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Adaptive survival mechanisms of *Lithops* sp. in arid environments: Morphological and water regulation strategies

Luthfiana Mutiara Sani[1], Tasya Preira Farrennina[1], Haoling Yang[2], Aura Balqis Nicheta Putri[1], Yusfi Afidah[1], Qori'atul Mustafidah[1], Mukhamad Su'udi[1*]
[1]Department of Biology
Faculty of Mathematics and Natural Sciences, Universitas Jember
Kalimantan Street No. 37, Jember, East Java, Indonesia. 68121
[2]Lithops Berg, China
*E-mail: msuudi52@gmail.com

Abstract: Succulents are plants whose body parts are thicker and fleshier as adaptation form to the arid environment in which they grow. *Lithops* sp. is a succulent plant often found in South Africa and Namibia. This plant belongs to the Aizoaceae family and has a total of 37 species. This study was carried out by collecting reference sources which were then used as a reference for studying *Lithops* sp. related to morphological structure and adaptation to extreme environment. *Lithops* sp. shaped like an inverted cone with the part above the ground being the surface of the leaves. This form is an adaptation carried out by *Lithops* sp. to reduce exposure to sunlight and prevent excess water loss during the transpiration process. Apart from its shape, the epidermis of *Lithops* sp. also undergoes special differentiation so that it can prevent excess water loss during transpiration. *Lithops* sp. also undergoes differentiation to form window cells on the surface of its leaves which function to increase the rate of photosynthesis by increasing sunlight radiation entering the photosynthetic tissue.

Keywords: adaptations, arid environment, *Lithops* sp., morphology, succulents

Abstrak: Sukulen adalah tumbuhan yang memiliki bagian tubuh lebih tebal dan berdaging sebagai bentuk adaptasi terhadap lingkungan kering tempat mereka tumbuh. *Lithops* sp. merupakan tanaman sukulen yang sering ditemukan di Afrika Selatan dan Namibia. Tanaman ini termasuk dalam famili Aizoaceae dan memiliki total 37 spesies. Penelitian ini dilakukan dengan mengumpulkan sumber referensi yang kemudian digunakan sebagai acuan untuk mempelajari *Lithops* sp. terkait struktur morfologi dan adaptasinya terhadap lingkungan ekstrem. *Lithops* sp. berbentuk seperti kerucut terbalik dengan bagian yang muncul di atas permukaan tanah merupakan permukaan daun. Bentuk ini merupakan adaptasi yang dilakukan oleh *Lithops* sp. untuk mengurangi paparan sinar matahari dan mencegah kehilangan air berlebih selama proses transpirasi. Selain bentuknya, epidermis *Lithops* sp. juga mengalami diferensiasi khusus sehingga dapat mencegah kehilangan air berlebih selama transpirasi. *Lithops* sp. juga mengalami diferensiasi untuk membentuk sel jendela pada permukaan daunnya yang berfungsi untuk meningkatkan laju fotosintesis dengan memperbesar radiasi sinar matahari yang masuk ke jaringan fotosintetik.

Kata Kunci: adaptasi, lingkungan kering, *Lithops* sp., morfologi, sukulen

INTRODUCTION

Succulents are a type of plant that has thicker and fleshy body parts as a form of adaptation for living in arid habitats (Aglave, 2018). Succulent comes from the Latin 'sucus' which means "juice" or "sap" due to its ability to retain water in some vegetative organs such as roots, stems, or leaves (Kolhe et al., 2019). One type of succulent that is rarely studied but has interesting adaptations is from the genus *Lithops*. Plants in this genus are known as "living stones" or living stones because their body shape resembles their substrate, namely stone (Cole, 2006). *Lithops* is included in the subfamily Ruschiodeae which is the largest subgenus with 112 genus and more than 1600 species (Klak et al., 2013). *Lithops* consists of more than 37 types of species (Kellner et al., 2011).

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The African continent, for example the country of South Africa, has many endemic succulents because of its environment which has unique characteristics such as *Lithops* sp. This plant has a limited and uneven distribution of species (Loots et al., 2019). *Lithops* sp. is one type of succulent that lives in desert areas with extreme hot weather. The habitat of *Lithops* sp. gets very strong direct sunlight and causes the temperature at ground level to exceed 70°C (Garrett et al., 2010). *Lithops* sp. is commonly found on the African continent, such as *L. ruschiorum* which grows in Namibia, a country located in southwestern Africa (Loots et al., 2019). The extreme habitat of *Lithops* sp. makes this plant adapt to its environment. This plant positions most of its shoots below the soil surface so as to reduce water loss. The morphology of *Lithops* sp. which is like a rock and grows flush with the surface of the soil makes this plant difficult to detect by herbivores (Garrett et al., 2010). *Lithops* sp. is generally considered to perform CAM photosynthesis, although experimental evidence is still rare (Oddo et al., 2021).

