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Research article

# Responses of physiological traits, growth and yield of rice to drought stress

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## Abstract

**Importance of the work**: Rice plants are sensitive to different levels of drought during all growth stages. Drought induces reduced rice growth and yield by affecting the growth parameters and physiological traits related to photosynthate production. The response of rice plants to drought stress is useful information for evaluating drought-tolerant characteristics in high yielding cultivars.

**Objectives**: To study the growth parameters and physiological traits, yield and yield components of two rice cultivars during various growth stages under polyethylene glycol (PEG)-induced drought stress.

**Materials & Methods**: The Khao Dawk Mali 105 (KDML 105) and Pathum Thani 1 (PT 1) rice cultivars were grown under two conditions (non-stress and drought stress) in a hydroponic system. The growth parameters, physiological traits and yield were evaluated after water stress induction during the seedling, tillering and flowering stages.

**Results**: The growth parameters and physiological traits of the two rice cultivars significantly decreased, while the free proline and spermidine contents increased under stress during all growth stages. However, the flowering stage was the most sensitive to drought. In addition, there was a greater decrease in all the studied growth and physiological traits of PT 1 under drought than for those of KDML 105. The grain yield was reduced by 35.9−50% for PT 1 and by 18.6−31% for KDML 105. Positive correlations were obtained between all the studied physiological traits and grain yield in both cultivars; however, the highest correlation to grain yield was obtained from the leaf water potential (LWP) and net photosynthetic rate.

**Main finding**: The magnitudes of drought response varied between the cultivars and among the growth stages. PT 1 was more sensitive to drought than KDML 105 and the flowering stage was the most sensitive stage. LWP could be used to study the plant-water status and to evaluate drought-tolerance characteristics, as it had the highest correlation to yield, was less influenced by other variables and could be measured easily during all growth stages without damaging the whole plant.

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## Introduction

Rice is an important economic crop in the world with increasing demand for international trade because it is a major staple food consumed by more than one-half of the world's population and is grown in more than 100 countries, especially in Asia (Fukagawa and Ziska, 2019). Rice production must be increased by at least 25% by 2030 due to global population growth and demand (Seck et al., 2012). Rice can be grown all year round; however, it requires a high water demand and is considered drought-susceptible (Schneider and Asch, 2020). The sensitivity of rice to drought varies with planting season, cultivar and growth stage (Oladosu et al., 2019). Indica rice [Chai Nat 1 (CNT 1), KDML 105, San-pah-tawng (SPT 1) and Rice Department 6 (RD 6) cultivars] are those that can be grown under low soil fertility and are tolerant to drought; thus, they are widely grown in the tropical zone of South Asia. Two rice cultivars, KDML 105 and PT 1 are of interest and were studied in the current experiment. KDML 105 has a distinctive texture and fragrance and can grow under drought conditions. However, its grain yield can be easily reduced due to grains falling off the panicles (Vanavichit et al., 2018; Sarutayophat et al., 2020). Likewise, PT 1 is a representative of non-photoperiod-sensitive cultivars and has a high yield (Cha-Um et al., 2010). It can be grown year-round in various environmental conditions but is commonly grown in irrigated areas of Thailand.

Nowadays, water resources for agriculture are limited and it is estimated that by 2025, it will be less available and irrigated rice production will suffer from water scarcity (Lampayan et al., 2015). Drought stress is the major environmental factor that is a constraint to rice productivity at various levels and all stages of the complete rice life cycle, as it can affect plant growth, physiological characteristics and some biochemical processes that are related to yield (Uyprasert et al., 2004; Singh et al., 2020). Closure of stomata and gas exchange restriction usually occur when rice is facing drought stress which is the plant's response to minimize water loss through evapotranspiration and to maintain cell turgor pressure (Liu et al., 2022). Additionally, drought stress directly leads to a decrease in rice growth (plant height, tiller number, fresh and dry weight) since approximately 80–95% of the plant cells is water (Piveta et al., 2020; Kuru et al., 2021)

