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Research article

Effects of alternate wetting and drying or low light intensity factors on increasing grain yield and 2AP content in fragrant rice

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Abstract

Importance of the work: Alternating wetting and drying (AWD) is a technology that can save water without affecting yield and may increase the 2-acetyl-1-pyrroline (2AP) content. Furthermore, low light intensity (LL) may reduce yield but increase the 2AP content.

Objectives: To investigate the effects of AWD and LL conditions and their interactions on Hom Malaiman (HMM) aromatic rice variety in paddy fields.

Materials and Methods: HMM was grown over three consecutive seasons. A randomized complete block split plot design was used to investigate water management (continuous flooding (CF) and AWD) and light intensity (natural light (NL) and low light) conditions.

Results: Water management (W) and light conditions (L) affected agronomic, physiological and grain quality traits. The W × L interaction had significant effects on grain yield and 2AP content. AWD significantly increased the grain yield by 16.31% compared to the CF condition, whereas LL decreased the grain yield by 16.00% compared to the NL condition. AWD × NL resulted in the highest grain yield, whereas CF × LL resulted in the lowest yield. AWD and LL increased the 2AP content in rice grains by 3.22% and 8.28%, respectively. In addition, AWD × LL produced the highest 2AP content, whereas CF × NL produced the lowest 2AP content.

Main finding: The interaction between AWD and LL may not be suitable for increasing yield together with increasing the 2AP content. In addition, the influence of LL was greater than that of AWD in terms of increasing the 2AP content.

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Introduction

Demand for high-quality rice is increasing in both rice-producing and rice-importing countries (Gao et al., 2024). Aromatic rice varieties, such as Thai Jasmine and Indian Basmati, are globally recognized for their superior quality and popularity among consumers (Prodhan and Qingyoo, 2020). The aromatic trait in rice is primarily controlled by the *Osbadh2* gene, operating under homozygous recessive conditions, with 2-acetyl-1-pyrrolin (2AP) identified as the key compound responsible for fragrance (Bradbury et al., 2005). However, the expression of this trait is influenced by the rice variety's genetic background and multiple environmental and agronomic factors throughout cultivation and postharvest management (Kongpun et al., 2024). Therefore, strategies to maintain or enhance aromatic quality are critical for sustaining the production of aromatic rice, especially in the face of climate change challenges.

Drought stress and low light intensity have been identified as important contributors among the various factors influencing the biosynthesis of 2AP in rice. For example, other studies have demonstrated that exposure to mild drought conditions during the flowering stage can lead to an increase in the 2AP content in rice grains (Wang et al., 2013; Gui et al., 2022). A water-saving irrigation strategy known as AWD has been proposed to induce mild drought stress while reducing overall water use. This method involves allowing the soil in paddy fields to dry to a certain threshold before reapplying irrigation, thereby creating alternating periods of flooded and non-flooded conditions (Lampayan et al., 2015). Bao et al. (2018) and Ashraf et al. (2022) confirmed that AWD not only increased 2AP levels but also conserved water without reducing the grain yield. Furthermore, AWD effectively reduced nitrogen losses (NH_4^+, NO_3^- and total N), especially when combined with deep fertilizer placement (Islam et al., 2018; Gbedourorou et al., 2025).

Low light intensity in rice-growing regions can result from prolonged cloudy conditions during the wet season (June–October) or from elevated levels of air pollution, such as particulate matter (PM_{10} and $PM_{2.5}$), during the dry season (January–April), both of which contribute to substantially reductions in surface-level solar radiation (Qian et al., 2006). Empirical evidence has indicated a decline in annual solar radiation attributable to persistent cloud cover and increased air pollution (Liu et al., 2014). In response to the global demand for alternative energy sources, many countries have promoted the adoption of renewable energy technologies, which offer benefits in terms of carbon emissions reduction and enhanced energy security (Irie et al., 2019). Rooftop photovoltaic systems have gained popularity for electricity generation, particularly in countries such as Japan. A growing trend in this context is the integration of solar energy systems with agricultural land commonly referred to as agrivoltaics (Dupraz et al., 2011). Therefore, rice paddies in Asia are being considered as potential sites for the deployment of solar farm systems. However, concerns remain regarding the possible impacts of these systems on rice yield and grain quality (Gonocruz et al., 2021).

Reduction in light intensity through artificial shading, particularly during the grain-filling stage, has been shown to enhance the accumulation of 2AP in rice grains, with the extent of this effect varying according to the rice variety and growth stage (Mo et al., 2015; Chen et al., 2021; Xie et al., 2021). Conversely, insufficient light during the grain filling period has been reported to negatively impact rice yield, physiological processes and grain quality; specifically, it has been associated with alterations in the activities of starch synthase and related enzymes (Wang et al., 2013; Mo et al., 2015). Therefore, it is necessary to investigate the effects of low light intensity on yield performance, grain quality and 2AP biosynthesis in rice under various conditions such as prolonged cloudiness or air pollution. Such studies are particularly relevant in the context of the potential expansion of solar energy systems over rice cultivation areas.

