

Unraveling the Tolerance of Rice Varieties to Single and Dual Salinity and Waterlogging Stresses: Impacts on Agronomic Traits and Yield Performance

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Abstract

Dual salinity and waterlogging alter metabolisms activity in rice, leading to reduced growth and yield. The use of tolerant varieties offers a promising strategy to enhance plant resistance, improving agronomic traits and yield performance. The main objective of this study is to reveal and evaluate rice tolerance to single and dual salinity and waterlogging stress and to assess their effects on agronomic traits and yield performance. A split-plot design was used with stress conditions as the main factor, consisting of control (no salinity or waterlogging), salinity stress, waterlogging stress, and dual salinity and waterlogging stress. Seven rice varieties were tested as subplots, including Inpari 30 Ciherang Sub 1, Inpari 34, Inpara 8, Inpari 79 Unsoed Agritan, Maros, Mawar, and IR 64. All stress conditions significantly reduced leaf area. Salinity and dual salinity-waterlogging stresses induced Na⁺ accumulation in the leaves and reduced K⁺ concentrations, whereas waterlogging and dual salinity-waterlogging stresses accelerated flowering age. Under dual salinity and waterlogging, rice varieties such as Inpari 30 Ciherang Sub 1, Inpari 34, Inpara 8, and IR 64 exhibited higher proline content than other varieties. All 3 stress treatments resulted in a reduced percentage of filled grain and lower grain yield in Inpari 30 Ciherang Sub 1, Inpari 34, and IR 64, whereas Inpari 79 Unsoed Agritan showed more stable performance across stress conditions, despite producing the lowest grain yield among the varieties tested. Based on the YSI and PCA analysis, Inpari 79 Unsoed Agritan was identified as the most stable variety under stress conditions, although its yield remained low. In contrast, Inpara 8, Maros, Mawar, and IR 64 recorded higher yields than the other varieties.

Keywords: Agronomic responses, Dual stress, Rice variety, Salinity, Susceptible, Tolerant, Yield stability index

Introduction

Salinity and waterlogging are direct consequences of climate change, particularly the rising sea level [1]. This phenomenon causes seawater intrusion to extend into agricultural lands. Data reveals that around 41% - 50% of coastal agricultural lands become unsuitable for crop cultivation due to increase salinity and waterlogging/flooding [2]. The negative impact on rice production by disrupting plant metabolism activity and reducing yields, ultimately resulting in crop failure.

Both salinity and waterlogging are well-established as limiting factors in crop production. According to the FAO, soil is classified as saline when its electrical conductivity (EC) exceeds 4 dS m⁻¹ [3].

Elevated salt concentrations hinder plants' ability to absorb water and essential minerals, causing ionic and osmotic stress, and nutrient imbalance [4]. These stresses can reduce cell turgor, low photosynthesis rate and chlorophyll degradation, as well as a decrease in leaf area, plant biomass, and crop yield [5]. Previous studies reported that salinity stress of 4 - 10 dS m⁻¹ increased Na content, proline content, and decreased K content in shoots and roots, along with an increase in the Na/K ratio [6,7]. Application of NaCl at concentrations ranging from 25 to 100 mM resulted in decreases in shoot and root fresh weight, shoot and root dry weight, plant height, and root length [8]. Salinity stress in the range of 6 - 8 dS m⁻¹ adversely affected

not only vegetative growth but also yield performance, as evidenced by reductions of 44.01% in the number of productive tillers, 29.12% in grains per panicle, 39.30% in 1,000-grain weight, and 60.61% in grain yield, compared to the control [9].

Furthermore, waterlogging reduces O₂ availability in the soil, leading to hypoxic or anoxic conditions and affects the root system and overall plant metabolism. This condition causes a low assimilate produce by inhibiting various physiological processes [10]. Waterlogging disrupts plant growth by reducing biomass and crop growth rate, while also inducing shoot elongation. Moreover, it leads to declines in the number of productive tillers, spikelets, and grain yield up to 49.60% [11]. According to Yu *et al.* [12], when waterlogging occurs during the jointing stage, grain yield can decrease by as much as 17.07%. Furthermore, different genotypes respond differently to waterlogging stress, with yield reductions ranging from 28.93% to 45.86%.

The use of high-yielding and salt-waterlogging tolerant rice varieties serves as a strategy to mitigate the adverse effects of these stresses by utilizing their defense mechanisms, which enhance physiological and biochemical processes. Rice varieties with the Sub 1 gene insertion could improve plant resistance to waterlogging stress, promoting the development of the root system, and increasing chlorophyll content [13]. Inpari 30 Ciherang Sub 1 rice variety has tolerance to 14-days single submergence stress with a harvest yield up to 6.29 tons ha⁻¹, compared to Inpara 3 and Inpara 5 [14]. Meanwhile, Inpari 34 is tolerant to single salinity up to an EC value of 4.18 dS m⁻¹ with a harvest yield of 2.85 tons ha⁻¹ [15]. Conversely, susceptible rice varieties to dual salinity and waterlogging stress cause a decline in various metabolism functions. Gautam *et al.* [16] reported that IR 64 rice variety is susceptible to abiotic stress and causes a decrease in photosynthesis rate, biomass production, chlorophyll degradation, and low harvest yield. Thus, selecting tolerant rice varieties is crucial under dual-stress to ensure optimal growth and harvest yield.

Based on the information presented previously, the novelty of our study lies in identifying tolerant rice varieties to single and dual-stress conditions. Many studies explored physiological, agronomic,

biochemical, anatomical, metabolomic, and other responses of rice plants to single stressors. Nevertheless, the study on the effects of dual-stress is limited. This gap underscores the need for further investigation, particularly in exposure to dual salinity and waterlogging stress. The main objective of this study is to reveal and investigate the rice plant tolerance to single and dual salinity and waterlogging stress and to assess their effects on agronomic traits and yield performance.

Materials and methods

Study area

The study was conducted at the Kebun Tridharma, Faculty of Agriculture, Universitas Gadjah Mada, located at the coordinates 7°48'16.1"S 110°24'44.9"E, from May to August 2024. A pot experiment was used in this study, utilizing soil as the planting medium, without the addition of organic matter, sourced from rice fields in the coastal agricultural land of Karangjaladri, Pangandaran Regency (7°41'45.4"S 108°31'02.1"E). Preliminary observations using the EC indicator revealed that the soil is likely saline, with an EC value of approximately 4.93 dS m⁻¹.

Experimental setup and seed nursery

The study used a split-plot design, with stress conditions as the main plot, including no salinity or waterlogging (control), salinity stress, waterlogging stress, and dual salinity and waterlogging stress. Rice varieties were tested as subplots, comprising Inpari 30 Ciherang Sub 1, Inpari 34, Inpara 8, Inpari 79 Unsoed Agritan, Maros, Mawar, and IR 64. There were 3 replications. Each rice variety was sowed in high-salinity (with an EC value of 4.93 dS m⁻¹) in ultisol soil for 28 days, like the soil used in the primary experiment. After 28 days, seedling from each variety was transplanted into a polybag and arranged according to the experimental design.

All treated plant pots are placed in a dead-end trench, with the size of 10 m in length, 1 m in width, and 0.8 m in depth. The trench bottom was covered with UV plastic to prevent water loss. Polybags are set in the hole according to the treatment. In the control and salinity treatments, water levels were maintained at the soil surface (simulating saturated conditions) at

plant height of 25 cm. The control treatment involved adding 3,000 L of water, while in the salinity treatment, as much as 3,000 L of water and 3 kg of NaCl per hole. For the waterlogging involved adding 8,000 L of water, and dual salinity and waterlogging treatments, 8,000 L of water and 8 kg of NaCl per hole. The salinity level, indicated by an EC value of approximately 4.93 dS m^{-1} , was carefully maintained throughout the growth and the rice plants in both the salinity and dual salinity and waterlogging treatments. Weekly measurements of potential of hydrogen (pH) and redox potential (Eh) were conducted as supporting observations. pH was assessed under all environmental conditions, while Eh was recorded only under waterlogging and dual salinity and waterlogging conditions.