Several experiments have been performed to simulate different water stress conditions induced by polyethylene glycol (PEG; Nio et al., 2018; Rahim et al., 2020; Sagar et al., 2020; Zhu et al., 2021). Studies of plant response to PEG-induced drought stress could be used to identify a drought-tolerant character for developing rice cultivars that are adapted to drought and have increased grain yield compared to other cultivars. Physiological characteristics such as net photosynthetic, stomatal conductance and chlorophyll content could be used to evaluate rice drought tolerance for a breeding program (Mishra et al., 2019; Salsinha et al., 2020; He et al., 2021). These traits are easy to observe and can be measured multiple times in large numbers with a non-destructive method compared to other growth parameters and yield components. The improvement of rice plants resistant to drought stress is the main target for rice growth and grain yield increment in many countries (Khan et al., 2021). In addition, information on growth and yield, such as plant height, tiller number, filled spikelets, numbers of panicles and seed weight, in response to drought could be used to evaluate drought tolerance. The main focus for the selection should be rice cultivars that maintain optimal growth with a high yield under water scarcity (Ghazy et al., 2021). Therefore, the current experiment aimed to study the responses of growth and physiological characteristics, yield and yield components of rice cultivars (KDML 105 and PT 1) to drought conditions.

## Materials and Methods

### *Experimental design and plant materials*

This experiment was conducted under greenhouse conditions at Suranaree University of Technology, Nakhon Ratchasima, Thailand during 2021–2022. During the experiment, the daily temperature was in the range 23.71–39.65°C and relative humidity was in the range 30.08–89.77%. Two rice cultivars (KDML 105 and PT 1) were planted into plastic trays (36 cm length × 600 cm width × 12 cm height) containing Hoagland's nutrient solution (Hoagland and Arnon, 1950) in a hydroponic system that was continuously aerated using an electric pump. The nutrient solution was adjusted every 5 d to maintain the nutrient concentration until the harvest stage. The experiment was conducted in a completely randomized design with 10 replications. Treatments consisted of water-saturated (non-stress) and three water deficit treatments (PEG-induced drought stress at the seedling, tillering and flowering stages). In the water-saturated treatment, the nutrient solution was adjusted every 5 d throughout the growing period. In the water deficit treatments, the nutrient solution was also adjusted every 5 d until the plants reached either the seedling, tillering, or flowering stage, according to the experimental design. Then, 5% of PEG-6000 was added to create a mild water stress condition (equivalent to -0.5 MPa) for 7 d (Neumann, 2003). Distilled water was adjusted every 5 d to replenish water lost through evaporation and transpiration. The pH of the nutrient solution was maintained in the range 5.8−6.5 and the nutrient concentration was maintained at electrical conductivity of 1.8 dS/m in both treatments throughout the experiment.

### *Measurement and data collections*

The growth and physiological parameters as well as osmotic adjustment of the rice plants were measured at 7 d after drought stress had been induced. Depending on the treatment, the measurements for drought stress at the seedling stage, tillering stage and flowering stage were carried out after germination when the rice plants were aged 15−20 d, 25−30 d and 80−85 d, respectively. The growth parameters (plant height and dry matter content) were recorded from 10 randomly selected plants in each replicate. Predawn leaf water potential was measured using a pressure chamber (3005F01 New Plant Water Status Console; Soilmoisture Equipment Corp.; USA). Photosynthetic parameters—net photosynthetic rate (A) and stomatal conductance ($g_s$)—were measured using a portable photosynthesis system (LCi T Compact Photosynthesis System; ADC BioScientific Ltd.; UK) at the third leaf counted from the shoot. The conditions of measurement were: 500 mmol/m$^2$/s of the molar flow of air per unit leaf area, 1,500 µmol/m$^2$/s of the photosynthetically active radiation at the leaf surface, a leaf temperature in the range 35.0−39.0°C and 400 µmol/mol $CO_2$. Chlorophyll fluorescence ($F_v/F_m$) was measured using a chlorophyll fluorimeter (Handy PEA; Hansatech Instruments Ltd; UK). Leaf clips were clamped on the chosen fully expanded leaves for 15 min to induce dark adaptation; afterward, the $F_v/F_m$ was measured (Mishra and Panda, 2017). The free proline content (Pro) and spermidine content (Spd) were determined following the methods described by Bates et al. (1973) and Huang et al. (2017), respectively. These two traits were chosen for measurement based on their roles in the regulation of osmotic adjustment as a strategy to mitigate drought stress (Ghosh et al., 2022). The yield and yield components (number of panicles and grain yield per plant) were determined at the harvesting stage.

