those in the leaf or tuber suggests that these crystals serve not only as a defense against herbivory, but may also contribute to tissue stiffness and mechanical strength in plant parts that support compound leaves (Arzate-Vázquez et al. 2022).

Table 3. Average number of Ca oxalate crystals in *Amorphophallus variabilis*

Organ	Raphide	Druse	Prism	Rhombohedral	Sand
Tuber (mm ²)	14±13	16±17	5±6	0±0	3437±1414
Petiole (mm ²)	17±16	27±27	1±1	52±112	1767±949
Leaf (mm ²)	22±44	61±50	1±1	0±0	1029±426

Table 4. Average size of Ca oxalate crystals in *Amorphophallus variabilis*

Organ	Raphide	Druse	Prism	Rhombohedral	Sand
Tuber (µm ²)	2,977.09±3,538.47	1,262.84±548.70	62.59±40.34	0±0	3.65±1.51
Petiole (µm ²)	4,102.22±2,032.63	822.02±307.14	68.26±37.51	23.40±23.31	4.38±0.69
Leaf (µm ²)	301.40±322.37	46.20±3.05	35.95±9.47	0±0	4.16±1.03

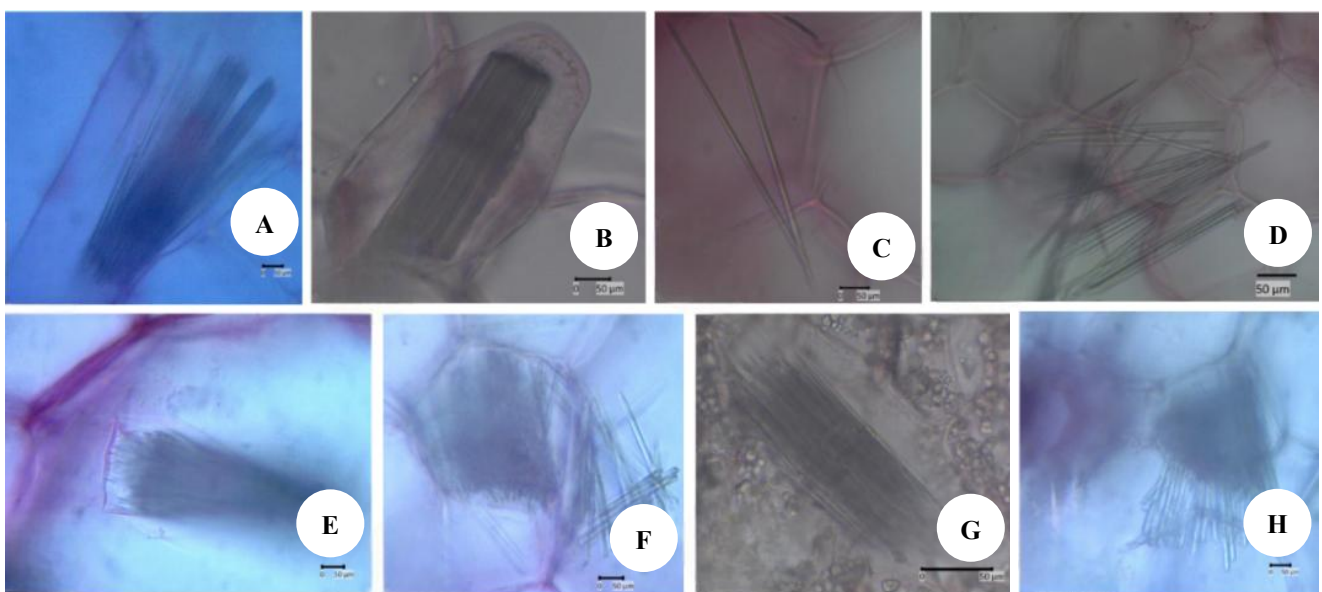


Figure 3. Various variations of raphide-shaped Ca oxalate crystals in *Amorphophallus variabilis*: A, B. Neatly arranged raphide bundles with edges aligned straight and flat with each other, C. Single raphides, D, F. Irregular bundles stabbing each other, E, H. Neat raphide bundles forming conical shapes, G. Irregular bundles like straw ties

