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Interrelationships of Air Canal Adaptation in the Leaves of Water Lilies and Water Depth of *Lebak* Swampland in Kalimantan Selatan

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Abstract:

Nymphaea pubescens grows in *Lebak* swampland in its different levels of water depth. This aquatic plant has an absorption system that moves gases through the laminae and has a convective flow system through air canals in midrib and petiole. This study aims to determine the adaptive structure of air canal in the water lilies (*Nymphaea pubescens*) laminae and how its structure varies along with water-depth fluctuations. The research was conducted by observing plants in 4 (four) different zones of water depth: (1) water depth between 28-95 cm (zone I), (2) 28-99 cm (zone II), (3) 54-112 cm (zone III), and (4) 55-124 cm (zone IV).

Every lamina area, lamina thickness, and cross-sectional area (XS) of petiole, a number and area of air canals in midrib and petiole were collected for analysis. The results showed that the cross-sectional area of the laminae *N. pubescens* increased along with water depth, but the correlation with laminae thickness decreased. The midrib air canals are symmetrically divided and there was one main canal pair, an additional three pairs of canals, and a pair of smaller canals.

The cross-sectional area of the midrib and air canal increased along with water depth. The calculation of the area of four pairs of air canals is 75%. Air canals make up 34% of midrib cross-sectional area. The midrib air canals produced one pair of air canals, an additional two pairs of canals and a pair of smaller canals. The calculation of the area of three pairs of airways is 93%. Air canals make up 31% of the cross-sectional area of the petiole. The length of the petiole, the volume of the petiole, and the volume of the air canal increased along with water depth, but the cross-sectional area of the petiole and the air canal were not related by water depth.

Keywords: air canal; laminae; *Lebak* swampland; midrib; *Nymphaea pubescens*; petiole.

JEL Classification: Q10; Q15; Q56; Q57; R11.

Introduction

The water level fluctuations in *Lebak* swampland cause the plants' attempt to adapt to these environmental conditions. The sessility of plants is undoubtedly their most disadvantageous feature compared to other living

organisms and implies that their survival can be threatened by environmental perturbations. However, plants have developed fascinating mechanisms enabling rapid detection of changing conditions accompanied by highly complex molecular responses, resulting in remarkable phenotypic plasticity (Dubois *et al.* 2018).

According to Shashika *et al.* (2016), species of *Nymphaea* show high morphological plasticity where the size of leaves and flowers are thought to be strongly dependent on hydrological and edaphic conditions. *Nymphaea odorata* petioles increase in size and number in deeper water but at a decreasing amount concerning lamina area (Richards *et al.* 2012). The area of the leaf that captures oxygen from the air is proportional to its size (Weisner 1988). Modification of the petiole structure has a morphological form that is capable to respond flood pressures and water depth (Grace 1989; Waters and Shay 1992; Sasidharan *et al.* 2017). Up to a certain age, a leaf rudiment will develop into a submerged or a floating leaf according to nutritive conditions (Conard 1905). The petioles of *Nymphaeas* necessarily vary in length according to the depth of water in which the plant grows, being always long enough to allow the leaf some freedom in floating about (Conard 1905; Richards *et al.* 2011; Yu and Yu 2011; Wu 2017). According to Richards *et al.* (2011), the petioles of *N. odorata* increase in width as well as length with increased water depth and also increase their mass per unit length.

Anatomical modification of the plants' petiolar structure with an internal ventilation system (Sorrell *et al.* 1997; Richards *et al.* 2012) or sufficiently large air space is the most common plants adaptation in swampland or aquatic environments (Seago 2018; Ford and Champion 2019). Plants that have this type of ventilation system have several anatomical modifications that support it, such as diaphragms and aerenchyma (Sorrell *et al.* 1997). Schizogenous aerenchyma air spaces almost always occur in the cortex or ground organ tissue (Seago 2018) that facilitate oxygen movement and survival. The response of limited internal gas transport is very important in the O₂ supplied to the roots in sediment (Weisner 1988; Sorrell and Tanner 2000; Colmer 2003). Oxygen stress due to gas transport limitations may be one of the factors limiting depth penetration in this species and other emergent aquatic plants (Sorrell and Tanner 2000) such as *Nymphaea* with floating leaves and rooted in the sediments (Conard 1905; Chen *et al.* 2017; Ismail *et al.* 2018).

Aquatic vascular plants commonly have an extensive system of internal gas spaces, and it is generally accepted that the primary role of these lacunae is the delivery of O₂ to respiring plant parts buried in the anaerobic sediment (Dacey 1981). According to Armstrong (1979); Große (1996); Matthews and Seymour (2014), swamp plants survive in an anoxic environment. Higher water depths increase O₂ transport distance from atmospheric sources to the parts in sediments (Dacey 1981; Armstrong *et al.* 1996; Richards *et al.* 2012), petiole gets more pressure from water (Richards *et al.* 2012), and the wind or wave condition from surrounding (Etnier and Villani 2007). To meet the requirements of rapid and efficient transport of oxidizing capacity to the roots and rhizosphere, vascular plants have a well-developed system of internal gas space (Dacey 1981) as a striking feature of the internal anatomy of aquatic plants (Dacey and Klug 1979). Air gaps between cells function as gas transport pathways, aerate organs under the sediment, and oxidize the rhizosphere, all of which contribute to plant growth (Armstrong 1979).

The Network of internal gas spaces in the yellow waterlily constitutes a pressurized flow-through system that forces oxygen to the rhizome buried in anaerobic sediment (Dacey and Klug 1982^a). When a leaf emerges on the water surface, the adaxial part of the leaf that has stomata exposed to the atmosphere (Kaul 1976; Dacey and Klug 1982^b; Tsuchiya 1988; Etnier and Villani 2007; Kordyum *et al.* 2021) to exchange gases (Dacey 1980; Dacey 1981; Tsuchiya 1991; Ribaudo *et al.* 2012). Water lilies and especially floating-leaved aquatic macrophytes absorb energy from sunlight or water with higher temperatures than ambient temperature to produce a gas-pumping system commonly powered by solar radiation, with air influx and pressurisation of the youngest, just emerged leaves along with positive humidity and temperature gradients between leaf aerenchyma and the ambient atmosphere (Große 1996).

