Jurnal Ilmu Pertanian Indonesia (JIPI), Januari 2025
(Indonesian Journal of Agricultural Sciences)
ISSN 0853-4217 EISSN 2443-3462

Vol. 30 (1): 55–63
http://journal.ipb.ac.id/index.php/JIPI
DOI: 10.18343/jipi.30.1.55

Diversity of Oil Palm Seedlings Jambi Accessions Exhibits Physiology Responses Differently During a Waterlogged

Evan Vria Andesmora[1], Hamim[2], Sulistijorini[2], Triadiati Triadiati[2]*

(Received May 2023/Accepted December 2024)

ABSTRACT

Cultivated oil palm is commonly found in several ecosystems with different topographies, including riparian areas. This ecosystem is expected to affect the morphology and physiology of oil palms. In addition, oil palm habitats in riparian or flooded ecosystems will experience anaerobic respiration. Indonesia has the potential to access quality palm oil that can be used for cultivation. This study aimed to determine which oil palm accessions could adapt physiologically to the duration of waterlogging. The accession of oil palm seedlings from Jambi tested were Merangin, Tebo, Muara Jambi, Tanjung Jabung, and Simalungun. The research design was to treat waterlogging in a greenhouse and then analyze the plant growth and physiology. Waterlogging was given for two, four, and six weeks. The results showed that the accession of oil palm seedlings and the duration of waterlogging affected photosynthesis rate, transpiration rate, and stomatal conductance. Growth parameters, i.e., fresh weight, dry weight, and root/shoot ratio, were significantly different in accession and waterlogging duration. In conclusion, accessions from Tebo and Merangin can adapt to waterlogging.

Keywords: Merangin accession, photosynthesis rate, stomatal conductance, Tebo accession

INTRODUCTION

Oil palm (*Elaeis guineensis* Jacq.) is one of the most essential plantation commodities in Indonesia. The palm oil industry in Indonesia is one of the industries that contribute to the country's economy. Indonesia is currently the world's largest palm oil producer, with around 55% of the world's total production. Oil palm in Indonesia is grown on the islands of Sumatra, Kalimantan, and Papua, which have climates and soils suitable for oil palm cultivation. One of the oil palm plantations in Sumatra is in Jambi Province. The area of oil palm plantations in this province was 1.13 million ha in 2022, an increase of 52.6 thousand ha from 2020 (Directorate General of Estates, 2020). Palm oil production increased by 331.330 tons in 2020, namely 3.02 million tons (BPS Provinsi Jambi 2020).

Oil palms need water for proper growth and development. However, oil palm plantations in Indonesia face several problems, including changes in rainfall patterns. In addition, the land profile for oil palm cultivation in Indonesia depends on geographical location, climatic conditions, and plantation management. Land for oil palm cultivation is also often found on uneven ground or in riparian sections. Uneven land can cause waterlogging when heavy rainfall can damage the roots of the oil palm plants. Under waterlogged conditions, plants will exhibit morphological changes such as developing adventitious roots, initiating hypertrophic lenticels (Ashraf 2012), and/or establishing aerenchyma (Herzog *et al.* 2016).

In waterlogged conditions, plants will experience hypoxia, which causes reduced oxygen content in soil and roots. Low oxygen availability in the soil will have an impact on root respiration. The roots will change the respiration path to alcoholic fermentation to produce energy (Bailey-Serres and Colmer 2014). Roots will minimize the allocation of oxygen during hypoxic conditions and respiration (Nakamura and Nakamura 2016). Roots in a hypoxic state will reduce energy requirements and ion transport in the roots (Gibson *et al*. 2013).. Hypoxic conditions will also increase radical oxygen species (ROS) activity (Lin *et al*. 2021) and affect the expression of aquaporins, which are water transporter genes (Zwiazek *et al.* 2017; Tan and Janusz 2019; Pawłowicz and Masajada 2019).