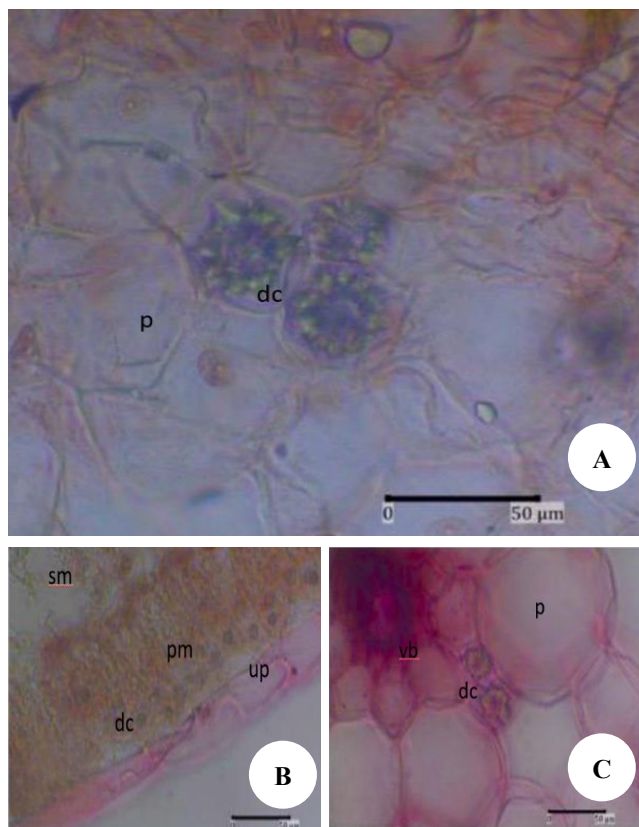


Figure 4. Ca oxalate crystals in the form of druse in: A. The tuber, B. Leaf, and C. Petiole in *Amorphophallus variabilis*. Note: dc: Druse crystal, p: Parenchyma, up: Upper epidermis, pm: Palisade mesophyll, sm: Sponge mesophyll, vb: Vascular bundle

Another type of Ca oxalate crystal found in *A. variabilis* is druse, spherical in shape with a spiny surface (Figure 4). Druse crystals have two forms: tightly arranged and loosely arranged. Similar to raphide crystals, druse crystals are found either inside idioblasts (A, B) or in cavities (C). The crystalline idioblasts that form druse crystals may contain a single crystal or multiple crystals. The druse crystal form in *A. variabilis* has an important role in regulating calcium ions in cells. These crystals can absorb and store excess calcium ions in the tissue. Furthermore, these crystals play a role in the plant's defense mechanism against heavy metals through phytoremediation. Ca oxalate, for instance, can bind heavy metals like lead, zinc, and cadmium, thus aiding plants in adapting to polluted soil conditions (Khan et al. 2023; Victório et al. 2023). Weber et al. (2015) have conducted several analyses that demonstrated that metals in the surrounding environment may interact with calcium oxalate, where metal ions replace calcium in crystalline unit cells, thus inducing size-dependent structural changes. This suggests that Ca oxalate in plants plays a role in calcium storage, detoxification mechanisms, and protection against environmental heavy metals. In addition, these crystals also contribute to the carbon cycle (He et al. 2024).

Other Ca oxalate crystals found in *A. variabilis* are sand-shaped and prism-shaped (Figure 5). Sand-shaped Ca

oxalate crystals are tiny and evenly distributed in the tissues, especially in the tubers. These crystals help regulate Ca levels in plant cells and are part of a natural defense mechanism. Meanwhile, prism-shaped Ca oxalate crystals are among the most common types in *A. variabilis* organs, especially in leaf palisade mesophyll tissue and tuber parenchyma. The presence of prism crystals in the palisade mesophyll is believed to play a role in increasing the efficiency of sunlight absorption and providing internal CO₂ reserves that can be used when stomata are closed due to environmental stress conditions. This suggests that Ca oxalate crystals are not just a metabolic by-product but have important physiological functions in maintaining photosynthetic efficiency (Tooulakou et al. 2016). In addition, prism crystals are also found in the sclerenchymal tissue of the petiole, where they play a role in strengthening the plant's supporting cell structure. Arzate-Vázquez et al. (2022) showed that the presence of Ca oxalate crystals in the sclerenchyma tissue on *Carya illinoensis* increased hardness and elastic modulus, thus strengthening the mechanical structure of the plant. In the genus *Amorphophallus*, the petiole organ functions as a pseudo-stem that supports large compound leaves, which require a sturdy supporting structure. Using the biomineralization mechanism, Ca oxalate crystals contribute to a significant increase in tissue stiffness. However, variations in mechanical properties do not always directly correlate with the volume and number of crystals. The variation in the shape of Ca oxalate crystals in *A. variabilis* reflects a complex adaptive mechanism in mineral regulation and supporting various plant physiological functions.