Oxygen transport through mass flow depends on the light absorbed by the leaves (Dacey 1981). This flow transports oxygen from young leaves to submerged organs and returns it to the environment through the ventilation of older leaves. This ventilation system represents an important adaptation by the waterlily to life in anaerobic sediments (Dacey 1980; Dacey 1981; Dacey 1982^a; Dacey 1982^b; Grosse and Mevi-Schultz 1987; Tsuchiya 1991).

Functional stomata in floating leaf have a prominently gas chambered mesophyll on the abaxial surface, the larger the laminae, the more prominent the gas chamber. Most floating leaves have prominently chambered mesophyll, and in some instances the chambers are locally enlarged and form buoys (Kaul 1979). According to Richards *et al.* (2012) the gas space in petiole increases in size and amount of air along with the increase of water depth. This study aims to describe how the modification of laminae, petiole, and air canal in *N. pubescens* is related to different levels of water depth in *Lebak* swampland. This study also explains the interrelationships of

petiolar air canal architecture in *N. pubescens* and water depth. Water from rain and upstream can be stored in the swampland's basin shape, which creates a topography that causes the swampland to have water level fluctuations (Fatah *et al.* 2017).

1. Literature Review

Richards *et al.* (2012) studied the relationship among air canal architecture, depth, and convective airflow in the petiole of *Nymphaea odorata*. Different air depths cause differences in the structure of the air canal and convective airflow, where and the number of air canals increases with increasing air size but decreases in the number of petioles. The convective flow will vary depending on the depth of the water and the amount of influx to the efflux lamina. Yu and Yu (2011) found that various leafy *Nymphoides peltata* plants floating on the water surface responded to changes in high water depth levels. The researchers compared the growth response of *Nymphoides peltata* to rapid rises in water levels treated with 1 g and 12 g of N-P-K:16-8-12 fertilizer per tub filled with 8 kg of washed sand. Increased water depth causes *Nymphoides peltata* to respond. Under low and high nutrient concentrations, the gradual increase in water lengthened the petiole 3.96 - 4.80 cm per day, the rapid increase in water lengthened the petiole 25.48 - 26.64 cm per day, and the constant increase in water lengthened the petiole 3.0 - 24.4 cm per day.

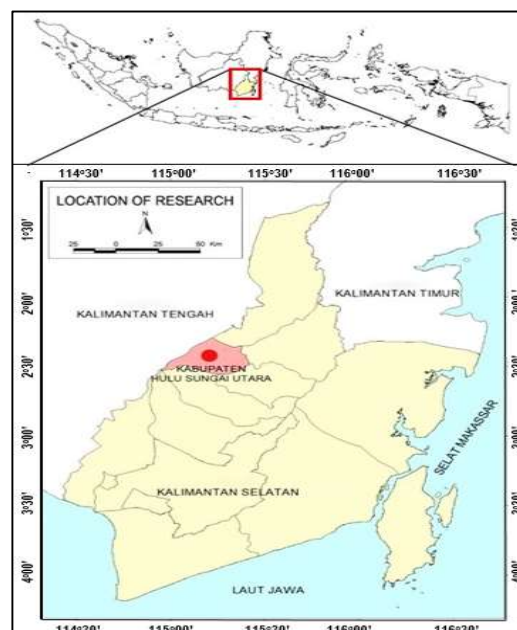
Richards *et al.* (2011) researched *Nymphaea odorata* growth, morphology, and biomass allocation in response to water surface depth. *Nymphaea odorata* was planted for 13 days at 30 cm, 60 cm, and 90 cm water depths. Water depths of 30 cm have smaller leaf sizes and shorter lifespans than depths of 60 cm and 90 cm. The laminate area and petiole length increased significantly as water depth increased, but biomass did not. Eugeniusz *et al.* (1985) studied how changes in lake water depth affected the morphology and anatomy of the petiole in *Nymphaea alba* L. and *Nuphar lutea* L. A series of responses to irregular water flow (fluctuation in water depth) and turbulence cause changes in the structure and anatomy of the plant, resulting in elongation and a decrease in the petiole cross-section.

2. Materials and Methods

2.1. Time and Location of Research

The research was conducted from February to June 2019 in the *Lebak* swampland in Desa Teluk Sinar, Kecamatan Sungai Pandan, Kabupaten Hulu Sungai Utara, Kalimantan Selatan, Indonesia (Figure 1). In 2019, rainfall in Kecamatan Sungai Pandan was 1.846 mm, at a height of 6 meters above sea level (MASL) and a slope of 0-2° (BPS-HSU, 2020). The research location is classified into four water depth zones with their respective positions: zone I with a depth of 28-95 cm at 2°30'5.7"S, 115°10'23.5"E; zone II at 2°30'4.3"S, 115°10'18.6"E; zone III at 2°30'4.3"S, 115°10'15.3"E; and zone IV at 2°30'4.3"S, 115°10'10.5"E.

Figure 1. Research location (●) Desa Teluk Sinar, Kecamatan Sungai Pandan, Kabupaten Hulu Sungai Utara, Kalimantan Selatan, Indonesia



2.2. Procedures

Determination of observation zone and water-depth level fluctuation

Swamplands' level of water depth differences was obtained by determining the observation zone from the edge of the swamp to a deeper spot or towards the basin. Zones were determined by measuring the distance from the swamp's edge to the basin as far as 150 meters in each zone. The zone determination was being taken as the research location consists of four zones: zones I, II, III, and IV. The obtained zone was marked with *galam* wood (*Melaleuca ericifolia*) and the ordinate points were determined by using the Global Position System (GPS) Handheld. Observations of water depth fluctuations were examined in each zone from February to June 2019. Measurement of water depth was carried out using the Secchi-disk.

