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# The Relationship between Relative Water Content of Leaves, Soluble Sugars, Accumulation of Dry Matter, and Yield Components of Rice (*Oryza sativa* L.) under Water-stress condition during the Generative Stage

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***Abstract*—This study aims to observe the relationship between leaves' relative water content (RWC), soluble sugar, dry matter accumulation, and rice yield components under water-stress conditions during the generative stage. Six rice varieties were observed under three different water stress treatments: non-stress, moderate water-stress (-0.35 bar), and severe (-0.70 bar). The results showed that under moderate and severe water-stress; the RWC at reproductive stage had correlation with RWC at maturity stage (r = 0.97), colored pollen (r = 0.87), the percentage of grains (r = 0.54) and grain weight (r = 0.57). The RWC at anthesis stage was closely related to the RWC at ripening stage (r = 0.99), the percentage of colored pollen (r = 0.87) and filled grains (r = 0.58), and the weight of grains per hill (r = 0.69). The RWC at the ripening stage was also closely related to the percentage of colored pollen (r = 0.87), the percentage of filled grains (r = 0.61), and the weight of filled grains per hill (r = 0.72). Furthermore, the percentage of colored pollen was closely related to the biomass dry weight (r = 0.47), and the soluble sugars at the reproductive stage were related to the percentage of filled grains (r = -0.68). The soluble sugars at the anthesis stage were closely related to the soluble sugars at the maturity stage (r = 0.75). The result might allow us to use the RWC as a determinant for rice under water stress, and it is important to maintain the RWC under water stress, especially during the generative stage.***

***Keywords*— Correlation; drought; environment; global warming.**

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## I. INTRODUCTION

Rice is a main staple food crop and is significantly influenced by environmental factors [1], [2]. The main environmental factor that limits rice production is water stress [3], [4]. Water stress affects various physiological activities, namely the formation of chlorophyll, sugar, various pigments, antioxidants, and osmotic compounds that regulate water balance in cells [5]. Rice tolerant of water stress can maintain high cell water potential to maintain cell activity [6].

A plant's water status can be seen from its leaf's relative water content [7]. This relative water content can change according to the soil's moisture and is strongly influenced by rice's environment and genetic characteristics, decreasing relative water content due to increasing drought [8]. Drought at the reproductive stage can decrease yields by 61.3%, flowering by 83.7%, and vegetative stage 76.7% [9]. The leaf's relative water content (RWC) affects leaf morphology, as indicated by the shape of leaf rolling due to water stress [8]. The relative water content in leaves determines the plant's ability to recover after experiencing water stress. IR 64 is the variety that needs more time to recover after being watered than other varieties [10] and is classified as a water stress-sensitive variety [11]–[13]. Rice that is tolerant of water stress has a high water status [13]. The water status of the plants is represented by the relative water content in the leaves that affects the activity of photosystem II [12].

Relative water content is related to compatible compounds such as proline, polyamine, and soluble sugars and is important for plant resistance to water stress [14]. Various mechanisms keep cell osmotic pressure low by accumulating compatible compounds [3], which consist of two parts containing nitrogen and hydroxyl components [15]. Compatible compounds containing nitrogen are amino acids, proline, quaternary ammonium, and polyamine. Meanwhile, the hydroxyl components include sucrose, polyhydric alcohols, and oligosaccharides [16]. Compatible compounds significantly affect osmotic adjustment to maintain plant water balance in water stress conditions [13].

Osmotic adjustment involves various osmotically active molecules and ions, namely soluble sugars, sugar alcohols, proline, glicinebetain, organic acids, potassium, chloride, and others [5]. Compatible compounds also act as antioxidants to avoid damage to cell membranes under drought conditions [17] and include soluble sugars, proline, polyamine, glycine betaine, and various other compounds that are osmotic regulators [15]. Among the compatible compounds, soluble sugars are the dominant compounds that affect the growth and development of plants in various stages [18].

The ability to accumulate sugar determines a drought-tolerant character in plants [13], [19], and the ability to accumulate soluble sugars plays an important role in preserving turgor pressure by reducing the osmotic potential of cells [20]. Among the compatible compounds, amino acids, especially proline, commonly accumulate in many plants in response to environmental stress [21]. When water stress occurs, it is followed by an acceleration of leaf aging, causing a decrease in photosynthate for grain filling [22].

In addition, aging leaves that have reduced sugar levels also have reduced chlorophyll levels [23]. The destruction of the chloroplast membrane causes the reduction in chlorophyll under stress conditions due to the swelling of the vascular lamellae by peroxidation of lipids in the membrane [24]. Low levels of chlorophyll under water stress limit the potential for photosynthesis [25]. Chlorophyll damage is avoided by maintaining high water content in cells [26]. Water stress-tolerant varieties can increase both their soluble sugars and chlorophyll in water stress conditions [27]. Increasing water stress is followed by increasing soluble sugars [28]. Water stress-tolerant varieties can maintain relative water content in water stress conditions.

