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RESEARCH ARTICLE

Soil Water Contents Affect the Physiological Traits of Duku Undergoing Sudden Death Disease, in Jambi

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ABSTRACT

Duku, also known as *Lancium domesticum* Corr, is a plant native to Jambi Province, Indonesia, which is currently facing a sudden death disease. The plant generally grows in the alluvial of the Batanghari River, which is among the widest and longest rivers in Indonesia. Duku is consumed as a fresh fruit that tastes sweet and contains many antioxidants. The phenomenon of duku disease has the potential to cause scarcity, as its population continues to decline. The disease begins with root rot and is prevalent in areas that are often flooded due to the overflow of the Batanghari River. This study aimed to investigate the physiological aspects of sudden death in duku seedlings grown at different water levels. The study involved three treatments on seedlings, each repeated three times, using planting media with different water contents - Field Capacity (100% FC = control), 150% FC (flooded), and 50% FC (drought). Planting media were derived from heavily infested duku fields. This study suggests that sudden death syndrome is more likely to occur under drought and waterlogged conditions. The results showed that stomatal conductance decreased significantly under flooded and drought conditions. However, under drought stress conditions (50% FC), photosynthetic rate, intercellular CO2, and respiration rate increased.

Keywords: Batanghari, Duku, Growing, Medium, Sudden death

Introduction

The Duku fruit, also known as *Lancium domesticum* Corr., is a famous and native fruit of Jambi Province, Indonesia. However, its production has significantly declined in recent years due to various reasons. These include the old age of the plants, improper cultivation methods, and most importantly, the presence of die-back or sudden death (SD) disease. This disease is found in areas that frequently experience flooding. Available data show that waterlogging and recurrent flooding are associated with SD epidemics caused by *Phytophthora palmivora*. The diseased duku displays symptoms such as root rot in seedlings and mature plants, neck rot, stem rot, stem base rot, stem canker, and sudden death.

Phytophthora palmivora is a soil-borne pathogen belonging to the water mold oomycete family. Various studies have been conducted to anticipate soil-borne oomycete spread. Erwin and Ribeiro[1] suggested that water management and phenyl amide pesticides can be used as control strategies. However, the use of phenyl amide is no longer recommended since some pathogens are resistant to it.[2] Therefore, managing Phytophthora disease should include activities related to avoiding infection, reducing susceptibility through good irrigation and drainage, and improving soil health.

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Numerous studies have shown that there is a connection between waterlogging and Phytophthora disease, which affects crops such as cherries,[3] raspberries,[4,5] strawberries, citrus, and Quercus.[6–8] In addition, some studies have analyzed the impact of soil moisture on other pathogens like Pythium and Fusarium.[9,10] Conversely, some reports suggest a correlation between drought and disease exacerbation.[11,12] Unfortunately, due to climate change, the severity of droughts and extreme rainfall has increased significantly in recent years.[13] *Phytophthora* epidemics are influenced by the duration of free water in the soil, particularly the length of inundation. This excess water facilitates the multiplication of zoospores, making them more infective.[14–16]

However, there is limited research on the relationship between soil moisture content and Phytophthora disease in duku. This study was conducted to examine the physiological response of diseased duku seedlings at different soil moisture levels.

Materials and methods

Preparation of plant material

Phytophthora epidemics are influenced by the duration of free water in the soil, particularly the length of inundation. This excess water facilitates the multiplication of zoospores, making them more infective. Duku seedlings were used as plant material, as all stages of plant growth can be subjected to SD in the field. The seedlings used were healthy 4-month-old duku plants about 20 cm tall and had 5 or 6 leaves. They were then transplanted into 25 cm diameter polybags containing natural growing medium from the infested rhizosphere, mixed with 30% (v/v) organic fertilizer.