Amorphophallus variabilis contains tannins that stored in idioblasts and secretory structures in the form of schizogenous cavities (Figure 6). Idioblasts are specialized cells distinct from the surrounding cells and serve as storage sites for secondary metabolites, including tannins. These compounds are widely used in food preservation and pharmaceuticals, such as astringency and antioxidant. Molnar et al. (2024) reported that Deep Eutectic Solvents (DES) can extract tannins efficiently and are environmentally friendly, increasing their practical value. *A. variabilis* has secretory cavities that play a role in the storage of secretions and resistance to environmental stress. The formation of these cavities is thought to occur through a schizogenous mechanism, which is cell separation due to differential growth in the middle lamella of the cell wall (Costa and Demarco 2024; Martínez-Quezada et al. 2025). Although this process has been described histologically in several species, the developmental regulation and the molecular mechanisms remain poorly understood.

The results indicate that the distribution of secretory structures differs among organs in *A. variabilis* (Table 5). Idioblasts are most abundant in tubers, with significantly fewer in petioles, and almost none in leaves. Meanwhile, schizogenous cavities are most prevalent in petioles, but relatively few in tubers and leaves. This pattern indicates functional differentiation of organs, with petioles likely serving as the primary site of secretion, while tubers serve as reservoirs for tannin storage.

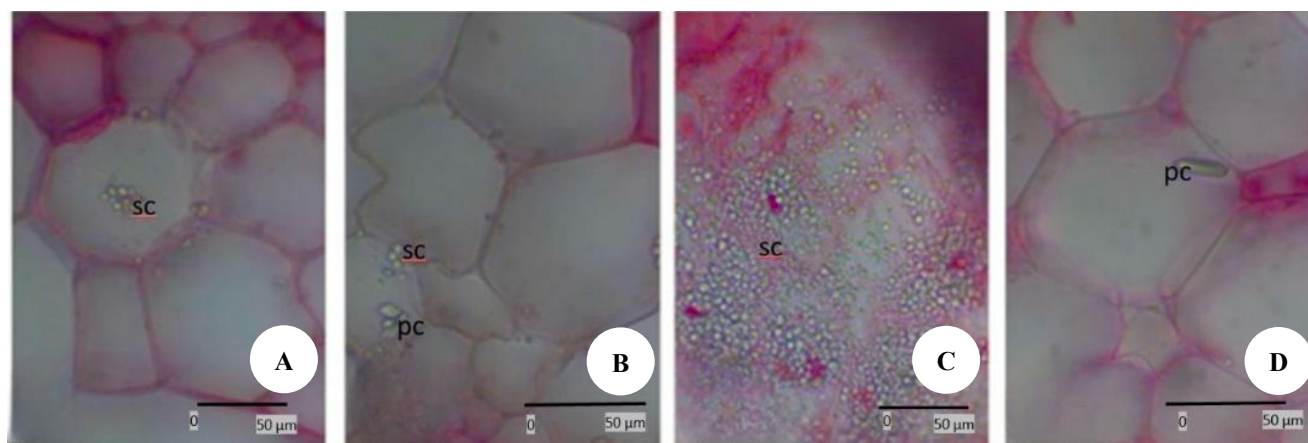


Figure 5. Ca oxalate crystals in *Amorphophallus variabilis*: A, C. Sand-shaped, D. Prismatic-shaped, B. Sand and prismatic-shaped. Note: sc: Sand crystal, pc: Prismatic crystal (pc)

Table 5. Average number of tannin structures in *Amorphophallus variabilis*

Organ	Idioblasts	Schizogenous cavity
Tuber (mm ²)	74±89	6±5
Petiole (mm ²)	9±4	86±41
Leaf (mm ²)	1±2	7±3

Table 6. Average size of tannin structures in *Amorphophallus variabilis*

Organ	Idioblasts	Schizogenous cavity
Tuber (µm ²)	152.05±72.79	2724.47±1378.62
Petiole (µm ²)	1993.64±1631.87	2142.04±1258.75
Leaf (µm ²)	103.20±52.81	1432.41±1107.28

Idioblasts in petioles are generally larger than those in tubers and leaves (Table 6). Meanwhile, schizogenous cavities also exhibit large dimensions, particularly in tubers, followed by petioles, and relatively smaller in leaves. This difference confirms the variation in storage and secretion capacity among organs, which aligns with the physiological functions of each organ.

The amount of tannin in *A. variabilis* petioles is relatively lower than that of starch granules in tubers, however, its importance should not be underestimated. Tannins possess antioxidant, antimicrobial, and astringent properties that hold significant potential in the pharmaceutical, cosmetic, and food industries. The use of tannins in leather tanning, natural ink production, and biofilm activation demonstrates high economic value and contemporary industrial relevance (Bele et al. 2010; Pizzi 2019). Moreover, tannins have been explored as bio-adhesives and anti-corrosion agents in sustainable biomaterial processing (Santulli et al. 2025). Tannins in *Acacia* have been extensively exploited for industrial purposes, therefore, *A. variabilis* tannins could be a valuable source if processed and marketed efficiently and demonstrating that each plant organ has a specific economic contribution.