The role of compatible compounds is important to maintain RWC so that cell activity can take place during drought conditions [29]. Therefore, there is a close relationship between RWC and compatible compounds. Compared to other parameters, RWC is an important determinant for plant water status [30]. Varieties producing high yields can maintain water content in cells and have balanced sources that can compensate for the sink under drought conditions [31].

This is important in areas with unpredictable rainfall patterns since selecting tolerant rice varieties is a short-term alternative to overcome water shortages. In the long term, it is necessary to increase the plants' ability to produce in water shortage conditions by improving compatible compounds [13]. Several studies have shown that soluble sugars increase resistance to water stress [32], and the ability to accumulate soluble sugars at the anthesis stage can increase the yields [3]. This occurs since there is an increase in sugar in rice grains under water stress conditions [27].

Drought stress causes soluble sugars to increase [13], [32]. The soluble sugar accumulation can regulate the osmotic pressure of cells, so that cell activity normally runs [26]. Water stress causes an increase in soluble sugar in rice plants [33]. A decrease in soluble sugar levels under water stress causes faster leaf aging [34]. Thus, leaf aging can be avoided by providing soluble sugars [4].

There is an increase in soluble sugars in the stem, leaves, and rice panicles under water shortage conditions [35] and an increase in soluble sugars at panicle initiation [35]. The soluble sugar content at flowering is higher than at the grain filling stage [36]. The total content of sugars in the Intani rice variety straw is 2.53% [2]. The soluble sugars in flag leaves increase with increasing water stress [25]. They are higher at the time of heading than during panicle initiation [37] and affect plant growth and development [36]. Soluble sugars are closely related to tolerance to water stress [38] since it provides carbon and energy for growth and regulation of osmotic pressure during water stress [26].

Sugar metabolism is a key determinant for stress resistance to the environment [39]–[41]. However, rice has different critical conditions for water stress at each stage. The critical point of soil water potential at the vegetative stage is -35.9 KPa, at the reproductive stage is -25.8 KPa and at the maturity stage is -0.30 KPa [42]. Maintaining rice productivity by planting varieties with relatively high water content is required under water stress conditions to accumulate dry matter. Selecting varieties that have balanced sources and sink is also a strategy in overcoming water shortages. Source and sink sizes are determined by the number of leaves and sink organs such as roots, shoots, panicles, and grains of rice [43]. Several dry-resistant rice varieties include Towuti and Situ Patenggang [44]–[46]. Water stress-tolerant varieties can yield under water stress conditions [3].

This study aims to determine the leaf relative water content changes, the soluble sugars at the reproductive stage, anthesis and maturity, and their relationship to dry matter accumulation and rice yield. This research was conducted to answer the mechanism of rice survival and yield production under water stress conditions. As previous studies have only examined the RWC in leaves in certain stages with short intervals. This study addresses the mechanism of tolerance to water stress during the critical generative stage of rice. This can be a reference for changing agronomic techniques at the generative stage under water stress conditions according to correlation among variables.

## II. MATERIALS AND METHODS

### A. *Materials and Growth Conditions*

This research was conducted in a plastic house at an experimental farm at the Faculty of Agriculture, Syiah Kuala University, Darussalam, Banda Aceh, Aceh, Indonesia. Twelve days after sowing, healthy and uniform rice seedlings were planted in 19 L pots filled with 10 kg dried podzolic soil (see Fig. 1). The soil had been saturated with water, stirred until muddy, and incubated for two weeks. Each pot was planted with one rice seedling. The seedlings were given 900 kg $ha^{-1}$ of NPK fertilizer (15:15:15)%, urea 150 kg $ha^{-1}$, SP36 150 Kg $ha^{-1,}$ and KCl 100 kg $ha^{-1}$. Urea and NPK were given three times: at planting, 30 and 60 days after planting (DAP), 1/3 dosage each time. Water stress treatment was controlled through different soil water potentials. The plant was flooded 2 cm above the surface for moderate water stress, unwatered until the soil water potential dropped at -0.35 bar, and re-irrigated. When the soil was dried at -0.70 bar for severe stress, the plant was re-irrigated until flooded 2 cm above the soil surface, repeated until harvest. Moreover, as a control, non-stress treatment was prepared, in which it was a condition of stable or irrigated soil water of 2 cm flooded until harvest.