Waterlogging procedures

To study the effect of moisture content on disease severity, all plants were cultivated on three different media with varying moisture content: drought (50% Field Capacity = FC), optimal moisture (100% FC), and inundation (150% FC). The soil condition with 100% FC was considered the control, as it is ideal for plant growth. For each waterlogging treatment, the plants were immersed in a bucket of water for a week to a depth of 5 mm above the surface of the soil media, after which they were allowed to flow freely for a day. After the waterlogging treatment, the plants were weighed to determine the subsequent water content corresponding to the treatment. During the experiment, the plants were maintained in a growth chamber with an air temperature of 25°C and humidity ranging from 60% to 80%. Finally, at the end of each experiment, predetermined variables were measured.

Observed variables

Disease severity

Since root rot is part of the sudden death disease syndrome, the severity of the disease was evaluated on affected roots at the final observation. Disease severity was calculated using a scale of 1-3 (1, healthy lateral and taproot; 2, lateral root with visible necrosis; 3, root system—lateral and taproot—with visible necrosis and (or) plant death).

Physiological aspects

Leaves chlorophyll and carotenoid content

The chlorophyll and carotenoid content of duku leaves were analyzed at the post-harvest laboratory at IPB University following the protocol of Sims and Gamon.[17] All collected leaves were placed in plastic bags and kept cool until they were returned to the laboratory for measurements.

Photosynthetic rate, stomatal conductance, CO_2 intercellular, respiration rate, and relative water content

Photosynthetic rate, stomatal conductance, CO_2 intercellular, and respiration rate were measured using a portable photosynthesis system (LI-6400, LI-COR, Inc., Lincoln, NE, USA). Measurements were taken on full-width, fully-developed leaves (fourth leaf) from the top of the main stem. Measurements were taken at the end of the research. Relative water content (RWC), calculated by the formula, RWC = (FW - ODW)/(TW - ODW) x100%, where RWC = relative water content, FW = fresh weight of sample leaves, ODW = oven dry weight, and TW = turgor weight.

Experimental design and data processing

Experimental treatments were arranged in a completely randomized design. The study consisted of 3 treatments (FC 150%, FC 100%, FC 50%). Growing medium with FC 100% served as a control; the experiment was repeated thrice. The comparison of observed variables was analyzed for variance and further tested by Student Newman Keul at $\alpha = 0.05$.

Results and discussion

Results

Disease severity

According to our findings, the symptoms were more severe in duku seedlings grown in flooded soil (150%

Table 1. Disease severity of duku plants at various soil water contents.

Treatment (% FC)	Disease severity (%)
(150% FC)	73.00 a
(100 % FC)	20.00 b
(50% FC)	45.00 c

Notes: The SNK test at a 5% level shows that numbers not followed by the same letter are significantly different.

FC), with a rate of 73%, followed by the water shortage or drought condition (50% FC), with a rate of 45%. In comparison, when grown in soil with a moisture content of 100% FC, the rate was only 20%, as shown in Table 1.

Physiological aspects

Chlorophyll and carotenoid content

The study indicated that the chlorophyll content of diseased duku seedlings remained unchanged despite varying soil water conditions. However, the leaf chlorophyll content was lower when the soil water content was at either 150% or 50% field capacity (FC). However, no significant difference was observed between the two or with 100% FC water content as shown in Table 2. On the other hand, the carotenoid content of duku seedlings varied based on the soil water content level. Soil moisture content of 150% FC and 50% FC resulted in carotenoid content of 0.405 $mg.g^{-1}$, and 0.410 $mg.g^{-1}$, respectively. Table 3 showed no significant difference between the two, but both differed significantly from the carotenoid content at 100% FC.

Photosynthetic rate, stomatal conductance, CO_2 intercellular, respiration rate, and relative water content

In this study, we recorded several physiological aspects affected by the state of diseased duku plants in various soil water contents of the growing medium, as displayed in Fig. 1.