Data sample collection from the field

The collection of materials being used for anatomical and morphological studies in the form of leaves and their petioles were collected in each of the designated observation zones. Plant samples were taken in four observation zones by selecting 18 plants, so that the total sample plants were 72 plants. Determination of the data sample was done by purposive sampling method. Plants that were selected as observation samples were marked with *galam* wood and observation labels. Harvesting is done by using a *jukung* or canoe as main transportation in swampland. Harvesting leaves are taken from the plant with mature leaves and their petioles, the leaves are fully opened, and the surface is green.

*Morphology and anatomy observation of *N. pubescens**

In each harvest, the length of petiole is measured by using a tape measure. The petiole and leaf were separated purposively for morphology and anatomy observation. Morphological studies concern with the width and length of the petiole. The area of separated leaves was measured by using a Leaf Area Meter. Anatomical studies were carried out by slicing the center of the leaf starting from the base, resulting in a laminae size of 5 x 5 cm. Because the petiole is too long, the petiole is cut into three parts, namely the top, middle, and bottom, each 5 cm long. Leaf and petioles were sliced thinly using a cutter, then to preserve the tissue, the material plant as put in 70% ethyl alcohol (Eugeniusz *et al.* 1985). The material plant was photographed and measured using a Dino Capture 2.0 digital microscope version 1.3.6.K. Photographs of the cross-section were used to measure leaf thickness, area, number, arrangement of air canal in leaf and petiole. The formed air canals tend to be paired in almost all cross-sections of the leaf and petiole. The volume of the petiole was calculated by modeling the petiole as a cylindrical shape, so that the length of petiole was multiplied by the petiole cross-section. Likewise, the volume of petiolar air canal is obtained from the length of petiole multiplied by the cross-section of petiole air canal.

2.3. Data Analysis

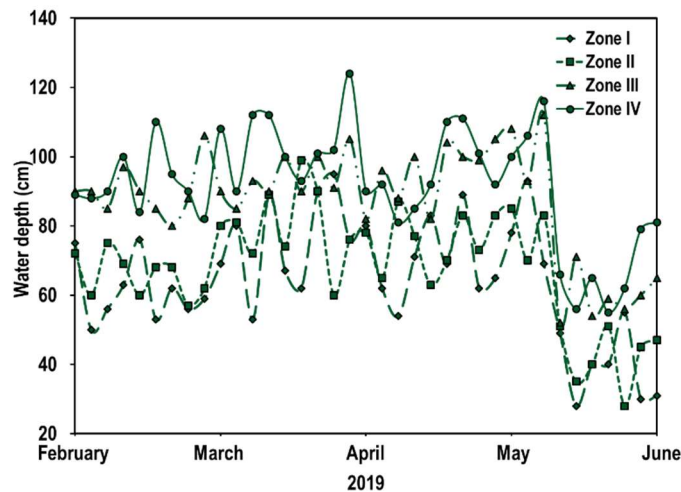
Data was analyzed using statistical software (SAS 9.4) and Microsoft Excel. The correlation of petiole morphology, leaf, leaf area, and air canal shape measurement were analyzed using linear regression, while differences among water depth levels were analyzed by ANOVA for normal distribution. The difference between the water depth in the percentage of air canal area is compared with the GLM (Generalized Linear Model) using the binomial error distribution. Post hoc comparisons were made using Tukey's HSD. Summary data are presented with \pm SD.

3. Results and Discussion

3.1. Water Depth

Lebak swampland had a fluctuating depth of water, whereas this water level fluctuation depends on meteorological conditions (Figure 2). The surface of swamp water level from February to May is almost in stable fluctuations, but there was a drastic decline at the beginning of June. The water depth fluctuations in each zone of the swamp had different minimum and maximum retentions. The minimum and maximum retention of the swamp water level are in zone I with a depth of 28-95 cm, zone II with a depth of 28-99 cm, zone III with a depth of 54-112 cm, and zone IV with a depth of 55-124 cm. Each research zone showed that zone I had the same minimum water surface retention as zones I and II, which was 28 cm, while in zones III and IV the water surface retention are 54 cm and 55 cm, respectively, which was higher than zones I and II. The maximum water surface retention for each zone is different and increasing, namely zone I with 95 cm depth, zone II with 99 cm depth, zone III with 112 cm depth, and zone IV with 124 cm depth.

Figure 2. The fluctuation of water-depth level in swampland surface of Desa Teluk Sinar. Data was acquired from the correlation of water depth level between 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV). Observation and measurement have been conducted from February until June 2019.