Lithops have an interesting adaptation mechanism behind their rock-like body shape, making them very interesting to study. Based on this, a review was conducted to understand the adaptive survival mechanisms of *Lithops* in arid environments through morphological strategies and water regulation. The findings outlined in the article can serve as a valuable information source to support conservation efforts aimed at protecting the species from extinction due to environmental changes. Thus, this research not only enriches the scientific literature on *Lithops* adaptation in arid environments but also holds potential for broader practical applications.

RESEARCH METHODS

The method used in this research is to conduct a scientific review. The writing begins with collecting reference sources using the keywords "*Lithops* sp., succulent, adaptation of *Lithops* sp., and morphology of *Lithops* sp. from various articles and books that contain supporting information. Collection of reference sources is done through various scientific databases such as *ResearchGate, PubMed, ScienceDirect,* and *Google Scholar.* The reference criteria used are research articles and reviews related to morphology and adaptation of *Lithops* sp. with a publication period of the last 15 years and available in full text. References will not be used if they exceed the publication period of the last 15 years unless there are no other relevant publications. The references obtained are then selected and used as the basis for writing to study the morphology of *Lithops* sp. and the influence of morphology in supporting adaptation patterns in dealing with habitat conditions in dry areas. Data analysis is done qualitatively through the extraction of important and relevant information while data synthesis is done narratively by grouping references into several categories such as characteristics of the morphological structure of *Lithops* sp., regulation of photosynthesis of *Lithops* sp. through the role of window cells and water regulation mechanisms in the leaves of *Lithops* sp.

RESULTS AND DISCUSSION

1. Morphology of *Lithops* sp.

Lithops sp. is a genus known for its adaptability to extreme climates in South Africa (Korn, 2011). This plant is also known as a stone plant or flowering stone because of its ability to blend with its substrate on gravel plains, rocks, and slopes making it difficult to detect (Loots et al., 2019). *Lithops* sp. belongs to the Aizoaceae family which is distributed in the western and southern central African regions, especially in Namibia and South Africa (Oddo et al., 2016). *Lithops* sp. consists of 37 species, of which one example is L. *ruschiorum* (Loots et al., 2019). According to Schoch et al. (2020), the following is the classification of *Lithops* sp.:

Kingdom	: Plantae
Phylum	: Tracheophyta
Class	: Magnoliopsida
Order	: Caryophyllales
Family	: Aizoaceae
Genus	: *Lithops*
Species	: *Lithops* sp.

Lithops has a shallow root system and draws water from the uppermost soil layer (about 5 cm from the soil surface). This plant is in the form of an inverted cone with the base or base above the ground and the apex shrinking in the soil and at the end there are roots (Figure 1) (Oddo et al., 2016). For example, the species *L. ruschiorum* has a tall body morphology with a heart shape, the surface of the leaves above the ground is generally very smooth, has a pale white to grayish color or has a yellowish leaf surface with a slight pattern (Loots et al., 2019).

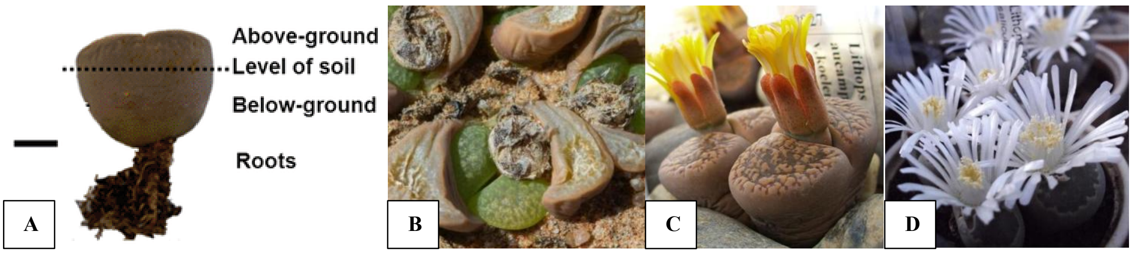
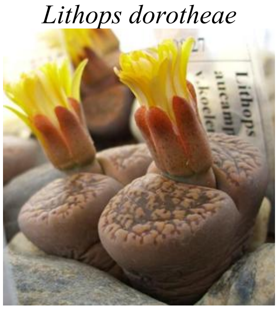
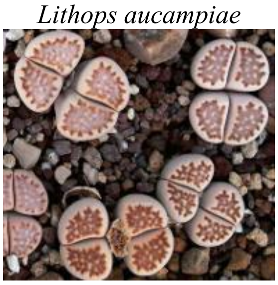


Figure 1. (A) Morphology of *Lithops* sp. (Field et al., 2013); (B) Leaves of *Lithops* sp. (Earle' & Young, 2020); (C) Flower buds of *Lithops aucampiae*; (D) Flower of *Lithops salicola* (Loana et al., 2015)