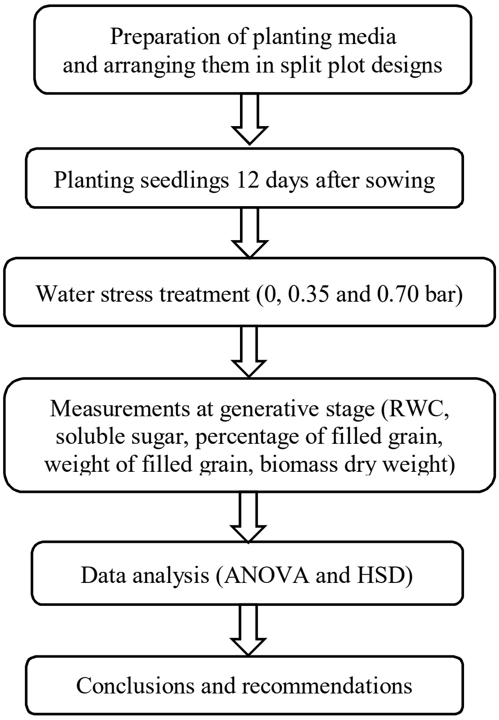


Fig. 1 Flowchart of the experiment

This study used a randomized block design of 3x6 with three replications. Water stress treatments were the main plots, and the varieties were the subplots. The varieties used included Situ Patenggang (V1), Towuti (V2), IR 64 (V3), Sipulo (V4), Sanbei (V5), and Bo Santeut (V6). V1 and V2 were the check varieties for tolerance to water stress (the positive control of water-control tolerant varieties); IR 64 was the sensitive water-stress variety (the negative control of water-stress sensitive variety); and V4, V5, and V6 were the tested varieties. Research on six varieties was carried out from September 2015 to February 2016 with a minimum/maximum temperature of 22/34.8°C and humidity at 40 to 93%.

### *B. Sampling and Measurements*

According to the method described by Barrs and Weatherley [47], relative water content (RWC) was analyzed on the fourth leaf from the top of the plant, which was taken when the soil water content reached -0.35 and -0.70 bar. Samples for soluble sugars were taken at each stage under water stress conditions. The soluble sugar content was determined based on the phenol sulfuric acid method [33], [48], in which 0.1 g of dry leaves was ionized with distilled water, and then the extracts were filtered and treated with 1% phenol and 98% sulfuric acid, then mixed for one hour. The absorbance reading was 485NM using a UV vis Shimadzu UV 1700 spectrophotometer. The analysis was conducted in the Food Analysis Laboratory, Department of Food Technology, Faculty of Agriculture, Syiah Kuala University. Productivity and yield components were measured based on IRRI [49]. The percentage of colored pollen was established using the Staining method with $I_2KI$ [50], [51]. Pollen was collected during the day when water stress reached -0.35 and -0.70 bar, after which the pollen grains were dripped with 1% of potassium iodide ($I_2KI$) on the object glass, covered with a glass cover, and viewed through a microscope with 400x magnification.

### *C. Data Analysis*

Data were analyzed using variants (ANOVA) at $p < 0.05$ to test the significance between factors with an HSD test. This study also used the Pearson correlation with SPSS package version 26.

## III. Results and Discussion

### *A. Correlation Between Parameters*

The correlation between the relative water content, soluble sugars, colored pollen, the percentage of filled grains, the weight of filled grains per hill, and biomass dry weight can be seen in Table 1.

TABLE I
THE CORRELATION COEFFICIENT MATRIX BETWEEN RELATIVE WATER CONTENT, SOLUBLE SUGARS, COLORED POLLEN, THE PERCENTAGE OF FILLED GRAINS, THE WEIGHT OF FILLED GRAINS PER HILL, AND BIOMASS DRY WEIGHT UNDER DIFFERENT WATER STRESS CONDITIONS

| | a | b | c | d | e | f | g | h | i | j |
|---|---|---|---|---|---|---|---|---|---|---|
| a | 1 | .981** | .978** | -0.319 | 0.188 | 0.209 | .876** | .544* | .670** | 0.350 |
| b | | 1 | .990** | -0.374 | 0.161 | 0.166 | .872** | .583* | .690** | 0.388 |
| c | | | 1 | -0.370 | 0.189 | 0.191 | .874** | .619** | .724** | 0.393 |
| d | | | | 1 | 0.123 | 0.119 | -0.360 | -.682** | -0,071 | -0.216 |
| e | | | | | 1 | .759** | -0.032 | 0.263 | 0.328 | -0.309 |
| f | | | | | | 1 | 0.085 | 0.244 | 0.459 | -0.046 |
| g | | | | | | | 1 | .491* | .642** | 0.362 |
| h | | | | | | | | 1 | .477* | .474* |
| i | | | | | | | | | 1 | .474* |
| j | | | | | | | | | | 1 |

a = RWC in leaves at reproductive stage; b = RWC in leaves at anthesis stage; c = RWC in leaves at maturity stage; d = soluble sugars in leaves at reproductive stage; e= soluble sugars in leaves at anthesis stage; f = soluble sugars in leaves at maturity stage; g = coloured pollen; h = percentage of filled grains; I = weight of filled grain pot; j = biomass dry weight

The Pearson correlation in Table 1 shows that relative water content in leaves at the reproductive stage was closely related to the relative water content of the leaves at the anthesis stage (r = 0.98), the relative water content of the leaves at the ripening stage (r = 0.97), the percentage of colored pollen (r= 0.87), the percentage of filled seeds (r =

0.64) and the weight of filled grains (r = 0.67). This is because, during the reproductive stage, the leaves' water status determined the perfection of the formation of the reproductive organs. The perfection of the reproductive organs determined the percentage of the number of filled grains and the weight of filled grains. In turn, grain weight was determined by the dry matter accumulation in the grains, which was influenced by the water status of the plant.

