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Phosphorus-Dipping Retained Higher Rice Shoot Biomass and Leaf Stomatal Conductance Under Drought-Stress Conditions

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Abstract

Rainfed upland and lowland cultivation systems account for over 70% of the total rice cultivated area in sub-Saharan Africa. However, drought stress and phosphorus (P) deficiency are significant abiotic stresses impacting rice production in the region. In two separate studies (Exp. 1 and 2), we evaluated the combined effects of drought stress (Well-watered, mild drought, moderate drought, and severe drought) and P treatments on the growth of NERICA 4 at the initial stages in rainfed upland-like conditions. In Exp. 1, P treatments consisted of P-dipping (P-dip), where rice seedling roots were dipped in a phosphorus-rich slurry before transplanting, and a control with no P application. In Exp. 2, P-dip and another broadcast P fertilizer level (Brod) were used. Compared to the control, the P-dipping treatment resulted in significant increases in mean shoot biomass of 21.1% and 44.4% under the well-watered and mild drought treatments, respectively, at 12 days after treatment (DAT) in Exp. 1. P-dipping also significantly increased shoot biomass (0.8 g plant^{-1}) compared to broadcasting (0.6 g plant^{-1}) under severe drought conditions, 12 DAT in Exp. 2. In Exp. 1, mean stomatal conductance (gs) under P-dip (0.7 mol m^{-2} s^{-1}) was significantly higher than that under the control (0.5 mol m^{-2} s^{-1}). Additionally, gs decreased more dramatically with reductions in soil volumetric water content under the control condition than in the P-dipping treatment, where a moderate decline was observed. As hypothesized, P-dipping increased rice shoot biomass and stomatal conductance under drought conditions.

Keywords: Chlorophyll content; Gas exchange; Inorganic fertilizers; Nutrient deficiency; *Oryza sativa* L; Specific leaf weight

Introduction

More than 70% of the rice-cultivated area in sub-Saharan Africa (SSA) is rainfed [1]. Thus, drought stress is a major limiting abiotic factor facing rice production in the region [2]. Van Oort [3] reported that a third of the rice-cultivated area is affected by drought stress. Phosphorus (P) deficiency is another yield-limiting factor in the highly weathered and inherently low-nutrient soils of SSA [4], which have low cation exchange capacities, low water-holding capacities, low pH, and high Fe and Al oxide contents that form complexes with P—making it unavailable for plant uptake [5, 6]. The first line of response to mitigating P deficiency across many SSA countries has been the promotion of inorganic fertilizer use [7]. Owing partly to the region's inherently low nutrient status, the use of large quantities of inorganic fertilizers has been recommended to improve crop yields [8], but the

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recommended rates have not been adopted because fertilizers are prohibitively expensive for most farmers.

Given that drought reduces soil P availability and plant uptake [9], approaches and techniques that promote localized soluble P uptake in rice production, even under minimal soil water conditions, should be studied and promoted. Considerable research has been conducted on the physiological and morphological techniques to improve P-acquisition efficiency in rice plants through modifying root physiology [10], altering root morphology [11], and improving colonization by mycorrhizal hyphae [12]. Agronomic research on P micro-dosing and the application of small amounts of P in nursery beds before transplanting has also been conducted to improve plant P uptake [13]. More recently, P-dipping, which involves dipping rice seedling roots into P-enriched slurry before transplanting, has shown improved early growth and P-use efficiency, with downstream benefits for yield-related traits in P-fixing soils [14-16]. However, almost all the stated studies on P-dipping were conducted in waterlogged conditions, where soil moisture content is not severely limiting. On the other hand, whether P-dipping–promoted root growth contributes to improved leaf gas exchange and shoot biomass under severe drought conditions remains unclear.

Because rice production in the rainfed lowland ecology—where the occurrence of transient water deficit in the soil or drought events is common—is predominant in many parts of SSA and other subtropical regions of the world, there is need to understand whether P-dipping can improve the resilience of transplanted rice to withstand drought events in rainfed lowland conditions at initial growth stages. Therefore, the major objective of this study was to evaluate the effect of P-dipping on rice shoot physiological and morphological characteristics during the initial growth stages under drought conditions. To that end, we hypothesized that P-dipping enhances the resilience of rice to retain higher leaf stomatal conductance and shoot biomass under severe drought conditions.

Materials and Methods

Plant material and planting environment

The mean temperature and relative humidity in the greenhouse, where the experiments were conducted, were 30.8 °C and 74.6%, respectively, throughout the experiment period. They were measured using a data logger (RTR-503B, T&D Corporation, Matsumoto, Japan) equipped with temperature and humidity sensors. We used rice variety NERICA 4, an interspecific progeny between *O. sativa* and *O. glaberrima.*

Experimental design and treatments

We conducted two concurrent experiments, Experiment 1 (Exp. 1) and Experiment 2 (Exp. 2), in separate experimental block structures, illustrated in Figure 1. The dimensions of the experimental block structures are consistent with those employed in comparable experiments, including those reported by Katsuhama [17], in which similar setups were sufficient to capture treatment effects under controlled conditions. Each structure featured four water regimes: well-watered (WLW), mild drought (MLD), moderate drought (MOD), and severe drought (SVD). The WLW regime served as the control; the average volumetric water content (VWC) in each water regime for Exp. 1 and 2 is presented in table 2. Each experimental block structure measured 382 cm long, 110 cm wide, and 100 cm high, and was filled with varying amounts of soil (bulk density: 1.2 g cm^{-3}): WLW contained 347 kg, MLD 545 kg, MOD 743 kg, and SVD 941 kg.