### *Statistical analysis*

Data were analyzed using the SPSS V.16 software (SPSS Inc.; USA). The treatment means were compared based on least significant differences. Correlation analysis based on the correlation coefficient (r) was performed between physiological traits and grain yield attributes of rice. The tests were considered significant at $p < 0.05$.

## Results and Discussion

The results regarding growth, yield and physiological traits were compared between the non-water stress and water stress treatments to identify the degree of responses of both rice cultivars to water stress in each growth stage.

**Table 1** Plant height and dry matter of rice cultivars at 7 d after introduction of drought stress during three different growth stages

| Rice cultivar | Treatment | Plant height (cm) | | | Dry matter (g/plant) | | |
|---|---|---|---|---|---|---|---|
| | | SS | TS | FS | SS | TS | FS |
| PT 1 | Non-stress | 24.27 | 48.90 | 89.90 | 6.05 | 7.98 | 76.48 |
| | Stress | 23.00 | 45.50 | 79.87 | 3.75 | 5.89 | 64.38 |
| | Reduction (%) | 5.23 | 6.95 | 11.16 | 38.02 | 26.19 | 15.82 |
| | Significance | ns | * | ** | * | * | * |
| | CV% | 5.96 | 2.21 | 3.43 | 51.94 | 3.35 | 8.87 |
| KDML 105 | Non-stress | 26.60 | 70.63 | 86.00 | 8.20 | 10.12 | 60.21 |
| | Stress | 24.27 | 66.20 | 65.07 | 3.38 | 8.81 | 44.03 |
| | Reduction (%) | 8.76 | 6.27 | 24.34 | 58.78 | 12.94 | 26.87 |
| | Significance | ns | ns | ** | * | ns | ** |
| | CV% | 8.19 | 2.02 | 5.76 | 33.91 | 3.65 | 2.68 |

SS = seedling stage; TS = tillering stage; FS = flowering stage; CV = coefficient of variation.

*, **, ns = significant differences at $p < 0.05$ and $p < 0.01$ and not significant, respectively.

*Effects of drought stress on growth parameters*

The plant height of both cultivars decreased under drought stress (Table 1). Plant height for PT 1 decreased under drought stress during the tillering and flowering stages (6.95% and 11.16%, respectively), whereas for KDML 105, plant height significantly decreased under stress during the flowering stage (24.34%). Growth reduction commonly occurred when the plant had less water absorption or low water potential, as reported in other experiments, such as Islam et al. (2018) and Piveta et al. (2020), where the plant height and dry weight decreased in all rice genotypes when the water stress levels increased. Under drought stress, plant height is reduced from impaired cell division and elongation, poor root development, leaf area reduction and the limitation of oxygen supply (Uyprasert et al., 2004; Farooq et al., 2010).

The dry matter content of PT 1 under drought stress significantly decreased during the seedling, tillering and flowering stages (38.02%, 26.19% and 15.82%, respectively), as shown in Table 1, while the KDML 105 dry matter content significantly decreased under stress during the seedling and flowering stages (58.78% and 26.87%, respectively). The reduction in the dry matter content caused by drought was the result of reductions in leaf expansion, tiller number, photosynthetic rate and leaf area. These plant responses reduced water loss and preserved the plant water content to survive through stress (Kumar et al., 2006). These results were similar to the findings of Larkunthod et al. (2018), who reported that the dry matter content in all there studied rice cultivars reduced by more than 55% after 7 d of stress, particularly in KDML 105.

*Effects of drought stress on leaf water potential and osmotic adjustment (free proline content and spermidine content)*

Under drought stress conditions, the predawn leaf water potential ($LWP_{pd}$) in PT 1 was significantly reduced during the seedling and flowering stages, while in KDML 105, $LWP_{pd}$ was significantly reduced for all growth stages (Table 2). These results were in agreement with Moonmoon et al. (2020), who reported that drought significantly reduced physiological traits, particularly LWP, in all their studied rice genotypes. LWP is directly related to water status; in a plant under drought stress conditions, water absorption is limited, leading to reductions in the turgor pressure and water potential in leaf cells (Reddy et al., 2021).