The relative water content in leaves at the anthesis stage was closely related to the relative water content at the ripening stage (r = 0.99), the percentage of colored pollen (r = 0.87), the percentage of filled grains (r = 0.58), and the weight of filled grains (r = 0.69). The relative water content determined the sugar and starch content in the pollen, which affected the percentage of colored pollen. The higher the percentage of colored pollen, the more flour in the pollen, which resulted in a higher rate of fertilization, causing the percentage and weight of the grains to increase. Because pollen consists of protein, fat, and starch [52], starch can be transformed into sugar for osmotic adjustment and energy used by the pollen for germination and movement towards the ovule [53].

The relative water content in leaves at the ripening stage was closely related to the percentage of colored pollen (r = 0.87), filled grains (r = 0.61), and the weight of filled grains (r = 0.72). The relative water content in leaves also determined the formation of starch, which affected the weight and percentage of filled grains.

Soluble sugars at the reproductive stage were closely related to the percentage of filled grains (r = -0.68). Soluble sugars became compatible compounds that regulated osmotic adjustments under water stress conditions, so that cell activity at the reproductive stage ran optimally for the formation of reproductive organs such as rice flowers, which would become filled grains. However, if the sugar content continued to increase, only a small amount of starch could be allocated for panicle formation at the reproductive stage. It caused the percentage of filled grains to decrease because too much starch was broken down into sugar for osmotic adjustment under water shortage conditions, as observed by Taiz and E. Zeiger [14].

Soluble sugars in leaves at the anthesis stage were closely related to soluble sugars in leaves at the ripening stage (r = 0.75). Soluble sugar levels from one stage to another influenced each other because they were produced by the breakdown of carbon in plant tissue.

The percentage of colored pollen was closely related to the percentage of filled grains (r = 0.49) and the weight of filled grains (r = 0.64). The pollen that was colored showed high levels of protein, fat, and starch, indicating that pollen has the energy to fertilize egg cells to become filled grains [50]. The percentage of filled grains was closely related to the weight of filled grains (r = 0.47) and biomass dry weight (r = 0.47). Filled grains per hill were closely related to biomass dry weight (r = 0.47). This was because the starch in filled grains came from plant tissue, a component of biomass dry weight.

### *B. The Effects of Water Stress*

The effect of water stress on relative water content, soluble sugars, colored pollen, the percentage of filled grains, the weight of filled grain per hill, and biomass dry weight can be seen in Table 2. There was a decrease in the leaf relative water content with increasing water stress at reproductive, anthesis, and ripening stages. However, there was an increase in soluble sugar levels at the reproductive stage with increasing water stress. In addition, the anthesis and maturity stages of soluble sugars were not significantly different at different levels of water stress.

TABLE II
AVERAGE VALUES OF RELATIVE WATER CONTENT, SOLUBLE SUGARS, COLORED POLLEN, THE PERCENTAGE OF FILLED GRAINS, THE WEIGHT OF FILLED GRAINS PER HILL AND BIOMASS DRY WEIGHT UNDER WATER STRESS CONDITIONS

| Parameter | Water Stress | | | HSD 0.05 | CV (%) |
|---|---|---|---|---|---|
| | WW | MS | SS | | |
| Relative water content in leaves at reproductive stage (%) | 88.49c | 80.97b | 1.05 | 1.4 | 1.05 |
| Relative water content in leaves at anthesis stage (%) | 94.98 | 79.34 | 1.02 | 1.31 | 1.02 |
| Relative water content in leaves at maturity stage (%) | 91.77 | 67.73 | 0.92 | 1.04 | 0.92 |
| Soluble sugars in leaves at reproductive stage (μmol $g^{-1}$ DW) | 27.08a | 28.28a | 3.43 | 1.63 | 3.43 |
| Soluble sugars in leaves at anthesis stage (μmol $g^{-1}$ DW) | 34.55a | 31.21a | 7.13 | 3.85 | 7.13 |
| Soluble sugars in leaves at maturity stage (μmol $g^{-1}$ DW) | 30.01a | 27.94a | 29.95 | 14.47 | 2.95 |
| Percentage of filled grains (%) | 67.16c | 51.68b | 2.37 | 2.12 | 2.37 |
| Weight of filled grain $pot^{-1}$ (g $pot^{-1}$) | 28.49c | 17.99b | 9.85 | 3.2 | 9.85 |
| Biomass dry weight (g $pot^{-1}$) | 91.84c | 59.53b | 5.47 | 6.16 | 5.47 |

Data followed by the same letter within the same row indicated no significant difference at $p < 0.05$ level of HSD test; CV = coefficient of variant; WW = well watered; MS = moderate water-stress; SS = severe water-stress

There was a decrease in filled grains, weight of filled grains, and biomass dry weight with increasing water stress. The moderate and severe water stress conditions caused a reduction of water taken up by plants, resulting in a decrease in relative water content in the leaves, which is in line with the research results of Swapna and Shylaraj [30]. The soluble sugars in leaves increased during the reproductive stage with increasing water stress because soluble sugars are compatible compounds that regulate osmotic adjustments in plants which increase when induced by water stress in certain stages. This is in line with the results of previous studies conducted by Chozin *et al.* [23] and Eslami *et al.* [54].