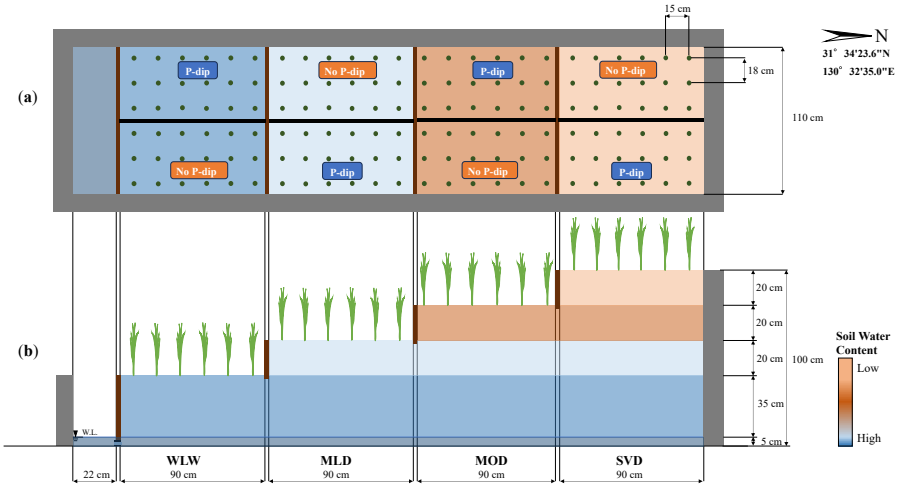

Figure 1: Top view (**a**) and side view (**b**) of one experimental block structure with four water regimes: WLW, which served as the control, MLD, MOD, and SVD. W.L., water level where 5 cm of water was maintained during the drought treatments; Each regime was subdivided into two parts using a plastic sheet (a) to randomize the P treatments. P-dipping was conducted in plots marked "P-dip", and the "No P-dip" plots indicate where no P-dipping or any P fertilizer application was conducted, which served as the control.

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In Exp. 1, water regimes were factorially combined with a P-dipping (P-dip) fertilizer treatment and a no-P-dipping (Ctrl) control, in which rice seedlings were transplanted without P-dipping or P fertilizer application. In Exp. 2, the four water regimes and the P-dipping treatment in Exp. 1 were maintained. However, non–P-dipped seedlings were transplanted in soil uniformly broadcast with 33 g (5.7 g P_2O_5 0.5 m^{-2}) SSP fertilizer to constitute the "Brod" treatment. To correct any deficiencies in the experimental soil N and K contents within each water regime for both experiments, 72 g of ammonium sulphate (15 g N 0.99 m^{-2}) and 20 g of potassium chloride (10 g K 0.99 m^{-2}) were homogeneously mixed with soil within each water regime.

Before transplanting, the soil in the experimental structures was adequately watered. NERICA 4 seedlings, grown in seedling trays until the 3-4 leaf stage, were identified, and seedling roots were carefully hand-washed and then dipped into P-enriched slurry for 30 minutes—as recommended by Oo [18]—to constitute the P-dip treatment. The P-enriched slurry was produced by mixing 45 g of air-dried soil, 14 mL of water, and 1.31 g of single superphosphate (SSP) fertilizer. All seedlings were transplanted using the dibble method at a spacing of 18 cm × 15 cm, and 4 replicates were taken from each treatment combination. Holes approximately 6 cm deep and 3 cm wide were made before transplanting to avoid root damage, and plants were watered for an additional 10 days after transplanting to minimize transplant shock. After 10 days, direct water irrigation was withheld. However, a 5-cm water level was maintained in a compartment at the lower end of the experimental structure, as water was allowed to infiltrate into the soil within the structure by capillarity (Figure 1). To avoid water leakage outside the experimental structures, impermeable plastic sheets were laid at the bottom before filling them with soil. During the experiment period, variations in soil volumetric water content (VWC) within each regime were monitored using sensors (10SH; METER Group, Inc., USA) installed at a depth of 15 cm and equipped with a data logger (Em50 Series; METER Group, Inc., USA). Upon exposing plants to drought, i.e., withholding direct water supply for 12 days after treatment (DAT), rewatering was resumed until 26 DAT, when the experiment was terminated. Soil VWC changes in Exp. 1 and 2 are presented in figure 2.

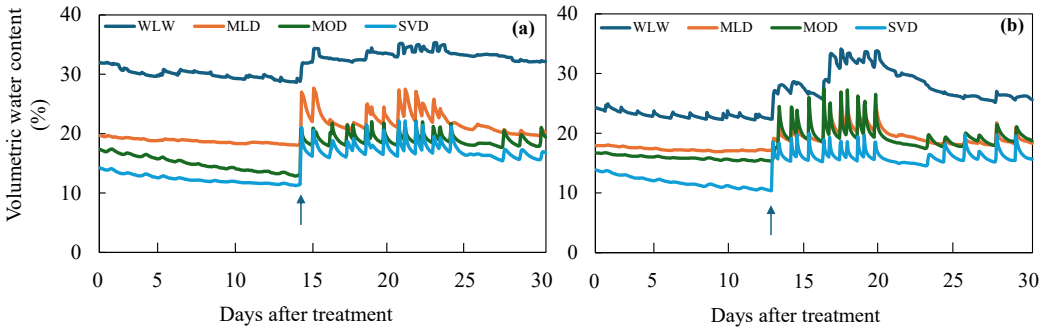

Figure 2: Changes in the soil VWC in Exp. 1 (a) and Exp. 2 (b) during the experimental period. The average soil volumetric water contents in the WLW, MLD, MOD, and SVD regimes are summarized in table 2. Upward-pointing arrows show the start of the rewatering period.

Table 1: Chemical and physical properties of the experimental soil.

