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The impact of straw application on growth dynamics and proline accumulation in drought-stressed rice

R.P. Ria[1], K. Kartika[2,*], B. Lakitan[1,3], F. Sulaiman[1] and M. Meihana[4]

[1]University of Sriwijaya, Faculty of Agriculture, Department of Agronomy, Jl. Raya Palembang-Prabumulih Km 32 Indralaya, Ogan Ilir 30662, Indonesia
[2]Research Center for Horticulture, Research Organization for Agriculture and Food, National Research and Innovation Agency (BRIN), Cibinong 19611, Indonesia
[3]Research Centre for Sub-optimal Lands, Universitas Sriwijaya. Jl. Padang Selasa No. 524, Bukit Besar, Palembang 30139, South Sumatra, Indonesia
[4]STIPER Sriwigama, Faculty of Agriculture, Department of Agronomy, Palembang 30137, South Sumatra, Indonesia
[*]Correspondence: kart011@brin.go.id

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Abstract. The frequent occurrence of unpredictable extreme droughts necessitates investigating measures to mitigate their impacts, as drought may occur at any growth phase of rice. This study evaluated the efficiency of straw applications to conserve soil moisture and mitigate the negative effect of drought stress on rice in tropical riparian wetlands. Rice straw was applied as organic matter (S1) and as mulch (S2) and then subjected to drought stress during early vegetative (D1), late vegetative (D2), and generative (D3) phases. The result of this study showed that the utilization of straw slowed down the water loss through evaporation as indicated by soil moisture. However, both rice straw applications, organic matter and mulch, were inefficient in maintaining the optimum plant growth when the soil moisture declined to < 10%. Drought stress at the early vegetative phase reduced the number of leaves by 63.68%, the number of tillers by 50.58%, and the total leaf area by 72.36%. Drought stress at the early vegetative phase also delayed flowering time for 11 days. Meanwhile, drought stress during the generative phase reduced the number of filled spikelets by 45.18% and increased sterile spikelets to 247.05%, which significantly reduced the yield. Plants that experienced drought stress during the vegetative and generative phases eventually increased the proline content by about 10 times (18.47 mmol g^{-1}) compared to unstressed plants (1.62 mmol g^{-1}). Straw mulching is recommended for mild to moderate droughts, but additional methods are needed to maintain soil moisture below 10%.

Key words: morpho-physiological adaptations, mulch, organic matter, soil moisture, wetland.

INTRODUCTION

Tropical riparian wetlands in Indonesia have been used as agricultural land for ages. However, the productivity of rice as the main cultivated crop remains low compared to the national average. Unfavorable environmental conditions are the prevalent challenges of rice cultivation within tropical riparian wetlands (Kartika et al., 2018). Excess water during the rainy period and drought in the dry period are widespread issues in tropical riparian ecosystems. The first growing season in the tropical riparian wetland occurs by the end of the rainy season. The second growing season is supposed to be planted immediately after the harvest of the first rice crops, simultaneously with the early dry season (Ria et al., 2020). Thus, the second rice crop is probably exposed to drought stress during germination until the late vegetative phase.

Drought stress commonly manifests during the reproductive phase of first-grown rice crops, representing a significant abiotic challenge that can constrain growth and substantially crop production (Usman et al., 2013; Palareti et al., 2016; Ndjiondjo, 2018; Kartika et al., 2020; Khalaf et al., 2024). Drought induces physiological, physicochemical, and morphological changes in plants, which adversely impact their growth and yield (Kartika et al., 2020). As noted by Ndjiondjop et al. (2018), rice has traditionally been cultivated under well-watered conditions, where the soil water potential is consistently near 0. Thus, rice plants are particularly susceptible to drought.

Previous research has documented a substantial decline in rice growth and yield under drought stress in tropical riparian wetland ecosystems (Kartika et al., 2020). Rice exhibits the reduction of stomatal conductance and increases leaf rolling as common physiological responses to drought (Ria et al., 2020; Kartika et al., 2021a). Furthermore, drought stress impairs plant growth by disrupting key biochemical processes, including proline. The accumulation of proline is an adaptive response of plants to drought stress, but its levels quickly decline once the plants recover (Dien et al., 2019; Saha et al., 2019). As such, proline can function as a metabolic indicator of drought stress in plants (Jain et al., 2019).

The application of straw may provide a sustainable solution to mitigating the effect of drought and enhancing crop yields through various mechanisms. The utilization of straw as a mulch can enhance the microclimate conditions and improve soil fertility (Melnyk et al., 2023). Rice straw is abundantly available in tropical riparian wetlands. Approximately about 78.10% of farmers in tropical riparian wetlands abandoned untreated rice straw in fields, 20.00% was burned and 0.95% was composted (Lakitan et al., 2016). Rice straw can be repurposed as organic fertilizer. Incorporating rice straw into the soil not only enhances soil fertility by supplying essential nutrients but also improves soil structure and aggregation, ultimately enhancing the overall quality and productivity of the soil (Liu et al., 2021). Rice straw application has been reported as an effective measure to mitigate the negative effect of environmental stresses on rice growth. The application of 1% rice straw enhanced rice growth under heavy metals contaminated soil and drought stress (Ahmad et al., 2022). Additionally, the application of 1.5% straw could increase soil biological properties and rice growth under low water irrigation (Novair et al., 2024).

Rice straws also can be applied as mulch to reduce evaporation during the dry season. Straw application is able to modify environmental factors, retain groundwater, reduce soil temperature, and increase organic matter accumulation in soil (Abbasi et al., 2013). Straw mulching also can maintain soil moisture, increase infiltration, and maintain the structure of the soil surface (Lucas-Borja et al., 2018). Yang (2015) reported that the utilization of rice straw as a mulch significantly improves water use efficiency, sustains high grain production, and enhances the overall quality of rice crops. Moreover, applying a rice straw mulch maintains soil moisture levels under drought conditions similar to when there is no drought stress (Abo-Ogiala & Khalafallah, 2019). Straw mulching has also been shown to increase the vegetative growth of rice under drought stress in non-flooded paddy fields in the subtropical moist climate of China (Qin et al., 2010).