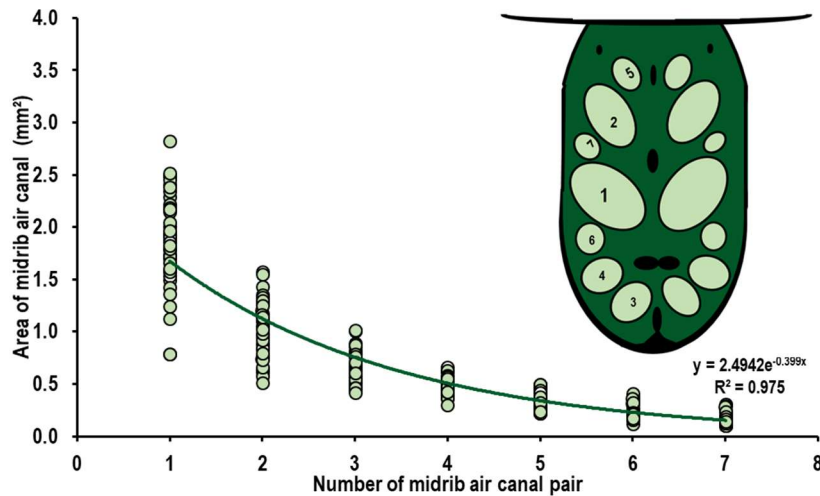
The water level difference in swampland surface was affected by the difference position in each observation zone and seasonal water input differences results in water level fluctuations. Swampland that was inundated either permanently, periodically, or prolongly saturated land could create a good environment for hydrophytes to grow (Tiner 2017; Fahmi and Wakhid 2017). The swamp in Desa Teluk Sinar is a type of *Lebak* swampland. According to Noor (2007) the word *lebak* is taken from the Javanese vocabulary which means valley or low. A lower position will form a basin, basin morphometry causes various depth measurements (van der Valk 2006), the occurrence of variations in height, and the duration of inundation (Nursyamsi *et al.* 2014). Changes or instability of the water surface also depends on the existence of two seasons in Indonesia, namely the wet season and the dry season. In Indonesia, the wet season occurs when the southwest monsoon blows, while the dry season occurs when the northeast monsoon blows (Wirjohamidjojo 2010). The rain that falls in the swamp area and its surrounds leads the surface of the swamp to rise fast; even if there is a rainy season, there will be runoff and floods; however, as the season changes, the rainfall decreases, which causes the surface of the swamp to lower. The average rainfall in Kabupaten Hulu Sungai Utara from February to May was recorded at an average of 247.48 mm and from May to June an average of 99.64 mm (BPS-HSU 2020). High rainfall from February to May causes an increase in the depth of the water surface, while in late May to June which is entering the dry season, there is a decrease in the depth of the water surface (Figure 2).

3.2. Air Canal Architecture

Midrib air canal

Nymphaea pubescens had floating leaves with air canals or gas space in the leaf veins. The most prominent are the leaf veins with the largest air canal size are found in midrib. The air canals in midrib have at least two pairs of canals in the center (Figure 3). Air canals in midrib tend to appear in pairs and surround the vascular tissue, however there are some unpaired canals. The first pair of the two largest air canals is located in the center of the midrib and opposite to each other, while the second pair is in posterior from the first pair. The third pair is exactly in the anterior with smaller size than the first and second pairs. Subsequent canals are additional and smaller in size than the previous canals. The pair of air canals in midrib decreased in area close to an exponential decay ($y = 2.4942e^{-0.399x}$, $R^2 = 0.975$; Figure 3). Three pairs of air canals in midrib accounted for air canal area of $65.7 \pm 6.80\%$, respectively $35.2 \pm 4.80\%$ for the first pair, $18.2 \pm 4.09\%$ for the second pair, and $12.2 \pm 1.88\%$ for the third pair. The air canals in midrib have different occurrence rates which cause the number of air canals to vary in each cross-section. The average number of air canals in midrib were 26 (range 13-34, $N = 72$) at 28-95 cm depth, 28 (range 17-38, $N = 72$) at 28-99 cm depth, 30 (range 17-38 cm). 21-40, $N = 72$) at 54-112 cm depth and 31 (range 22-41, $N = 72$) at 55-124 cm depth.

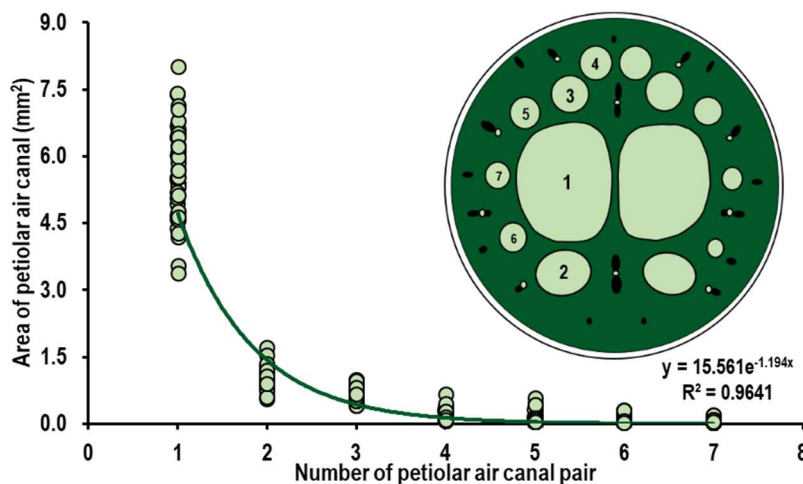
Figure 3. Midrib Cross sectional area (XS) *N. pubescens* for the air canal pair, number in canals means the occurrence rates of air canal in cross sectional (XS) midrib. Data of plants are acquired from water depth level combination of 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV).



Petiolar air cannal

The air canals in the petiole of *N. pubescens* have large size. The petiolar air canal contains one pair of canals which is very dominant as the first pair of canals (Figure 4). The second pair of air canal is at abaxial and the third pair of canals is at adaxial of the center of the first air canal. The next cannals have additional cannals which are smaller than the previous pair of channels. The pair of petiolar air canals reduced in area close to an exponential decay ($y = 15.561e^{-1.194x}$, $R^2 = 0.9641$; Figure 4). Three pairs of air canals on the petiole generated for the air canal area of $93.2 \pm 7.1\%$, respectively $72.5 \pm 9.5\%$ for the first pair, $12.1 \pm 2.1\%$ for the second pair, and $8.6 \pm 2.1\%$ for the third pair. The petiole air canals have different occurrence rates which cause the number of air canals to vary in each cross section (Figure 4). The average number of air canals in the petiole at 28-95 cm depth was 13 (range 10-19, $N = 72$), 28-99 cm depth was 14 (range 10-21, $N = 72$), 54-112 cm depth was 15 (range 10-24, $N = 72$), and 55-124 cm depth is 17 (range 10-31, $N = 72$).

Figure 4. Cross sectional area (XS) of petiole *N. pubescens* for air canal pairs. Numbered canal is the occurrence rates of air canals that appear in cross sectional (XS) of petiole. Data of plants are acquired from water depth level combination of 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV). Number in the diagram shows the pair order placement in cross sectional area.