Parameter	Exp. 1	Exp. 2
pH (1:2.5 H_2O)	7.4	7.5
Available P (mg kg^{-1})	80.3	71.8
Exchangeable K (mg kg^{-1})	199	256
Total N (mg g^{-1})	0.08	0.08
Total C (mg g^{-1})	0.2	0.2
C: N ratio	2.5	2.6
OM content (%)	0.34	0.35
Particle size distribution (%)		
Sand	94	95
Clay	3	3
Silt	2	3
Textural name	Sand	Sand

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The chemical and physical properties of the experimental soil are presented in table 1. Experimental soils were analyzed for pH (1:2.5 H_2O), available P using Truog's method, exchangeable potassium using the 1 mol L^{-1} ammonium acetate extraction method, total nitrogen and carbon using the dry combustion method via an NC analyzer (JM1000CN/HCN TOC.TN, J-Science Lab Co., Ltd., Japan), and soil texture using the pipette method. Soil organic matter content was determined by multiplying the per cent value of organic carbon by the conventional Van Bemmelen's factor of 1.724 [19].

Briefly, the available P content in Exp. 1 soil was slightly higher than that in Exp. 2. Conversely, the exchangeable K content in Exp. 2 soil was higher than that in Exp. 1 soil. A summary of the P and drought treatments is presented in table 2.

Data collection and measurements

Data on shoot parameters, i.e., plant height, leaf area, and stomatal conductance (gs), were collected at 12 DAT (i.e., post-drought period) and 26 DAT (i.e., post-recovery period) in both Exp. 1 and 2. In comparison, data on leaf age and tiller number were collected at only 12 DAT in both Experiments. Plant height was measured from the base of the stem (at the soil surface) to the highest part of the plant. Stomatal conductance was measured on the youngest fully expanded leaf between 9:00 AM and 12:00 PM using a porometer (AP4, Delta-T Devices, UK). At the end of the drought treatment period (12 DAT), rice shoots were cut. The leaves were removed to measure leaf area using a digital image analysis machine (LIA32, Nagoya University, Nagoya, Japan), and the data were used to calculate specific leaf weight (SLW; ratio of leaf dry weight to leaf area measured in mg cm^{-2}).

To determine leaf chlorophyll content via spectrophotometric analysis of chemically extracted pigments, we collected leaf samples using a leaf disk having an area of 1.0 cm^2 from a section of the youngest fully expanded leaf and placed the samples in plastic tubes. We then added 3.0 ml dimethylformamide, and samples were stored in a refrigerator for 24 hours for pigment extraction [20]. Thereafter, we measured pigment absorption at 647, 664, and 750 nm using a spectrophotometer (Spectronic 200, Thermo Fisher Scientific Inc., USA), and the readings were converted to chlorophyll content using the equations defined by Porra [20]. The cut rice leaves and stems were oven-dried at 80 °C for 48 hours to determine shoot biomass per treatment at 12 and 26 DAT.

Statistical analyses

We analyzed data using a two-way ANOVA to determine the main and interaction effects of P treatments (P-dip, Brod, and Ctrl) and water regimes (WLW, MLD, MOD, and SVD) in IBM SPSS Statistics (Version 18.0.0). Treatment means from the replicates and mean values among treatment groups were compared at the 5% level of probability using Tukey's HSD test. To measure the level of significance between the P treatment groups, two-tailed t-tests assuming equal variances were used at a 5% level of probability using Microsoft Excel.

Table 2: Summary of the P and water treatments in Exp. 1 and 2

Exp. 1			Exp. 2		
P Treatments	**Total application (g P_2O_5 0.5 m^{-2})**	**Application method and timing.**		**Total application (g P_2O_5 0.5 m^{-2})**	**Application method and timing.**
P-dip[1]	-	P-dipping at transplanting	P-dip[1]	-	P-dipping at transplanting
Ctrl	0	-	Brod	5.7	Broadcasting at transplanting
Water Treatments[2]		Av. soil VWC in Exp. 1 during 12 DAT (% *v/v*)	Av. soil VWC in Exp. 2 during 12 DAT (% v/v)		Amounts of soil within each water regime in each experimental structure (kg)
WLW	Well-watered	30.1	23.7		347
MLD	Mild drought	18.9	17.6		545
MOD	Moderate drought	15.1	16.5		743
SVD	Severely drought	12.5	12.5		941

[1]The P-enriched slurry was produced by mixing 45 g of air-dried soil, 14 mL of water, and 1.31 g of single superphosphate fertilizer. To correct deficiencies in the soil N and K contents within each water regime for both experiments, the topsoil was homogeneously mixed with 72 g of ammonium sulphate (15 g N 0.99 m^{-2}) and 20 g of potassium chloride (10 g K 0.99 m^{-2}).

[2]The four water regimes were applied for 12 days, and rewatering was resumed until 26 DAT

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Results

Changes in shoot morphological and physiological traits

At the end of the drought treatment (12 DAT), mean shoot biomass decreased with a reduction in water content under both P-dip and Ctrl (Exp. 1) and P-dip and Brod (Exp. 2) treatments (Tables 3 and 4). In contrast to Ctrl, there were significant increases of 21.1% and 44.4% in mean shoot biomass for the P-dip treatment under WLW and MLD water regimes at 12 DAT, respectively. Notably, mean shoot biomass under the SVD moisture regime for the P-dip treatment (0.8 g plant^{-1}) in Exp. 2 was significantly higher ($p = 0.015$) than that for the Brod treatment (0.6 g plant^{-1}). Overall, at the end of the drought period, mean shoot biomass from the P-dip treatments (1.2 g plant^{-1} in Exp. 1; 1.3 g plant^{-1} in Exp. 2) was significantly higher than that under Ctrl and Brod in Exp. 1 and 2, respectively.