The agronomic variables

Leaf area was measured at the early heading stage by removing all leaves from a single clump, placing them on a leaf area meter, and calculating the data using winDIAS 3 (version 3.2.1) application. The number of tillers was counted manually per clump and plant height with a ruler during the early heading stage. Assimilate partitioning was assessed by measuring the shoot and root biomass collected destructively during the early heading stage. The shoots and roots were separated, dried in a Memmert Type UN 260 oven at $80 \text{ }^\circ\text{C}$ for 48 h, and weighed using a digital scale with $500 \text{ g} \times 0.01$ accuracy. The net assimilation rate (NAR) was determined using leaf area and plant biomass with data collected when the plants were 4 and 8 WAP. The formula of NAR in Eq. (1), following [17].

$$\text{Net assimilation rate (g dm}^{-2}\text{week}^{-1}) = \frac{w_2 - w_1}{t_2 - t_1} \times \frac{\ln La_2 - \ln La_1}{La_2 - La_1} \quad (1)$$

Where W_2 represent plant biomass at 8 WAP and W_1 plant biomass at 4 WAP, t_2 represent time 8 WAP and t_1 time 4 WAP, La_2 represent leaf area at 8 WAP and La_1 leaf area at 4 WAP.

K^+ , Na^+ , and proline content determination in the leaves

The concentration of K^+ and Na^+ were determined following modified method by Trivedi, using the $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ digestion technique [18], while

proline content was determined using the method of Bates by extracting fresh leaves [19].

Yield performance variables

The flowering age of the rice plants was determined when 80% of plants in a treatment exhibited panicles, marking the transition into the generative stage. Pollen viability was determined using a modified staining technique from Skrzypkowski *et al.* [20]. Pollen samples were collected from panicles in the morning and placed on microscope slides. Acetocarmine dripped to stain viable pollen pink to red, while dead pollen remained colorless and transparent. Observation using a Yazumi light microscope and an OptiLab SIGMA. The following harvest, manually count the number of filled grain per panicle. Calculation of the percentage of filled grains using Eq. (2). The grain weight for each treatment is converted to tons per hectare to assess the overall grain yield. The yield stability index (YSI) evaluates the rice tolerance to dual-stress conditions based on the method by Gitore [21] and calculated using Eq. (3).

$$\text{Percentage of filled grain (\%)} = \frac{\text{Weight of filled grain per clump (g)}}{\text{Total weight of grain per clump (g)}} \times 100 \quad (2)$$

$$\text{Yield stability index} = \frac{\text{Grain yield of each variety under stress conditions}}{\text{Grain yield of each variety under normal conditions}} \quad (3)$$

Statistical analysis

The data were analyzed using an F-test, followed by Duncan's multiple range test ($\alpha = 5\%$). To classify the stability of rice varieties under stress conditions based on grain yield, yield component, and YSI using principal component analysis (PCA). Data processing was carried out using Statistical Tools for Agricultural Research (STAR) version 2.0.1 and PCA analysis using SPSS 27.0, following the method described by Sruthi [22].

Results and discussion

Treatment-induced environmental conditions

Environmental parameters measured in the soil included pH, Eh, the concentration of Na and K, and EC. Based on the observations, the soil used as the growing medium originated from the coastal land of Pangandaran, with an EC value of 4.93 dS m^{-1} , which remained stable throughout the experiment. The Na

content was $21.30 \text{ cmol kg}^{-1}$ of soil, categorized as very high, while the K content was $2.56 \text{ cmol kg}^{-1}$ of soil, also classified as very high. Although both were in the very high category, the Na content was significantly higher than that of K.

Under normal conditions, soil pH fluctuated throughout the planting period. From the initial stage until the plants reached 5 weeks after planting (WAP), the soil pH ranged from 7.8 to 8.0, falling within the alkaline category. However, as the plants reached 6 WAP, the pH decreased to a neutral range between 7.2 and 7.5. Under salinity conditions, the soil pH during the early growth stage (up to 4 WAP) ranged from 7.6 to 7.8, classifying it as alkaline. From 6 WAP to harvest, the pH shifted to a neutral, range between 7.1 and 7.5. Consistent with control and salinity treatments, soil under waterlogged conditions also exhibited pH fluctuations, although with higher values than the other treatments. During the entire growth period, the pH ranged from 7.4 to 8.6, indicating alkaline conditions. Under dual salinity and waterlogging conditions, soil pH remained predominantly alkaline throughout the planting period, ranging from 7.3 to 8.6. The soil under all stress conditions, including waterlogging stress, was classified as alkaline due to its origin from saline soil, with an EC value of 4.93 dS m^{-1} , previously influenced by tidal seawater intrusion. Continuous waterlogging leads to an increase in soil pH, rendering the soil alkaline [23]. This is attributed to anaerobic conditions that promote the dissolution of salts and the release of basic cations such as calcium and magnesium, ultimately leading to a rise in pH toward alkalinity.

Redox potential (Eh) is a key indicator of a soil's capacity to accept or donate electrons, which is closely associated with oxidation-reduction (redox) reactions in the soil environment. Eh measurements are particularly useful for evaluating soil aeration status, microbial activity, and the bioavailability of certain nutrients and elements [24]. Observational data indicate that Eh values ranged from -45 to 49 mV under waterlogging conditions and -30 to 39 mV under dual salinity and waterlogging conditions. Under waterlogging and dual salinity and waterlogging, Eh values fell within the

reduced soil range of -100 to $+100 \text{ mV}$ [25], indicating anaerobic conditions with limited oxygen availability. Within this range, the solubility and mobility of elements such as iron (Fe), manganese (Mn), and arsenic (As) are significantly affected. Moreover, microbial activity is highly responsive to redox dynamics, and facultative anaerobes often dominate under these conditions, promoting key biogeochemical processes such as denitrification and methanogenesis [26].

Agronomic traits

Salinity and waterlogging stress can hinder the growth of plant parts like height, leaf size, biomass, and root function, ultimately reducing rice production. Additionally, salinity stress causes ion toxicity, primarily due to the accumulation of Na^+ , which disrupts cellular processes [27]. Leaf Na^+ concentration increased under salinity and dual salinity- waterlogging stresses, whereas it remained relatively low under waterlogging stress. The highest leaf Na^+ concentration under salinity stress were observed in the Inpari 30 Ciherang Sub 1, Inpari 34, Inpara 8, Inpari 79 Unsoed Agritan, Maros, and Mawar, ranging from 66.86 to $83.30 \text{ mmol g}^{-1}$. Under dual salinity and waterlogging stress, Inpari 30 Ciherang Sub 1 and IR 64 accumulated the highest leaf Na^+ concentrations, ranging from 63.13 to $65.37 \text{ mmol g}^{-1}$ (**Figure 1**).

These findings suggest that plants subjected to salinity stress experience physiological disruptions that affect ionic balance and cellular metabolism [28]. Salt-tolerant rice varieties exhibit lower leaf Na^+ concentrations, whereas salt-sensitive varieties tend to accumulate higher Na^+ concentrations. Excess Na^+ in the leaves competes with K^+ and Ca^{2+} for absorption and transport within the plant, thereby reducing the concentration of these essential nutrients in various tissues. This imbalance leads to nutrient deficiencies, decrease photosynthetic efficiency, causes tissue damage, and inhibits rice growth. Such effects are mediated through mechanisms including chlorophyll degradation, oxidative stress, electrolyte leakage, and disruption of ion homeostasis [8].