### *C. The Effect of Varieties*

The effects of varieties on relative water content, soluble sugars, colored pollen, the percentage of filled grains, the weight of filled grains per hill, and biomass dry weight can be seen in Table 3. Relative water content in leaves at the reproductive stage varied between varieties. The highest relative water content in leaves at the reproductive stage was found in the Situ Patenggang variety, followed by Sanbei, Towuti, and Sipulo, and the lowest RWC in leaves was IR 64. At the anthesis stage, the highest RWC in leaves was in Sanbei, followed by Situ Patenggang, Sipulo, and Bo Santeut, while the lowest was IR64. The highest relative water content in leaves at the ripening stage was in Situ Patenggang, followed by Sanbei, Sipulo, Towuti, and Bo Santeut and the lowest was in IR 64. This is in line with the results of research by Sovannarun *et al.* [8]. There were differences in the relative water content in leaves of several local varieties. These findings are also in line with the study results of Prathap [10] study that IR 64 had a lower water content and, therefore, leaf recovery took longer [3], [12]. Since IR 64's leaves have a relatively low water content, it takes a long time to recover from drought, and it is classified as a water stress-sensitive variety [11].

TABLE III
AVERAGE VALUES OF RELATIVE WATER CONTENT, SOLUBLE SUGARS, COLORED POLLEN, THE PERCENTAGE OF FILLED GRAINS, THE WEIGHT OF FILLED GRAINS PER HILL, AND BIOMASS DRY WEIGHT IN DIFFERENT VARIETIES

| Parameter | Variety | | | | | | HSD | CV |
|---|---|---|---|---|---|---|---|---|
| | V1 | V2 | V3 | V4 | V5 | V6 | | |
| Relative water content in leaves at reproductive stage (%) | 82.44f | 81.14d | 75.72a | 80.13c | 81.77e | 78.36b | 0.38 | 0.47 |
| Relative water content in leaves at anthesis stage (%) | 80.74e | 78.01c | 69.24a | 79.09d | 80.96e | 75.55b | 0.34 | 0.43 |
| Relative water content in leaves at maturity stage (%) | 72.03f | 67.87c | 58.65a | 68.72d | 71.21e | 64.52b | 0.58 | 0.85 |
| Soluble sugars in leaves at reproductive stage (µmol $g^{-1}$ DW) | 28.09b | 27.49a | 29.73c | 30.53c | 26.59a | 28.59b | 0.98 | 3.39 |
| Soluble sugars in leaves at anthesis stage (µmol $g^{-1}$ DW) | 40.53e | 29.35b | 31.65c | 27.05a | 31.45c | 34.45d | 1.33 | 4.06 |
| Soluble sugars in leaves at maturity stage (µmol $g^{-1}$ DW) | 35.13b | 26.47a | 24.07a | 27.91a | 31.93a | 28.47a | 9.1 | 30.96 |
| Percentage of filled grains (%) | 49.74d | 51.35b | 42.62a | 65.25e | 54.77c | 57.91d | 2.81 | 5.17 |
| Weight of filled grain $pot^{-1}$ (g $pot^{-1}$) | 24.94d | 15.81b | 13.21a | 29.19e | 16.17b | 17.69c | 1.83 | 9.27 |
| Biomass dry weight (g $pot^{-1}$) | 35.39a | 51.78c | 41.95b | 134.40e | 71.80d | 70.36d | 3.75 | 5.48 |

Data followed by the same letter within the same row indicate no significant difference at $p < 0.05$ level of HSD test; CV = coefficient of variant; HSD = honesty significant different; DW = dry weight

At the anthesis stage, the highest soluble sugars were in Sipulo, followed by IR 64, Bo Santeut, Situ Patenggang, and Towuti, and the lowest was in Sanbei. The highest soluble sugars in leaves at the ripening stage were in Situ Patenggang, followed by Sanbei, Bo Santeut, Sipulo, and Towuti, and the lowest was in IR 64; this is in line with a previous study [23].

The highest percentage of filled grains was found in Sipulo, followed by Bo Santeut, Sanbei, Towuti, and Situ Patenggang, and the lowest was in IR 64. The highest weight of filled grains was found in Sipulo, followed by Situ Patenggang, Bo Santeut, and Sanbei, and the lowest was found in Towuti and IR 64. This was because Situ Patenggang is a water stress-tolerant variety planted in lowland and upland areas [46], [47]. The rice landraces, Sipulo, Bo Santeut, and Sanbei, had a higher percentage of filled grains and weight of filled grains than Towuti, which is a water stress-tolerant variety [44]. This shows that varieties of Sipulo, Sanbei, and Bo Santeut can produce higher yields than Towuti.