The Pro value of both cultivars increased under stress compared to non-stress conditions (Table 2). The Pro value of PT 1 under stress significantly increased for all growth stages (54.29%, 66.16% and 62.69%, at the seedling, tillering and flowering stages, respectively). In KDML 105, the Pro value under stress significantly increased for the seedling to flowering stages (56.08% and 52.43%, respectively). Generally, under drought stress, rice cultivars accumulate a high Pro content to maintain plant water status and turgor pressure by promoting the uptake of $K^+$, $Ca^{2+}$, P and N to reduce stomatal opening and the evapotranspiration rate, which can reduce the negative effect of drought on membrane organelles, proteins and enzymes (Hayat et al., 2012; Nio et al., 2018). Pamuta et al. (2022) indicated that the leaf proline contents in all their studied rice cultivars significantly increased under drought stress and it was tightly associated with rice growth.

**Table 2** Predawn leaf water potential ($LWP_{pd}$), free proline content (Pro) and spermidine content (Spd) of rice cultivars at 7 d after introduction of drought stress during three different growth stages

| Rice cultivar | Treatment | $LWP_{pd}$ (bar) | | | Pro (µg/g FW) | | | Spd (nmol/g FW) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | SS | TS | FS | SS | TS | FS | SS | TS | FS |
| PT 1 | Non-stress | -5.43 | -9.63 | -6.00 | 11.93 | 10.26 | 17.84 | 176.41 | 219.37 | 603.22 |
| | Stress | -10.07 | -13.57 | -17.70 | 26.10 | 30.32 | 47.81 | 1,593.62 | 1,810.52 | 2,498.07 |
| | Reduction (%) | 46.08 | 29.03 | 66.10 | | | | | | |
| | Significance | ** | * | ** | ** | ** | ** | ** | ** | ** |
| | CV% | 3.83 | 10.27 | 21.86 | 23.52 | 7.01 | 19.95 | 8.39 | 8.66 | 15.51 |
| KDML 105 | Non-stress | -9.57 | -12.40 | -5.00 | 10.90 | 13.02 | 19.16 | 224.42 | 287.22 | 589.34 |
| | Stress | -16.58 | -14.60 | -16.57 | 24.82 | 28.11 | 40.28 | 1,453.65 | 2,187.53 | 2,755.51 |
| | Reduction (%) | 42.28 | 15.07 | 69.82 | | | | | | |
| | Significance | * | ns | ** | ** | ** | ** | ** | ** | ** |
| | CV% | 17.17 | 9.49 | 11.76 | 4.68 | 19.16 | 3.89 | 9.34 | 8.67 | 3.86 |

SS = seedling stage; TS = tillering stage; FS = flowering stage; CV = coefficient of variation.

*, **, ns = significant differences at $p < 0.05$ and $p < 0.01$ and not significant, respectively.

The Spd value of both cultivars increased under drought stress (Table 2). In PT 1, the value was significantly increased by 88.93%, 87.88% and 75.85% for the seedling, tillering and flowering stages, respectively, under stress conditions, while in KDML 105, it significantly increased for the seedling, tillering and flowering stages (84.56%, 86.87% and 78.61%, respectively). These results were in agreement with Zhang et al. (2017), who reported that the Spd significantly increased while the number of sterile spikelets decreased in rice young panicles under drought stress. Spd can increase the relative water content, chlorophyll content, photosynthetic rate and antioxidant enzyme activities but decreased the malondialdehyde, total soluble sugar and abscisic acid contents under drought stress (Chen et al., 2017). Spd acts as a free radical scavenger that protects the membranes from oxidative damage, stabilizes the cell membrane and optimizes stomatal opening and closing to reduce plant water loss (Hasan et al., 2021).

### *Effects of drought stress on photosynthetic function of net photosynthetic rate and chlorophyll fluorescence and stomatal conductance*

The net photosynthetic rate (A) of both cultivars decreased under stress (Table 3). The A values of PT 1 and KDML 105 during seedling and flowering stages reduced under stress conditions. In PT 1, the A value was reduced by 69.30% and 70.87%, respectively, while in KDML 105, the value was reduced by 65.29% and 75.08%, respectively. The reduction in A under stress conditions was mainly the result of a decrement in $g_s$. Punchkhon et al. (2020) recorded that all photosynthetic performance parameters (A, $g_s$ and the transpiration rate) significantly decreased (44–70%) in all their studied rice lines under drought stress during the vegetative stage compared with non-stressed plants. In addition, Moonmoon et al. (2020) observed that drought reduced all physiological attributes, such as LWP, A and $g_s$.