Ca oxalate and tannin crystals in tubers are higher than in the leaves and petioles, suggesting that tubers serve as a source of bioactive compounds and as a storage organ. These compounds play a role in dormancy regulation by affecting phytohormone metabolism, responding to oxidative stress, and controlling apical dominance. These adaptations allow the plant to survive in extreme environmental conditions, such as dormancy periods or dry seasons in its habitat (Dogramaci et al. 2024). Secretory structures in *A. variabilis* support its self-defense and show great potential in its economic utilization. Tannins, for example, can be used as raw materials for traditional medicines and products of high economic value (Fraga-Corral et al. 2021; Ciriminna et al. 2025). Its astringent properties can be utilized in cosmetic and medicinal products, while Ca oxalate crystals have applications in the field of bioremediation of heavy-metal-polluted soil (Prasad and Shivay 2017; Karabourniotis et al. 2020). These opportunities open up opportunities for local communities to develop sustainable utilization of this plant.

Ergastic substances distribution

The distribution of ergastic substances in *A. variabilis* showed a clear distinction among plant organs, reflecting the complex specialization of physiological and ecological functions. The tuber is the organ with the most abundant ergastic substances, particularly starch granules. Starch granules in the tuber attain the highest average density, at approximately 8400 per mm² (Figure 7). This number significantly exceeds those in other organs, reinforcing the role of the tuber as the main energy storage center and enabling the plant to survive in suboptimal environments. Starch is synthesized in leaf chloroplasts during the day and can be classified as either temporary or storage starch. Temporary starch is used for respiration and growth at night, while storage starch is retained in non-photosynthetic organs, such as tubers, roots, and stems as a long-term energy source (Pfister and Zeeman 2016). In contrast, the number of starch granules in the petiole and leaves is relatively low, reflecting the primary role of these organs in photosynthesis and the transport of metabolic products, rather than energy storage. The results showed that Ca oxalate crystals were dominant, with sand and druse types

being the most prevalent in the tubers. This suggests that tubers serve as a significant storage center for secondary metabolite compounds that are important for plant survival in their natural habitat (Li et al. 2022; Plunkert et al. 2024). This also suggests another function of the tuber as a storage site for excess Ca and as a plant defense mechanism against herbivores or pathogens (Konyar et al. 2014).

The secretory structures containing tannins exhibit a distribution pattern distinct from that of starch and Ca oxalate crystals. Although the number of tannin structures in the tuber is relatively lower than the other two substances, their presence remains important, as these structures contribute to dormancy regulation and protection against environmental stress. Tannins in the tuber are stored in idioblasts and are likely to support the plant's resilience to extreme conditions, such as dry seasons or dormancy in Selo Arjuno Forest. The role of tannins as part of secondary metabolites is not limited to tolerance against abiotic stress, but is also crucial in plant defense mechanisms against biotic stress, such as attacks by pathogens and herbivores. Tannins can exert direct toxic effects, inhibit digestion, or attract natural enemies of harmful organisms. Tannins also help regulate molecular signaling and enzymatic activity that strengthen the plant's adaptive responses to environmental pressures (Al-Khayri et al. 2023).

The petiole shows a markedly different profile of ergastic substance distribution. Although the starch granule and Ca oxalate crystal contents in the petiole are relatively low, the number of tannin structures is quite prominent. This suggests that the petiole acts as a center for the secretion of bioactive compounds, particularly tannins, which are stored in idioblasts and schizogenous cavities. This distribution supports the hypothesis that the petiole is a primary site for the secretion of secondary metabolites that play a vital role in the plant's defense system against external pressures, including herbivore attacks, considering that tannins are known for their antimicrobial and anti-herbivore effects (War et al. 2012). This is consistent with the findings of Divekar et al. (2022), who explained that secondary metabolites such as tannins function in plant defense by inducing direct toxicity, inhibiting digestion, or attracting the natural enemies of herbivores. Tannins are also found in relatively high amounts in the tuber, possibly serving as an additional protective mechanism against underground pathogens (Adamczyk et al. 2017). The biosynthesis of tannins is also regulated by hormonal signaling, enabling the plant to respond adaptively to herbivore attacks and enhance long-term resilience to environmental stress (Divekar et al. 2022). The large size of the tannin structures in the petiole further reinforces its role as a producer of functional compounds with potential for economic utilization.

Visualization of the distribution of ergastic substances in this plant provides important insights into optimizing the utilization of *A. variabilis*. The dominance of starch and Ca oxalate in the tuber indicates that the main utilization is more likely to be directed as a source of carbohydrates and bioactive ingredients for further processing (Islam et al. 2023). The higher tannin content in the petiole suggests that this part has potential as a source of antioxidant and

antimicrobial compounds, which could be explored for the pharmaceutical or cosmetic industries (Jasim 2018).