Significant interaction effects for mean shoot biomass existed only in Exp. 2 at 12 DAT, and analysis of the simple main effects for P treatments showed that P-dip had the highest effect size ($p < 0.05$; Partial $\eta^2 = 0.92$) and that the interaction effect was only under the WLW ($p < 0.05$; Partial $\eta^2 = 0.58$) water regime. After rewatering (26 DAT), the P-dip treatment showed significantly higher mean shoot biomass values in Exp. 1 (3.1 g plant^{-1}) in contrast to Ctrl (2.5 g plant^{-1}), and in Exp. 2 (3.4 g plant^{-1}) in contrast to the Brod (2.8 g plant^{-1}) P treatment. Significant interaction effects ($p = 0.05$) between P treatments and water regimes also emerged for shoot biomass under Exp. 1 and 2 by the end of the rewatering period.

The leaf area (LA) in Exp. 1 was significantly affected by water treatments at 12 DAT. However, during the same period in Exp. 2, both water regimes and P treatments significantly affected LA, with mean values of 256.5, 128.7, 95.3, and 63.3 cm^2 resulting from the WLW, MLD, MOD, and SVD, respectively. The P-dip (150.2 cm^2) treatment showed the highest mean LA in contrast to Brod (121.7 cm^2), and the mean LA under P-dip in the SVD regime (70.3 cm^2) was significantly higher ($p = 0.0002$) than that under Brod (56.2 cm^2) within SVD regime in Exp. 2. Significant interaction effects between P treatments and water regimes emerged for LA at 12 DAT in only Exp. 2 (Table 4). At 26 DAT, P-dip (320.5 cm^2) showed a significantly higher mean LA than Ctrl (234.6 cm^2) in Exp. 1; and in Exp. 2, the P-dip (287.2 cm^2) treatment also showed a significantly higher mean value in contrast to that under the Brod (260.9 cm^2) treatment. During the same period, there were significant interaction effects ($p = 0.05$) between P treatments and water regimes for LA under Exp. 1 and 2 (Tables 3 and 4). A strong positive correlation existed between leaf area and total chlorophyll content in Exp. 1 at 12 DAT (Figure 3a), but not in Exp. 2 at 26 DAT (Figure 3b).

Plant height was significantly affected by water treatments in Exp. 1 at 12 DAT, with an average two-fold increase in mean value under the sufficient water regimes (WLW and MLD) than the drier (MOD and SVD) ones (Table 3). There existed a significant interaction effect between water regimes and P treatments for plant height ($p < 0.05$; Partial $\eta^2 = 0.53$). In Exp. 2, water treatments significantly affected plant height only under the P-dip treatment, with the WLW

Table 3: Changes in shoot morphological traits and stomatal conductance at 12 and 26 DAT in Exp. 1

Phosphorus Treatment (P)	Water Treatment (W)	Shoot biomass (g)		Leaf area (cm² plant⁻¹)		Plant height (cm d⁻¹)	Leaf age	Tiller No.	Stomatal conductance (mol m⁻² s⁻¹)		Specific leaf weight (mg cm⁻²)	
		12 DAT	26 DAT	12 DAT	26 DAT	12-0 DAT	12 DAT	12 DAT	12 DAT	26 DAT	12 DAT	26 DAT
Ctrl	WLW	1.9a	4.3a	294.8a	423.0a	31.4a	8.5a	3.0a	0.76a	0.86a	3.9a	4.9a
	MLD	0.9b	2.9b	134.1b	265.0b	25.9a	7.5a	2.3a	0.55b	0.67b	3.2a	5.5a
	MOD	0.7c	1.9c	78.8c	169.5c	9.6b	5.3b	1.3b	0.43c	0.60b	4.0a	5.5a
	SVD	0.5c	0.9d	71.8c	80.8d	5.7b	5.3b	1.3b	0.27d	0.40c	3.1a	5.0a
P-dip	WLW	2.3a	5.5a	309.5a	559.8a	19.3b	9.5a	2.8a	0.77a	0.87a	3.7b	5.0a
	MLD	1.3b	3.4b	154.0b	333.1b	27.6a	7.3b	2.3a	0.72a	0.82b	4.7a	4.9a
	MOD	0.7c	1.8c	90.4c	270.2c	12.7bc	5.3c	1.3b	0.64b	0.79b	4.4ab	3.2b
	SVD	0.6c	1.2c	78.3c	118.8d	6.3c	5.0c	1.0b	0.46b	0.56c	3.9ab	3.9b
Two-way ANOVA	P	*	*	ns	*	ns	ns	ns	*	*	*	*
	W	*	*	*	*	*	*	*	*	*	*	*
	P × W	ns	*	ns	*	*	ns	ns	*	*	*	*

NERICA 4 shoot morphological and physiological traits to P treatments Pdip and Ctrl, and water treatments WLW, MLD, MOD, and SVD in Exp. 1 at 12 and 26 DAT ($n = 4$). *, $p < 0.05$; ns, not significant; both according to Tukey's HSD test. Different lowercase letters after parameter values indicate significant differences at $p < 0.05$ within each P treatment.

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regime showing a 4.6-fold increase in mean plant height in contrast to the SVD regime. No significant interaction effects between water regimes and P treatments for plant height were observed in Exp. 2

Leaf age and tiller number showed similar tendencies, where they were significantly affected by only the water regimes rather than the P treatments in Exp. 1 at 12 DAT. However, though not statistically different, the P-dip treatment showed higher (3.0%) mean leaf age values compared to Ctrl (Table 3). In Exp. 2, leaf age and tiller number were also significantly affected by water regimes only. The mean leaf age value under the P-dip treatment within the WLW regime was significantly higher ($p = 0.005$) than its mean value under Brod P within the same water regime. Likewise, the mean tiller number from the P-dip treatment under the WLW was also significantly higher ($p = 0.04$) than that from the Brod P treatment within the same regime. Significant interaction effects between P treatments and water regimes were shown for leaf age ($p < 0.05$; Partial $\eta^2 = 0.62$) and tiller number ($p = 0.007$; Partial $\eta^2 = 0.39$) in Exp. 2 at 12 DAT (Table 4).