Changes in plant physiological processes during waterlogging can cause an increase in stomatal conductance and transpiration rate due to excess water in the environment. Oil palm seeds submerged in water

[1] Graduate Program in Plant Biology, Department of Biology, Faculty of Mathematics and Natural Sciences, IPB University, IPB Campus Darmaga, Bogor 16680, Indonesia
[2] Department of Biology, Faculty of Mathematics and Natural Sciences, IPB University, IPB Campus Darmaga, Bogor 16680, Indonesia
* Corresponding Author: Email: triadiati@apps.ipb.ac.id

have higher stomatal conductance and transpiration levels than those without submerging (Ponte *et al.* 2019). In addition, photosynthesis results in submerged plants were lower than those not submerged (Lamade *et al.* 1998). Oil palm seedlings that were given waterlogging showed that their photosynthetic rate was lower than oil palm plants in their field capacity (Rivera-Mendes *et al.* 2016). However, the growth of oil palm accessions from Jambi in waterlogged conditions needs to be studied to determine if the oil palm accessions could acclimate physiologically to the duration of waterlogging.

METHODS

Research Locations and Materials

The research was conducted at the Greenhouse and Laboratory of Plant Physiology and Genetics, Department of Biology, IPB University. The accessions used were three-months old oil palm seedlings, namely Muara Jambi (MJ), Tebo (TB), Tanjung Jabung Barat (TJB), Merangin (MR), and Simalungun (SM).

Research Design

This study used a factorial randomized block design with accession and waterlogging treatments. Accessions were obtained from Muara Jambi (MJ), Tebo (TB), Tanjung Jabung Barat (TJB), Merangin (MR), and Simalungun (SM), and waterlogging duration at two, four and six weeks, with three replications. Oil palm seedlings were planted in 30 cm ´ 30 cm pots containing 20 kg of soil and then transferred to a greenhouse for acclimatization for 14 days before treatment. During the acclimatization period, all plants are watered every day as needed. At the end of acclimatization, the seedlings were waterlogged as high as 2 cm above the soil surface and maintained by daily checking to maintain the water level during the experiment.

Photosynthesis, Transpiration and Stomatal Conductance, Chlorophyll and Carotenoid Content

Photosynthesis rates (*Amax*), transpiration rates (E), and stomatal conductance (g) were measured using LICOR-6400, LI-COR Inc., Lincoln, USA, on mature leaves of each plant at two, four, and six weeks. Chlorophyll and carotenoid content were measured by extracting 0.1 g of fresh, mature leaves with 80% acetone p.a. The extract was centrifuged for 10 minutes at 4 °C. Chlorophyll and carotenoid content were determined using a spectrophotometer with absorbances of 470, 646, and 663 nm (Lichtenthaler 1987; Turhadi *et al*. 2020).

Plant Growth

Growth measurements were carried out on oil palm seedlings treated with waterlogging at two, four, and six weeks of planting. The fresh weight of above- and below-ground plants was weighed and then dried in an oven at 60 °C until a constant weight. The root-to-shoot ratio was obtained by comparing the dry biomass of above- and below-ground plants (Mašková *et al*. 2022).

Data Analysis

All data were tested by Analysis of Variance, followed by Duncan's New Multiple Range Test at α = 5% using IBM SPSS Statistics 20.

RESULTS AND DISCUSSION

In waterlogging conditions, plants experience various physiological changes and adaptations to overcome the decreased oxygen availability and excessive moisture. Plants will experience hypoxia, where the oxygen content is reduced due to the pressure of the abundant water on the soil (Gurevitch *et al*. 2002). Waterlogging causes the synthesis of pyruvate decarboxylase and alcohol dehydrogenase to produce ethanol under hypoxic conditions (Kreuzwieser *et al.* 2004; Wu *et al.* 2022). Oxygen supply will directly impact the root organs responsible for respiration that produce energy in cells. Low oxygen levels in the roots can interfere with metabolic activity and energy production. The duration of waterlogging will also impact plant survival (Tamala *et al*. 2019). The roots will change the respiration path to alcoholic fermentation to produce energy (Bailey-Serres and Colmer 2014). In respiration, plants will minimize the allocation of oxygen during hypoxic conditions (Nakamura and Nakamura 2016). Furthermore, plants will reduce energy requirements and ion transport in the roots in hypoxia (Gibson *et al.* 2013). Hypoxic conditions will also increase the activity of radical oxygen species (ROS) (Lin *et al.* 2021).