The highest biomass dry weight was found in Sipulo, Sanbei, Bo Santeut, Towuti, IR 64, and Situ Patenggang. This is because the Sipulo and Bo Santeut have a greater ability to form productive tillers and roots than IR 64 and Situ Patenggang. However, Situ Patenggang has a better proportion of yields and shoots. Only a few tillers have longer panicles, greater weight, and a high percentage of filled grains [44].

### *D. The Interaction between the Effects of Water Stress and the Varieties of Rice Plants*

The interaction between the effects of water stress and the varieties of rice plants on relative water content, soluble sugars, colored pollen, the percentage of filled grains, the weight of filled grains per hill, and biomass dry weight can be seen in Table 4. There was a decrease in the relative water content of the leaves at the reproductive stage in all varieties with increasing water stress and varying degrees of reduction. However, in severe water stress, the highest relative water content was in Situ Patenggang, followed by Towuti, Sanbei, and Sipulo, and the lowest was in Bo Santeut, followed by IR 64. Since IR 64 is a susceptible water stress variety, with low recovery ability after drought and lower relative water content, it is classified as a water stress-sensitive variety [3], [10], [12].

TABLE IV
AVERAGE VALUES OF RELATIVE WATER CONTENT, SOLUBLE SUGARS, COLORED POLLEN, THE PERCENTAGE OF FILLED GRAINS, THE WEIGHT OF FILLED GRAINS PER HILL, AND BIOMASS DRY WEIGHT UNDER DIFFERENT WATER STRESS CONDITIONS

| Parameter | | Variety | | | | | | HSD -0.05 |
|---|---|---|---|---|---|---|---|---|
| | | V1 | V2 | V3 | V4 | V5 | V6 | |
| Relative water content in leaves at reproductive stage (%) | WW | 89.99k | 88.21j | 86.74h | 87.91i | 90.19l | 87.88i | 0.47 |
| | MS | 82.61g | 81.80f | 75.30e | 82.02 | 81.96fg | 82.13g | |
| | SWS | 74.72d | 73.42c | 65.12b | 70.47b | 73.15c | 65.08a | |
| Relative water content in leaves at anthesis stage (%) | WW | 96.29m | 95.15l | 91.36k | 94.92l | 97.43 | 94.70l | 0.42 |
| | MS | 82.37j | 80.02h | 73.52f | 80.32h | 81.82i | 77.99g | |
| | SWS | 63.57e | 58.84c | 42.85a | 62.04d | 63.63e | 53.97b | |
| Relative water content in leaves at maturity stage (%) | WW | 94.69q | 90.99o | 84.23m | 90.33o | 94.30p | 89.85n | 0.726 |
| | MS | 70.24l | 67.48i | 59.85g | 68.11j | 69.74k | 64.72h | |
| | SWS | 51.17f | 45.14c | 31.88a | 47.73d | 49.59e | 38.98b | |
| Soluble sugars in leaves at reproductive stage (µmol $g^{-1}$ DW) | WW | 30.69c | 24.51a | 30.03bc | 24.45a | 24.03a | 28.77b | 1.23 |
| | MS | 24.63a | 24.69a | 28.47b | 37.89e | 24.99a | 29.01b | |
| | SWS | 28.95b | 33.27d | 30.69c | 29.25b | 30.75c | 27.99b | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Soluble sugars in leaves at anthesis stage (µmol $g^{-1}$ DW) | WW | 59.31g | 28.83c | 33.81e | 25.41b | 32.07d | 27.87c | 1.67 |
| | MS | 32.97d | 25.71b | 32.61d | 23.73a | 28.95c | 43.29f | |
| | SWS | 29.31c | 33.51d | 28.53c | 32.01d | 33.33d | 32.19d | |
| Soluble sugars in leaves at maturity stage (µmol $g^{-1}$ DW) | WW | 46.35c | 24.57a | 25.53a | 29.85a | 28.59a | 25.17a | 11.38 |
| | MS | 29.19a | 23.19a | 22.47a | 27.09a | 34.83b | 30.87a | |
| | SWS | 29.85a | 31.65a | 24.21a | 26.79a | 32.37a | 29.37a | |
| Percentage of filled grains (%) | WW | 67.91gh | 60.51f | 55.77e | 85.29i | 64.66g | 68.82h | 3.51 |
| | MS | 48.45c | 53.42de | 37.67b | 60.60f | 54.12e | 55.84e | |
| | SWS | 32.86a | 40.13b | 34.41a | 49.85d | 45.53c | 49.08d | |
| Weight of filled grain $pot^{-1}$ (g $pot^{-1}$) | WW | 44.77i | 22.69g | 18.33d | 35.64h | 21.93e | 27.61g | 2.29 |
| | MS | 19.07d | 14.33c | 11.09b | 27.26g | 22.18e | 14.03c | |
| | SWS | 10.99b | 10.42b | 10.22b | 24.66f | 4.40a | 11.44b | |
| Biomass dry weight (g $pot^{-1}$) | WW | 36.48a | 63.69d | 47.91b | 225.38h | 93.50g | 84.08f | 4.7 |
| | MS | 36.20a | 47.14b | 43.87b | 92.00g | 64.17d | 73.82e | |
| | SWS | 33.50a | 44.52b | 34.07a | 85.81f | 57.74c | 53.17c | |