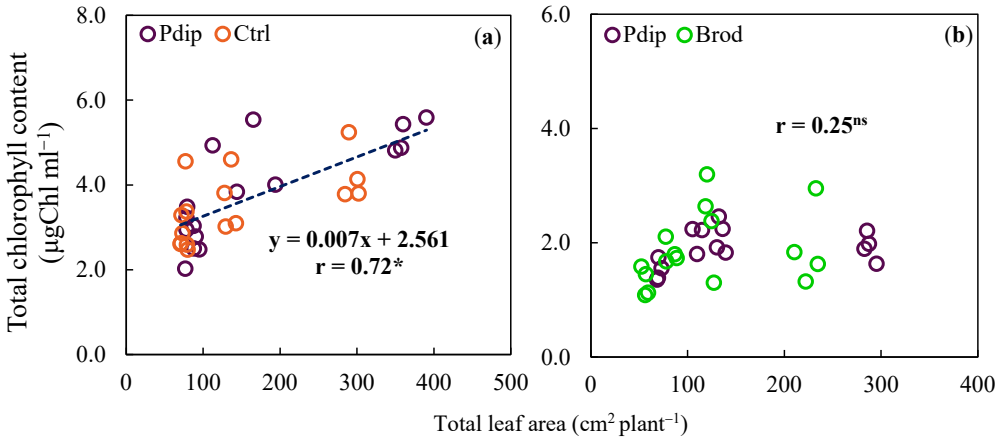

Figure 3: Relationship between total leaf chlorophyll content and leaf area in Exp. 1 (**a**) and Exp. 2 (**b**) at 12 DAT. Purple circles represent the P-dip treatment; orange circles represent Ctrl; and green circles represent the Brod treatment.

Table 4: Changes in shoot morphological traits and stomatal conductance at 12 and 26 DAT in Exp. 2

Phosphorus Treatment (P)	Water Treatment (W)	Shoot biomass (g)		Leaf area (cm² plant⁻¹)		Plant height (cm d⁻¹)	Leaf age	Tiller No.	Stomatal conductance (mol m⁻² s⁻¹)		Specific leaf weight (mg cm⁻²)	
		12 DAT	26 DAT	12 DAT	26 DAT	12-0 DAT	12 DAT	12 DAT	12 DAT	26 DAT	12 DAT	26 DAT
Ctrl	WLW	1.7a	4.4a	225.1a	357.1a	11.5a	8.3a	2.5a	0.66a	0.48a	4.1a	4.6a
	MLD	1.0b	4.1a	122.7b	330.9b	16.8a	8.0ab	2.5a	0.38b	0.39a	4.3a	5.5a
	MOD	0.8b	1.8b	82.8c	235.2c	10.5a	6.8ab	1.5a	0.32b	0.51a	4.6a	3.1b
	SVD	0.6b	0.9c	56.2d	120.4d	9.1a	6.5b	1.5a	0.22b	0.47a	4.7a	2.7b
P-dip	WLW	2.3a	7.5a	287.9a	588.6a	18.5a	11.3a	3.5a	0.43a	0.48a	3.8b	5.1a
	MLD	1.2b	2.7b	134.7b	241.4b	13.5ab	6.5b	1.5b	0.47a	0.35b	4.3ab	5.7a
	MOD	0.9c	2.1bc	107.8c	188.2c	10.5ab	6.3b	1.0b	0.24b	0.49a	4.0ab	5.1a
	SVD	0.8c	1.2c	70.3d	130.6d	4.0b	6.3b	1.3b	0.41a	0.50a	4.5a	3.2b
Two-way ANOVA	P	*	*	*	*	ns	ns	ns	ns	ns	ns	*
	W	*	*	*	*	*	*	*	*	*	*	*
	P × W	*	*	*	*	ns	*	*	*	ns	ns	*

NERICA 4 shoot morphological and physiological to P treatments P-dip and Ctrl, and water treatments WLW, MLD, MOD, and SVD in Exp. 2 at 12 and 26 DAT ($n = 4$). *, $p < 0.05$; ns, not significant; both according to Tukey's HSD test. Different lowercase letters after parameter values indicate significant differences at $p < 0.05$ within each P treatment.

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P treatments affected stomatal conductance (gs) in Exp. 1 at 12 DAT, with the mean gs under P-dip (0.7 mol m^{-2} s^{-1}) showing significantly higher values than that under Ctrl (0.5 mol m^{-2} s^{-1}) (Table 3). Notably, gs reduced more drastically with a reduction in soil volumetric water content (VWC) under Ctrl than the relatively mild reduction observed under P-dip in Exp. 1 at 12 DAT (Figure 4a). Significant interaction effects in gs existed between P treatments and MOD ($p < 0.05$; Partial $\eta^2 = 0.79$), SVD ($p < 0.05$; Partial $\eta^2 = 0.74$), and MLD ($p < 0.05$; Partial $\eta^2 = 0.70$) water regimes. In Exp. 2, no significant differences in gs were observed between P-dip and Brod P treatments. However, water treatment affected gs, with no significant decline in gs values within the WLW and MLD water regimes under P-dip, yet a significant 1.7-fold decline in gs within the same water regimes in the Brod treatment (Table 4, Figure 4b). There were significant interaction effects in mean gs values between P treatments and WLW ($p = 0.001$; Partial $\eta^2 = 0.40$) and with SVD ($p = 0.003$; Partial $\eta^2 = 0.31$) water regimes.