The effectiveness of the straw application is highly influenced by environmental conditions. Straw mulching tends to be more beneficial in cooler climates, while straw incorporation performs better in warmer climates (Qin et al., 2021). Although many studies report the positive impact of straw application on improving plant growth under drought conditions, few have demonstrated the extent to which straw application can maintain soil moisture and rice growth, particularly under severe drought conditions in tropical riparian wetlands. Therefore, this study aimed to assess the effects of straw application on growth, yield, and proline accumulation in rice subjected to drought stress in tropical riparian wetlands, with the goal of evaluating the effectiveness of straw application in mitigating the adverse impacts of drought stress.

MATERIALS AND METHODS

This study was conducted in an outdoor setting located in Jakabaring (104°46'44"E; 3°01'35"S), Palembang, South Sumatra, Indonesia. The study area is situated in a tropical lowland climatic region. Seeds of Inpago 10 of more than 90% germination were used in this study. The seeds were obtained from the Indonesian Center for Rice Research at Sukamandi, West Java, Indonesia. Inpago 10 was selected for this study due to its strong performance under drought stress conditions (Ria et al., 2020). For clarity, this information has now been added in the materials and methods section. After a 24-hour germination period, the seeds were directly sown into pots containing a mixture of ultisol soil and chicken manure (2:1 v/v). The pot dimensions were 22 cm (base diameter), 26 cm (height), and 30 cm (upper diameter). A single seed was planted in each pot. The plants were provided with NPK compound fertilizers (16:16:16) at a rate of 5 g per plant two weeks after transplanting.

Rice straw was used in this study. The straw was applied as organic matter (S1) and as mulch (S2). As organic matter, straw is mixed with the planting media and applied 2 weeks prior to the seed planting. A mulch straw was placed on the planting media surface and applied 2 weeks after planting. The amount of straw applied was 75 g pot^{-1} for both treatments S1 and S2.

Before the drought stress treatment, all plants were placed in open areas and thoroughly watered to ensure they were well-hydrated. During the drought stress treatment period, the plants were arranged in plastic houses to shield them from any potential precipitation and expose them solely to the intended drought conditions. The average temperature was 30 ± 5 °C, with relative humidity of 80% to 90%. The plants were subjected to drought conditions for 21 days during the early vegetative phase and 7 days during the late vegetative and generative phases. The duration of the drought stress treatment was determined by the soil moisture level, and it was terminated when the soil moisture dropped below 10%. This threshold ensured that the plants experienced severe drought stress but could still recover once the stress was alleviated (Kartika et al., 2020).

Data collection

During drought treatments, soil moisture content was observed daily using a Lutron PM-714 soil moisture meter. A digital image analysis system developed by Easlon and Bloom was utilized to precisely measure the leaf area of the plants.

Temperature and air humidity were measured using a digital multifunction environment meter (CEM DT-8820). Leaf rolling was observed at noon on the last 3 days of drought stress treatment, scored according to the Standard Evaluation System for Rice (IRRI, 2002). Proline levels were quantified using the protocol outlined by Bates et al. (1973). The results of the analysis were then obtained by running the samples through a UV/VIS-6100 spectrophotometer set to a wavelength of 520 nm. The dry weight of the plant biomass was quantified following oven-drying of the samples at 70 °C for 48 hours.

Experimental design and data analysis

This experiment utilized a factorial randomized block design. The first experimental factor involved straw application, with treatments consisting of without straw (S0), straw as organic matter (S1), and straw as mulch (S2). The second factor involved four distinct drought stress treatments: no stress with adequate water supply (D0), stress during the early vegetative phase at 4 weeks after planting (D1), stress during the late vegetative phase at 8 weeks after planting (D2), and stress during the generative phase at 10 weeks after planting (D3). The experimental design involved three replications for each factor combination, with each replication comprising three pots. This approach ensured the reliability and robustness of the results. Collected data were analyzed using SAS 9.0 statistical analysis software. The differences between treatments were evaluated using the Least Significant Difference at a significance level of $P \leq 0.05$. Significant differences between the unstressed and drought stress conditions were analyzed using the Student's *t*-test in the R software. $P < 0.05$ was considered statistically significant for both the *LSD* and Student's *t*-test.

RESULTS

The applications of straw only significantly affected the number of tillers at the early vegetative growth at 5 weeks after planting (WAP) (Table 1). Exposure to drought stress during the early vegetative phase led to a substantial decline in the number of tillers produced by the rice plants. The detrimental impact of drought stress on tiller formation manifested within one week of initiating the drought conditions during the vegetative growth phase. However, straw application as mulch (S2) produced relatively more tillers than without straw or its application as organic matter (S1).

Drought stress exposure was evaluated at three distinct developmental phases of rice cultivation: early vegetative, late vegetative, and reproductive phases. The utilization of straw as mulch consistently showed the highest soil moisture over other treatments under drought stress (Table 2). However, the application of straw both as mulch and organic matter was unable to maintain soil moisture at adequate levels when the plants experienced drought conditions during their late vegetative and reproductive phases. This study found that drought stress at the early vegetative phase up to 21 days to reach 8.62% but only 6 days when drought stress was applied at the late vegetative and generative phases. The long duration of this phase of drought was not only due to the effect of straw application, but plants require and absorb less water and low transpiration during the vegetative phase. Thus, the soil water content decreases slowly. Water requirements for each growth phase are different, depending on the availability of soil content, the ability of soil particles to hold water, and the ability of roots to absorb water.