There was no difference in the photosynthetic rate of diseased duku seedlings at 150% FC soil water content (23.01 $g.cm^{-2}.min^{-1}$), at 100% FC (27.22 $g.cm^{-2}.min^{-1}$), and x 50% FC soil moisture condition (29.78 $g.cm^{-2}.min^{-1}$), as displayed in Fig. 1A. There was also no significant difference in leaf stomatal conductance among these 3 growing media: 0.33 mmol $H_2O.m^{-2}.min^{-1}$ at 150% FC, 0.39 mmol $H_2O.m^{-2}.min^{-1}$ at 100% FC, and 0.42 mmol $H_2O.m^{-2}.min^{-1}$ at 50% FC as displayed in Fig. 1B. There was also no significant difference in intercellular CO_2 levels of duku seedlings in these 3 soil water conditions: 203.4 $\mu mol.mol^{-1}$ in 150% FC, 216.32 $\mu mol.mol^{-1}$ in 100% FC, and 249.34 $\mu mol.mol^{-1}$ in 50% FC as displayed in Fig. 1C. Furthermore, the highest respiration rate was found in 50% FC soil water conditions (8.40 μmol $CO2.g^{-1}.sec^{-1}$) followed by 150% FC soil water conditions (8.36 μmol $CO_2.g^{-1}.sec^{-1}$) and significantly differed from the respiration rate of duku plants in 100% FC soil water conditions (8.12 μmol CO_2. $g^{-1}.sec^{-1}$) as shown in Fig. 1D. The average relative water content (RWC) of duku seedlings was highest at 100% FC soil moisture content of 33.55%. Fig. 1E shows a decrease in RWC at 150% FC soil moisture content, 32.31%, and 32.19% at 50% FC soil moisture content.

Discussions

Crops can suffer from soil waterlogging, a major abiotic stress caused by excessive rainfall and poor soil drainage, which can further affect the health of the plants. These conditions are often observed in the duku growing area in Jambi, mainly due to the impact of climate change, especially in our research location. Duku plants are primarily cultivated on the river banks of Batanghari, where recurrent flooding is common, and it can negatively impact various physiological aspects of the duku plants.

The study found that diseased duku seedlings, submerged in water (150% FC), had different disease severity and levels of chlorophyll and carotenoid concentrations than those in the control group (100% FC). Interestingly, the same results were also observed in plants deprived of water (50% FC). This led to yellowish leaves, which indicated a decrease in chlorophyll concentration due to its degradation. This finding was consistent with a report by Xu et al. [18] that

Table 2. Chlorophyll content of leaves in various soil water content treatments.

	Chlorophyll Content (mg/g)			
Treatment (% FC)	Chlorophyll a	Chlorophyll b	TotalChlorophyll	Ratio (a/b)
(150% FC)	1,115 a	0,469 a	1,584 a	2,380
(100% FC)	1,204 a	0,497 a	1,701 a	2,430
(50% FC)	1,176 a	0,477 a	1,653 a	2,464

Note: The numbers in each column followed by the same letters are significantly different at the 5% level of the SNK test.

Table 3. Carotenoid content of leaves in various soil water content treatments.

Treatment (% FC)	Carotenoid Content (mg/g)
(150% FC)	0,405 a
(100 % FC)	0,428 b
(50% FC)	0,410 a

Note: The numbers in each column followed by the same letters are significantly different at the 5% level of the SNK test.

found a decrease in chlorophyll content (a + b) and the photosynthetic rate when soil moisture content decreased during the tillering stage of rice.

In stressful environments, plants often lack Nitrogen availability, which affects the formation of chlorophyll. This is because chlorophyll formation depends on the citric acid and amino acid cycle, which produces the amino acid levulinate.[19] However, under water exposure and N deficiency conditions, the amino acid precursor for chlorophyll formation is reduced, leading to a decrease in chlorophyll formation. Nitrate reduction requires energy and reducing power from carbohydrate respiration, which is supplied by photosynthesis. Therefore, photosynthesis increases the supply of carbohydrates and NADH needed for nitrate reduction.