The chlorophyll fluorescence ($F_v/F_m$) is the ratio of variable to maximum fluorescence after dark adaptation. In PT 1, this value for the seedling, tillering and flowering stages of the stressed plants significantly decreased by 19.23%, 9.86% and 19.95%, respectively, compared to the non-stress conditions (Table 3). Similarly, the $F_v/F_m$ value of KDML 105 was significantly reduced under stress conditions for the seedling, tillering and flowering stages (19.92%, 25.16% and 24.48%, respectively). Under drought conditions, the photosynthetic activity and chlorophyll content decrease due to early leaf senescence and chlorophyll degradation (Batool et al., 2022). Yang et al. (2014) reported that the net photosynthetic rate and chlorophyll fluorescence decreased under severe drought stress. In addition, Nio et al. (2019) revealed that leaf total chlorophyll content decreased due to PEG-induced water stress, causing reductions in the photosynthetic and transpiration rates. Mafakheri et al. (2010) reported that drought inhibits photosynthesis by causing changes in the chlorophyll content and light capacity by affecting chlorophyll components and damaging the photosynthetic apparatus.

The response of stomatal conductance ($g_s$) to drought stress is shown in Table 3. The $g_s$ value in PT 1 significantly decreased under stress compared with non-stress during the seedling and flowering stages (65.22% and 25.35%, respectively). The $g_s$ value of KDML 105 also decreased significantly under stress conditions during the seedling and tillering stages (60.00%

**Table 3** Net photosynthetic rate (A), chlorophyll fluorescence ($F_v/F_m$) and stomatal conductance ($g_s$) of rice cultivars at 7 d after introduction of drought during three different growth stages

| Rice cultivar | Treatment | A (μmol/m²/s) | | | $F_v/F_m$ ratio | | | $g_s$ (mol/m²/s) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | SS | TS | FS | SS | TS | FS | SS | TS | FS |
| PT 1 | Non-stress | 8.73 | 13.93 | 15.62 | 0.749 | 0.811 | 0.737 | 0.46 | 0.60 | 0.71 |
| | Stress | 2.68 | 3.21 | 4.55 | 0.605 | 0.731 | 0.590 | 0.16 | 0.26 | 0.53 |
| | Reduction (%) | 69.30 | 79.96 | 70.87 | 19.23 | 9.86 | 19.95 | 65.22 | 56.67 | 25.35 |
| | Significance | ** | ** | ** | ** | ** | ** | ** | ** | ** |
| | CV% | 7.38 | 17.70 | 4.09 | 4.67 | 4.10 | 4.77 | 3.30 | 19.69 | 3.91 |
| KDML 105 | Non-stress | 6.54 | 12.61 | 15.45 | 0.763 | 0.791 | 0.813 | 0.35 | 0.55 | 0.71 |
| | Stress | 2.27 | 2.92 | 3.85 | 0.611 | 0.592 | 0.614 | 0.14 | 0.16 | 0.35 |
| | Reduction (%) | 65.29 | 76.84 | 75.08 | 19.92 | 25.16 | 24.48 | 60.00 | 70.91 | 50.70 |
| | Significance | ** | ** | ** | ** | ** | ** | ** | ** | ** |
| | CV% | 3.37 | 3.88 | 6.80 | 4.60 | 9.15 | 4.43 | 4.44 | 6.50 | 7.09 |

[1]SS = seedling stage; TS = tillering stage; FS = flowering stage; A, net photosynthetic rate; $g_s$, stomatal conductance; CV = coefficient of variation.
** = significant difference at $p < 0.01$.

and 70.91%, respectively). These results were in agreement with Dien et al. (2017), who reported that drought stress significantly decreased plant growth and $g_s$ in all their studied rice varieties. Chareesri et al. (2020) reported that drought consistently and strongly decreased the $g_s$ value by more than 75% compared to well-watered treatments. This reduction is a physiological mechanism that helps reduce water loss through leaf transpiration. In addition, the drought-induced ABA and signaling proteins biosyntheses also contributed to stomatal closure and a reduction in $g_s$ (Gujjar et al., 2020).