Khao Dok Mali 105 (KDML105) is the most widely cultivated aromatic rice variety in Thailand (Vanavichit et al., 2018). Despite its popularity, this variety has several agronomic limitations, including tall plant height, susceptibility to lodging, vulnerability to multiple pests and diseases, high sensitivity to photoperiod and a relatively low yield potential (Vanavichit et al., 2018). Therefore, substantial national efforts have been directed toward the development of high-yielding aromatic rice varieties through advanced breeding programs (Chimthai et al., 2024). Nevertheless, the adoption of newly developed aromatic rice varieties requires not only agronomic superiority in terms of yield but also consumer acceptance, particularly in terms of sensory quality and cooking characteristics (Calingacion et al., 2014).

A recent example of an aromatic rice breeding program is the development of the Thai aromatic rice variety "Hom Malaiman" (HMM), which was derived from the Hom Nil variety through fast neutron irradiation (Center of Rice Science, 2024). That program identified the mutation site at

the *Osbadh2* gene locus. Furthermore, the program noted that HMM possesses several improved characteristics, including early maturity, long and slender grains, low amylose content (15–16%), moderate resistance to pests and diseases and enhanced yield performance (3.75 t/ha) compared to KDML105 (2.37 t/ha). Notably, HMM retains its strong aromatic quality even under irrigated field conditions in the central region of Thailand (Center of Rice Science, 2024).

The present study was a field experiment conducted over three consecutive growing seasons to evaluate the impacts of AWD throughout the growing season (approximately 4mth) and of reduced light intensity during the early grain-filling stage (20 d). The objective was to determine which of these factors, either independently or in combination, most influenced the grain yield, 2AP content, grain quality and their interactions in the newly developed aromatic rice variety, HMM. The hypothesis was that mild drought stress through AWD and reduced light intensity during grain filling could enhance 2AP accumulation in aromatic rice grains without negatively affecting yield.

Materials and Methods

Plant materials and field conditions

The field experiment was conducted using the newly developed aromatic rice variety HMM over three consecutive growing seasons, beginning with the dry season of 2023 (January–April 2023; DS2023), followed by the wet season of 2023 (June–October 2023; WS2023) and concluding with the dry season of 2024 (November 2023–March 2024; DS2024). The experimental site was located at the rice research field of Kasetsart University, Kamphaeng Saen Campus, Nakhon Pathom Province, Thailand (14°02'07.6" N, 99°58'03.0" E), which is situated in a humid tropical monsoonal climate zone.

Prior to the initiation of the experiment, soil samples were collected from 10 randomly selected locations within each plot. These samples were analyzed by the Soil Science Laboratory, Kasetsart University, Kamphaeng Saen Campus, Nakhon Pathom Province, Thailand and classified as sandy loam. The detailed soil characteristics for both the AWD and CF treatments are presented in Table 1. Meteorological data (air temperature, relative humidity, light intensity and rainfall) were recorded at 30 min intervals using a WatchDog 2000 Series Weather Station (Spectrum Technologies, Inc.; USA), which was installed at the center of the experimental field.

Experimental design and crop management

The experiment was laid out in a split plot within a randomized complete block design with three replications. Water irrigation management treatment was designated as the main plot, comprising two treatments (CF and AWD). The CF treatment maintained a water level of 10 cm above the soil surface, while the AWD treatment allowed water to decrease to 15 cm below the soil surface before re-irrigation. A buffer distance of 2 m was maintained between the CF and AWD plots to prevent water seepage. Light intensity was assigned as a subplot, consisting of two levels: full natural light (NL) and low light intensity (LL). The LL treatment was implemented using a 50% black shading net installed over the designated plots to simulate low light conditions.