Water is crucial in many physiological processes involved in plant growth, development, and metabolism.[20,21] This study found the carotenoid content in the leaves of diseased duku did not vary across three different soil water contents. Phytophthora species cause tree mortality due to environmental conditions like warmth, flooding, and drought. Despite drought being a significant factor that affects crop growth, carotenoids play a vital role in drought resistance in higher plants.[22,23]

Flooding and drought harm duku crop farming, and this exacerbates sudden death disease in duku caused by *Phytopthotara* with 73% severity in waterlogged soil (150% FC) and 45% in low soil moisture content (50% FC), compared to FC 100% as a control. These environmental events occur when excess water saturates the soil with inadequate soil drainage. High rainfall inundated the Batanghari riverbank, resulting in flooding periodically.[24] This was in line with the finding that Phytophthora species cause tree mortality due to environmental conditions like warmth and flooding.[8]

Several authors previously explained that anaerobic roots produce ATP mainly through glycolysis. This pathway also incorporates pyruvic acid into ethanol fermentation and lactic acid fermentation, especially in the first hours of anoxia before the cytosol becomes acidic.[25–28] So it is hypothesized that this mechanism allows *Phytophthora* to be supplied with oxygen to survive and thrive under anaerobic conditions that cause the development of sudden death in Jambi duku plants that have recently experienced recurrent flooding. There was no relationship between disease severity and stomatal conductance and intercellular CO_2. On the other hand, Dron[29] reported that waterlogging of the soil minimizes the ability of *P. medicaginis* to infect plants, and the pathogen cannot reproduce under hypoxic conditions. Thus, waterlogging reduces disease resistance. However, both inundation and drought conditions increase stomatal resistance and limit water uptake, and further lead to internal water deficit.[30,31] Low O_2 levels can also reduce hydraulic conductivity, which results in decreased root permeability.[32]

As hypoxia conditions develop in waterlogged soils, increased by-products of fermentation metabolism accumulates in the root environment, and levels of CO_2, methane, and volatile fatty acids also increase.[33] The decrease in available energy impacts cellular processes, leading to water and nutrient imbalances and deficiencies. In addition, these environmental changes can also make plants more susceptible to other stresses, particularly to pathogen infection.[34] In contrast, Zahra et al.[35] reported that plants have complex ways of responding to different types of stress. Plants sense stress signals from living and non-living factors and use these cues to decide how to adapt. The combination of abiotic stresses can impact plant performance and reduce the risk of biotic stress. To adapt to various stresses, plants prioritize response pathways and regulate feedback. This enables the plant to adapt using minimal energy.[36]

One of the mechanisms of plant tolerance to water stress (waterlogging) and water shortage is the stomatal movement response or stomatal conductance. In flooded conditions, the stomatal conductance of plants often decreases due to the decrease in the value of root conductance.[37] In this study, the duku plants did not experience a significant decrease in stomatal conductance or show any notable differences, indicating that their stomata remained relatively open at all soil water content levels. This suggests that this variety of duku plants has adapted to respond to waterlogging and water scarcity by maintaining root permeability, which ensures efficient water absorption. The high water content that the plant roots can absorb helps meet the plants' needs, keeping the turgidity of their tissues intact. When water is abundant, the plant cells, including the guard cells of the stomata, become more turgid, causing the stomata to open. The increase in turgor pressure causes water movement from neighboring cells into the guard cells. This condition allows the amount of CO_2 that diffuses into