### *Effects of drought stress on yield traits*

The number of panicles per plant for both cultivars under drought stress for all growth stages was lower than for the non-stress treatment (Table 4). In both cultivars, the number of panicles under stress during the seedling and flowering stages significantly decreased. In addition, the grain yield for both cultivars decreased under stress conditions for all growth stages (Table 4). The grain yields of the PT 1 and KDML 105 plants subjected to drought stress introduced during the seedling, tillering and flowering stages significantly decreased compared to those of the controls (40.98%, 35.89% and 50.08% reductions, respectively) for the PT 1 cultivar. Similarly, for the KDML 105 cultivar, grain yields significantly decreased by 31.11%, 18.63% and 25.76% under stress conditions during the seedling, tillering and flowering stages, respectively. The grain yield reductions were in the ranges 35.89−50.08% for PT 1 and 18.63−31.11% for KDML 105. These results indicated that based on yield reduction, PT 1 was more sensitive to drought than KDML 105.

Drought stress significantly affected growth, physiological traits and biochemical processes that resulted in reductions on rice growth, yield and yield components. The yield of both rice cultivars decreased under stress by 35.9−50% in PT 1 and 18.6−31% in KDML 105. Reduction in the grain yield under drought was mostly the result of reductions in the seed weight and the numbers of panicles and fertile panicles. Moonmoon and Islam (2017) indicated that all yield parameters were reduced under drought, including total spikelets per panicle, filled grains per panicle, 1,000-grain weight, percentage of sterility and grain yield. These traits are important yield components of rice that have a direct effect on the rice yield (Haider et al., 2012). The grain yield could have reduced due to panicle formation being disturbed by drought during the reproductive and ripening stages. The responses of physiological traits to drought occurred for all growth stages; however, the highest responses were recorded during the flowering stage. Many researchers have suggested that the flowering stage is the critical one for rice yield reduction and quality formation due to spikelet sterility and grain yield reduction occurring when the rice has been exposed to severe drought (Yang et al., 2019; Vijayaraghavareddy et al., 2020 Zhao et al., 2020). Furthermore, the yield of rice plants exposed to drought stress during the flowering stage decreased more than due to drought stress during other growth stages because rice plants normally cannot fully recover from drought stress during the flowering stage before panicle formation (Shamsudin et al., 2016; Zhang et al., 2018; Yang et al., 2019).

**Table 4** Number of panicles and grain yield of rice cultivars in response to drought introduced during three different growth stages

| Rice cultivar | Treatment | Number of panicles (panicles/plant) | | | Grain yield (g/plant) | | |
|---|---|---|---|---|---|---|---|
| | | SS | TS | FS | SS | TS | FS |
| PT 1 | Non-stress | 16.67 | 16.67 | 16.67 | 19.67 | 19.67 | 19.67 |
| | Stress | 11.00 | 13.00 | 9.67 | 11.61 | 12.61 | 9.82 |
| | Reduction (%) | 34.01 | 22.02 | 41.99 | 40.98 | 35.89 | 50.08 |
| | Significance | * | * | * | ** | ** | ** |
| | CV% | 9.67 | 21.26 | 21.26 | 6.02 | 5.35 | 5.64 |
| KDML 105 | Non-stress | 12.67 | 12.67 | 12.67 | 13.47 | 13.47 | 13.47 |
| | Stress | 8.33 | 11.00 | 9.67 | 9.28 | 10.96 | 10.00 |
| | Reduction (%) | 34.25 | 13.18 | 23.68 | 31.11 | 18.63 | 25.76 |
| | Significance | * | ns | * | * | * | * |
| | CV% | 12.83 | 6.90 | 15.07 | 11.17 | 3.81 | 3.94 |

SS = seedling stage; TS = tillering stage; FS = flowering stage; CV = coefficient of variation.
*, **, ns = significant differences at $p < 0.05$ and $p < 0.01$ and not significant, respectively.