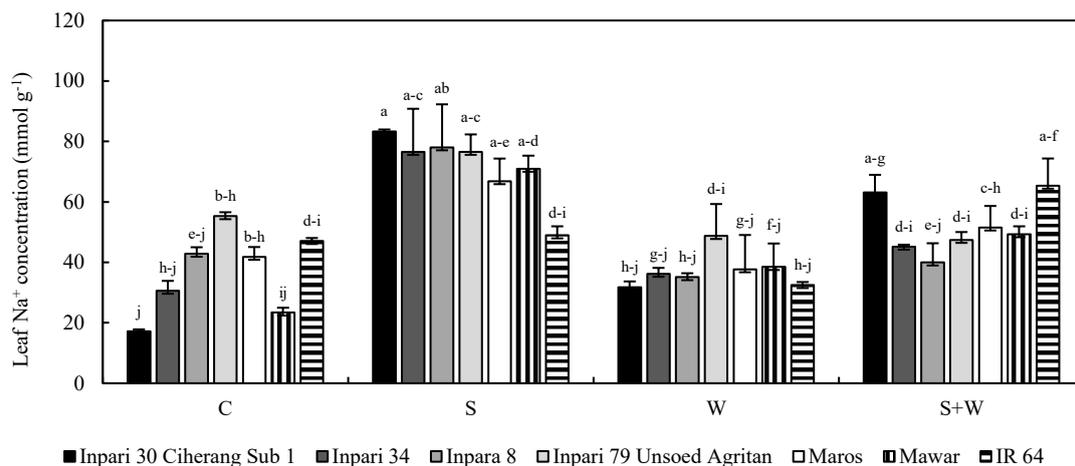


Figure 1 Interaction between stress conditions and rice varieties on leaf Na⁺ concentration at 8 WAP. Remarks: Bars represent mean values of 3 replicates with error bars showing the standard error (SE). Different letters represent significant differences in the interaction between stress conditions and rice varieties based on DMRT at α = 5%; C (control); S (salinity); W (waterlogging); S + W (dual salinity and waterlogging).

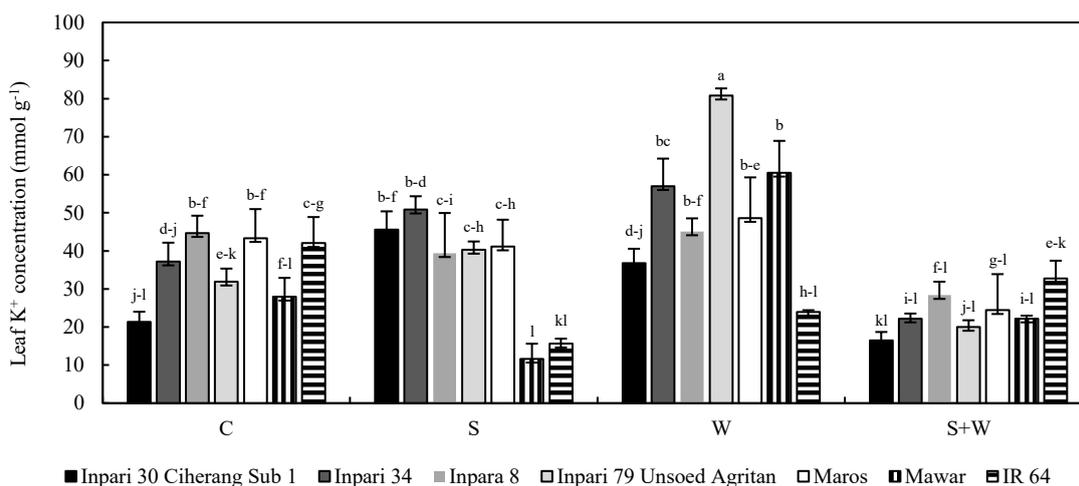


Figure 2 Interaction between stress conditions and rice varieties on leaf K⁺ concentration at 8 WAP. Remarks: Bars represent mean values of 3 replicates with error bars showing the standard error (SE). Different letters represent significant differences in the interaction between stress conditions and rice varieties based on DMRT at α = 5%; C (control); S (salinity); W (waterlogging); S + W (dual salinity and waterlogging).

K⁺ ions are vital for plants to cope with salinity stress by maintaining ion homeostasis, enhancing antioxidant defences, regulating stomatal function, and interacting with other nutrients and signaling pathways [29]. As shown in **Figure 2**, leaf K⁺ concentrations were higher under control and waterlogging conditions compared to salinity and dual salinity and waterlogging stress. However, under salinity and dual salinity and waterlogging stress, leaf K⁺ concentrations tended to be lower than Na⁺ concentrations. Under waterlogging, Inpari 34, Inpara 8, Inpari 79 Unsoed Agritan, and

Mawar showed the highest leaf K⁺ concentrations, whereas under control conditions, Inpari 34 dan Maros exhibited the highest concentrations. Dual salinity and waterlogging stress markedly reduced leaf K⁺ concentrations across all varieties. Under waterlogging, tolerant rice varieties were able to maintain higher leaf K⁺ concentrations, likely due to their favorable root morphology. Varieties with longer roots and well-developed root systems can sustain greater K⁺ availability, supporting survival under waterlogged conditions [30]. In contrast, dual salinity and

waterlogging stress significantly disrupts K^+ homeostasis and promotes Na^+ accumulation in rice leaves, leading to severe physiological and growth impairments. Adaptive mechanisms and genetic tolerance play crucial roles in mitigating these adverse effects [31].

These findings suggest that K^+ compete with Na^+ for uptake and distribution within the plants, as reflected by the elevated Na^+/K^+ ratio observed under salinity and dual salinity and waterlogging conditions. The study results indicate that stress conditions and rice varieties had no significant effect on the Na/K ratio. However, the Na/K ratio was 1.21 under salinity stress and 0.83 under combined salinity and waterlogging stress. These values were 69.42% and

55.42% higher, respectively, than those of rice grown under normal conditions (**Table 1**). The accumulation of Na^+ ions in leaves strongly suggests a malfunction in the Na^+ exclusion system or selective ion transport mechanisms in the roots. Effective management of Na^+ through exclusion, compartmentalization, and competitive interactions with K^+ is essential for plant health under saline conditions [32]. In susceptible varieties, high Na^+ accumulation leads to chloroplast damage, impaired photosynthesis, and leaf necrosis, which can inhibit growth and ultimately cause plant death. In contrast, tolerant rice varieties typically possess mechanisms to limit Na^+ transport to the leaves, either by reducing uptake at the root level or by compartmentalizing Na^+ into vacuoles [33].

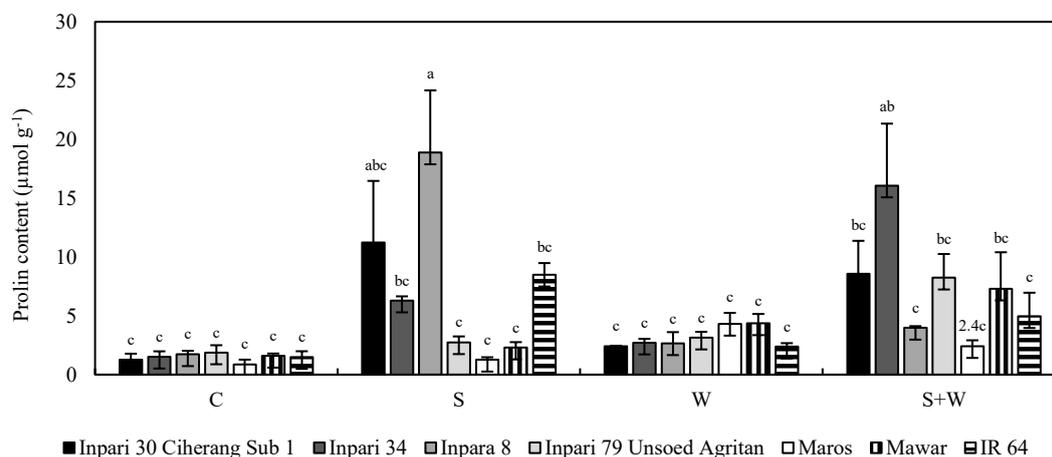


Figure 3 Interaction among stress conditions and rice variety on proline content. Remarks: Bars represent mean values of 3 replicates with error bars showing the standard error (SE). Different letters represent significant differences in the interaction between stress conditions and rice varieties based on DMRT at $\alpha = 5\%$; C (control); S (salinity); W (waterlogging); S + W (dual salinity and waterlogging).