Table 1. The number of tillers of Inpago 10 from 5 WAP to 9 WAP affected by straw application and drought stress

Treatment	5 DAP	7 DAP	9 DAP
Straw application (S)			
Without straw (S0)	3.91 b	13.79 a	19.37 a
Straw as organic matter (S1)	4.75 a	14.7 a	20.45 a
Straw as mulch (S2)	4.7 a	15.29 a	20.87 a
LSD	0.77	2.63	3.43
Drought stress (D)			
Unstressed (D0)	5.16 a	16.66 a	21.88 a
Early vegetative phase (D1)	2.61 b	7.72 b	16.38 b
Late vegetative phase (D2)	5.16 a	18.05 a	20.72 a
Generative phase (D3)	4.88 a	15.94 a	21.94 a
LSD	0.9	3.04	3.97
Interaction of S and D			
S0D0	4.17 bc	15.17 bc	20.83 ab
S0D1	6.00 a	17.17 ab	23.00 a
S0D2	5.33 ab	17.67 ab	21.83 ab
S0D3	2.33 d	6.67 d	13.83 c
S1D0	3.50 cd	10.00 cd	20.00 abc
S1D1	2.00 d	6.50 d	15.33 bc
S1D2	5.00 abc	18.83 ab	20.67 abc
S1D3	4.17 bc	14.67 bc	18.33 abc
S2D0	5.17 a	20.67 a	23.17 a
S2D1	4.17 bc	14.50 bc	22.17 ab
S2D2	5.33 ab	17.00 ab	20.50 abc
S2D3	5.17 ab	16.33 ab	23.17 a
LSD	1.56	5.27	6.87

Note: Means followed by different letters indicated statistically significant differences at $LSD_{0.05}$. WAP = Weeks After Planting.

Table 2. The soil moisture content at the end of the drought stress period, in relation to the application of rice straw in the Inpago 10 rice variety

Last day of drought stress	Straw application	Soil Moisture (%)		D/U Ratio
		Unstressed	Drought	
Early vegetative phase	Without straw	21.95 ± 1.82	8.62 ± 0.96	0.39 *
	As organic matter	22.93 ± 2.87	9.78 ± 0.73	0.43 *
	As mulch	21.67 ± 2.68	9.42 ± 0.63	0.43 *
Late vegetative phase	Without straw	18.18 ± 0.03	4.47 ± 0.80	0.69 **
	As organic matter	16.82 ± 0.15	5.23 ± 1.13	0.58 **
	As mulch	18.35 ± 1.68	6.48 ± 1.03	0.72 *
Generative phase	Without straw	19.88 ± 1.30	2.80 ± 1.23	0.14 *
	As organic matter	22.67 ± 7.43	4.08 ± 1.19	0.18 *
	As mulch	18.65 ± 0.80	4.65 ± 1.69	0.25 **

Note: D/C ratio, Ratio between drought treatment to the unstressed. Means of soil moisture with drought treatment and unstressed were compared by the Student's *t*-test (**, $p < 0.01$; *, $p < 0.05$).

The straw application did not affect to leaf rolling score. Fig. 1 depicts the leaf rolling scores of the plants in the last 3 days of drought stress. Leaf score increased continuously during the last three days of stress and the highest leaf score appeared in the plants imposed to drought stress during their generative phase. The plants applied with straw as mulch tended to exhibit less leaf rolling than those treated with other treatments, particularly when drought occurred during the early and late vegetative phase.

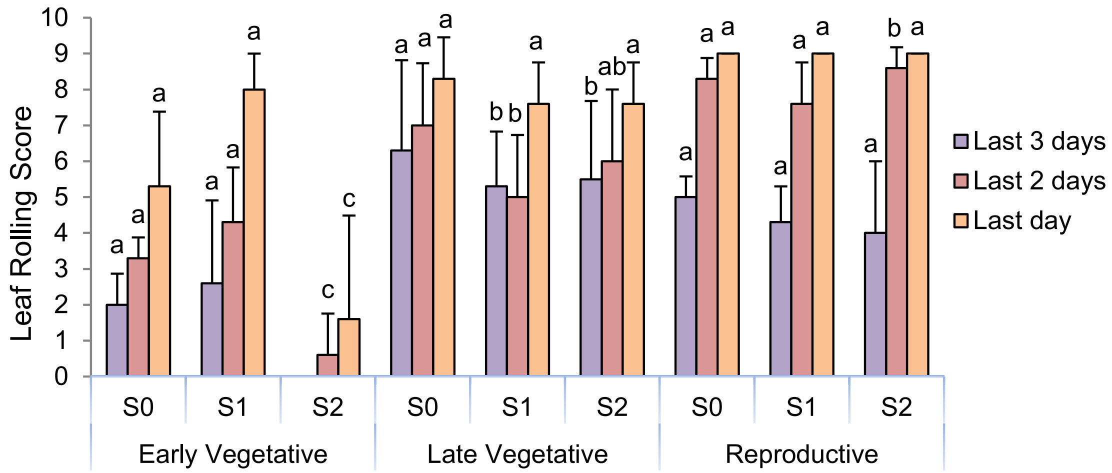

Figure 1. Leaf rolling score at the last three days was affected by straw application and drought stress. Bars (means ± SD, $n = 3$) with different letters are significantly different based on $LSD_{0.05}$. S0 = Without straw; S1 = Straw as organic matter; S2 = Straw as mulch.

In addition to leaf rolling, rice has a tolerant mechanism (drought tolerance) in taking on drought stress. The plant will increase the concentration of proline content. The findings indicate that proline levels increased substantially on the 7th day of drought stress implementation during the late vegetative phase of the plant's growth cycle (Fig. 2).

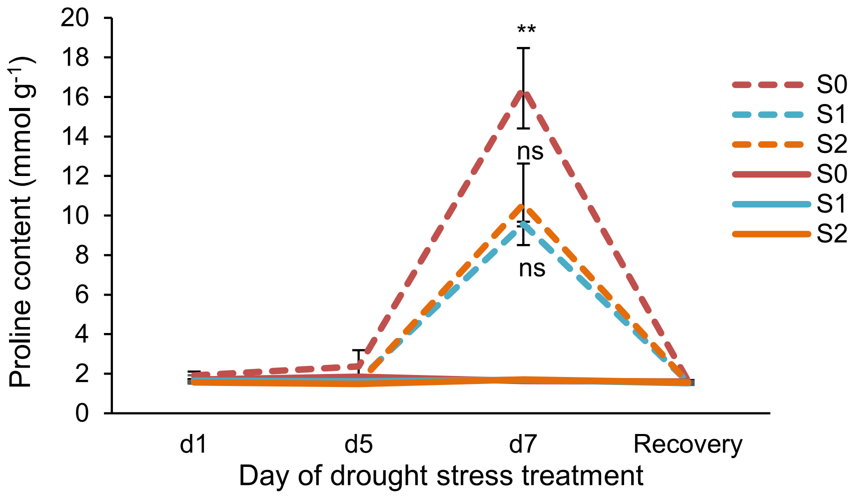

Figure 2. Effect of straw application and drought stress during the late vegetative phase on leaf proline content at the 1st day (d1), 5th day (d5), and 7th day (d7) of drought treatment, and during the 7th day of recovery. Solid lines are for untreated and broken lines are for drought treated plants. The vertical bars represent the standard deviation. Asterisks (**) above the bars indicate results that are significantly different at the $LSD_{0.05}$, while 'ns' denotes a non-significant difference. S0 = Without straw; S1 = Straw as organic matter; S2 = Straw as mulch.