### *Correlation analysis between physiological responses and grain yield of rice cultivars*

The correlation coefficients between the physiological characteristics and grain yield for the rice cultivars are presented in Table 5. For PT 1, there were highly positive correlations between the grain yield and $LWP_{pd}$, $g_s$, A and the $F_v/F_m$ ratio. A had the highest positive correlation with grain yield (r = 0.996, significant at $p \leq 0.01$). Similarly, in KDML 105, there were positive correlations between the grain yield and all physiological traits, with $LWP_{pd}$ and A having the highest positive correlations with grain yield (r = 0.956 and 0.957, respectively, with both at $p \leq 0.01$). In contrast, the Pro and Spd contents of both cultivars were negatively correlated with grain yield.

Correlation coefficient analysis between physiological traits is one of the methods used to obtain information on drought tolerance traits. In the current study, the grain yield was positively correlated with all the studied physiological traits for both cultivars. Conversely, Pro and Spd were negatively correlated with the grain yield and all the studied physiological traits. However, Liu et al. (2016) reported that the grain weight and grain-filling rate were significantly and positively correlated with free Spd concentrations in wheat under drought conditions. Similarly, Pro and Spd were positively and significantly correlated with the rice yield, chlorophyll content and number of filled grains per panicle of rice under sodicity stress (Gopikannan and Ganesh, 2013). In the current study, $LWP_{pd}$, $g_s$ and A had the highest positive correlations with the grain yield, which agreed with Yang et al. (2019), who reported that both traits had a strong influence on the rice yield during the flowering stage.

In conclusion, the current results indicated that drought stress had negative effects on water absorption. A limited amount of water led to reductions in physiological and growth traits, yield and yield components, while osmotic adjustment (Pro and Spd) increased under drought conditions. The grain yield of PT 1 was more sensitive to drought than was KDML 105, especially to drought during the flowering stage. All the studied physiological traits responded to drought for all growth stages; however, the most sensitive period was during the flowering stage. Positive correlations were obtained between the grain yield and all the studied physiological traits. However, $LWP_{pd}$ and A had the highest and most consistent correlation to grain yield. $LWP_{pd}$ normally indicates the whole plant's water status and it is usually less influenced by other variables because it represents the mean soil moisture potential next to the roots that is closely correlated to transpiration rate (Améglio et al., 1999). The $LWP_{pd}$ could be repeatedly observed throughout the rice growth cycle without damaging the whole plant samples; therefore, it is proposed for evaluating drought-tolerant characters and as a criterion for drought-tolerance selection in rice breeding programs.

**Table 5** Correlation coefficients of physiological traits, osmotic adjustment and grain yield of rice cultivars under stress

| Rice cultivar | Trait | $g_s$ | $LWP_{pd}$ | $F_v/F_m$ ratio | Pro | Spd | GY |
|---|---|---|---|---|---|---|---|
| PT 1 | A | 0.974** | 0.926** | 0.967** | -0.996** | -0.993** | 0.996** |
| | $g_s$ | | 0.907* | 0.964** | -0.971** | -0.928** | 0.977** |
| | $LWP_{pd}$ | | | 0.976** | -0.997** | -0.976** | 0.948** |
| | $F_v/F_m$ ratio | | | | -0.992** | -0.948** | 0.979** |
| | Pro | | | | | 0.979** | -0.991** |
| | Spd | | | | | | -0.957** |
| KDML 105 | A | 0.987** | 0.985** | 0.969** | -0.996** | -0.990** | 0.957** |
| | $g_s$ | | 0.999** | 0.990** | -0.983** | -0.998** | 0.951** |
| | $LWP_{pd.}$ | | | 0.994** | -0.975** | -0.994** | 0.956** |
| | $F_v/F_m$ ratio | | | | -0.944** | -0.976** | 0.941** |
| | Pro | | | | | 0.993** | -0.983** |
| | Spd | | | | | | -0.996** |

A = net photosynthetic rate; $g_s$ = stomatal conductance; $LWP_{pd}$ = predawn leaf water potential; Pro = proline content; Spd = spermidine content; GY = grain yield.

*, ** = significant differences at $p < 0.05$ and $p < 0.01$, respectively.

## Conflict of Interest

The authors declare that there are no conflicts of interest.

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