Proline functions as a biochemical indicator in plants under salinity stress, functioning as part of a complex defense mechanism. It plays multiple roles, including acting as an osmoprotectant, stabilizing membrane structures, scavenging ROS, serving as a reservoir for energy and nitrogen, and as a molecular signal that regulates the expression of stress-responsive genes [34]. In this study, rice plants subjected to salinity and dual salinity and waterlogging stress exhibited higher proline concentrations than those under control and waterlogging conditions. Specifically, the rice varieties Inpara 8 and Inpari 30 Ciherang Sub 1 under salinity stress, and Inpari 34 under dual salinity and

waterlogging stress, showed elevated proline accumulation. In contrast, Inpari 79 Unsoed Agritan, Mawar, and Maros under salinity stress, along with Inpara 8, Mawar, and IR 64 under dual salinity and waterlogging, exhibited the lowest proline concentrations (**Figure 3**). It is presumed that the rice varieties Inpari 30 Ciherang Sub 1, Inpari 34, and Inpara 8 emitted signals indicating that the plants were under salinity stress.

While high proline concentration is a widespread physiological response to various abiotic stresses, including salinity, its role in salinity tolerance is not straightforward. It may reflect a general stress response

rather than a specific adaptation to salinity. In tolerant rice varieties, elevated proline concentrations are crucial for maintaining osmotic balance, preserving cellular integrity, and reduce ROS-induced damage, thereby enhancing the plant's ability to withstand various abiotic stresses [35]. Conversely, in susceptible

rice varieties, increased proline concentration often functions as a stress signal associated with physiological damage, manifesting as chlorosis, necrosis, and inhibited growth. This accumulation is linked to oxidative stress and cellular damage, highlighting the complex role of proline in salinity

Table 1 Response of leaf area, net assimilation rate, and tiller numbers of rice under single and combined stress conditions.

Treatments	Leaf area at the early heading stage (cm ²)	Net assimilation rate (g dm ⁻² week ⁻¹)	Number of tillers at the early heading stage	Na ⁺ /K ⁺ ratio in leaf
Stress conditions				
C	350.50 ^a ± 2.99	1.66 ^a ± 0.17	8.56 ^a ± 0.25	0.37 ^a ± 0.08
S	222.60 ^b ± 3.93	1.53 ^a ± 0.56	7.52 ^a ± 0.36	1.21 ^a ± 0.18
W	285.70 ^{ab} ± 3.07	1.15 ^a ± 0.17	8.13 ^a ± 0.21	0.29 ^a ± 0.12
S + W	241.90 ^b ± 2.80	0.78 ^a ± 0.08	7.56 ^a ± 0.22	0.83 ^a ± 0.18
Varieties				
Inpari 30 Cihorang Sub 1	197.90 ^q ± 5.32	1.90 ^p ± 0.99	8.26 ^p ± 0.39	0.66 ^p ± 0.44
Inpari 34	341.90 ^p ± 3.64	1.36 ^p ± 0.38	8.17 ^p ± 0.30	0.44 ^p ± 0.19
Inpara 8	294.30 ^{pq} ± 3.43	1.44 ^p ± 0.31	7.81 ^p ± 0.42	0.47 ^p ± 0.18
Inpari 79 Unsoed Agritan	238.70 ^q ± 3.62	1.02 ^p ± 0.38	8.19 ^p ± 0.28	0.60 ^p ± 0.07
Maros	317.60 ^p ± 4.25	1.19 ^p ± 0.23	7.53 ^p ± 0.19	0.53 ^p ± 0.24
Mawar	312.30 ^p ± 5.42	1.07 ^p ± 0.13	7.19 ^p ± 0.48	1.38 ^p ± 0.23
IR 64	223.40 ^q ± 4.18	0.97 ^p ± 0.18	8.43 ^p ± 0.48	0.67 ^p ± 0.35
ANOVA				
Stress conditions (S)	*	ns	ns	ns
Varieties (V)	**	ns	ns	ns
S×V	ns	ns	ns	ns

Remarks: Values are presented as mean ± standard error (SE) of 3 replicates. Means in the same column marked with the same letter are not significantly difference based on DMRT ($\alpha = 5\%$); C (control); S (salinity); W (waterlogging); SW (dual salinity and waterlogging).

Leaves, as key organs in plants are essential for producing nutrients through photosynthesis, transpiration, and gas exchange, which are crucial for plant growth and development [37]. The result showed that rice grown under salinity and combined salinity and waterlogging developed narrower leaves (**Table 1**). Osmotic stress alters the water movement across the cell membrane, causing reduced water uptake. As a result, the roots face difficulty absorbing water, leading to a decline in leaf water potential and transpiration rate. Additionally, high concentration of Na⁺ ions in the soil create ionic stress, resulting in nutrient imbalances [27]. Low water and mineral absorption impair the production of assimilates in plants, subsequently

inhibiting leaf area growth and resulting in narrower leaves.

Additionally, when both stresses occur, waterlogging causes low light interception, affects the low rate of photosynthesis and reduces chlorophyll content. This also impacts the production and distribution of assimilates to the plant organs [38]. However, based on the F-test, stress conditions had no significant effect on the net assimilation rate and number of tiller (**Table 1**). A decrease in net assimilation rate did not follow the reduction in leaf area, possibly due to several factors, including the remaining leaves having more efficient photosynthetic capacity, greater thickness, and higher chlorophyll

content. In addition, the plant prioritized assimilate translocation to root and stem organs rather than to the leaves to survive under stress conditions [39]. **Table 1** indicates that tiller growth in rice exposed to single and combined stress tends to be lower. Osmotic and ionic stress reduces potassium concentrations in the soil, further suppressing tiller growth [40]. While combined stress affects root growth and increases oxidative stress, it does not significantly reduce tiller numbers [41].

The rice varieties tested exhibit distinct characteristics, as evidenced by variations in leaf area (**Table 1**). Some varieties, including Maros, Mawar, dan Inpari 34, have wider leaves than Inpari 30 Ciherang Sub 1, Inpari 79 Unsoed Agritan, dan IR 64. The leaf area is affected by environmental factors and genetic traits specific to each variety. Tolerant rice varieties to salinity and waterlogging stress tends to increase leaf area, as they can still generate assimilates to support the growth of plant organs. The Inpari 34 rice variety is more tolerant to salinity and increased leaf area than susceptible varieties. Similarly, rice varieties tolerant to waterlogging and possessing the Sub 1 gene tend to maintain more stable growth [42]. In contrast, susceptible rice varieties accumulate oxidative stress, leading to cellular damage and leaf narrowing. Green leaves, rich in chlorophyll, capture more sunlight, which enhances the photosynthesis rate, resulting in increased assimilate production, then translocate to the plant's sink [43].

Based on **Table 1**, the net assimilation rate revealed no significant differences among the 7 rice varieties tested, a finding also observed in the number of tillers. Single and dual stress impair the plant ability to develop optimally, even in susceptible varieties. Tolerant and susceptible rice varieties can exchange carbon dioxide, resulting in relatively stable biomass across various genotypes, even under abiotic stress [44]. This condition affects the growth of other plant organs, including tillers and plant height.

Environmental conditions influence the assimilates translocation across various plant organs. Under normal conditions, the assimilates translocation to both root and shoot organs is generally predominant in most varieties (**Figure 4(a)**). However, Mawar and Inpari 30 Ciherang Sub 1 rice varieties have a higher assimilates translocation is observed in the grain, with comparatively lower distribution to the roots and

shoots. Under normal conditions, rice plants efficiently store assimilates from photosynthesis to support the growth of vegetative organs, ultimately contributing to increase grain yields [45]. However, under salinity or waterlogging, the vegetative growth is hindered, leading to a decline in grain yields. Abiotic stress affects gene expression, and rice-tolerant varieties will enhance physiological activity, while rice-susceptible varieties lead to a reduce in grain yields [46].