Photosynthesis rates (A_{max}), Transpiration Rates (E) and Stomatal Conductance (g), Chlorophyll and Carotenoid Content

The A_{max}, E, and g were affected by the interaction between accessions and the duration of waterlogging (p<0.05). The highest A_{max} was shown by TB and MR accessions at 6 weeks after waterlogging treatment

Table 1 Photosynthesis rates (A_{max}), transpiration rates (E), and stomatal conductance (g) of oil palm accessions treated by waterlogging at PAR 1000

Accessions	Treatment	Duration (weeks)	A_{max} (µmol CO_2 m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})	g (mol H_2O m^{-2} s^{-1})
Tebo (TB)	Control	2	26.17 $^{e-i}$	1.68 ^{cde}	0.42 ^{bcd}
		4	28.43 ^{cde}	2.32 ^{ab}	0.15 ^{d}
		6	32.68 ^{a}	1.65 ^{cde}	1.57 ^{a}
	Waterlogged	2	25.87 ^{ghi}	1.76 ^{cd}	0.17 ^{cd}
		4	28.11 $^{c-f}$	2.50 ^{a}	0.19 ^{cd}
		6	33.07 ^{a}	1.78 ^{cd}	1.48 ^{a}
Merangin (MR)	Control	2	26.01 $^{f-i}$	1.33 ^{ef}	0.32 ^{bcd}
		4	27.86 $^{c-g}$	2.45 ^{a}	0.18 ^{cd}
		6	31.56 ^{ab}	1.08 ^{f}	0.83 ^{b}
	Waterlogged	2	25.09 ^{hi}	1.46 ^{de}	0.15 ^{d}
		4	26.93 $^{d-h}$	2.47 ^{a}	0.18 ^{cd}
		6	33.06 ^{a}	1.79 ^{cd}	1.50 ^{a}
Muara Jambi (MJ)	Control	2	24.41 ^{i}	1.43 ^{de}	0.39 ^{bcd}
		4	24.30 ^{i}	2.38 ^{a}	0.15 ^{d}
		6	28.57 ^{cd}	1.56 ^{de}	0.56 ^{bcd}
	Waterlogged	2	24.29 ^{i}	1.74 ^{cd}	0.16 ^{cd}
		4	28.29 ^{cde}	2.28 ^{ab}	0.15 ^{d}
		6	31.16 ^{ab}	1.68 ^{cde}	1.74 ^{a}
Tanjung Jabung Barat (TJB)	Control	2	25.66 ^{hi}	1.63 ^{de}	0.73 ^{b}
		4	28.36 ^{cde}	2.44 ^{a}	0.17 ^{cd}
		6	29.11 ^{cd}	1.44 ^{de}	0.70 ^{bc}
	Waterlogged	2	25.30 ^{hi}	1.73 ^{cd}	0.18 ^{cd}
		4	24.29 ^{i}	2.27 ^{ab}	0.16 ^{cd}
		6	31.54 ^{ab}	1.74 ^{cd}	0.83 ^{b}
Simalungun (SM)	Control	2	24.03 ^{i}	2.00 ^{bc}	0.52 ^{bcd}
		4	28.17 $^{c-f}$	2.52 ^{a}	0.18 ^{cd}
		6	30.10 ^{bc}	1.52 ^{de}	0.50 ^{bcd}
	Waterlogged	2	24.55 ^{i}	1.48 ^{de}	0.16 ^{cd}
		4	25.50 ^{hi}	2.37 ^{a}	0.19 ^{cd}
		6	28.43 ^{cde}	1.74 ^{cd}	1.72 ^{a}

Note: Data followed by the same letter (s) are not significantly different at $P \leq 0.05$ according to Duncan's multiple range test.