Lithops sp. has a pair of succulent leaves that are fused along the edge, and are inserted on very short stems separated by narrow slits. The leaf surface of *Lithops* sp. has a structure called window cells. These window cells have a function to receive light. Light entering through the window will diffuse to the chlorophyll side, adaxial surface, and abaxial leaf. Each species of *Lithops* sp. differs in expressing the clarity of its reticulation pattern. The reticulation pattern surrounds a polygonal areola with a varying number of sides, with the largest number of sides being hexagons. The most prominent feature of this reticulation pattern is the incomplete closure of the marginal polygons, except for the polygons at the adaxial edge of the leaf. This incompleteness can also be found in small paired internal polygons (Korn, 2011).

The apical meristem on *Lithops* sp. will produce a new pair of leaves (Figure 1B) or sometimes flower buds during each growing season (Figure 1C). The new pair of leaves will develop in the cavity of the previous leaf. The new leaf of this plant will grow through a gap in the old leaf or the previous leaf by forming a 90° angle from the angle of the old leaf (Figure 2). The leaves of *Lithops* sp. only the adaxial is exposed to light so that this plant can grow in extreme conditions or habitats because this plant is able to reduce water loss through transpiration. The seed capsules of this plant are elliptical in shape measuring 5-6 locules and contain seeds without any features to enhance their dispersal. *Lithops* seeds adapt physically and physiologically to survive long periods of dormancy until they need only a small amount of moisture to begin germinating. In addition, this plant is a small succulent that requires less water for growth compared to larger plants (Oddo et al., 2016). The morphological characteristics of several *Lithops* species are shown in Table 1.

Table 1. Morphological characteristics of several *Lithops* species

No.	***Lithops* species**	**Morphological Character**
1.	 *Lithops salicola*	It grows in clusters of up to 20 or more pairs of leaves, overall gray in color with the window portion olive green. It has a slightly convex upper leaf surface with a smooth texture, measuring up to 30 mm in length and 15 mm in width, and has white flowers (Kellner et al., 2009; Loana et al., 2015).
2.	 *Lithops dorotheae*	Overall, it is cream or light yellowish-brown in color, with a convex upper surface of the leaf and a smooth texture. It measures up to 30 mm in length and 20 mm in width. The window area is dark in color with thick red lines and features yellow flowers (Kellner et al., 2009; Loana et al., 2015).
3.	 *Lithops aucampiae*	It has a reddish-brown color with a flat to slightly convex leaf surface. It is relatively large, measuring 40 mm in length and 20 mm in width, with yellow flowers. The window area is dark olive green to reddish-brown with patterns of lines or horn-like branches along the outer edges (Loana et al., 2015).
4.	 *Lithops julii* ssp. *fulleri*	The surface of the body is pale cream in color, with a windowed surface featuring numerous intersecting lines forming a pattern resembling a net in shades ranging from light to dark brown, and it has white flowers (Stancher, 2017).
5.	 *Lithops amicorum*	Very small in size, dull white in color with flat leaves that lie flat on the ground, it has white flowers (Loots *et al*., 2019).

6.	 *Lithops karasmontana*	Growing in clusters of up to 60 pairs of leaves or more, with flat to convex leaf surfaces. Some varieties have red markings, while others do not. Has white flowers (Loots et al., 2019).

2. Mechanisms of water regulation in *Lithops* sp. leaves

Leaves are an important part because they are composed of parenchymal tissue that is used to store water as a form of adaptation to habitat in arid environments (Sajeva & Oddo, 2007). *Lithops* morphology is composed of a pair of leaves with a small stem mediated role as a form of adaptation in the face of extreme environments in the form of lack water. Body parts that mostly grow in the soil cause this plant to be able to reduce exposure to light, limit excess heat, and lose water during transpiration (Martin et al., 2013).

Regulation of water transfer between vegetative organs is one of the adaptations of some plants as a survival strategy in limited water conditions. Succulent plants have the ability to produce a new pair of leaves from the cavity between the previous leaves without additional external water (Yang et al., 2021). New leaves that grow from between old leaves have the ability to utilize existing water from old leaves. This recycling can occur through a potential gradient because the water potential in young leaves is always lower than the old leaves, allowing water transfer to occur (Oddo et al., 2016). The epidermis in plants living in arid regions generally undergoes special differentiation that serves to reduce transpiration that causes water shortages. Epidermal differentiation in *Lithops* is in the form of window cells that allow light to penetrate into the photosynthetic tissue underground. This differentiation allows photosynthesis to occur without having to expose the entire leaf to the outside surface, reducing water loss through transpiration (von Wilert et al., 1992).