While leaf rolling score increased earlier, from the 5th day, and sharply increased on the 7th day after drought stress initiation (Fig. 3). Proline levels decreased back to pre-stress levels after 7 days of recovery following the termination of drought stress.

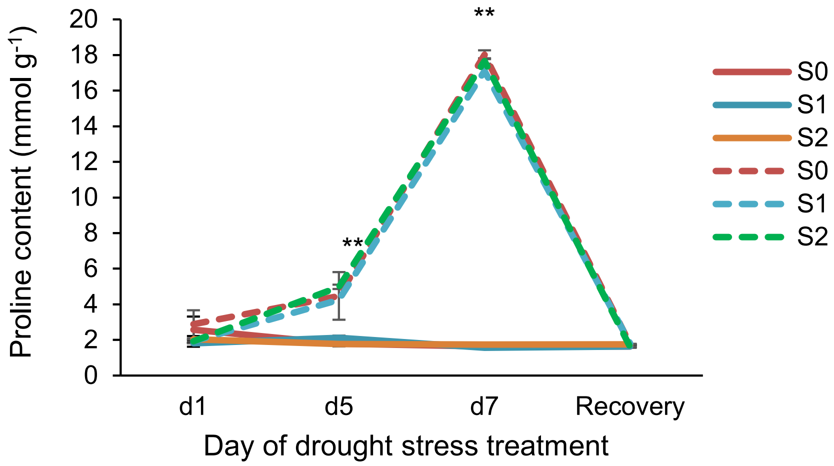

Figure 3. Effect of straw application and drought stress during the generative phase on leaf proline content at the 1st day (D1), 5th day (D5), and 7th day (D7) of drought treatment, and during the 7th day of recovery. Solid lines are for untreated and broken lines are for drought treated plants. The vertical bars represent the standard deviation. Asterisks (**) above the bars indicate results that are significantly different at the $LSD_{0.05}$, while 'ns' denotes a non-significant difference. S0 = Without straw; S1 = Straw as organic matter; S2 = Straw as mulch.

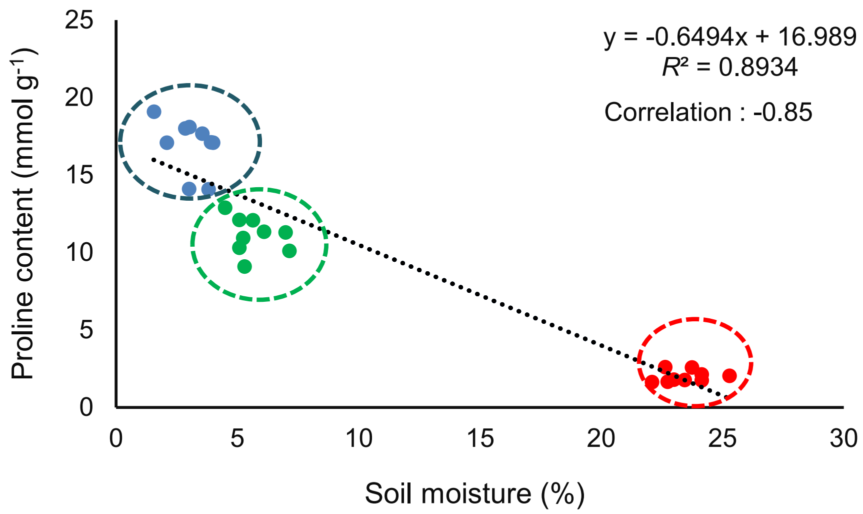

Figure 4. Regression and correlation of soil moisture x proline content of rice inpago 10 under unstressed condition (red), moderate (green), and severe (blue) drought stress.

Soil moisture showed a negative correlation with proline content in leaves, as indicated by the regression line (y = -0.6494x + 16.989) and the correlation coefficient of -0.85 (Fig. 4). This finding suggests the levels of proline will increase as soil moisture decreases. The red group represents the unstressed condition, where soil moisture content is high (20–25%) in association with low proline content. In contrast, the green group indicates moderate drought stress conditions when soil moisture content is 10–15% and proline content of between 7–11 mmol g^{-1}. In severe drought stress (blue group), the soil moisture drops (1–5%), and the level of proline content increases. The increase in proline contents demonstrates an adaptive process, where proline acts as an osmolyte, enabling the plants to maintain osmotic balance during a deficiency of water.

The study determined that the use of straw was insufficient to alleviate the effects of drought stress on the development of shoots and roots. Drought stress significantly impacted the vegetative organs, as evidenced by reductions in the number of leaves, total leaf area, shoot-to-root ratio, and an increase in organ death rates (Table 3).