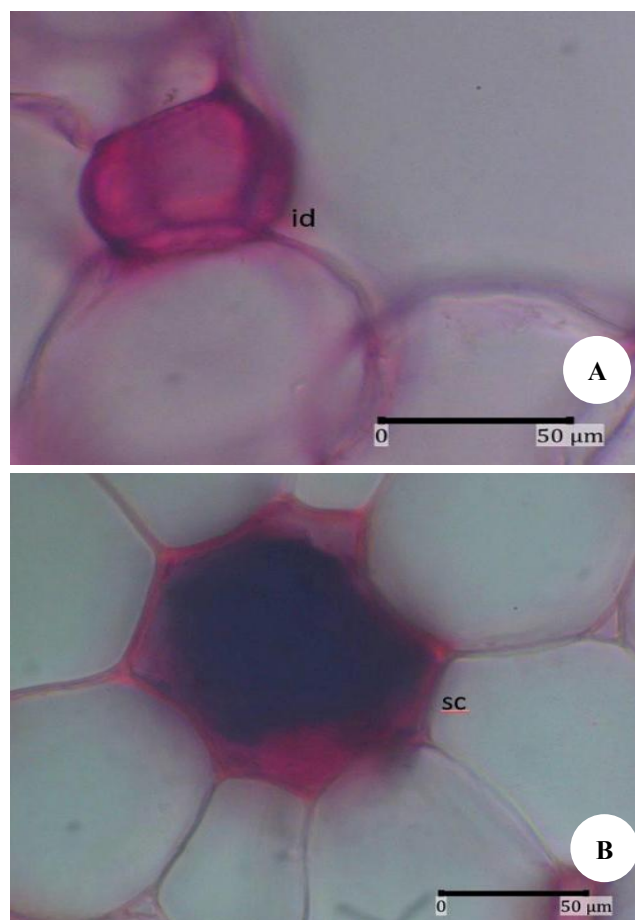


Figure 6. Structure of tannins found in *Amorphophallus variabilis*. Note: id: Idioblast, sc: Schizogenous cavity