Leaves are places where air canals exist as a means of transportation used to transport O_2 . According to Armstrong (1979) the survival of aquatic plants is highly dependent on their ability to transport O_2 to the flooded tissues. According to Matthews and Seymour (2006) the gas flow system of the water lilies plant consists of a number of pairs of gas canal that flow along the leaves, petioles and rhizomes. Gas flow in leaves is located in air canals, including those in the midrib or main veins on the underside of the leaf. The architecture of the air canals in midrib and petiole shows a typical arrangement as an aquatic plant (Figures 3 and 4). Air canals that are

composed of various sizes, in pairs provide the strength, elasticity, and buoyancy for lamina (Kaul, 1976), and has a plasticity that reflects a response to environmental changes. Changes of air canals numbers in both midrib and petiole at various water depths were related to the larger air canal (Figures 3 and 4). Minor modifications to anatomy and/or morphology greatly change their mechanical properties, permitting them to exist in both aquatic and aerial environments (Etnier and Villani 2007).

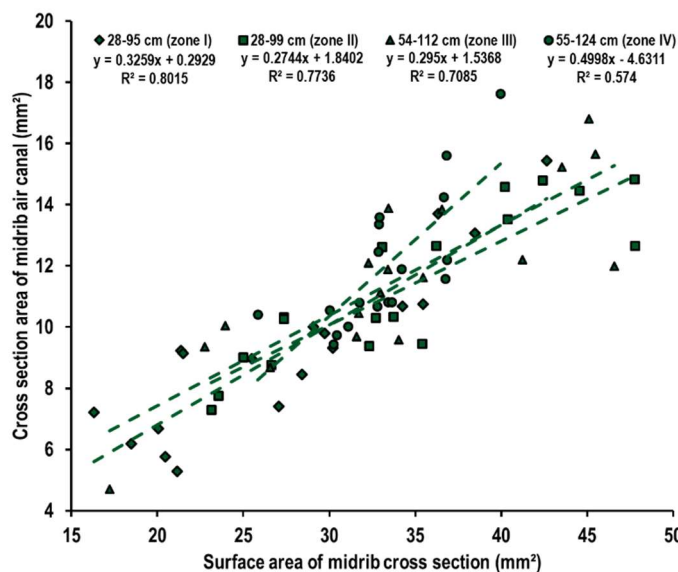
3.3. Adaptation to Water Depth

Growing Macrophytes have differences in terms of their live adaptation. Different water depth fluctuations form a sinusoidal curve with the period of each month of observation (Figure 2). This water depth fluctuation causes various adaptation behaviors attempted by *N. pubescens*. Adaptation is indicated by the formation of air canals in both midrib and petiole (Figures 3 and 4), as well as changes in leaf area and thickness (Table 1). Leaf area, leaf cross-sectional thickness, midrib cross-sectional area, midrib air canal cross-sectional area, petiole length, petiole volume, and petiole air canal volume were affected by different levels of water depth (Table 1 and 2). Leaf area, midrib cross-sectional area, and petiole length at a water of 28-95 cm depth (zone I) were significantly different with water at the depth of 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV), but between zones II, III, and IV did not show a significant difference (Tables 1 and 2).

Adaptation of midrib and petiole *N. pubescens* growing at different water depth zones had variations in the cross-sectional area of midrib, the cross-sectional area of midrib air canal, the cross-sectional area of petiole, and the cross-sectional area of petiolar air canal (Figure 5 and 6). The midrib air canal occupied $32.1 \pm 1.2\%$ of midrib cross-sectional area. The percentage of midrib air canal position from the midrib cross-sectional area at different water surface depths was not significantly different (Figure 5; ANOVA $F = 0.26$, $df = 3$, $P = 0.8538$). Furthermore, the petiole air canal occupied $31.7 \pm 0.5\%$ of the petiole cross-sectional area with the petiole air canal position from the petiole cross-sectional area at different water depths was not significantly different (Figure 6; ANOVA $F = 0.66$, $df = 3$, $P = 0.5972$).

The relationship between the cross-sectional surface area of midrib and the cross-sectional area of midrib air canal correlated with the water depth according to the regression equation in zone I ($y = 0.3259x + 0.2929$, $R^2 = 0.8015$), zone II ($y = 0.2744x + 1.8402$, $R^2 = 0.7736$), zone III ($y = 0.295x + 1.5368$, $R^2 = 0.7085$), and zone IV ($y = 0.4998x + 4.6311$, $R^2 = 0.574$), elaborated in Figure 5. Different surface levels of water depth simultaneously affect the cross-sectional area of midrib and the cross-sectional area of midrib air canal, the effect on each zone is 80.15% (zone I), 77.36% (zone II), 70.85% (zone III), and 57.4% (zone IV), elaborated in Figure 5.

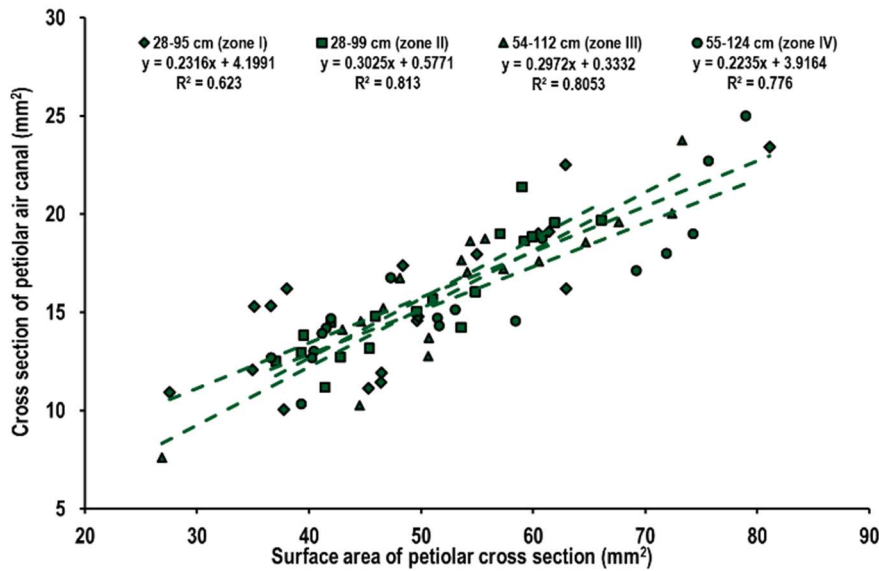
Figure 5. Cross sectional (XS) of midrib air canal area *Nymphaea pubescens* vs Cross sectional (XS) of midrib air canal area of plants growing at Lebak swampland in Desa Teluk Sinar in the zone at the depth of 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV).