Table 3. Number of leaves, total leaf area (TLA), specific leaf area (SLA), shoot to root ratio, and percent dead organ in Inpago 10 as affected by straw applications and drought stress

Treatment	Number of leaves	Total leaf area (cm^2)	Specific leaf area (cm^2 g^{-1})	Shootto root ratio	Dead organ (%)
Straw application (S)					
Without straw (S0)	57.91 a	2,587.80 a	3.63 a	4.78 a	34.33 b
Straw as organic matter (S1)	63.37 a	2,681.10 a	4.42 a	5.04 a	41.85 a
Straw as mulch (S2)	63.62 a	2,714.00 a	3.44 a	4.58 a	32.09 b
LSD	8.99	443.11	1.28	1.52	4.68
Drought stress (D)					
Unstressed (D0)	69.00 a	2,895.10 a	4.03 ab	5.90 a	27.67 c
Early vegetative phase (D1)	43.94 b	2,094.90 b	3.94 ab	6.19 a	37.64 b
Late vegetative phase (D2)	63.94 a	2,844.10 a	4.44 a	3.83 b	45.67 a
Generative phase (D3)	69.66 a	2,809.60 a	2.92 b	3.30 b	33.83 bc
LSD	10.38	511.66	1.42	1.76	7.49
Interaction of S and D					
S0D0	67.50 ab	2,873.52 a	5.41 bc	5.29 ab	27.50 cd
S0D1	71.16 ab	2,862.73 a	6.37 abc	5.51 ab	29.31 cd
S0D2	68.33 ab	2,949.22 a	5.71 bc	6.88 a	26.18 d
S0D3	36.83 d	1,773.07 c	9.03 a	6.46 a	30.30 cd
S1D0	55.83 bc	2,651.14 abc	9.23 a	6.57 a	46.40 ab
S1D1	39.16 cd	1,860.56 bc	7.79 ab	5.53 ab	36.23 bcd
S1D2	60.66 ab	2,794.28 a	7.66 ab	3.21 b	45.48 ab
S1D3	58.16 ab	2,510.59 abc	7.99 ab	5.15 ab	52.47 a
S2D0	73.00 ab	3,227.52 a	5.38 bc	3.14 b	39.07 bcd
S2D1	66.67 ab	2,910.20 a	3.94 c	4.17 ab	34.04 bcd
2D2	68.33 ab	2,700.10 ab	4.97 bc	2.93 b	39.22 bc
S2D3	74.00 a	2,818.57 a	3.78 c	2.79 b	26.87 cd
LSD	17.99	886.22	3.08	3.04	12.97

Note: Means followed by different letters indicated statistically significant differences at $LSD_{0.05}$.

Drought stress during the early vegetative phase significantly diminished the number of leaves and total leaf area (Table 3). Drought stress in the early vegetative phase significantly reduced root, leaf, and stem growth, whereas plants subjected to later drought phases exhibited greater resilience (Table 4 and Table 5). Meanwhile, specific leaf area (SLA) is one of the parameters used to indicate leaf thickness which is the result of the comparison of leaf area and leaf dry weight. Drought stress significantly reduces SLA, especially when it occurs during the generative phase. The proportion of dead plant organs markedly increased when rice plants experienced drought stress at any growth phase. Interestingly, straw mulching enabled the plant to develop a greater number of leaves and a larger leaf area, with a lower percentage of dead organs during drought at the generative phase. In addition, straw mulching consistently enhanced root length and biomass, suggesting it facilitates deeper rooting and supporting vegetative growth under drought stress.

Table 4. The root length, fresh weight, and dry weight of Inpago 10 subjected to drought stress and straw applications

Treatment	Root length (cm)	Root fresh weight (g)	Root dry weight (g)
Straw application (S)			
Without straw (S0)	43.12 a	65.64 a	23.59 a
Straw as organic matter (S1)	46.19 a	81.85 a	22.79 a
Straw as mulch (S2)	44.05 a	87.51 a	27.77 a
LSD	6.29	23.98	7.11
Drought stress (D)			
Unstressed (D0)	46.74 a	80.37 a	23.15 ab
Early vegetative phase (D1)	34.16 b	41.85 b	15.21 b
Late vegetative phase (D2)	47.94 a	95.66 a	30.57 a
Generative phase (D3)	48.97 a	94.66 a	29.95 a
LSD	7.26	27.69	8.21
Interaction of S and D			
S0D0	51.50 a	67.88 bcd	23.46 bcd
S0D1	45.00 ab	86.41 abc	22.07 bcd
S0D2	43.73 ab	86.80 abc	23.92 bcd
S0D3	25.66 c	28.94 d	12.22 d
S1D0	39.66 ab	43.86 cd	16.65 cd
S1D1	37.16 bc	53.05 bcd	16.76 cd
S1D2	45.50 ab	93.25 ab	30.49 abc
S1D3	48.00 ab	77.69 abc	20.20 bcd
S2D0	50.33 a	116.02 a	41.04 a
S2D1	49.83 a	72.08 abcd	28.21 abc
S2D2	52.10 a	118.63 a	32.26 ab
S2D3	45.00 ab	94.15 a	29.38 abc
LSD	12.58	47.96	14.22

Note: Means followed by different letters indicated statistically significant differences at $LSD_{0.05}$.

Table 5. Fresh weight and dry weight of leaf and stem at harvest in Inpago 10 subjected to drought stress and straw applications

Treatment	Leaf		Stem	
	Fresh weight (g)	Dry weight (g)	Fresh weight (g)	Dry weight (g)
Straw application (S)				
Without straw (S0)	26.64 a	7.78 ab	132.14 a	27.28 a
Straw as organic matter (S1)	22.46 a	6.53 b	124.69 a	27.05 a
Straw as mulch (S2)	28.61 a	8.50 a	139.17 a	29.44 a
LSD	6.16	1.91	23.76	4.66

Table 5 (continued)

Drought stress (D)				
Unstressed (D0)	28.03 ab	7.52 b	151.07 a	31.67 a
Early vegetative phase (D1)	18.69 c	5.64 b	107.55 b	22.34 b
Late vegetative phase (D2)	24.07 bc	7.24 b	128.43 ab	29.70 a
Generative phase (D3)	32.82 a	10.01 a	140.65 a	27.99 a
LSD	7.12	2.20	27.44	5.38
Interaction of S and D				
S0D0	27.66 abc	8.14 abcd	159.70 a	30.81 ab
S0D1	26.85 abc	6.46 bcd	138.39 a	28.36 abc
S0D2	29.56 ab	7.96 abcd	155.11 a	35.86 a
S0D3	19.06 bc	5.57 d	90.82 b	20.67 c
S1D0	17.1 c	5.19 d	117.73 ab	22.83 bc
S1D1	19.91 bc	6.16 cd	115.00 ab	23.53 bc
S1D2	26.18 abc	6.06 cd	131.84 ab	29.45 abc
S1D3	17.17 c	5.98 cd	115.91 ab	28.78 abc
S2D0	28.84 abc	9.66 abc	137.53 ab	30.87 ab
S2D1	33.66 a	11.34 a	146.18 a	28.19 abc
S2D2	28.68 abc	8.46 abcd	126.72 ab	28.26 abc
S2D3	36.1 a	10.21 ab	149.05 a	27.53 abc
LSD	12.33	3.82	47.52	9.32

Note: Means followed by different letters indicated statistically significant differences at $LSD_{0.05}$.