(WAT). The highest E occurred at the four WAT, and the highest g occurred at 6 WAT (Table 1).

The interaction between the duration of waterlogging and the oil palm accession in this study affected the rate of photosynthesis, stomatal conductance, and transpiration ($p<0.05$). TB accession had the highest A_{max} among other waterlogging and control treatments, namely 28.89 and 29.22 µmol CO_2 m^{-2} s^{-1}. A_{max} in oil palm seedlings increases with the duration of waterlogging. Plants that are well adapted to waterlogging will continue to increase A_{max} during waterlogging. *Distylium chinense* demonstrated an increase in A_{max} during waterlogging. This species survived and had an A_{max} that increased with the duration of the waterlogging (Liu *et al.* 2014). Water and CO_2 are essential factors that are the main ingredients in photosynthesis. Waterlogging can inhibit the Krebs cycle by limiting NADH reoxidation due to low O_2 concentrations, and hypoxia increases nitric oxide (NO) production, a potent aconitase inhibitor (Gupta *et al.* 2012). *Aconitase* is an enzyme sensitive to NO and ROS and participates in the interconversion pathway of three tricarboxylic acids (citrate, cis-aconite, and isocitrate). Aconitase is located in plant cells' mitochondria, which are involved in the TCA cycle (Zemlyanukhin *et al.* 1984). NO plays a significant role in controlling plant respiration. In suppressing the respiratory chain, cytochrome c oxidase (COX, complex IV)'s oxygen binding sites are competitively bound by NO (Brown 2001). This impacts the mitochondrial electron transport chain and oxidative phosphorylation (Yamasaki *et al.* 2001). One of the causes of NO's toxicity is its inhibitory action on the electron transport chain, which leads to the suppression of respiratory oxygen intake and the production of superoxide (Shiva *et al.* 2001).

The A_{max} of control oil palm seedlings in this study was higher than that of the treatments. This result is confirmed by a study on oil palm seedlings that were waterlogged, which revealed that their A_{max} was lower than oil palm plants in their field capacity (Rivera-Mendes *et al.* 2016). Submerged plants had lower A_{max} than non-submerged plants (Lamade *et al*. 1998). Research on *Melaleuca alternifolia* showed that the waterlogged A_{max} was lower than the control (Jing *et al.* 2009) in *Genipa americana* (Mielke *et al.* 2003). Under normal conditions, the speed of water flow to plants will be affected by genes located in roots, stems, and leaves. The rate will weaken when one of these genes is disturbed, thereby reducing water availability as a material for photosynthesis. One of the genes that play a role in waterlogged or hypoxic conditions is aquaporin, which helps regulate the physiological processes of cells (Kadam *et al.* 2017).

The *E* of oil palm accessions under waterlogging treatments was higher than the control. TB had the highest *E* in waterlogging treatments, which was 6.9% higher than for those that control. The SM accession control has the highest transpiration rate among the other accessions but was lower than the waterlogging treatments. This resulting study about transpiration rate shows that the two accessions can remove excess water, thereby reducing physiological disturbances. This result also aligns with the highest *g* in the treatment accession: SM, 72.5% higher than the control. However, the average *g* of submerged oil palm accessions was higher than that of the control. High stomata opening will also increase *E* so that it will maximize the excess water in the environment. Species less tolerant of waterlogging usually have a more significant reduction than more resistant species and a smaller acclimation capacity in their physiological potential (Copolovici and Niinemets 2010).