Correlation with the surface of water depth was also found in the cross-sectional area of petiole and the cross-sectional area of petiolar air canal (Figure 6). The regression equation for the cross-sectional area of petiole and the cross-sectional area of petiolar air canal to the surface of water depth in zone I ($y = 0.2316x +$

4.1991, $R^2 = 0.623$), zone II ($y = 0.3025x + 0.5771$, $R^2 = 0.813$), zone III ($y = 0.2972x + 0.332$, $R^2 = 0.8053$), and zone IV ($y = 0.2235x + 3.9164$, $R^2 = 0.776$), elaborated in Figure 6.

Figure 6. Cross sectional (XS) of petiolar air canal area *Nymphaea pubescens* vs Cross sectional (XS) of petiolar air canal area of plants growing at *Lebak* swampland in Desa Teluk Sinar in the zone at the depth of 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV).



The cross-sectional area of petiole and the cross-sectional area of petiolar air canal are also simultaneously affected by different surface levels of water depth in each zone, respectively, the effect is 62.3% (zone I), 81.3% (zone II), 80.53% (zone III), and 77.6% (zone IV). The regression slope for the cross-sectional area of midrib and petiole increased as air pathways increased in midrib and petiole (Figure 5 and 6). The water depth of 55-124 cm (zone IV) has a steeper slope than the depth of 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III). This steeper slope indicates a higher increase in the cross-sectional area of midrib air canal per unit of increasing the cross-sectional area of midrib air canal (Figure 5). In contrast to the midrib, on the petiole, the steeper regression slope is found at a water surface depth of 28-95 cm (zone I) compared to a depth of 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV) (Figure 6). This steeper slope indicates a higher increase in the cross-sectional area of petiole air canal per unit of increasing cross-sectional surface of petiole at a depth of 28-95 cm (zone I).

Figure 7. Cross-sectional (XS) area of midrib air canal vs leaf area of the plants growing on *Lebak* swampland in Desa Teluk Sinar at the zone with water depth of 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV).

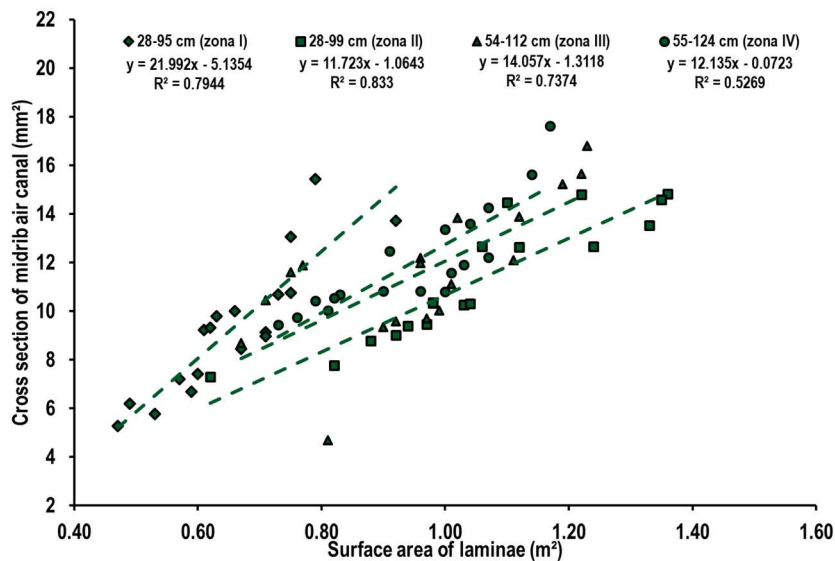
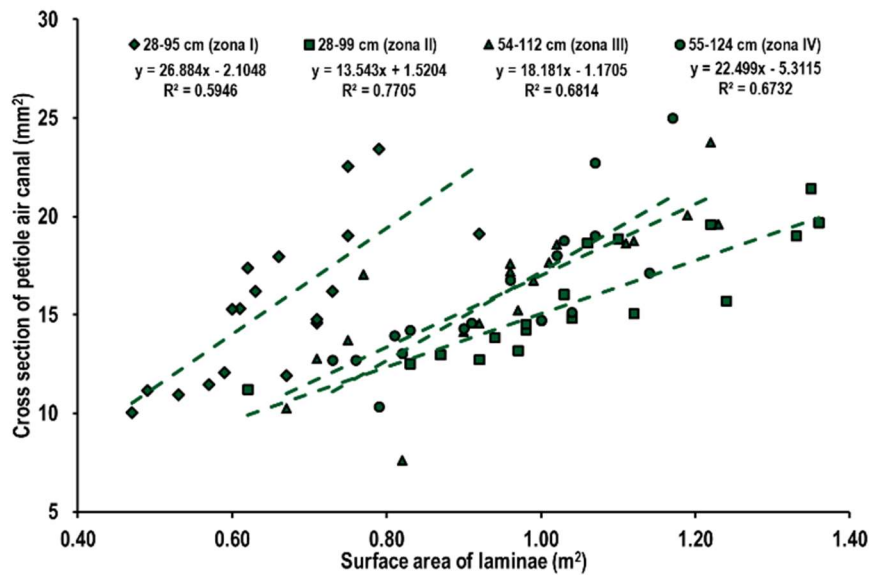


Figure 8. Cross-sectional (XS) area of petiolar air canal vs leaf area of plants growing on *Lebak* swampland in Desa Teluk Sinar at the zone with water depth of 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV)



The area of midrib air canal and the area of petiolar canal increased as the leaf area increased (Figure 7 and 8). Likewise, the regression slope of the leaf area increases as the airways increase in midrib and petiole. The water depth at 28-99 cm (zone II) has a shallower slope than the depths of 28-95 cm (zone I), 54-112 cm (zone III), and 55-124 cm (zone IV), the slope is shallower indicating a lower increase in the air canal cross-sectional area per unit of increasing leaf area.