Table 1 Comparison of soil properties between alternate wetting and drying (AWD) and continuous flooding (CF) plots

Soil property	AWD plot		CF plot	
	Value	Rating	Value	Rating
1. pH (soil:H_2O, 1:1)	5.62	Moderately acid	5.49	Moderately acidic
2. Electrical conductivity (EC_e; dS/m)	0.49	Non-saline	0.61	Non-saline
3. Organic matter (%)	1.37	Moderately low	0.91	Low
4. Available P (mg/kg)	36.23	High	39.87	High
5. Exchangeable K (mg/kg)	69.73	Medium	59.19	Low
6. Exchangeable Ca (mg/kg)	846.06	High	612.36	High
7. Exchangeable Mg (mg/kg)	106.6	Medium	81.41	Medium
8. CEC; cmol/kg	9.69	Moderately low	8.61	Moderately low
9. Soil texture		Sandy loam		Sandy loam
Sand (%)	47.34		53.17	
Silt (%)	35.62		31.83	
Clay (%)	17.04		15.00	
10. Bulk density (g/cm^3)	1.64		1.78	

In the CF treatment, irrigation was initiated 7 d after transplanting (DAT) by maintaining a water level of 5 cm. Subsequently, the water depth increased to 10 cm at 20 DAT and was maintained throughout the growing period (the water level was not permitted to fall below 5 cm). Irrigation ceased and the field was drained 7 d prior to harvest. In the AWD treatment, water management commenced at 20 DAT. Four field water tubes were installed per plot to monitor the water level, each positioned 15 cm below the soil surface and extending 10 cm above the ground. Water levels were monitored daily 0800 – 0900 hours using a watermark indicator placed within each water tube, following the method described by Lampayan et al. (2015). In addition, soil moisture tension was recorded using tensiometers installed at depths of 10 cm and 15 cm below the soil surface. The AWD cycle was suspended approximately 1 wk before the booting stage (R2), as defined by Counce et al. (2000), to prevent water stress during critical panicle development. AWD management resumed at the early grain-filling stage and continued until 7 d before harvest, after which the plots were fully drained.

Light intensity treatments were implemented following the method described by Mo et al. (2015). The LL treatment reduced incident radiation by at least 67% compared to NL conditions. Shading was achieved by installing a single layer of black shade netting, which was applied during the early grain-filling stage (R5) through to the hard dough stage (R7), for a total of 20 d. The net was positioned at 1 m above the rice canopy to ensure adequate air circulation and to minimize microclimatic effects.

Crop management

Initially, the rice seedlings were raised in a field nursery. At 20 d after sowing, uniform seedlings were transplanted into each subplot (2 m × 4 m) with a spacing between plants of 25 cm × 25 cm. All plots received the same rate of chemical fertilizer application, with a basal dose of 375 kg/ha of 18-8-8 (N-P-K) fertilizer applied 15 DAT, followed by 188 kg/ha of 46-0-0 (N-P-K as urea) fertilizer applied at 45 DAT. A pre-emergence herbicide was applied at 11 DAT and manual hand weeding was performed as needed to control weed growth. Pest and disease management practices were uniformly implemented across all treatments in accordance with the recommendations of Rice Department of Thailand (2023).

Water measurement

The total volume of water applied in the AWD treatment was estimated in two steps. First, the depth of water in the soil profile was calculated using Equation 1:

$$d = [(Ps-Pw) \times Bd \times D] / 100 \quad (1)$$

where d is the water depth in the soil (measured in millimeters), Ps is the percentage soil moisture content under flooded conditions, Pw is the percentage soil moisture content in dry soil before reflooding, Bd is the soil specific gravity and D is the soil depth (measured in millimeters).

Next, the amount of water was calculated using Equation 2:

$$Q = [(Ht – d) \times A] / 100 \quad (2)$$

where Q is the amount of irrigation water applied at -15 cm to 10 cm (measured in cubic meters), Ht is the water level from -15 cm to 10 cm (measured in millimeters), d is the water depth in the soil (measured in millimeters) and A is the area of the paddy field (measured in square meters).

The amount of irrigation water applied in the CF plot was calculated using Equation 3 (Ruensuk et al., 2021):

$$Q = (H \times A) / 1000 \quad (3)$$

where Q is the amount of irrigation water applied at 10 cm (measured in cubic meters), H is the water level at 10 cm (measured in millimeters) and A is the area of the paddy field (measured in square meters).

The total rainfall was recorded continuously from the transplanting date until harvest. Seasonal water use for each treatment was calculated as the sum of all irrigation water applied and the cumulative rainfall during the growing period. In addition, water use efficiency (WUE) was determined by dividing the grain yield by the total volume of water used (irrigation + rainfall) throughout the growth period.

Determination of grain yield and agronomic traits

The agronomic traits recorded were: days to flowering, plant height, tillers per plant, panicles per plant, seed set rate, 1,000-grain weight and grain yield. Days to flowering was defined as the number of days until 100% of the plants in each plot had flowered. Plant height, tillers per plant and panicles per plant were measured at maturity from

10 randomly selected hills per plot prior to harvest. Seed set rate and 1,000-grain weight were determined based on samples collected from the harvested area (8 m²/plot). Grain yield was measured in tonnes per hectare, with the grain moisture content adjusted to 14%. For the 1,000-grain weight, three replicates were randomly sampled from each plot.