The total leaf area accounts for 97.65% of the variation in the number of productive tillers, as indicated by an R^2 value of 0.9765. This demonstrates a very strong relationship between total leaf area and the number of productive tillers, suggesting that total leaf area can effectively predict most of the variance in productive tiller numbers. Additionally, the positive correlation coefficient of 0.745 further supports this strong association (Fig. 5).

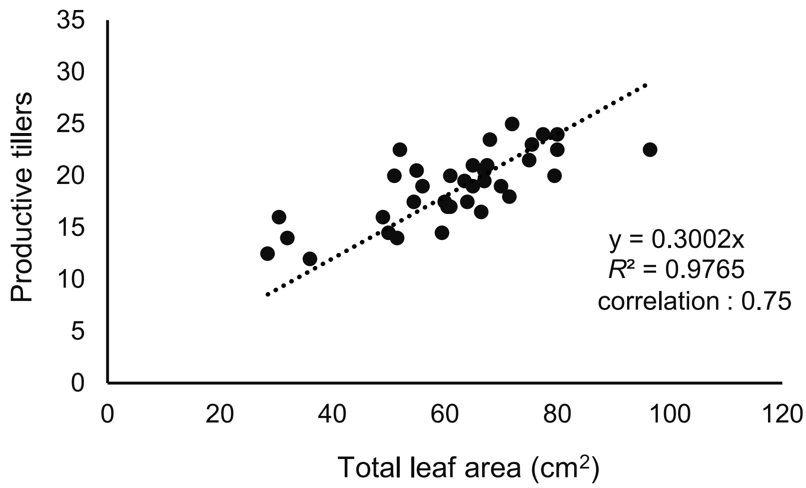

Figure 5. Regression and correlation total leaf area with productive tiller of rice inpago 10 under drought stress condition.

Exposure to drought conditions during the early and late phases of vegetative growth can delay the onset of flowering in plants. Drought stress during the vegetative phase causes plants to extend their vegetative development, requiring additional time to progress through growth phases. However, drought stress did not affect the productive tillers, as over 90% of tillers produced panicles. In this study, plants under unstressed and drought stress at generative phase treatment had the same flowering time (Table 6). The plants had already initiated flowering before experiencing drought stress. Straw application as mulch could alleviate the negative impact of drought on reproductive traits, particularly a higher number of productive tillers under drought stress conditions at vegetative and generative growth phases.

Table 6. Efflorescence and yield traits of Inpago 10 subjected to drought stress and straw applications

Treatment	Day of flowering	Number of tillers	Productive tiller	Penicle length (cm)
Straw application (S)				
Without straw (S0)	76.08 a	19.37 a	18.62 a	26.42 a
Straw as organic matter (S1)	74.83 a	20.45 a	18.95 a	27.04 a
Straw as mulch (S2)	75.33 a	20.87 a	19.25 a	27.6
LSD	1.91	3.43	2.63	1.26
Drought stress (D)				
Unstressed (D0)	71.16 c	21.88 a	20.05 ab	27.21 ab
Early vegetative phase (D1)	82.83 a	16.38 b	16.22 c	27.74 a
Late vegetative phase (D2)	75.5 b	20.72 a	18.83 bc	26.26 b
Generative phase (D3)	72.16 c	21.94 a	20.66 a	26.85 ab
LSD	2.2	3.97	3.04	1.46
Interaction of S and D				
S0D0	71.00 d	20.83 ab	19.50 a	26.50 ab
S0D1	71.00 d	23.00 a	20.00 a	27.25 ab
S0D2	71.50 cd	21.83 ab	20.66 a	27.89 ab
S0D3	82.50 a	13.83 c	13.66 b	27.04 ab
S1D0	82.50 a	20.00 abc	19.00 b	27.49 ab
S1D1	83.50 a	15.33 bc	16.00 ab	28.70 a
S1D2	76.00 b	20.67 abc	20.33 a	26.08 b
S1D3	75.16 bc	18.33 abc	16.00 b	25.91 b
S2D0	75.33 b	23.17 a	20.16 a	26.79 ab
S2D1	74.83 bc	22.17 ab	21.00 a	26.04 b
S2D2	70.66 b	20.50 abc	20.83 a	27.50 ab
S2D3	71.00 d	23.17 a	20.16 a	27.02 ab
LSD	3.82	6.87	5.27	2.53

Note: Means followed by different letters indicated statistically significant differences at $LSD_{0.05}$.

Grain weight and the percentage of spikelets filled per hill were diminished due to drought stress, with much of the negative impact being during the reproduction phase (Fig. 6). When straw was applied as mulch (S2), it managed to alleviate some of these effects and thereby produced higher grain weight and improved spikelet fertility than other treatments.