Under salinity stress, tolerant rice varieties typically exhibit a predominant translocation of assimilates to the grain compared to susceptible varieties (**Figure 4(b)**). In the rice varieties of Inpari 30 Ciherang Sub 1, Inpari 34, Inpara 8, and Inpari 79 Unsoed Agritan assimilates are primarily directed to the vegetative organs, particularly the shoot, but low to the grain filling. Research findings that under salinity stress, assimilate partitioning to the shoot increased by 19.6%, whereas it declined in the roots and grains by 6.5% and 13.8%, respectively. Several factors affect to influence this process, including the characteristics of the grains produced influenced by genetic factors, grain morphology, and environmental [47], pollen viability, and the plant's capacity to absorb water and essential minerals during the generative stage [48].

Under waterlogging conditions, all tested rice varieties demonstrated relatively balanced translocation of assimilates (**Figure 4(c)**). The results showed that under waterlogging stress, assimilate partitioning to the shoot and grain increased by 6.4% and 6.4%, respectively, while it decreased in the roots by 13.1%. Water availability in waterlogged conditions supports optimal growth, even under stress conditions. When rice plants under anaerobic conditions, increased formation of aerenchyma for exchange facilitates the venting of O₂ to the roots and shoots [49]. Furthermore, photosynthesis activity continues, as some leaf organs remain above the water surface. Plants under waterlogging conditions maintain the capacity to light intercept, as a portion of their leaf organs remain exposed above the water. Under submerged conditions, rice plants form a leaf gas film that facilitates the exchange of O₂ and CO₂ for supporting photosynthesis activity [50].

Under dual stress conditions, rice varieties of Inpara 8, Mawar, and Maros exhibit a significant

assimilates partitioning to the grain and shoot, while the translocation to the root is relatively low (**Figure 4(d)**). The results demonstrated that under dual salinity and waterlogging stress, assimilate partitioning to the shoots, roots, and grains decline by 2.5%, 21.4%, and 9.6%, respectively. This indicates that dual stress conditions severely hinder assimilate accumulation and translocation across different plant organs. These varieties may possess enhanced stress tolerance compared to others. In contrast, rice varieties of Inpari 30 Cihérang Sub 1, Inpari 34, Inpari 79 Unsoed Agritan, and IR 64, show a predominant assimilates partitioning to the shoot, with low translocation to the grain. The oxidative stress impairs the plant’s ability to synthesize and translocate assimilate effectively [51]. Furthermore, environmental stress adversely affects various growth parameters, including reductions in plant height, thereby underscoring its overall impact on plant development

and productivity [52].

Inpari 30 Cihérang Sub 1, Inpari 34, and Inpari 79 Unsoed Agritan showed reduced assimilate translocation to the grains under salinity, waterlogging, and combined stress conditions. This reduction may have resulted from impaired photosynthesis, limited ATP availability in transport tissues, and Na⁺ accumulation that damaged cell membranes, including those in the phloem. Under stress, plants tend to allocate more energy to maintaining vegetative organs as a survival strategy, rather than supporting grain filling, with assimilates preferentially allocated to shoots and roots. Although Inpari 79 Unsoed Agritan consistently showed low assimilate translocation to the grains across all stress conditions, this appears to be a genetically inherent trait, associated with a low harvest index and poor grain-filling capacity due to its small grain size and low grain number [45].

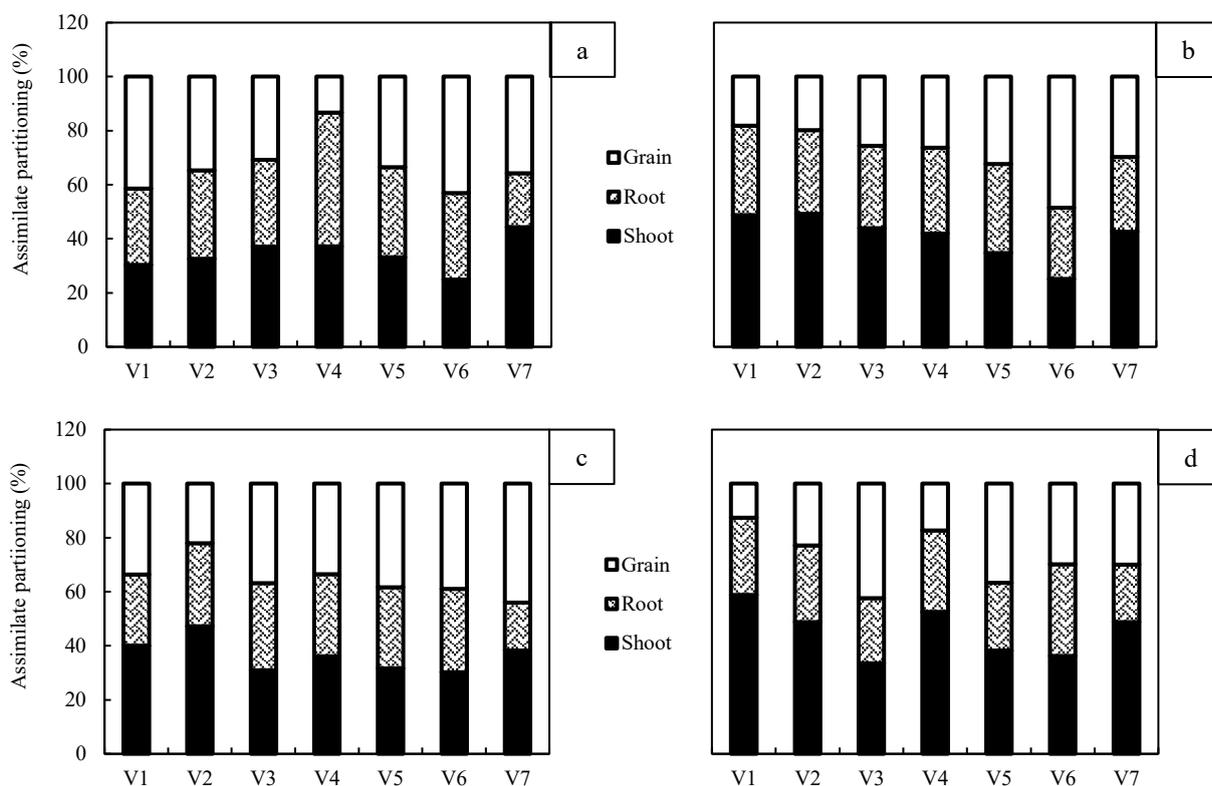


Figure 4 Assimilate partitioning under conditions of (a) control, (b) salinity, (c) waterlogging, and (d) dual salinity and waterlogging. Remarks: V1-V7 represent rice varieties, among which V1 (Inpari 30 Cihérang Sub 1); V2 (Inpari 34); V3 (Inpara 8); V4 (Inpari 79 Unsoed Agritan); V5 (Maros); V6 (Mawar); V7 (IR 64).

Plant height is an indicator of rice plant growth. Generally, most rice varieties exhibit greater height

when grown under waterlogging or dual salinity and waterlogging conditions than under control or saline

conditions. The Inpari 30 Ciherang Sub 1 variety consistently shows shorter plant height across various conditions, whereas Inpari 34 achieves the highest under waterlogging. IR 64, a variety considered susceptible to salinity and waterlogging stress, displays a similar height to Inpari 30 Ciherang Sub 1 under control and saline conditions. Under waterlogging and dual salinity and waterlogging conditions, IR 64 demonstrates better growth performance than Inpari 30 Ciherang Sub 1 (**Figure 5**).