The opening and closing of the stomata will affect CO_2 absorption. When the stomata are open, the opportunity for CO_2 absorption will be more significant. The opening of the stomata also corresponds to a higher *E*. The opening and closing of stomata will also depend on environmental conditions. When the temperature is very high, the stomata will close to prevent water loss, and abscisic acid will cause the stomata to close. Species tolerant to waterlogging will maintain their growth by increasing *g* and A_{max} during waterlogging times. Plants maintain increased biomass when waterlogging occurs (Zúñiga-Feest *et al.* 2017). The process of photosynthesis in plants cannot be separated from the role of chlorophyll. Chlorophyll is necessary for photosynthesis to absorb light and transfer energy (Wang and Grimm 2021).

Leaf chlorophyll (chl) content was not affected by the interaction between the duration of waterlogging and accession but was affected separately. The highest chlorophyll content was found in TB accession control (Table 2). In addition, the chlorophyll content also increases with the duration of waterlogging (Table 3).

The content of chlorophyll a, b, and total chlorophyll increased with the duration of the waterlogging. The waterlogging treatment has a lower value than the control. Total chlorophyll was lower in waterlogging than

Table 2 Chlorophyll content in oil palm seedling accessions treated by waterlogging treatment

Treatments		Chlorophyll a (mg. g^{-1} leaf fresh weight)	Chlorophyll b (mg. g^{-1} leaf fresh weight)	Total Chlorophyll (mg. g^{-1} leaf fresh weight)	Carotenoid (mg. g^{-1} leaf fresh weight)
Tebo (TB)	Control	8.13 ^{a}	2.70 ^{a}	10.83 ^{a}	2.24 ^{ab}
	Treatment	7.03 $^{a-d}$	2.45 ^{a}	9.48 ^{abc}	2.08 ^{abc}
Merangin (MR)	Control	7.57 ^{abc}	2.02 ^{a}	9.59 ^{abc}	2.16 ^{abc}
	Treatment	6.41 ^{cd}	2.32 ^{a}	8.73 ^{bc}	2.19 ^{abc}
Muara Jambi (MJ)	Control	6.67 ^{bcd}	2.24 ^{a}	8.91 ^{abc}	1.94 ^{abc}
	Treatment	5.88 ^{d}	2.24 ^{a}	8.12 ^{c}	1.73 ^{c}
Tanjung Jabung Barat (TJB)	Control	6.31 ^{cd}	2.51 ^{a}	8.82 ^{abc}	2.05 ^{abc}
	Treatment	6.03 ^{d}	2.68 ^{a}	8.71 ^{bc}	1.82 ^{bc}
Simalungun (SM)	Control	7.99 ^{ab}	2.35 ^{a}	10.34 ^{ab}	2.34 ^{a}
	Treatment	7.82 ^{ab}	2.51 ^{a}	10.33 ^{ab}	2.28 ^{ab}

Note: Data followed by the same letter (s) are not significantly different at P > 0.05 according to Duncan's multiple range test.

in non-waterlogged plants in *Bactris gasipaes* Kunth (De Carvalho and Ishida 2002), and *Melaleuca alternifolia* (Jing *et al.* 2009). The TB and SM accessions in the control had the highest chlorophyll content than all other accessions, or 33% and 19.6% higher than the lowest accession, MJ. The high chlorophyll content in TB and SM accessions gave both accessions a higher A_{max} than the other accessions.

The carotenoid content of oil palm accessions was, on average, the highest in the control. The SM accession is the accession that has the highest carotenoid content overall, with an increase of 2.6% from the waterlogged accession. In comparison, the accession with the lowest value was MJ, 1.73 mg. g^{-1} leaf fresh weight, or 10.8% lower than the MJ accession in control. Carotenoids are pigments that help the process of photosynthesis, where their role is to transfer energy to chlorophyll. In addition, carotenoids also play a role in antioxidant compounds that protect plants from the harmful effects of ROS, thereby preventing oxidative damage (Stra *et al.* 2023). Plant physiological processes affect growth because they are interrelated to increase plant biomass.