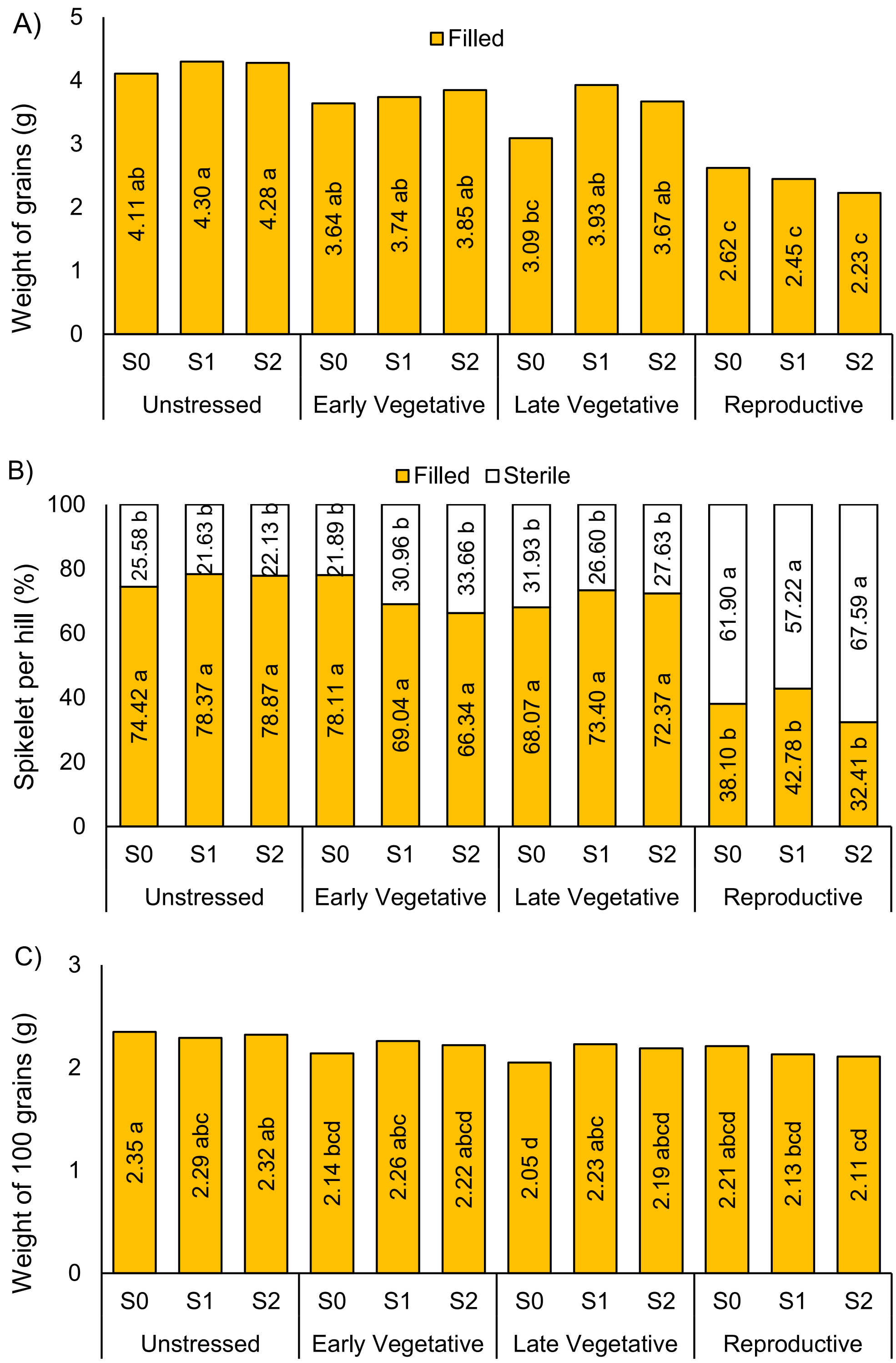

Figure 6. Interaction between straw application and drought stress at different growth phases for the weight of the total of grains (A), the percentage of filled and sterile spikelet (B), and the weight of 100 grains (C). Different letters indicate significant differences between pairs of treatments based on $LSD_{0.05}$.

DISCUSSION

Growth dynamic and yield of rice

The vegetative growth phase is a critical period for plants, as it lays the foundation for the overall development and productivity of crops. During this stage, the plant builds its essential structures, such as leaves, stems, and roots, which are vital for the subsequent reproductive phase. The vegetative growth phase requires sufficient water for cell elongation and division. Water deficiency leads to abnormal plant physiological and morphological processes, and inhibits cell division and elongation thereby inhibiting plant growth. Insufficient water availability leads to stunted growth, ultimately culminating in reduced plant biomass and overall development.

The results of this study further corroborate the adverse impacts of drought stress on rice during the vegetative stage. Our results indicate that drought significantly diminished critical growth metrics, such as leaf count, tiller number, as well as number, total area, and biomass of leaves. This growth reduction aligns with previous research, like Abbasi et al. (2013), which demonstrated that drought negatively affects key plant growth aspects, including plant height, tiller production, and leaf formation. The disruption of these growth parameters during the vegetative phase underscores the pivotal role of water availability for proper plant establishment.

The negative effects of drought stress extend beyond the vegetative stage, as it also hinders root development, compromising the plant's ability to acquire water and nutrients. This ultimately impairs the plant's capacity to accumulate biomass, leading to significant declines in yield and other yield-related parameters (Pirdashti et al., 2009; Hussein & Khursheed, 2014; Golabadi et al., 2015). In the current study, drought stress at generative phases resulted in reductions in key yield components, including a reduction number of tillers (25.13%), productive tillers (19.19%), total filled spikelet (62.45%), and weight 100 grain yield less than unstressed plant. These findings align with previous research, indicating that drought stress during the reproductive phase can severely impact carbohydrate synthesis, assimilation, and the translocation of nutrients from the leaves to the grain, ultimately reducing grain weight and overall yield potential (Ji et al., 2012). Additionally, plants exposed to drought stress during the reproductive phase exhibited a notable decrease in filled spikelets, further highlighting the critical impact of drought on rice productivity (Hossain et al., 2016).

Effect of straw mulching on soil moisture and plant growth

Drought stress is influenced by a complex interplay of factors beyond just the direct availability of water. Microclimate conditions, including temperature, humidity, sunlight, wind, and the surrounding vegetation, collectively contribute to the rate of water loss from the plant through processes such as transpiration and evaporation. When environmental factors like high temperatures, low humidity, and strong winds are present, the rates of transpiration and evaporation can increase significantly, leading to a faster depletion of soil moisture.

In several previous studies, rice straw mulching reported the potential to maintain soil moisture. Mulching is recognized for improving soil moisture retention, reducing temperature fluctuations, and preventing soil erosion. Previous research has demonstrated that rice straw mulching can significantly increase soil water availability and lower soil temperatures, especially at depths of 0–30 cm (Su et al., 2014). This creates an environment more conducive to plant growth, especially during drought periods. However, the effectiveness of straw mulching varies across different conditions. It is influenced by environmental and climatic factors, soil moisture levels, and the rate of straw decomposition (IRRI, 2002; Abo-Ogiala & Khalafallah, 2019). While straw mulch is highly effective under mild to moderate drought, its capacity to retain moisture diminishes under severe drought. In this study, although straw mulching consistently showed higher soil moisture, it was insufficient to maintain adequate moisture when plants were exposed to more severe drought stress.