Water and P treatments affected specific leaf weight at both 12 and 26 DAT in Exp. 1 (Table 3), and only at 26 DAT in Exp. 2 (Table 4). In Exp. 1, the mean SLW at 12 DAT from the P-dip treatment (4.2 mg cm^{-2}) was significantly higher than that from Ctrl (3.5 mg cm^{-2}). On the contrary, at 26 DAT, mean SLW under Ctrl (5.2 mg cm^{-2}) was significantly higher than the mean value under P-dip (4.2 mg cm^{-2}). Water treatments showed significant differences in SLW at 12 and 26 DAT only under the P-dip treatments in Exp. 1, with an overall reduction in mean SLW values as soil water content reduced. Significant interaction effects for SLW existed between water regimes and P-dip in Exp. 1. In Exp. 2, significant differences in SLW emerged between water regimes only under the P-dip treatment at 12 DAT. However, at 26 DAT, both water and P treatments significantly affected SLW, with mean value under P-dip (4.8 mg cm^{-2}) being significantly higher than that under Brod (4.0 mg cm^{-2}). Significant interaction effects also existed for SLW between water and P treatments at 26 DAT in Exp. 2 (Table 4).

Changes in leaf chlorophyll content

Water regimes significantly affected Chl a content at 12 DAT, and the effects existed only within the P-dip treatments in Exp. 1 and 2 at 12 DAT (Figure 5a). Though not statistically different, mean Chl a content under P-dip (2.7 µg Chl mL^{-1}) was slightly higher than that under Ctrl (2.4 µg Chl mL^{-1}) in Exp. 1. Within the same Exp. 1, WLW showed 100% and 63.6% significant increases in mean Chl a content values compared to MOD and SVD treatments, respectively. There were no significant differences in the Chl b content between the P treatments and between the water treatments in both Exp. 1 and 2 at 12 DAT (Figure 5b). However, in Exp. 1, Chl b content tended to reduce with a reduction in the soil water content for both P treatments, which tendency was not observed in Exp. 2.

Total leaf chlorophyll content ranged from 0.66 to 5.59 µg Chl mL^{-1} in Exp. 1, and from 0.89 to 4.72 µg Chl mL^{-1} in Exp. 2. Water treatments significantly affected the total chlorophyll content in both Exp. 1 and 2 at 12 DAT. In Exp. 1, the moisture-sufficient regimes (WLW and MLD) showed a combined mean 50.5% increase in total chlorophyll content compared to the combined mean of the drier (MOD and SVD) regimes at 12 DAT (Figure 6a). Though to a lesser extent, a similar trend was observed during the same period in Exp. 2 (Figure 6b). While no significant differences in total chlorophyll content were observed between water regimes in Exp. 1 at 26 DAT, P-dip showed significantly higher total chlorophyll content in contrast to control within the MLD regime (Figure 6c). In Exp. 2 at 26 DAT, P-dip also showed a significantly higher value for total chlorophyll content in contrast to the Brod treatment under the MLD regime, and the P-dip treatment generally posted higher non-significant values than the Brod treatments under the rest of the water regimes (Figure 6d).

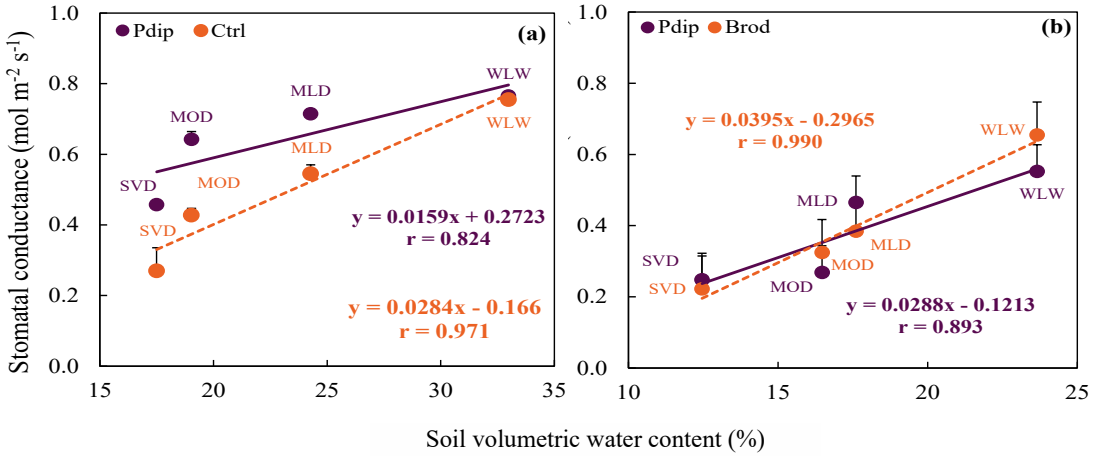

Figure 4: Changes in stomatal conductance in response to changes in volumetric water content within WLW, MLD, MOD, and SVD regimes, and (i) P-dip and Ctrl in Exp. 1 (**a**), and (ii) P-dip and Brod in Exp. 2 (**b**) at 12 DAT. Error bars show standard deviations ($n = 4$).

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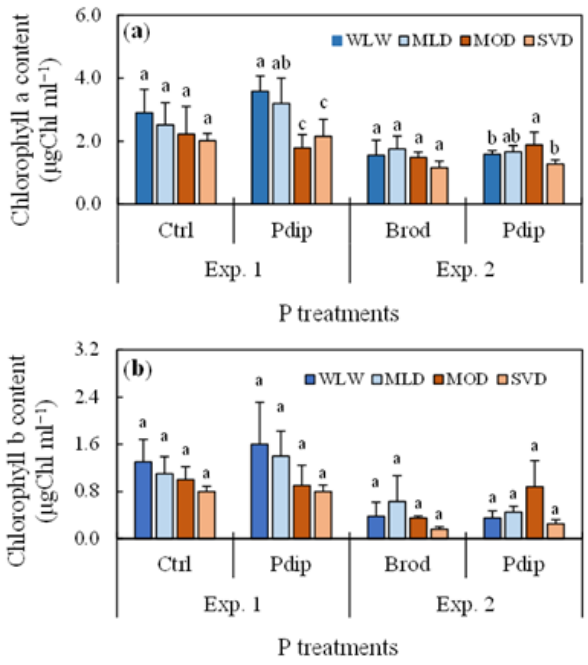

Figure 5: Changes in chlorophyll *a* content to changes in water content within WLW, MLD, MOD and SVD regimes in Exp. 1 and 2 (**a**), and changes in chlorophyll *b* content to changes in water regimes in Exp. 1 and 2 (**b**) at 12 DAT. Different lowercase letters above P treatments indicate significant differences between P treatments in Exp. 1 and 2 at $p < 0.05$ according to Tukey's HSD test. Error bars show standard deviations ($n = 4$).