Plant Growth

Plant growth was not affected by the interaction between waterlogging duration and accession but was influenced by waterlogging duration and accessions separately. Oil palm growth increases with waterlogging

Table 3 Content of chlorophyll a, b, total chlorophyll, and carotenoids of oil palm accessions during the duration of waterlogging

Duration (week)	Chlorophyll a (mg. g^{-1} leaf fresh weight)	Chlorophyll b (mg. g^{-1} leaf fresh weight)	Total Chlorophyll (mg. g^{-1} leaf fresh weight)	Carotenoid (mg. g^{-1} leaf fresh weight)
2	5.75 c	1.63 b	7.38 c	2.18 a
4	6.78 b	1.97 b	8.75 b	1.99 c
6	8.42 a	3.74 a	12.16 a	2.08 b

Note: Data followed by the same letter (s) are not significantly different at P > 0.05 according to Duncan's multiple range test.

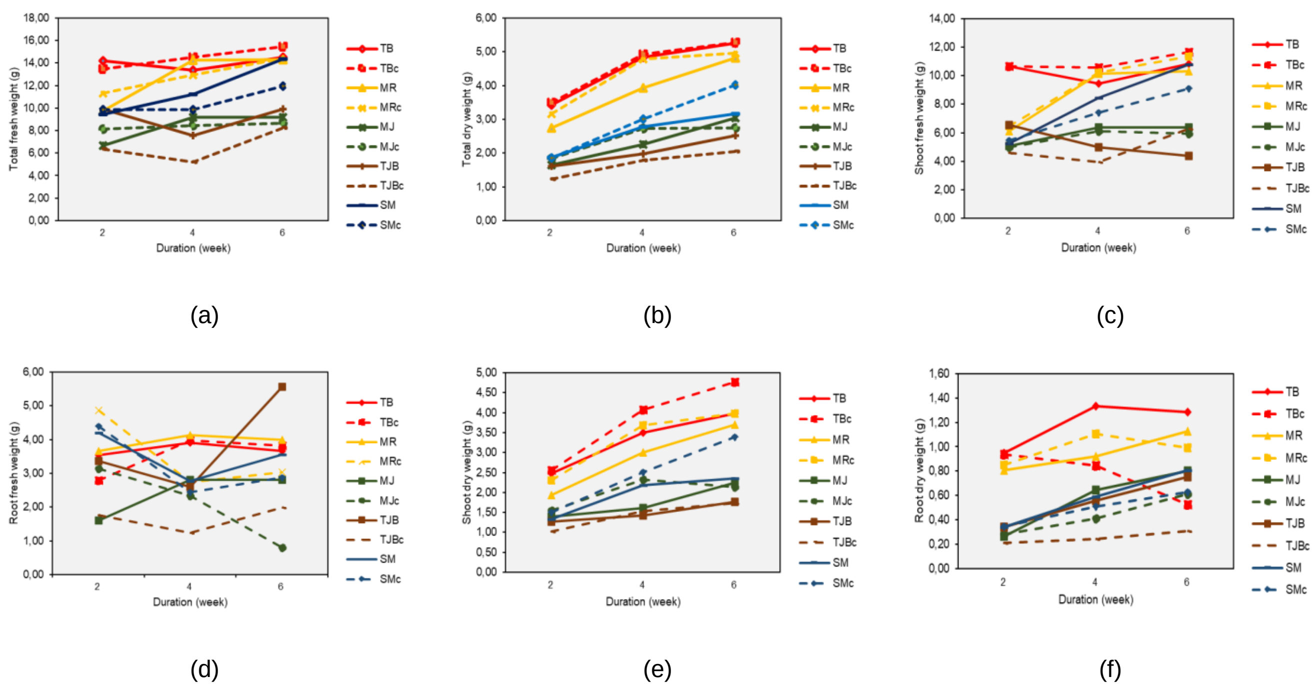

Figure 1 Fresh and total dry weight of oil palm plants with waterlogging treatment. A. Total fresh weight, B. Total dry weight, C. Shoot fresh weight, D. Root fresh weight, E. Shoot dry weight, F. Root dry weight, TB (Tebo), TBc (Tebo control), MR (Merangin), MRc (Merangin control), MJ (Muara Jambi), MJc (Muara Jambi control), TJB (Tanjung Jabung Barat), TJBc (Tanjung Jabung Barat control), SM (Simalungun), SMc (Simalungun control).