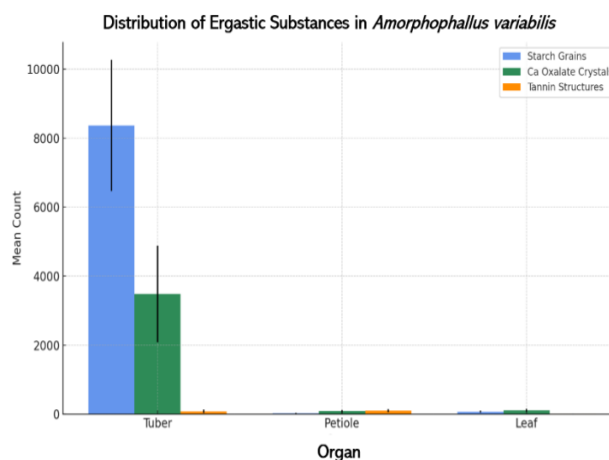


Figure 7. Distribution of ergastic substances in *Amorphophallus variabilis*

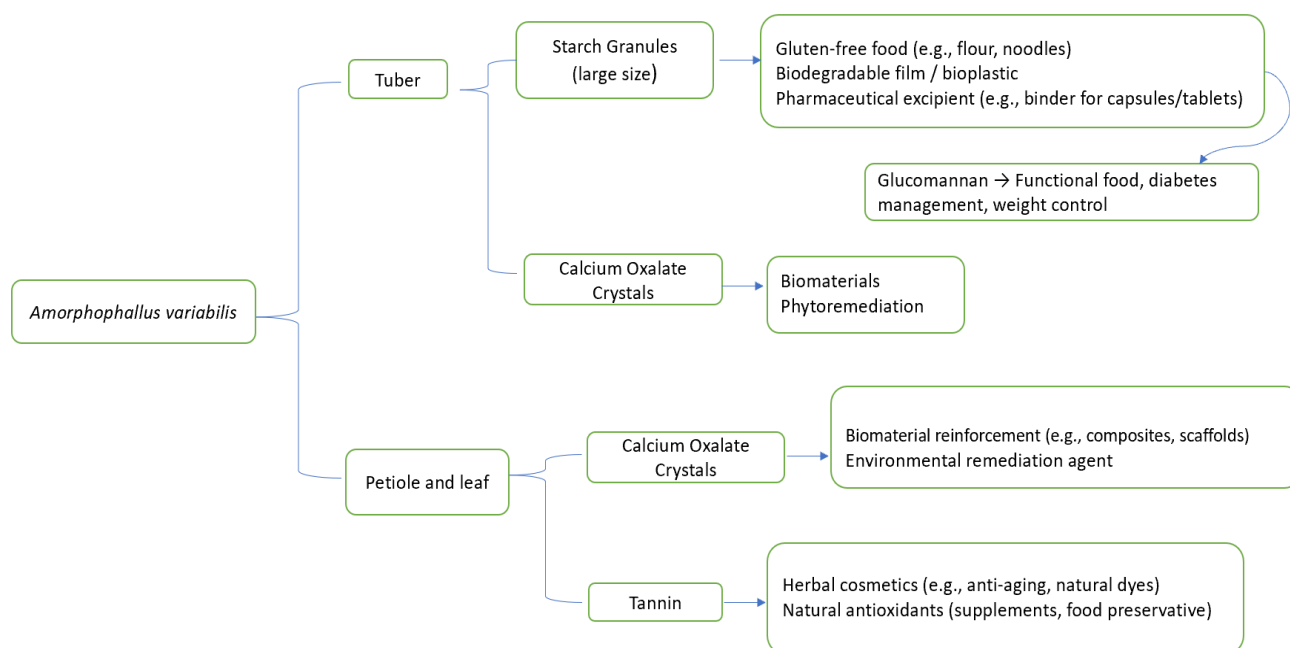


Figure 8. Economic value diagram of *Amorphophallus variabilis* based on plant organs and ergastic compounds

Low tannin concentration in *A. variabilis* tubers is helpful in conservation and economic sense, since it enables their use as food or pharmaceutical raw materials without the need for expensive detannination processes. However, the high Ca oxalate content still needs to be considered because it can cause irritation or toxicity if not processed properly, for example, by boiling, fermentation, or soaking in saline solution (Handayani et al. 2023). Reducing Ca oxalate levels in *A. muelleri* tubers by soaking in a 5% acetic acid solution may apply to processing *A. variabilis* tubers (Wardani and Arifiyana 2020). Therefore, the utilization strategy of *A. variabilis* should focus on processing the tubers with techniques that can reduce oxalate content. At the same time, tannin extraction from the petiole can be developed as a value-added product. Tannin extraction is generally done through solid-liquid extraction methods, such as maceration or decoction, which can be adapted to obtain high-quality extracts from the petiole of this plant (Fraga-Corral et al. 2021).

Economic value

The economic potential of *A. variabilis* can be explored through the presence of ergastic substances found in various plant organs. The large-sized starch granules present in the tuber allow for the development of value-added products, such as gluten-free food, environmentally friendly biofilms, and pharmaceutical excipients. Ca oxalate crystals have potential applications in the development of biomaterials and phytoremediation. Meanwhile, the tannin content, primarily found in the petiole, creates opportunities for use in the cosmetics sector and as natural antioxidants. An economic value diagram has been constructed based on the bioactive components and their corresponding plant organs to illustrate these utilization pathways (Figure 8).

Amorphophallus variabilis has significant economic value, mainly through the utilization of ergastic substances present in this plant. Ergastic substances, such as Ca oxalate crystals, starch granules, and tannins have various industrial and economic applications. Ca oxalate crystals, for example, are known to have potential in the field of phytoremediation, which is the process of restoring soil and water polluted by heavy metals. The ability of Ca oxalate crystals to bind toxic metal ions, such as lead, cadmium (Cd), and zinc (Zn) makes them an important ingredient in green technology to improve environmental quality. Pongrac et al. (2018) reported that Cd was associated with oxalate in Ca oxalate crystals, where more than 88% of Cd is bound to oxalate ligands in *Gomphrena claussenii* Moq. This demonstrates that Ca oxalate crystals play a role in absorbing and reducing heavy metal toxicity in plants, which can be applied in phytoremediation and phytoextraction strategies. Considering that *A. variabilis* also contains Ca oxalate crystals, this plant could be utilized in the management of land and water contaminated with heavy metals, providing new economic opportunities in the environmental field and green industry.

According to Prasad and Shivay (2017), oxalate content in plants not only serves as a phytoremediation agent, but also has other economic roles. Oxalates can be used in the pharmaceutical and food industries, especially as natural preservative agents or in the formulation of nutritional supplements. Ca oxalate crystals in *A. variabilis* also play a role in the plant's natural defense against pests, thus potentially reducing the need for chemical pesticides and opening up opportunities in the development of sustainable agricultural systems. Therefore, this plant not only contributes to environmental rehabilitation but also has added value in the bio-based industrial sector. Although the tannin content in *A. variabilis* is less than that of Ca oxalate

crystals and starch, these compounds still have significant economic value in the industrial and health sectors. Tannins are known to have astringent, antioxidant, and antimicrobial properties, making them widely used in the pharmaceutical, cosmetic, and food industries (Pizzi 2019). In available amounts, tannins from *A. variabilis* can still be utilized in ink manufacturing and leather tanning processes, where these compounds form complexes with proteins, providing durability and natural color to leather products. Therefore, processing tannin extracts from *A. variabilis* holds potential to create additional economic opportunities, especially in the development of bio-based products. For local communities, at the Small and Medium-Sized Enterprise (MSME) scales, the utilization of tannins can be combined with other *A. variabilis*-based products, such as starch or phytoremediation additives, to enhance added value and product diversification.