Data followed by the same letter within the same row and column indicate no significant difference at $p < 0.05$ level of HSD test; HSD = honesty significant different; DW = dry weight

Relative water content in leaves at the anthesis stage decreased with increasing water stress, with different reduction levels in each variety. At the level of severe water stress, the highest relative water content in the leaves was found in the Sanbei variety, followed by Situ Patenggang, Sipulo, and Towuti. The lowest was IR 64, followed by Bo Santeut. The low relative water content at the anthesis stage at IR 64 indicates its inability to adjust the osmotic pressure to water stress conditions [3]. The varieties of Sipulo and Sanbei, as rice of local landraces, have a higher relative water content when compared with Towuti, which is a water stress-tolerant variety [44].

Generally, the relative water content at the maturity stage decreased, but the decrease varies between varieties. However, the highest relative water content in severe water stress was found in Situ Patenggang, followed by Sanbei, Sipulo, and Towuti, while the lowest was found in IR 64 and Bo Santeut. A high relative water content indicates the ability to adjust the osmotic pressure in water shortage conditions. This shows that compatible compounds can play a vital role in soluble sugars and polyamine compounds [14].

Soluble sugar content at the reproductive stage decreased in all varieties during moderate water stress, except for Sipulo, which was significantly different from other varieties. There was a decrease in soluble sugars in the Situ Patenggang and Bo Santeut varieties during severe water stress compared to non-stress conditions, but there was an increase in soluble sugars in Towuti Sipulo, and Sanbei, which exceeded of soluble sugars of non-stress treatment. This shows that Sipulo and Sanbei have an osmotic adjustment mechanism that increases soluble sugar content in severe water stress, similar to Towuti, a water stress-tolerant variety. In contrast, the IR 64 variety has lower soluble content, which makes it sensitive to water stress [23], [26], [38].

The soluble sugar content in the leaves of the anthesis stage generally increases with increasing water stress. The greatest increase was found in Bo Santeut, followed by Sipulo and Towuti, which are different from non-stress. This shows that at the anthesis stage, the Bo Santeut and Sipulo varieties have an osmotic adjustment mechanism that increases compatible compounds in the form of soluble sugars. Increases in soluble sugars under water stress have also been reported in other studies [3], [25], [32], [36], [37].

The soluble sugar content in leaves at the ripening stage generally varies between varieties with increasing water stress. There was an increase in soluble sugars during severe water stress in Sanbei, followed by Towuti, Bo Santeut, and Sipulo, while the lowest was found in the IR 64 variety. These show that Sanbei, Bo Santeut, and Sipulo can adapt to water stress by increasing soluble sugar content. An increase in soluble sugars is a mechanism to maintain cell activity in water stress conditions [2], [36], [55].

The percentage of filled grains decreased in all varieties with increasing water stress, with the highest decrease during severe water stress found in IR 64. The lowest percentage of filled grains was in Situ Patenggang, IR 64, Towuti, Sanbei, Bo Santeut, and Sipulo. Meanwhile, the lowest weight of filled grains per hill during severe water stress was found in Sanbei, followed by IR 64, Towuti, Situ Patenggang, Bo Santeut, and Sipulo. The differences in adaptation of plants from other factors such as temperature and relative humidity were at the anthesis stage, which affects the pollination and fertilization of rice and the water stress factor.

These findings are in line with the results of a study conducted by Herawati *et al.* [56]. However, varieties that have a defense mechanism through compatible compounds and relative water content can perform pollination and fertilization under water stress, as seen in the Sipulo, Bo Santeut, and Situ Patenggang varieties; this is in line with some previous studies [37], [39]–[41].

The biomass dry weight decreased with varying degrees of reduction due to increasing water stress. The largest decrease was in Sipulo, followed by Bo Santeut, Sanbei, and Towuti. While Situ Patenggang was relatively stable, the decrease in IR 64 was greater than others. This suggests that the accumulation of dry matter determines rice yield because the assimilates allocated to grains were assimilates mobilized from plant tissues. The proportional biomass weight varieties can produce high yields because of the balanced carbon accumulation between parts of the yield organs and other parts of the plant, as shown by the Situ Patenggang, which is a water stress-tolerant variety [44]–[46]. Drought-tolerant varieties are required for planting in upland areas that often experience water shortages due to climate change [57]. Varieties with a balanced allocation of dry matter, for example, for plant height, can be characterized as water stress-tolerant, as reported by Warman *et al.* [58]. The selection of water stress-resistant varieties is needed to obtain plants that can adapt to water stress conditions [59].