duration (Figure 1). The increase in plant biomass is related to A_{max}. The increase in biomass is because the photosynthate produced is utilized by plants for growth (Martínková *et al.* 2021). Photosynthate production in some species submerged in water may be an attempt to maintain the transport of sugars from mature leaves (source) to roots and new leaves, and this may continue if the waterlogging process occurs (Zúñiga-Feest *et al.* 2017).

Oil palm seedlings treated with waterlogging for six weeks experienced plant morphology and physiology changes. The shape of the morphological changes can be seen from the increase in weight. One of the plant's adaptation is through an increase in weight, which varies for each type of oil palm seedling. Changes that occur during waterlogging will affect growth and physiological processes (Jackson and Colmer 2005). Plant biomass refers to the total dry weight of all organic matter produced by plants. Plants produce biomass through the process of photosynthesis, in which sunlight is used to convert carbon dioxide (CO_2) and water into glucose and oxygen. Environmental factors such as light intensity, temperature, water availability, and nutrient availability will affect the rate of plant biomass production. Fresh and dry weight of roots and shoots of oil palm seedlings were affected by accession and duration of waterlogging separately (Figure 1). The treatment on *Holcus lanatus*, which was given waterlogging, showed a positive effect with an increase in above- and below-ground biomass (Boigné *et al.* 2017).

Total dry weight and A_{max} are important plant adaptation parameters (Phule *et al.* 2019). Biomass in wet and dry weight in waterlogged oil palm accessions showed a significant difference. The duration of waterlogging provides an increase in growth. Research on *Melaleuca alternifolia* showed increased biomass when waterlogged (Jing *et al.* 2009). *Plant biomass is one of the products of processes that occur throughout the growth stage. Photosynthesis is one of the mechanisms that contribute to the growth of biomass. The* TB accession is an accession that can utilize existing resources optimally, as indicated by the highest fresh and dry weight compared to other accessions. With the availability of sufficient water, the plants will process the water more. Water is used in photosynthesis during the light reaction through photolysis (Taiz *et al.* 2018). In contrast, the accessions with the lowest fresh and dry weights were MJ and TJB. Under certain conditions, the lack of increase in biomass during waterlogging could be due to the low capacity of the species to carry out internal gas diffusion (Garssen *et al.* 2015). Plants with stable physiological conditions can still carry out metabolic processes if the roots are waterlogged with a depth of waterlogging that does not exceed the height of the plant. An increase in the rate of photosynthesis in this study can demonstrate this.

The root-to-shoot ratio of oil palms shows that they are affected by accessions ($p<0.05$). The root-to-shoot ratio of waterlogging treatment was higher than the control. The highest root-to-shoot ratio was TJB, with a 100% increase from control, followed by SM and TB, 61.90% and 56.52%, respectively. The lowest increase ratio is MR and MJ to the control, which is less than 35% (Figure 2).

The root-to-shoot ratio between accessions has a significant difference. The TJB accession has the highest