Amorphophallus variabilis has potential as a food crop that can be consumed, provided that the processing is carried out appropriately. The species contains glucomannan like *porang* (*A. muelleri*) and *suweg* (*A. paeoniifolius*), a water-soluble polysaccharide that is beneficial for digestive health as well as weight control. However, the tubers of this plant also contain Ca oxalate, which can cause itching or irritation if consumed without proper processing. An appropriate processes, such as soaking in acetic acid or sodium chloride solution, heating, and drying have been proven effective in reducing the Ca oxalate content in *A. muelleri* tubers, thus making them safe for consumption (Azhar et al. 2023). *Amorphophallus variabilis* tubers have the potential to be used as healthy food ingredients with proper processing, including as an alternative flour source that is rich in fiber and low in calories, suitable for functional food products (Pambudi et al. 2020).

Local community understanding is another crucial aspect in assessing the economic value of *A. variabilis*. Interviews with five local farmers around Selo Arjuno Forest revealed that they had actually been familiar with *A. variabilis*. However, they considered it as a weed, thus leaving it unexploited. After gaining information that it has potential for development, their perceptions tend to be positive. Despite their lack of technical information, seed availability, and market certainty, their experience cultivating *A. muelleri* is believed to provide a starting point for developing *A. variabilis* as a new source of income. Market dynamics also play a significant role in determining the economic value of the species. Despite the absence of specific price data for this plant in the Selo Arjuno region, comparisons with similar commodities in Central Java can provide an indication of its potential. The price of *porang* (*A. muelleri*) at the domestic level reaches around IDR 14,000/kg, while in the export market it ranges from IDR 53,000-98,000/kg. Meanwhile, *A. variabilis* has a lower economic value, around IDR 3,000/kg domestically and IDR 9,000-15,000/kg internationally. The low economic value of the species is not primarily due to its active compound content, but rather because this commodity is not as popular as *A. muelleri* in the domestic and export markets, resulting in limited demand and supply chains. Upon proper development, *A. variabilis*' potential value could follow a similar pattern: its bioactive content provides

significant opportunities, but popularity and market access will largely determine the price. Seasonal factors can also influence availability and price, with prices trending downward during peak harvests.

Amorphophallus variabilis has the potential to be an antidiabetic and cholesterol-lowering therapeutic agent, similar to other better-known *Amorphophallus* species. The glucomannan content in its tuber is reported to help regulate blood sugar and cholesterol levels. Sood et al. (2008) showed that glucomannan has hypoglycemic (lowers blood sugar) and hypolipidemic (lowers blood fat) effects by slowing the absorption of glucose in the intestine and increasing the excretion of bile acids. In addition, glucomannan can also lower total and LDL cholesterol levels, which contribute to cardiovascular health (Musazadeh et al. 2024). These prospects highlight the need to develop herbal products or health supplements aimed at special markets like diabetics and patients with hypercholesterolemia. The integration of economic development and conservation of *A. variabilis* suggests that conservation through utilization is an appropriate strategy in biodiversity management. By utilizing the valuable parts of the plant, communities can earn additional income without destroying the plant's natural habitat. For example, communities can develop healthy food products based on *A. variabilis* tubers or use them as raw materials in herbal medicine products. Through training and empowerment, local communities can transform the raw materials into value-added products, such as herbal tea, supplement capsules, or processed food products.

Amorphophallus variabilis has broad economic prospects as an industrial raw material, a functional food, and a health product. Collaboration between the government, academia, and the private sector is needed to optimize this potential. The government can provide economic incentives, capital assistance, and regulations that support economically based conservation efforts. Academics and researchers can provide the community with scientific data, processing innovations, and training. Meanwhile, the private sector can partner in building a supply chain of *A. variabilis*-based products for domestic needs and export. With an integrated approach, *A. variabilis* can become a natural resource that contributes to the local economy while supporting sustainable environmental conservation.