Discussion

Changes in shoot morphology under water and P application treatments

Water and P treatments affected NERICA 4 shoot biomass, plant height, and leaf area, with P-dipping and WLW regime combination treatments showing higher significant mean values than the other treatments in Exp. 1 (Table 3). Even under the highest moisture stress treatment (SVD) in Exp. 2, the mean shoot biomass for the P-dipping treatment was significantly higher than that for P broadcasting (Table 4). This may be explained by the localized soluble P hotspots created by P-dipping around the root system [21], which may have contributed to the better access of P by roots, thus the better performance of the shoot parameters under the P-dipping treatment. Oo [21] demonstrated that P-dipping accelerates surface root system development relative to P incorporation, and in a recent study, Odama [14] found that P-dipping improved the resilience of NERICA 4 rice seedlings to P stress, which may further explain the observed better shoot performance under P-dipping.

Rice, being a water-intensive crop, requires ample moisture for optimal production [22]. Adequate water availability also enhances phosphorus concentration in the soil solution, making it more readily available for plant uptake [23]. Studies have demonstrated that plant growth is influenced by a complex interplay of factors, including cell

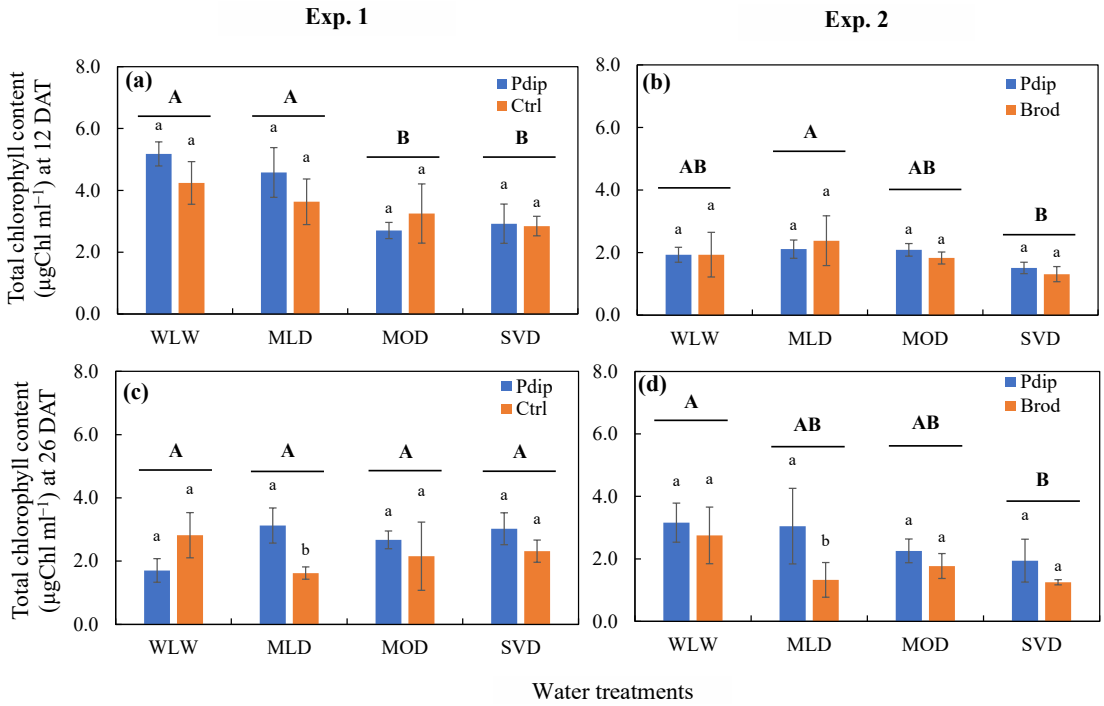

Figure 6: Changes in total chlorophyll content in response to changes in soil water content within WLW, MLD, MOD and SVD regimes and P treatments in Exp. 1 (**a**) and Exp. 2 (**b**) at 12 DAT, and in Exp 1 (**c**) and Exp. 2 (**d**) at 26 DAT. Different lowercase letters indicate significant differences in total chlorophyll content between P-dip and Ctrl within each water regime at $p < 0.05$ according to Tukey's HSD test. Different uppercase letters indicate significant differences in total chlorophyll content between the water regimes at $p < 0.05$ according to Tukey's HSD test. Error bars show standard deviations ($n = 4$).

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division, expansion, and genetic, physiological, ecological, and morphological characteristics. Water deficit significantly impacts these factors, affecting the overall quality and quantity of plant growth [24, 25]. These factors may have come into play under the WLW and MLD moisture treatments, where there was minimal water stress, resulting in better shoot parameters in contrast to the drier MOD and SVD regimes.