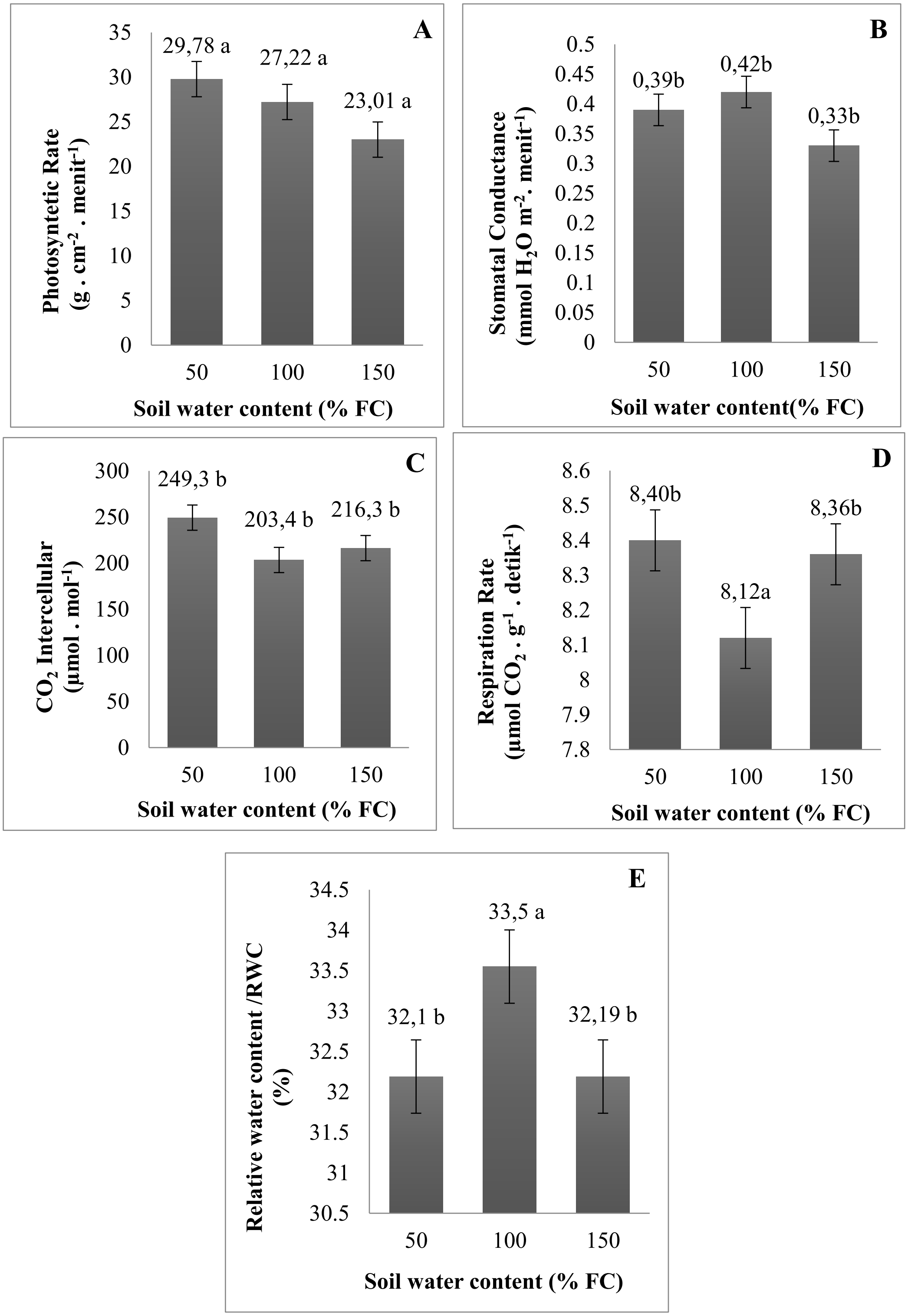

Fig. 1. Physiological characteristics of the duku seedlings at 3 variations of soil moisture content: Photosynthetic rate (A); Stomatal conductance (B); Intercellular CO_2 (C); Respiration rate (D); Relative water content. (E).

the leaf through the stomata to be relatively the same, thus showing no difference in photosynthesis rate.

The difference in soil moisture content affected the relative water content (RWC). There was a decrease in RWC at the soil moisture content of 150% FC and 50% FC compared to RWC at the soil moisture content of 100% FC, but the decrease was relatively small. Nonetheless, this indicates an obstacle in water absorption by plant roots at 150% FC soil moisture content and 50% FC soil moisture content. It is suspected that waterlogging at the 150% FC level started to damage the plant roots, which is thought to be self-poisoning by anaerobic metabolic products. The most well-known toxin is excess protons that acidify the cytoplasm and vacuoles.[38] Another possible toxin is acetaldehyde. In alcoholic fermentation, the activity of the enzyme that converts acetaldehyde to ethanol (alcohol dehydrogenase - ADH) usually exceeds the activity of the enzyme that promotes the production of acetaldehyde from pyruvic acid (pyruvate decarboxylase - PDC) which can damage the roots, reducing their ability to absorb water. In contrast to the reduction in Relative Water Content (RWC) observed under water-deficient conditions (50% Field Capacity), the decline in RWC in this case is believed to occur because the rate of water loss due to transpiration exceeds the rate of water absorption by the roots. Our results indicate that while the decrease in RWC at both levels of soil water content did not significantly affect stomatal conductance, there was a tendency for stomatal conductance to increase, whereas the photosynthetic rate tended to decrease.