Increased plant height under waterlogging or dual salinity and waterlogging stress is closely associated with the variety’s defence mechanisms. Rice varieties

that exhibit shoot elongation under waterlogging or dual salinity and waterlogging conditions employ an escape strategy. Ethylene promotes internode elongation, allowing the plant to extend its shoots above the water surface, thereby facilitating light capture and gas exchange [53,54]. Based on the study results, nearly all tested rice varieties appear to utilize this escape mechanism, including Inpari 34, Inpara 8, Inpari 30 Ciherang Sub 1, Mawar, and Maros. These 5 varieties exhibit enhanced shoot elongation under waterlogging and dual salinity and waterlogging stress conditions.

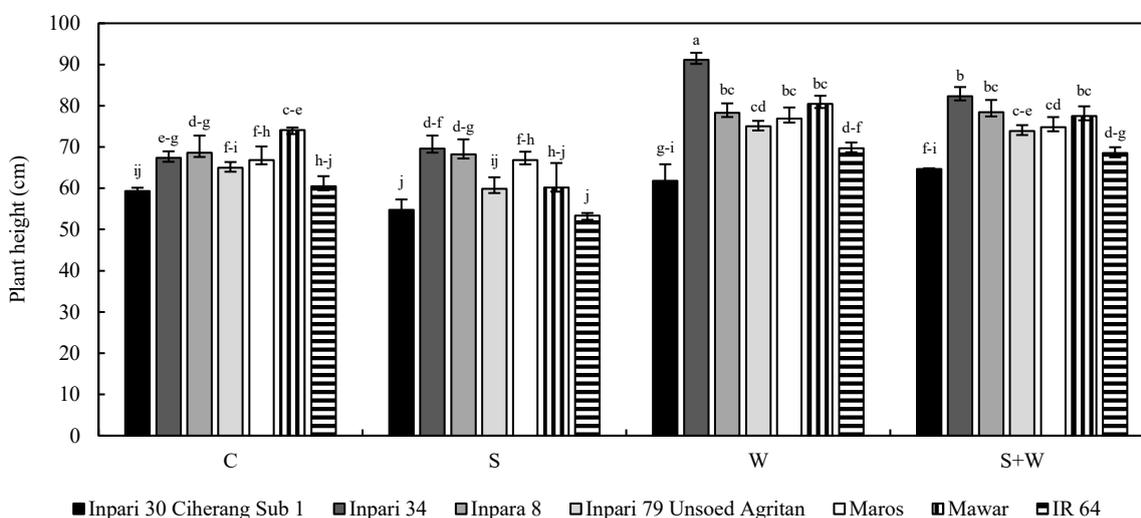


Figure 5 Interaction between stress conditions and rice varieties on plant height. Remarks: Bars represent mean values of 3 replicates with error bars showing the standard error (SE). Different letters represent significant differences in the interaction between stress conditions and rice varieties based on DMRT at $\alpha = 5\%$; C (control); S (salinity); W (waterlogging); S + W (dual salinity and waterlogging).

Meanwhile, the rice varieties of Inpari 30 Ciherang Sub 1 and IR 64 exhibited relatively stagnant shoot elongation under normal conditions, as well as under waterlogging and dual salinity and waterlogging. These findings suggest that both varieties may adopt a quiescence-based adaptive strategy, characterized by suppressed shoot elongation and reduced carbohydrate utilization, to conserve energy efficiency under waterlogging stress [55]. Furthermore, rice plants grown under salinity stress generally exhibited reduced height compared to those under normal conditions. This reduction results from osmotic stress, which limits water uptake and inhibits cell expansion and elongation.

Yield performance and yield stability index

Salinity, waterlogging, and their combination significantly influence the flowering time of rice plants. The study results indicated that rice subjected to dual salinity and waterlogging stress exhibited earlier flowering, followed by those grown under waterlogged conditions. In contrast, rice grown under normal conditions and salinity stress tended to flower later (**Table 2**). Under waterlogging or dual salinity and waterlogging stress, rice plants may active a defense mechanism through an escape strategy, accelerating their life cycle in response to prolonged hypoxic conditions [56]. This response correlates with increased ethylene synthesis, promoting earlier flowering

mediated by ABA and various genetic pathways. Conversely, salinity stress delays rice flowering by causing ionic toxicity and osmotic stress, which disrupt physiological processes during vegetative phase. This delay worsens due to reduced photosynthetic efficiency, increased oxidative stress, and significant changes in gene expression and metabolic profiles, all contributing to a hindered transition to the reproductive phase [57].

Furthermore, none of the stress treatments significantly affected pollen viability or the number of grains per panicle. However, plants subjected to salinity, waterlogging, and dual salinity and

waterlogging exhibited lower pollen viability and fewer grains per panicle than the control (**Table 2**). Salinity and waterlogging stress significantly reduce pollen viability, induce grain abortion, and damage reproductive tissues [58]. In addition, metabolic disruptions caused by Na⁺ ion toxicity and hypoxic conditions significantly impair grain formation and filling by affecting source-sink dynamics. These disruptions lead to oxidative stress, ion imbalances, altered signaling pathways, and inefficient metabolite transport, ultimately reducing grain yield and quality [59].

Table 2 Yield and yield components of rice under single and combined stress conditions.

Treatments	Flowering age (DAP)	Pollen viability (%)	Number of grains per panicle
Stress conditions			
C	65.60 ^a ± 2.33	87.14 ^a ± 2.27	91.10 ^a ± 6.11
S	65.83 ^a ± 1.93	81.14 ^a ± 2.58	79.67 ^a ± 6.25
W	63.67 ^{ab} ± 2.24	87.05 ^a ± 1.46	90.47 ^a ± 4.86
S + W	62.45 ^b ± 2.18	84.24 ^a ± 2.06	74.85 ^a ± 2.82
Varieties			
Inpari 30 Ciherang Sub 1	69.42 ^p ± 0.26	80.33 ^q ± 0.49	73.82 ^{qr} ± 1.73
Inpari 34	54.46 ^s ± 0.95	88.83 ^p ± 2.70	80.87 ^q ± 1.53
Inpara 8	68.96 ^{pq} ± 0.51	88.50 ^p ± 0.35	95.06 ^p ± 1.79
Inpari 79 Unsoed Agritan	66.00 ^q ± 1.39	78.17 ^q ± 1.89	80.48 ^q ± 1.19
Maros	66.96 ^q ± 1.08	84.75 ^{pq} ± 2.84	94.91 ^p ± 1.59
Mawar	66.08 ^q ± 1.23	86.00 ^p ± 4.42	95.18 ^p ± 2.24
IR 64	58.67 ^r ± 1.28	87.67 ^p ± 2.12	67.99 ^r ± 1.21
ANOVA			
Stress conditions (S)	*	ns	ns
Varieties (V)	**	*	*
S×V	ns	ns	ns

Remarks: Values are presented as mean ± standard error (SE) of 3 replicates. Means in the same column marked with the same letter are not significantly difference based on DMRT ($\alpha = 5\%$); C (control); S (salinity); W (waterlogging); SW (dual salinity and waterlogging).