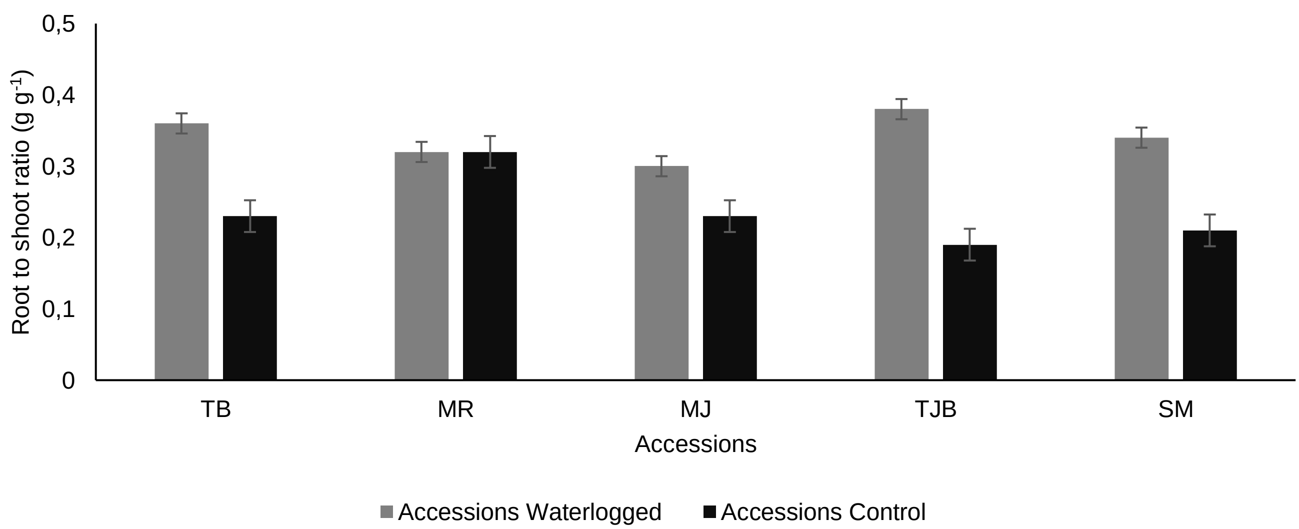

Figure 2 The root-to-shoot ratio of oil palm accessions treated by waterlogging. TB (Tebo), MR (Merangin), MJ (Muara Jambi), TJB (Tanjung Jabung Barat), SM (Simalungun).

root-to-shoot ratio, twice as high as the control accession. Roots are vital plant organs because they absorb nutrients for growth needs (Taiz *et al.* 2018). The low root-to-shoot ratio is due to assimilation only being translocated to the leaves (Putra *et al.* 2023). Root growth is affected by soil mechanical impedance and moisture content. Photosynthate from leaves and environmental factors such as temperature and soil water content affect root elongation rates (Salsinha *et al.* 2020). In addition, when the soil becomes denser or the water content increases, oxygen availability becomes a determinant of root growth (Centenaro *et al.* 2018). When plants are in a state of oxygen deficiency, it can affect the distribution of nitrogen. Nitrogen distribution increases from roots to shoots in plants (Liu *et al.* 2015). This condition causes shoot growth to increase.

Plants respond to water stress primarily through their leaves and roots. Their morphological and anatomical characteristics reflect their adaptability to unfavorable environments (Wu *et al.* 2022). Species that grow in waterlogging conditions can completely change their phenotype through various forms of adaptation (Ranawakage *et al.* 2013). Under waterlogged conditions, vascular plants have developed functional strategies to obtain nutrients and light (Hough-Snee *et al.* 2015). Some species will develop aerenchyma tissue under anaerobic conditions (Pedersen *et al.* 2021), forming pneumatophores to aid respiration (Garssen *et al.* 2015). In addition, leaf growth will be affected by the waterlogging treatment applied to annual crops (Putra *et al.* 2023). When plant species are sufficiently adapted to survive, biomass can be maintained, or regrowth can occur after waterlogging (Lambers *et al.* 2008).

CONCLUSION

The oil palm from Tebo (TB) and Merangin (MR) were well acclimated to the six weeks of waterlogging treatment through increased growth, such as an increase in fresh and dry weight. Acclimation in physiological processes, including photosynthesis, transpiration, and stomatal conductance rate. In addition, the duration of waterlogging also affects oil palm physiology.

ACKNOWLEDGEMENTS

This study was partly funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation), project ID 192626868, SFB 990 on behalf of the fourth author, and the IPB University for providing laboratory facilities.

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