Conservation strategies

Amorphophallus variabilis is one of the wild species with potential economic value that is still relatively abundant in Selo Arjuno Forest. However, it is vulnerable to habitat changes and human activities (Santosa et al. 2018). This species is often considered a weed by local communities and is rarely utilized (Wahidah et al. 2022). Deforestation, land use change, and intensive agricultural practices are the main threats that can affect the sustainability of *A. variabilis* populations in the wild. Given its economic and ecological functions, it is critical to develop suitable conservation plans to sustain its population stability in its natural habitat (Santosa et al. 2012; Li 2025). One of the recommended conservation approaches is in situ conservation. This

strategy allows the plants to preserve their adaptive traits, maintain ecological interactions, and sustain genetic diversity (Susmianto 2017). In this term, Selo Arjuno Forest, which has environmental conditions that support the growth of *A. variabilis*, can be used as a nature conservation area or wildlife reserve. Management of this area should include regular monitoring and protection against threats to habitat destruction.

Ex situ conservation through controlled cultivation also can be an effective strategy for maintaining the sustainability of *A. variabilis*. Cultivation of this species has the potential to be developed by referencing *A. muelleri* cultivation system, which has proven ecologically and economically successful. *Amorphophallus variabilis* shares morphological and physiological characteristics with *A. muelleri*, particularly in its ability to regenerate through tubers, shade tolerance, and adaptation to marginal soil conditions. Through cultivation, harvesting pressure on wild populations can be reduced, while also opening up opportunities for more sustainable use for food, industry, and environmental purposes. Furthermore, the implementation of community-based cultivation, such as through agroforestry or intercropping systems, has the potential to integrate conservation efforts with improving the economic well-being of local communities.

Reintroduction is also promising alternatives. Reintroduction involves planting *A. variabilis* seedlings or tubers in areas where populations are declining or in rehabilitated habitats. This technique can help expand the plant's population distribution and increase the number of individuals in the wild. In its implementation, reintroduction needs to be supported by good nurseries, selection of suitable habitats, and evaluation of plant adaptation after replanting. For example, the Bogor Botanical Garden has reintroduced nine rare plant species to their natural habitat, demonstrating the importance of evaluation and monitoring in reintroduction programs (Dodo 2018). The involvement of local communities in reintroduction activities is also important to ensure the sustainability of this conservation program. Active community participation in nurseries, monitoring, and habitat protection of *A. variabilis* can increase the effectiveness of reintroductions and ensure that plant populations remain stable in the long term. The reintroduction of the closely related *A. titanum* has been successfully carried out through propagation and planting in suitable natural habitats, demonstrating the feasibility of this approach for species within the genus (Setiawan et al. 2025).

The conservation strategy for *A. variabilis* also needs to take into account the anatomical characteristics of the plant that indicate a high adaptive capacity to environmental stress. The results show that the tuber is the richest organ in ergastic substances, particularly starch granules and Ca oxalate crystals. The starch granules highlight the tuber's role as the main energy storage center, allowing the plant to survive during dry seasons and in nutrient-poor soils. Ca oxalate crystals of the sand and druse types are evenly distributed throughout the tuber tissue. These not only serve as Ca ion regulators, but also function as a defense mechanism against herbivores and pathogens. Secretory structures containing tannins, although present in smaller

quantities, contribute to dormancy regulation and responses to environmental stress, and are stored in idioblasts that act as internal protective structures. In the petiole, although the content of starch granules and Ca oxalate crystals is relatively low, tannin-containing structures are found in notable quantities, indicating that this organ plays an active role in secreting secondary metabolites that function as antimicrobial and anti-herbivory defenses.

Understanding the distribution patterns and functions of these ergastic structures is a key to determining appropriate conservation strategies. Populations with large tubers and complex storage organ anatomy are more suitable for in situ conservation, particularly in undisturbed habitats. Meanwhile, populations threatened by overharvesting of tubers can be directed toward ex situ conservation, such as cultivation based on functional anatomy to preserve the plant's adaptive traits. Thus, an anatomy-based approach not only deepens the understanding of species ecology, but also strengthens conservation policies grounded in scientific data and sustainable practices. By recognizing the adaptive anatomical characteristics and economic potential of *A. variabilis*, conservation programs can be designed to integrate habitat protection, sustainable utilization, and local community participation. Incorporating anatomical data into conservation planning ensures that implemented strategies are not only ecologically appropriate but also account for the species' physiological resilience, in line with biodiversity conservation policies that emphasize both ecological and socio-economic benefits.

This study concludes that *A. variabilis* exhibits diverse ergastic and secretory structures with distinct distributions across different organs, reflecting its adaptive and functional potential. The integrative approach combining anatomical analysis and socio-economic insights highlights the species' previously underutilized potential value and its relevance for functional use and conservation. These findings provide a scientific basis for strengthening conservation strategies through sustainable utilization that supports biodiversity protection and community well-being.

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