Changes in stomatal conductance and specific leaf weight

Rice plants employ stomatal closure as a drought avoidance mechanism to mitigate the effects of water stress [26]. Stomatal conductance is a key factor influencing photosynthetic rate in rice [27]. Our findings demonstrated that P treatments and soil water content affected gs, with mean values under P-dipping being significantly higher than those under control at both 12 and 26 DAT in Exp. 1. We also observed a relatively mild reduction in mean gs values under P-dipping than a drastic reduction in gs under control, as soil moisture content reduced from WLW to SVD treatments (Figure 4a). This suggests that P-dipping could have boosted the plant's ability to withstand drought stress—as evidenced by the slow rate of stomatal closure relative to control—thus a prolonged rice photosynthetic activity [28, 29]. This may also be explained by the late start time at which rice roots sense soil drying conditions and signal leaf stomatal closure. It was inferred that this leads to favourable conditions for gas exchange in the leaves and improves drought tolerance.

In Exp. 2, we did not observe the trend where gs under the Brod treatment reduced drastically with an increase in drought, suggesting that P application has a major effect on stomatal conductance regardless of the application method (P-dipping or broadcasting). Given that both the P-dip and Brod treatments in Exp. 2 had some amount of P at transplanting, the resilience of the rice plant against the effect of drought may have been boosted, unlike under the control treatment in Exp. 1. Overall, there was a reduction in stomatal conductance with water stress in both experiments. Studies have shown that rice plants respond to drought stress partly by inducing stomata closure [26]. Relatedly, the dry atmosphere in the greenhouse may have increased water evaporation from leaves, resulting in stomatal closure regulated by the plant hormone abscisic acid transport to prevent excessive loss of water [30]. In their study on how reducing stomatal density affects water use, drought tolerance, and heat stress tolerance, Caine [31] concluded that rice plants with fewer stomata are drought-tolerant and more conservative in water use.

Specific leaf weight (SLW) and leaf chlorophyll content are leaf traits associated with photosynthetic rate, stomatal conductance, and transpiration rate [32]. High SLW shows more leaf thickness and or stomatal density [33], which are important morphological traits for enhancing drought tolerance in plants [34]. Findings from this study showed that P-dipping resulted in significantly higher SLW values than control during drought stress. However, SLW values under control increased more than values under P-dipping after the rewatering period in Exp. 1. In contrast to the control and Broadcasting P treatments, the better results posted under P-dipping may be due to enhanced root morphology associated with P-dipping [18, 35], which could have promoted wider and deeper foraging of the soil volume for nutrients to support healthier plant growth. On the other hand, the increased SLW values under the control treatment relative to P-dipping after rewatering in Exp. 1 may be a result of the better plant recovery response upon elimination of the water stress, owing to an enhanced root system in the P-deficient control treatment. Studies have shown that soil phosphorus deficiency often results in the development of highly branched and elongated root growth with proliferated root hairs[36], which could have contributed to promoting soil resource exploration to ultimately drive up SLW during the recovery phase.

Effect of drought and P application on leaf chlorophyll content

Leaf chlorophyll content directly influences photosynthetic rate and dry matter production [37]. On the other hand, drought stress and P deficiency are known to affect chlorophyll quantity and its potential to optimally function [38]. In this study, water stress affected chlorophyll (Chl a, Chl a+b), with a general decline in the pigment content as drought stress increased (Figures 5 and 6). This finding agrees with Sharma and Dubey [39], who established that rice exposed to drought stress undergoes chlorophyll degradation. Thus, at a molecular level, drought stress could have damaged the efficiency of photosystem II, resulting in photoinhibition [40].

Whereas P-dipping did not have a significant effect on chlorophyll content in contrast to control, the former showed higher mean values than the latter at both 12 and 26 DAT in Exp. 1—demonstrating that P application may have influenced the observed increase in the pigment content. Similar findings have been reported by Starck [41], who found that P starvation caused stomatal limitation and disturbances in the chloroplast photosystem, leading to an overall photosynthesis inhibition. Relatedly, results from a study on the effect of phosphorus deficiency on the photosynthetic characteristics of rice plants revealed that there was a significant decline in chlorophyll content in P-deficient rice plants [42]. Siaga [43] noted an inverse relationship between leaf chlorophyll density and leaf area, where plants with smaller leaf area tend to compensate for that by increasing chlorophyll density. On the contrary, however, our finding showed a strong positive linear relationship between total chlorophyll content and leaf area (Figure 3a), which agrees with Liu [44], who observed that stability in rice chlorophyll content had a direct relationship with leaf area.

Conclusion

We evaluated the combined effect of drought stress and phosphorus treatments on the early-stage growth of NERICA 4 in rainfed upland-like conditions. As hypothesized, P-dip resulted in higher rice shoot biomass and stomatal conductance under drought conditions. Mean shoot biomass under the severe drought treatment for P-dip was significantly higher than that for broadcasted P. P-dip significantly increased leaf area compared to broadcasting. This effect was particularly pronounced under the severe drought conditions. P-dip significantly increased stomatal conductance compared to the control. Additionally, stomatal conductance declined less dramatically under P-dip as soil volumetric water content decreased compared to the control. This demonstrated that P-dip not only increased stomatal conductance compared to the control but also maintained stomatal opening for longer periods under dry soil conditions. The findings of our study shed additional light on the ongoing research on the importance of the P-dip technique to improve rice production in rice cultivation areas prone to drought or where supplementary irrigation is limited.

Conflicts of interest

The authors declare no conflicts of interest.

Author Contributions

Emmanuel Odama: Conceptualization, methodology, data collection, data curation, data analysis, writing, editing, proofreading, and experiment management. **Yasuhiro Tsujimoto**: Methodology, editing, and reviewing. **Isao Akagi:** Soil analyses and reviewing. **Keita Goto:** Data analysis, editing, and reviewing. **Shin Yabuta:** Methodology, data analysis, and reviewing. **Shotaro Tamaru:** Methodology and reviewing. **Jun-Ichi Sakagami:** Conceptualization, methodology, reviewing, supervision, and experiment administration. All authors read and approved the final manuscript.

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