Water transfer between vegetative organs occurs when the apical meristem produces a new pair of leaves each growth season (Rabas & Martin, 2003). The regulation that is carried out is that the young leaves take water from the old leaves. Water transport can be through apoplastic and symplastic pathways (including transmembrane flow through the plasma membrane and transmembrane flow through plasmodesmata) (Xiong & Nadal, 2020). Based on research conducted by Veca et al. (2011), most water is transported via the apoplastic pathway (74.2%) compared to transportation via the symplastic pathway (59.2%). The symplastic pathway involves the movement of water and solutes from one cell to another through the cytoplasm. Water that moves symplastically will meet with two sets of membranes per cell and must diffuse across the inside of the cell (Buckley, 2014). Meanwhile, the apoplastic pathway is the process of water and solute transport that takes place in the intercellular space. The movement of water through this pathway prioritizes the outside of the cell, so that water will pass through the plasma membrane and cell membrane (Zarebanadkouki et al., 2019).

3. Role of windows cell in photosynthesis regulation

Epidermal differentiation in plants in arid regions affects the optimization of photosynthetic rates and regulation of energy regulation (Gibson, 1998). *Lithops* plants experience this epidermal differentiation in an extreme form known as windows cell on the leaf surface (Egbert & Martin, 2002). Windows cells besides being found in *Lithops* sp. are also found in several other succulent plants such as *Howarthia*. Windows cells on *Howarthia* have a smooth and shiny surface or are covered by protrusions or spines (Theodoris, 2018). This specific epidermal differentiation in succulent plants serves as a store of various secondary metabolites and mineral crystallization (Cote, 2009). This morphology allows light to penetrate deep into the photosynthetic tissue below the ground. The function of window cells is thought to increase the rate of photosynthesis underground by increasing the radiation of sunlight to enter the photosynthetic tissue (Field *et al*., 2013). The shape of the epidermis in large window cells increases the internal temperature in the leaf due to the large amount of incoming sunlight radiation (Martin et al., 2013).

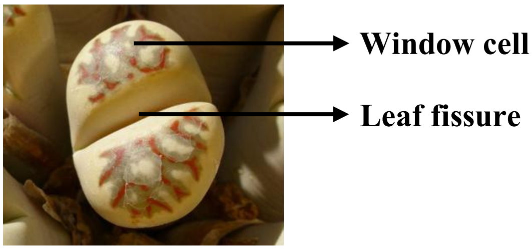


Figure 2. Window cell of *Lithops dorotheae*

The type of photosynthetic process that occurs in *Lithops* plants is Crassulacean Acid Metabolism (CAM) (Winter, 2021). This photosynthesis helps plants reduce water transpiration by optimizing the photosynthetic rate by opening stomata for CO_2 assimilation only at night when temperatures are cooler. This condition also causes a decrease in the concentration of water vapor from the leaves to the air when it is minimal (Arakaki *et al*., 2011). Stomata in leaves play an important role in the regulation of light intensity, light quality, osmolyte concentration, temperature, humidity, and the circadian rhythm of photosynthesis (Males & Griffiths, 2017). The CAM cycle consists of two sequential metabolic components that occur in the mesophyll cells of the leaf or stem collenchyme. This photosynthetic process is temporarily separated into two long cycles that occur over 24 hours (Borland et al., 2014).

CAM plants take up CO_2 at night throught stomata that have high conductivity, then convert it into HCO_3^- by carbonic anhydrase. Carbon fixation then occurs into malic acid by PEP carboxylase (PEPC) and malate through the Calvin cycle. Malic acid will accumulate overnight (Brautigam et al., 2017). Under high stomatal light during the day, the stomata are closed and malic acid is processed through decarboxylation to release CO_2 which is fixed by RuBisCO. PEPC in CAM plants that occurs at night causes water transpiration and CO_2 absorption from the atmosphere to be reduced (Cheung et al., 2014). The accumulation of CO_2 inside the cell during decarboxylation when the stomata are closed helps RuBisCO works more efficiently and lowers the risk of photorespiration by oxygenase enzymes. The mechanism aims to limit the amount of water lost through leaf stomata (Abraham et al., 2016).

CONCLUSION

The window cells on the surface of Lithops sp. leaves show a distinctive differentiation of the epidermis. These window cells serve to increase the rate of photosynthesis underground and support photosynthetic regulation aimed at limiting the amount of water lost from the leaves. Understanding the mechanisms of water regulation and the role of window cells in photosynthesis regulation as an adaptation of Lithops to extreme environments can serve as a foundation for research into the details of photosynthesis experienced by CAM plants. Further research can be conducted to explore the regulatory mechanisms and role of window cells in enhancing CAM photosynthesis efficiency, including metabolic pathway regulation, the role of specialized anatomy in light absorption, and physiological responses to environmental stress changes. This study is expected to broaden our understanding of succulent plant adaptation, support conservation efforts, and unlock their potential in the development of drought-resistant plants.

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