Flowering time varied significantly among the rice varieties tested. Inpari 34 and IR 64 exhibited the earliest flowering, followed by Inpari 79 Unsoed Agritan, Mawar, Maros, and Inpara 8, while Inpari 30 Ciherang Sub 1 showed the latest flowering time (**Table 2**). Both genetic and environmental factors play a crucial role in regulating flowering time. Each rice variety possesses specific genes that regulate the timing of flowering and the duration of vegetative

growth, and these processes depend on the plant's adaptability to environmental conditions [60]. Exposure to abiotic stress can alter flowering time, either accelerating or delaying it, depending on the variety's specific defence mechanisms. Pollen viability varies among rice varieties. Five varieties, including Inpari 34, Inpara 8, Mawar, Maros, and IR 64 exhibited higher pollen viability than Inpari 79 Unsoed Agritan and Inpari 30 Ciherang Sub 1 (**Table 2**). This variation

results from physiological and genetic adaptation mechanisms that help maintain reproductive function, including the preservation of pollen viability. Rice genotypes exhibiting stress tolerance, when exposed to salinity and waterlogging stress, maintain reproductive integrity by regulating energy metabolism under hypoxic conditions and alleviating ionic stress through Na^+ exclusion or its sequestration in vacuoles [61]. In contrast, susceptible varieties may experience a decline in pollen viability of up to 64.52%, which can negatively impact grain yield [45]. Under salinity and waterlogging stress, reduced pollen viability is one of the key factors contributing to a lower number of grains per panicle. The number of grains per panicle in rice is a complex trait influenced by multiple genetic, nutritional, and environmental factors that regulate panicle initiation and flowering. The results showed that Maros, Mawar, and Inpara 8 rice varieties produced the highest number of grains per panicle, followed by Inpari 34, Inpari 79 Unsoed Agritan, Inpari 30 Ciherang Sub 1, while IR 64 recorded the lowest grain number per panicle (Table 2). The number of spikelets formed, which depends predominantly on genetic factors, directly influences the number of grains per panicle. Optimal vegetative growth supported by adequate nutrient supply, water availability, and favorable environmental conditions promotes the development of large, highly branched panicles. Holistic strategies combining these factors can significantly enhance rice yield and panicle architecture [62]. Salinity or waterlogging stress can reduce pollen viability, thus impairing fertilization and decreasing the number of grains per panicle.

Pollen viability significantly influences the percentage of filled grains, as higher viability enhances fertilization success and subsequent grain development. Rice varieties that exhibit tolerance to salinity and waterlogging stress generally produce a higher percentage of filled grains, whereas susceptible varieties tend to yield fewer. All tested rice varieties showed reduce levels of filled grains under salinity. However, certain varieties, including Inpara 8, Inpari 79 Unsoed Agritan, Maros, and Mawar increase in percentage of filled grain under waterlogging or dual salinity and waterlogging. In contrast, Inpari 34 and IR 64 experienced a reduction in percentage of filled grain under all stress conditions, including salinity, waterlogging, and dual salinity and waterlogging (Table 3).

All tested rice varieties showed a reduction in filled grain percentage under salinity, waterlogging, and dual salinity and waterlogging stress conditions. Salinity caused a greater decrease in filled grain percentage than waterlogging in Inpara 8, Inpari 79 Unsoed Agritan, Maros, and Mawar. Conversely, the other 3 varieties maintained higher filled grain percentages under waterlogging than under salinity stress. Inpari 34 and IR 64 recorded the lowest filled grain percentages under dual salinity and waterlogging, compared to either single salinity or waterlogging. Meanwhile, Inpari 30 Ciherang Sub 1, Inpara 8, Inpari 79 Unsoed Agritan, Maros, and Mawar showed lower filled grain percentages under dual salinity and waterlogging than under single waterlogging, although the values remained higher than those under salinity stress.

Table 3 Interaction between stress conditions and rice varieties on the percentage of filled grains and grain yield.

	Stress conditions	Varieties							Average
		Inpari 30 Ciherang Sub 1	Inpari 34	Inpara 8	Inpari 79 Unsoed Agritan	Maros	Mawar	IR 64	
Percentage of filled grain (%)	C	67.25 ^{a-d}	77.80 ^{a-c}	68.59 ^{a-d}	14.18 ^g	55.28 ^{b-c}	81.97 ^{ab}	79.64 ^{a-c}	63.53
	S	43.80 ^{d-f}	56.58 ^{a-e}	56.52 ^{a-c}	10.77 ^g	54.86 ^{b-f}	70.64 ^{a-d}	56.13 ^{a-e}	49.90
	W	26.87 ^{fg}	55.83 ^{b-e}	81.88 ^{ab}	41.76 ^{d-f}	81.26 ^{a-c}	85.52 ^a	64.38 ^{a-d}	62.50
	S + W	27.84 ^{e-g}	51.93 ^{c-f}	75.51 ^{a-c}	14.91 ^g	80.61 ^{a-c}	71.04 ^{a-d}	45.31 ^{d-f}	52.45
	Average	41.44	60.54	70.63	20.41	68.00	77.29	61.37	57.10 (+)
	C	2.53 ^{bc}	2.16 ^{cd}	2.21 ^{cd}	0.55 ^{fg}	2.59 ^{bc}	4.34 ^a	2.51 ^{bc}	2.41

		Varieties							
Stress conditions	Inpari 30			Inpari 79				Average	
	Ciherang Sub 1	Inpari 34	Inpara 8	Unsoed Agritan	Maros	Mawar	IR 64		
Grain yield (t ha ⁻¹)	S	1.26 ^{d-g}	0.94 ^{e-g}	1.16 ^{d-g}	0.76 ^{e-g}	1.59 ^{c-f}	1.85 ^{c-e}	1.02 ^{e-g}	1.23
	W	0.98 ^{e-g}	1.36 ^{d-g}	2.57 ^{bc}	1.28 ^{d-g}	2.24 ^{cd}	3.46 ^{ab}	1.84 ^{e-e}	1.96
	S + W	0.38 ^g	0.80 ^{e-g}	1.58 ^{c-f}	0.54 ^{fg}	1.69 ^{c-e}	1.71 ^{c-e}	0.88 ^{e-g}	1.08
	Average	1.29	1.32	1.88	0.78	2.03	2.84	1.56	1.67 (+)

Remarks: Means followed by the same letter are not significantly difference based on DMRT ($\alpha = 5\%$); lowercase letters are read vertically, indicating comparisons between 2 stress conditions within the same variety; uppercase letters are read horizontally, indicating comparisons between 2 varieties under the same stress conditions. C (control); S (salinity); W (waterlogging); SW (dual salinity and waterlogging).

The decrease in the percentage of filled grains in rice under salinity results mainly from reduced pollen viability, which prevents flowers from developing into filled grains. Additionally, salinity and waterlogging can impair anther dehiscence, reduce pollen viability and germination rates, and ultimately lead to lower fertilization [63]. Ionic and osmotic stress further impacts source-sink dynamics by impairing the transfer of non-structural carbohydrates (NSC) into grains, resulting in low translocation efficiency, poor grain filling, and reduces yield [64]. In contrast, when exposed to waterlogging and dual salinity and waterlogging, rice varieties including Inpara 8, Mawar, and Maros tend to show an increased percentage of filled grains. These 4 varieties possess high tolerance to waterlogging and dual salinity and waterlogging stress. Once waterlogging stress subsides, stored photoassimilates mobilized to the grains in tolerant varieties. This remobilization is crucial for grain filling, especially in the later stages of development [65]. Inpari 30 Ciherang Sub 1, Inpari 34, and Inpari 79 Unsoed Agritan exhibited reduced filled grain percentages under waterlogging and dual salinity-waterlogging stress. Salinity and waterlogging inhibit the grain filling rate, reduce total starch content, and

affect key enzyme activities associated with starch synthesis. These findings result in poor sink-filling efficiency and yield performance, especially in susceptible varieties.

Grain yield declines under stress conditions, highlighting their adverse effects. Six rice varieties, including Inpari 30 Ciherang Sub 1, Inpari 34, Inpara 8, Maros, Mawar, and IR 64 produced lower grain yields than their performance under control conditions. Although Inpari 79 Unsoed Agritan recorded the lowest overall yield among the 6 varieties, it demonstrated yield stability under salinity, waterlogging, and dual salinity and waterlogging (**Table 3**). The relatively higher yields observed in the other 6 varieties under salinity and waterlogging suggest that despite stress-related declines, assimilates were still effectively translocated for grain filling. As is well established, a storing sink strength, indicated by high grain-filling rates and efficient assimilate transport, is vital for achieving high grain yield [66]. In contrast, Inpari 79 Unsoed Agritan appears to maintain stable pollen viability, regulate osmotic pressure, and mitigate oxidative damage by controlling ROS accumulation, contributing to consistent adaptability under abiotic stress [67].