Diseases caused by *Phytophthora* species cause tree mortality due to warm temperatures, flooding, and drought.[8] In plants that experienced water stress, respiration was slightly higher at 150% FC soil moisture content, than at 50% FC soil moisture content. To our knowledge, limited studies have analyzed the respiration response to water stress in duku plants. Nevertheless, these observations are in agreement with some published studies on tomato[39,40] but not another like soybean.[41]

Conclusion

The physiological behavior of diseased duku plants at different soil moisture levels shows differences in the respiration rate, leaf relative water content, and photosynthesis rate. Both soil moisture conditions in the form of flooding and lack of water (drought) trigger an increase in the severity of sudden death disease in duku plants caused by *Phytophthora.* In the study, it was found that the root suffered damage due to low relative water content. The findings suggest that sudden death syndrome is more likely to occur in both drought and waterlogged conditions. Considering this evidence is essential when making impactful decisions about duku plant disease management

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Authors' declaration

- Conflicts of Interest: None.
- We hereby confirm that all the Figures and Tables in the manuscript are ours. Furthermore, any Figures and images, that are not ours, have been included with the necessary permission for re-publication, which is attached to the manuscript.
- No animal studies are present in the manuscript.
- No human studies are present in the manuscript.
- Ethical Clearance: The project was approved by the local ethical committee at the University of Jambi.

Authors' contribution statement

I.H was primarily responsible for designing the study, analyzing and interpreting data obtained from other sources, and contributing significantly to the writing, critical revision, and overall structure of the manuscript. **S.N** assisted in analyzing and interpreting data. **M.M. B.I., M.M., and N.N** were responsible to ensuring accurate data acquisition and supervision. All of the authors participated in overall structure of the manuscript.

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تأثير محتوى المياه في التربة على مرض الموت المفاجئ لأشجار الدوكو (.Lancium sp) الفسيولوجي في جامبي

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الخلاصة

الدوكو، المعروف علمياً باسم Lancium domesticum Corr، هو نبات متوطن في مقاطعة جامبي بإندونيسيا، يواجه حالياً مرض الموت المفاجئ. ينمو النبات عموماً في السهول الفيضية لنهر باتانغهاري، الذي يعد من أعرض وأطول الأنهار في إندونيسيا. يستهلك الدوكو كفاكهة طازجة ذات مذاق حلو وتحتوي على العديد من مضادات الأكسدة. ان ظاهرة مرض الدوكو قد تؤدي الى حدوث ندرة في النبات، حيث يستمر تعداده في الانخفاض. يبدأ المرض بتعفن الجذور وينتشر في المناطق التي تتعرض للفيضانات المتكررة بسبب فيضان نهر باتانغهاري. هدفت هذه الدراسة إلى التحقيق في الجوانب الفسيولوجية للموت المفاجئ في شتلات الدوكو التي تنمو في مستويات مائية مختلفة. تضمنت الدراسة ثلاث معالجات على الشتلات، كررت كل منها ثلاث مرات، باستخدام وسائط زراعة ذات محتويات مائية مختلفة - السعة الحقلية (100% FC = معاملة المقارنة)، و150% FC (مغمور بالمياه)، و50% FC (جاف). تم اشتقاق وسائط الزراعة من حقول الدوكو شديدة الإصابة. تشير هذه الدراسة إلى أن متلازمة الموت المفاجئ أكثر احتمالاً للحدوث في ظروف الجفاف والغمر بالمياه. أظهرت النتائج انخفاضاً ملحوظاً في توصيل الثغور تحت ظروف الغمر والجفاف. ومع ذلك، في ظروف إجهاد الجفاف (50% FC)، ازداد معدل التمثيل الضوئي، وثاني أكسيد الكربون داخل الخلايا، ومعدل التنفس.

الكلمات المفتاحية: باتانغهاري، دوكو، نمو، وسط زرعي، الموت المفاجئ.