The level of water depth affects environmental conditions, related to its function such as providing oxygen, regulating nutrient levels, and controlling water conditions (Cronk and Fennessy 2001; Li *et al.* 2019). Changes in water depth can affect O₂ transport distances (Weisner and Strand 1996), the extent to which nutrients are limited as a resource available for plant growth (Grace 1989), and water conditions in the form of water temperature which appear to be a limiting factor for leaf production (Klok and van der Velde 2017). The limit of water depth as a place for growing water lilies can reach a depth of 3 m (Sculthorpe 1967; Les 2018). Various morphological changes are carried out by aquatic plants to adapt to their habitat so that plants can continue to carry out their physiological processes.

Adaptation was carried out by *N. pubescens* which grew in the zone of increased water depth by producing leaves with larger leaf, more prominent midrib, longer petioles, and decreased leaf thickness. Differences in depth in the growing zone with a depth of 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV) have a relationship and create differences between strands, leaves, and petioles. Significant differences were found in leaf area, leaf cross-sectional thickness, midrib cross-sectional area, petiole length, petiole volume, but they did not differ in petiole cross-sectional area.

Table 1. Laminae area, leaf cross-sectional area, midrib cross-sectional area, and midrib air canal cross-sectional area of *Nymphaea pubescens* growing in *Lebak* swampland at the water depth of 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV). Value of *P* is the probability > χ^2 from the GLM test, *df* = 3; data followed by the same letter on the same line is the significant difference (*P* < 0.05).

Variable	Water depth in each growing zone				<i>P</i>
	28-95 cm (zone I)	28-99 cm (zone II)	54-112 cm (zone III)	55-124 cm (zone IV)	
Area of laminae (cm ²)	656 ± 113 ^b	1052 ± 195 ^a	962 ± 172 ^a	946 ± 133 ^a	<.0001
Thickness of XS laminae (mm)	0.51 ± 0.03 ^a	0.43 ± 0.04 ^b	0.35 ± 0.06 ^c	0.31 ± 0.03 ^d	<.0001
Area of XS midrib (mm ²)	27.6 ± 7.6 ^b	34.2 ± 3.4 ^a	34.1 ± 8.1 ^a	34.4 ± 8.0 ^a	0.0077
Area of XS midrib air canal (mm ²)	9.3 ± 2.8 ^b	11.3 ± 2.5 ^{ab}	11.6 ± 2.9 ^a	12.0 ± 2.2 ^a	0.0145

Understanding the adaptation of air canal architecture in midrib and petiole towards the changes in water depth, allows us to understand the modification of air canal structure in midrib and petiole, including the internal ventilation system. The presence of an internal ventilation system can increase O₂ transport to the rhizomes and roots of *Nuphar lutea*, along with that, CO₂ faster movement to the leaves is achieved, resulting the leaves can be assimilated (Dacey 1980, 1981; Dacey and Klug 1982^b). The unique thermodynamic gas transport mechanism pushes O₂ gas from leaves on the water surface to rhizomes in anoxic sediments (Abd. Rasyid *et al.* 2019).

The increase of water depth causes the flow in the internal aeration system to have a longer path length (Richards *et al.* 2012) and O₂ diffusion will take longer time (Weisner 1988) due to the increasing of O₂ transport distance (Grosse *et al.* 1991; Armstrong *et al.* 1996) thus enabling the transport of this gas to be one of the factors limiting the depth penetration (Sorrell and Tanner 2000). Internal transport of O₂ can be achieved at high water depths by convective gas flow (Grosse *et al.* 1991). Convection flow in aquatic plants through air canal depends on the pressure gradient between the influx and efflux of the leaves and the flow resistance in the plant aerenchyma (Colmer 2003). Aerenchyma provides a pathway for gas movement (Raven 1996) and stores the minimum amount of O₂ required by plants in O₂-poor aquatic environments (Cronk and Fennessy 2001).

Gas flow in plants is influenced by different water depths, but plants will be resistant and adapt to differences in water depth by modifying the air pathways, both in midrib and petiole. The modification was similar to the increase in water depth, leaf area, the cross-sectional area of midrib, and the cross-sectional area of petiole, but these increases were not proportional. Observations for the cross-sectional area of petiole and the cross-sectional area of air canal were not significantly different at each water depth, in contrast to the volume, both the cross-sectional volume of petiole and the cross-sectional volume of air canal, which were significantly different at different water depths.

Aeration of submerged plant parts involves the leaf, air canals located in the midrib and petiole. The increase of the lamina area following the increase in water depth causes area to capture of O₂ extends which then flows through the canals in midrib that prominently increasing, then the flow enters the petiolar air canals which extends along with the water depth. The larger the top surface of the plant, with a wider area for light absorption causes the release of O₂ from the roots to the surrounding water environment more effectively (Albuquerque *et al.* 2020). The role of the leaf and petiole as a place for gas flow through the canals in it becomes limitation factor of water lilies' ability to grow.

Table 2. The length of petiole, cross-sectional area of petiole, cross sectional area of petiolar air canal, and the volume of petiolar air canal in *Nymphaea pubescens* growing in *Lebak* swampland at zone with the water depth of 28-95 cm (zone I), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV). The value of *P* is the probability > χ^2 from the GLM test, *df* = 3; data followed by the same letter on the same line is the significant difference (*P* < 0.05).