The percentage of colored pollen varies between varieties, as shown in Table 4. The difference is also due to the level of water stress. Quantitative differences have been shown in Tables 3 and 4. Morphologically, there is a difference in the color of the pollen after being dripped with 1% potassium iodide. Dark round pollen indicates fertile pollen that can fertilize egg cells and become filled grain (see Fig. 2).

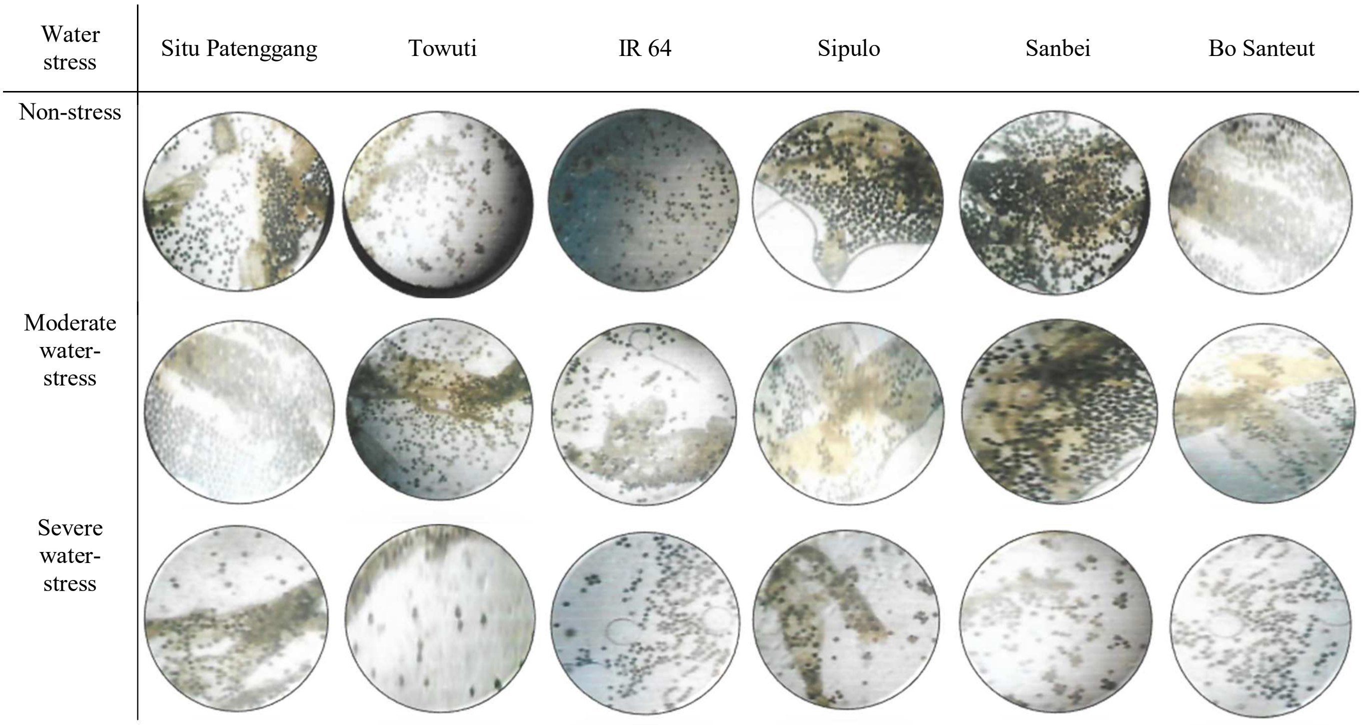


Fig. 2 The colored pollen of the varieties under different levels of water stress: dark and round pollen is fertile; shrinking and wrinkling pollen is sterile

This is because fertile pollen contains protein, fat, and starch, which can be converted into sugar for energy to germinate the pollen and penetrate the ovule to carry out fertilization, as noted in the results of previous studies by Waheed *et al.* [50] and Nugroho *et al.* [52].

## IV. Conclusion

The relative water content in leaves during the reproductive, anthesis, and ripening stages affects rice yields. Under severe water stress, varieties with high relative water content can produce higher yields than varieties with lower relative water content. The soluble sugars at the reproductive stage affect the yield components of rice. The percentage of colored pollen is closely related to filled grains, grains per hill, and biomass dry weight. Varieties with a proportional dry matter accumulation between the yield organs and other components can produce higher grains under water stress. The relative water content of the leaves is suitable as a reference for the water status of plants under water stress. Varieties with high relative water content in severe water stress give higher rice yields. The relative water content can be a key criterion for tolerance to water stress based on its relationship with yield components and dry matter accumulation. The correlation between variables during the generative stage can be used as a reference for choosing tolerance varieties and changing agronomic techniques under water stress conditions and needs to be studied further.

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