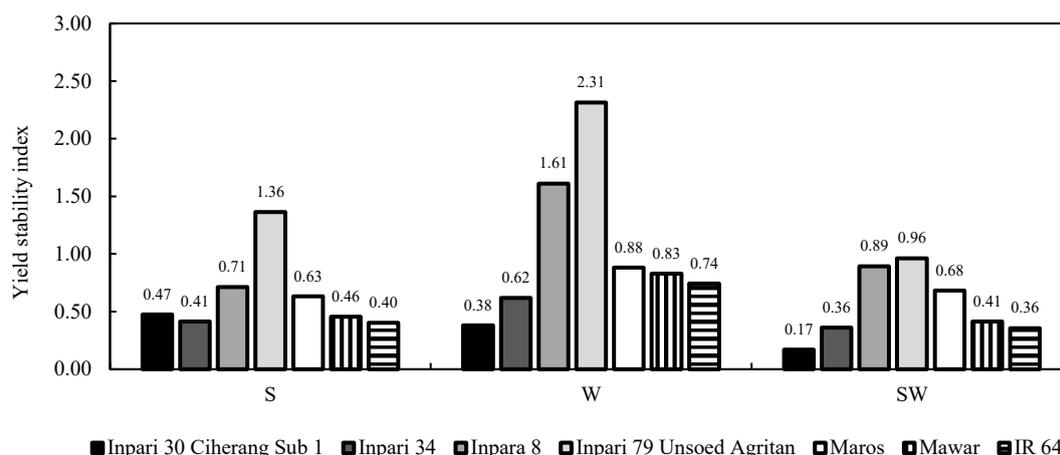


Figure 6 Yield stability index of 7 rice varieties under salinity, waterlogging, and dual salinity and waterlogging.

The stability of rice variety adaptability under stress relies on the yield stability index (YSI), which reflects a variety’s capacity to maintain yield across diverse environmental conditions. According to the study results, the Inpari 79 Unsoed Agritan variety, despite having a relatively low grain yield, exhibited the highest YSI under various stress conditions. In contrast, the Inpari 30 Ciharang Sub 1, Inpari 34, and IR 64 varieties recorded the lowest YSI values, suggesting lower adaptability to fluctuating or adverse

environments (**Figure 6**). A high YSI value reflects physiological tolerance to abiotic stress, likely associated with enhanced osmotic adjustment and increased antioxidant activity to mitigate ROS damage. Conversely, rice varieties with low YSI values likely lack critical genetic traits associated with salinity and waterlogging tolerance, rendering them more vulnerable to oxidative stress, impaired metabolic function, and consequent yield reduction [68].

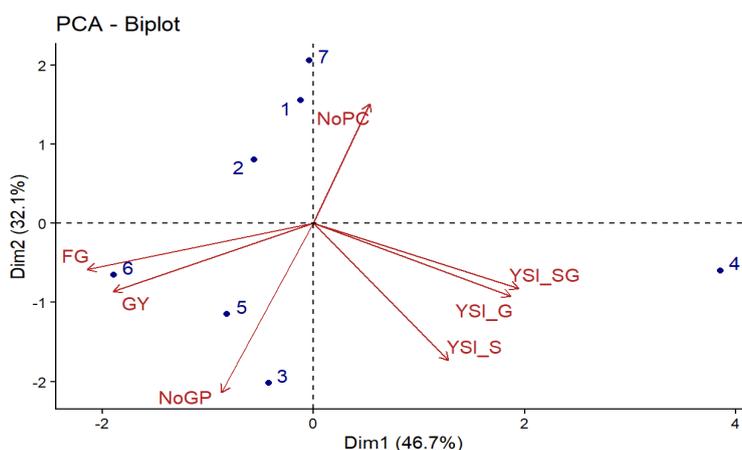


Figure 7 Grouping rice varieties based on YSI, grain yield, and yield component using principal component analysis. Remarks: NoPC (panicle number per clump), PFG (percentage of filled grains), NoGP (grain number per panicle), GY (grain yield), YSI_S (YSI under salinity), YSI_W (YSI under waterlogging), YSI_SW (YSI under dual salinity and waterlogging), 1 (Inpari 30 Ciharang Sub 1), 2 (Inpari 34), 3 (Inpara 8), 4 (Inpari 79 Unsoed Agritan), 5 (Mawar), 6 (Maros), 7 (IR 64)

PCA results showed that the Inpari 79 Unsoed Agritan rice variety remained stable under different abiotic stress conditions, including salinity, waterlogging, and their combination, although it produced lower yields. In contrast, the Inpara 8, Maros,

and Mawar varieties exhibited superior performance in terms of panicle number per clump, grain number per panicle, percentage of filled grains, and overall grain yield. These performance indicators were significantly higher than those observed in the Inpari 30 Ciharang

Sub 1, Inpari 34, and IR 64 varieties, suggesting that the latter lack the potential for high or stable yields under stress conditions (**Figure 7**). These findings are consistent with the YSI results (**Figure 6**), which further confirm the stability of Inpari 79 Unsoed across all 3 stress environments. Meanwhile, the 3 high-performing varieties, including Inpara 8, Maros, and Mawar, consistently achieved higher yields under stress conditions (**Table 3**).

Generally, all stress conditions, including salinity, waterlogging, and dual salinity and waterlogging, lead to physiological disorders that cause a decline in crop yields. Tolerant rice varieties maintain low cytosolic Na^+ concentrations by sequestering excess Na^+ into intracellular compartments, thereby sustaining a high K^+/Na^+ ratio. This mechanism minimizes toxic ion accumulation, preserves membran integrity, and supports better growth under saline conditions. Tolerant rice varieties generally exhibit more stability under abiotic stress conditions, despite having lower yields. In contrast, newly developed high-yielding varieties are often less stable when grown under salinity, waterlogging, or dual salinity and waterlogging stress.

Conclusions

Salinity, waterlogging, and dual salinity and waterlogging caused growth disorders in rice, as evidenced by a reduction in leaf area. Under salinity and dual salinity and waterlogging, there was an increase in Na^+ concentrations and decrease in K^+ . Waterlogging and dual salinity and waterlogging also accelerated flowering age and increased plant height. In salinity-tolerant rice varieties, assimilates were predominantly translocated to the grain rather than the shoot or root organs. The Inpari 79 Unsoed Agritan variety exhibited the lowest pollen viability, resulting in a lower percentage of filled grains and decreased yields. All varieties, except Inpari 79 Unsoed Agritan, experienced a yield reduction under stress conditions compared to control. Despite its low yield, Inpari 79 Unsoed Agritan demonstrated more stability across different stress conditions, as reflected in its higher YSI under salinity, waterlogging, and dual salinity and waterlogging. PCA revealed that the Inpara 8, Maros, and Mawar varieties produced more panicles per cump and achieved higher grain yields than the other tested

varieties. These results indicate that Inpari 79 Unsoed Agritan may serve as a useful genetic source for breeding programs targeting multi-stress tolerance. Further study is needed to connect these agronomic responses with physiological and molecular mechanisms. At the same time, practical efforts should focus on disseminating tolerant varieties to support farmers in region affected by salinity and waterlogging.

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Declaration of generative AI in scientific writing

I declare that generative AI and AI-assisted were used to support the writing and refinement of this work. Grammarly and Google Translate were employed, particularly for language refinement and grammar correction. The AI tools were limited to supporting tasks and did not replace original critical thinking, analysis, or authorship. All ideas, interpretations, conclusions, and contributions presented in this work are our own unless otherwise cited. The use of AI tools complies with the ethical standards and authorshhip guidelines of the target journal and the affiliated institutions.

CRedit author statement

Nasrudin: Conceptualization, Formal analysis, Writing - Original draft; **Budiastuti Kurniasih:** Methodology, Writing - Review & editing, Supervision; **Eka Tarwaca Susila Putra:** Validation, Data curation, Supervision; **Eko Hanudin:** Investigation, Visualization, Supervision.

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