Variable	Water depth in each growing zone				<i>P</i>
	28-95 cm (zone I)	28-99 cm (zone II)	54-112 cm (zone III)	55-124 cm (zone IV)	
The length of petiole (cm)	102 ± 14 ^b	125 ± 27 ^a	130 ± 21 ^a	142 ± 22 ^a	<.0001
Area of XS petiole (mm ²)	48.9 ± 13.3 ^a	50.3 ± 9.0 ^a	53.8 ± 11.4 ^a	54.1 ± 14.4 ^a	0.4100
Area of XS petiolar air canal (mm ²)	15.5 ± 3.9 ^a	15.8 ± 3.0 ^a	16.3 ± 3.8 ^a	16.0 ± 3.7 ^a	0.9229
Volume of petiole (mm ³)	49744 ± 15062 ^b	62971 ± 18969 ^{ab}	70023 ± 18646 ^a	76873 ± 24433 ^a	0.0003
Volume of petiolar air canal (mm ³)	15829 ± 4636 ^b	19837 ± 6410 ^{ab}	21186 ± 5758 ^a	22650 ± 5950 ^a	0.0031

The growing environment in swampland is very influential on plant life around it and provides opportunities for changes in vegetation (Smith *et al.* 2020). Basin morphometry affects the level of water depth (van der Valk, 2006), as well as in the *Lebak* swampland which has a basin shape that affects the height and duration of inundation (Susilawati and Nazemi, 2017). Indonesia, which has two seasons, utilizes *Lebak* swampland as a place to meet the needs of life. *Lebak* swampland in the dry season is used for rice fields, while in the rainy season it is used as a producer of fish and water lily seeds which are processed into various traditional food preparations. *Lebak* swampland is divided into three types, namely shallow, middle, and deep *Lebak* (Subagyo, 2006).

Shallow *Lebak* has a puddle height between 25-50 cm, middle *Lebak* between 50-100 cm, and deep *Lebak* 100 cm. The zones in this study have a depth of 28-95 cm (zone 1), 28-99 cm (zone II), 54-112 cm (zone III), and 55-124 cm (zone IV) fall into all three categories of swampland, for instance shallow, middle, and deep basin. The depth is 28-95 cm (zone 1) and 28-99 cm (zone II) because the depth is 100 cm, the zone is categorized as shallow to mid-range, then 54-112 cm (zone III) and 55-124 cm. (zone IV) because it is 100 cm, the zone is categorized as mid to deep. The division of three levels with a water depth range of 25 cm to 100 cm indicates that *N. pubescens* can grow in shallow, middle, and deep basin, but at each different level of water depth the plants will adapt. Leaf growth in shallow water depths will grow denser, because excessive density causes the petiole to be shorter (Etnier and Villani 2007).

The shadow effect of plants along the coastline will have an influence on plant growth in the swampland called the effect of shade. The deeper the shadow effect will disappear as the distance of swampland extends from the shoreline. Leaf growth of *N. pubescens* between growth zones showed significant differences, at a water

depth of 28-95 cm (zone 1) the smallest leaf area and petiole were shorter than at a depth of 28-99 cm (zone II), 54-112 cm. (zone III), and 55-124 cm (zone IV), while between zones II, III, and IV there was no difference (Tables 1 and 2).

When the dry season begins in the *Lebak* swampland, the water level is receding. The surrounding community will switch the use of swampland for farming. The water recedes until the swamp water no longer stagnates except in the deep zone causing the water lilies seeds and bulbs to go into dormancy. As the rainy season comes again, the swamp begins to stagnate. This is when the seeds and tubers of the waterlily begin to grow again. At the beginning of the rainy season, the swamp water is still not deep so that the growth of young waterlily leaves can remain on the surface of the water and get maximum light, thus in this phase the plant is not dependent on the availability of dissolved inorganic carbon. As the water level rises, water lilies grow according to the water depth, so when the water level is high, the produced leaves are submerged, but the leaves actively respond to rising water with rapid growth and elongation of the petiole to make the leaves float again (Ridge and Amarasinghe 1984; Wu *et al.* 2017).

The response is induced by the phytohormone ethylene (Polko *et al.* 2015; Bakshi *et al.* 2015; Binder 2020) which plays a major role in growth regulation (Munné-Bosch *et al.* 2018) and accumulates in submerged tissues (Voeselek and van der Veeon 1994). Ethylene regulates development, growth (Iqbal *et al.* 2017; Binder 2020), and response to various environmental stressors (van der Poel *et al.* 2015; Savada *et al.* 2017; Dubois *et al.* 2018; Binder, 2020; Zhang *et al.* 2020), both biotic (Dubois *et al.* 2018) and abiotic (Savada *et al.* 2017; Wu *et al.* 2017; Dubois *et al.* 2018) stresses.

Ethylene plays a major role in promoting petiole elongation by increasing the number and size of cells (Ridge and Amarasinghe 1984) resulting in under-water rapid growth (Jackson 2008). The accumulation of ethylene in submerged tissues has been shown to contribute to returning photosynthetic organs or flowers to the surface of the water (Sculthorpe 1967; Cookson and Osborne 1978), thus these organs can carry out their functions in the photosynthesis process optimally and flowers as reproductive organs will be pollinated in the soil water level.

Conclusion

Nymphaea pubescens will adapt to changes in its habitat to maintain its life. The level of water depth was one of the factors causing *N. pubescens* to adapt. The response of plants to changes in the level of water depth lies in changes in morphology and anatomy. *Nymphaea pubescens* will expand the leaf, reduce the thickness of the leaf, expand the midrib, and lengthen the petiole as the water depth increases. Air canals are also formed by *N. pubescens* as a place for gas flow that connects the surface of the plant to the part buried in the sediment. The midrib air canals of *N. pubescens* increase in the air canal area along with the water depth. The petiolar air canals, on the other hand, did not experience a significant difference in size at different water depths, but the volume of the air canals increased with the increasing of water depth.

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