Although straw mulching only might be most effective in less extreme drought conditions, the application of straw mulching is still beneficial in all drought scenarios. The straw will be decomposed over time and provide organic material that can enhance plant growth, particularly during the later stages of the vegetative and reproductive phases. However, the decomposition of straw is a gradual process that is heavily influenced by environmental factors such as temperature, rainfall, and microbial activity. While straw decomposition initially occurs at a faster rate under favorable conditions of temperature and moisture, the process slows down over time. As reported by Zribi et al. (2015), the effectiveness of straw mulch in reducing evaporation and maintaining soil moisture decreases as the mulch breaks down.

The decomposition of straw can supply essential plant nutrients like nitrogen, phosphorus, and potassium, which support optimal growth and development (Yan et al., 2018). These nutrients can be available in the soil for up to three years (Yan et al., 2019). This makes straw mulching not only a short-term solution for moisture retention but also a long-term strategy for improving soil fertility. However, the rate and effectiveness of nutrient release depend on the duration and conditions of decomposition. As the straw breaks down, it improves soil structure, enhances nutrient cycling, and supports soil organisms that contribute to long-term soil health. Therefore, returning straw residue to the soil following the initial growing season may be the most effective approach to maximize the benefits of straw mulching for improving soil quality. This strategy aids in replenishing vital organic matter, which is crucial for maintaining soil structure and fertility.

Morpho-physiological adaptations of rice under drought stress

The morphological responses of rice to drought stress include changes in both the aboveground shoot system and the belowground root system. Rijal et al. (2020) identified the reduction in shoot length, along with changes in pubescence, senescence, leaf thickness, size, shape, and waxiness, as key responses to drought stress. The leaf, recognized as the most sensitive aboveground plant organ, serves as a crucial indicator for analyzing plant growth and behavior during drought (Widuri et al., 2020). According to Abbasi et al. (2013), plants use leaf area reduction as an adaptive strategy to deal with drought conditions. A frequent reaction to drought circumstances is a reduction in leaf surface area in a variety of crop species, such as rice (Ria et al., 2020), maize (Nelissen et al., 2018), and wheat and chili peppers (Rijal et al., 2020). In the present study, drought stress significantly reduced the number of leaves and total leaf area. This reduction is attributed to the smaller size of newly formed leaves, inhibited expansion of emerging foliage, and an increased rate of leaf death. In order to mitigate the effects of drought, plants exhibit morphological and physiological adaptations, such as leaf characteristics, size of stomata, water use efficiency, and root architecture (Lonbani & Arzani, 2011). Reducing the number and area of leaves mitigates water loss through transpiration.

Furthermore, a rice plant's dry weight and root length are good predictors of how it will react to drought stress (Beena et al., 2021). In drought conditions, deeper roots were thought to be more efficient in preserving production. The plant's growth and productivity are determined by the root system's ability to absorb water and nutrients. Under drought stress conditions, the growth of fine roots with a high specific root length increases the surface area in contact with soil moisture, improving the plant's hydraulic conductivity and facilitating the uptake of nutrients and water (Kim et al., 2020; Kartika et al., 2021b). Unfortunately, the roots in this study failed to elongate under severe drought stress conditions.

Plants employ leaf rolling as a defensive mechanism to reduce the leaf's surface area under drought stress. This physiological reaction reduces transpiration and acts as a method to preserve water (Pandey & Shukla, 2015; Shahzad et al., 2016). The results of this study demonstrated a strong association between soil moisture and leaf rolling score, with more severe drought stress leading to higher leaf rolling scores. However, the variation degrees of tolerance and reaction depends on the genotype, development phase, and drought timing (Pandey et al., 2016). Research on rice under drought stress has made extensive use of leaf rolling scores (LRS). Plants under drought stress will have quickly rolling leaves, which will reduce their leaf area and the rate at which transpiration occurs.

As a physiological adaptation to drought, plants enhance the production and accumulation of free amino acids, with proline being particularly abundant (Zadehbagheri et al., 2014). This study found that drought stress increased proline levels more than tenfold compared to unstressed conditions. Under drought stress, particularly in the absence of straw, plants in both vegetative and generative phases exhibited the highest proline content. Saeedipour (2013) reported that proline content accumulated faster and in higher proportions in drought tolerant genotypes than in sensitive counterparts under drought-stress conditions. This argument is in line with the result of a previous study that Inpago 10 shows strong performances under drought stress conditions (Ria et al., 2020), suggesting its value in breeding for drought tolerance. Proline, along with glucose, fructose, and branched-chain amino acids, serves as an important storage compound, accumulating primarily in the meristematic regions where cell division occurs (Palareti et al., 2016). The enzymes involved in proline synthesis exhibit elevated activity, driven by the increased energy demands of respiration during drought stress (Rady et al., 2019). This accumulation of proline and other compatible solutes helps maintain cellular osmotic balance and protects essential cellular structures and functions, enabling the plant to better withstand the adverse effects of drought. Proline is easily metabolized and recovered in plant tissues (Singh et al., 2021). After recovery from drought stress, proline levels returned to their typical values.

However, the weak positive and non-significant correlation observed between proline content and stressed yield under controlled conditions suggests that, although proline plays an important role in osmoprotection, it may not be a reliable indicator of yield under drought stress. Furthermore, genes encoding desiccation tolerance may not necessarily enhance yield in agricultural drought conditions (Mwadzingeni et al., 2016).

CONCLUSIONS

The application of straw as mulch and organic matter offers limited benefits for mitigating severe drought stress in rice. Straw application is unable to maintain soil moisture levels in extreme drought conditions. Although straw mulch can reduce water loss and moderate drought symptoms, it only partially offsets the negative impacts on growth and yields when soil moisture falls below 10%. However, this study was conducted in controlled conditions and may not fully reflect field variability. Straw mulching remains a cost-effective option for mild drought, but in areas prone to severe drought, combining straw with additional drought mitigation methods may improve crop resilience.

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