Determination of crop growth rate

At harvest, five uniformly grown rice plants were randomly selected from each plot to estimate the harvest index. The above-ground biomass of these plants was dried in a hot-air oven at 75°C for 72 hr. After drying, the total dry matter weight of each plant was recorded. The harvest index was calculated using Equation 4:

$$\text{Harvesting index} = \text{Grain yield (t/ha)} / \text{Above ground dry matter (t/ha)} \quad (4)$$

The net assimilation rate (NAR) was computed using Equation 5:

$$NAR = [(W_2 - W_1) / T_2 - T_1)] / [(InLA_2 - InLA_1) / LA_2 - LA_1)] \quad (5)$$

where NAR is the net assimilation rate; W_2 and W_1 are the dry biomass weights of the plant at times T_2 and T_1, respectively, and LA_2 and LA_1 are the respective leaf areas corresponding to T_2 and T_1, respectively, and ln is the natural logarithm.

Determination of plant physiology traits

The physiological parameters measured were: photosynthetic rate, intercellular CO_2 concentration, stomatal conductance, transpiration rate and leaf temperature (Tleaf). These parameters were measured on flag leaves during the grain-filling stage under both the NL and LL conditions using a portable photosynthesis system (LI-6400; LI-COR, Inc.; USA). The leaf chlorophyll content was determined using a SPAD–502 Plus Chlorophyll Meter (Konica Minolta Sensing Inc.; Japan). Measurements were taken under both ambient conditions and with exposure to 400 µmol m^{-2} s^{-1} CO_2, under available light. All data were presented as mean ± SD values from three flag leaves randomly selected from each plot.

Determination of grain quality

The harvested grains were air-dried and stored at room temperature for 1 mth prior to grain quality analysis. A 300 g paddy grain sample was collected from each plot. Each sample was dehulled and polished using a mini rice polisher (Natrawee Technology Co. Ltd.). Three key grain quality parameters (gelatinization temperature, amylose content and percentage of chalkiness) were evaluated following the standard procedures described by Juliano (1985).

Determination of proline contents

The proline content in the grain samples was collected and analyzed at the soft dough stage (R6) according to the method of Sahin (2019). Subsequently, the amount of proline was calculated based on comparison with a standard curve of proline and expressed in micrograms per gram fresh weight.

Determination of 2AP contents

At the maturity stage, fresh paddy grain samples were randomly collected from 15 panicles located at the center of each plot. A 20 g sample of rice grains was immediately stored at -20°C for further analysis. The 2AP content was determined following the method described by Pitija et al. (2021). Instrument operation, data acquisition and processing were performed using the Agilent ChemStation software (versions A.01.04 and B.01.03; Agilent Technologies; Germany). The 2AP content was expressed in parts per million.

Statistical analysis

The recorded data were analyzed using the Statistix 10 software (Analytical Software; USA.). A combined analysis of variance was conducted across the three seasons for all measured traits. The interpretation of results focused on two experimental factors: water management (W) and light intensity (L), as well as their interactions, namely W × L and W × L × S. When both main effects and interactions were statistically significant, only the interaction effects were interpreted. Conversely, if only the main effects were significant without significant interactions, interpretation was limited to the main effects (Freund et al., 2010). Treatment means were compared using the least significant difference (LSD) test at a 95% confidence level and error bars represent ± standard deviation (SD). Correlation analyses were conducted using JASP software (version 0.18.1).

Results

Weather parameter

The photosynthetically active radiation (PAR), daily rainfall, relative humidity (RH) and air temperature for each growing season are presented in Fig. 1A. During DS2023, the mean PAR was 903 µmol/m²/s, while the mean day/night air temperatures were 28.8°C and 25.2°C, respectively, and the corresponding mean day/night RH values were 49.77% and 51.88%, respectively. In WS2023, the mean PAR increased slightly to 933 µmol m^{-2} s^{-1}, with day/night air temperatures of 29.4°C and 26.6°C, respectively, and mean RH values of 67.45% (day) and 69.64% (night). In the subsequent DS2024, the mean PAR declined to 866 µmol m^{-2} s^{-1}, with mean day/night temperatures of 28.08°C and 24.77°C, respectively, and RH values of 61.37% and 63.46%, respectively. The cumulative rainfall amounts recorded during DS2023, WS2023 and DS2024 were 26 mm, 260 mm and 71 mm, respectively (Figs. 5A–5C).

During the 20 d grain filling period, the mean PAR values under the NL conditions were 1,015 µmol/m²/s, 884 µmol/m²/s and 940 µmol/m²/s in DS2023, WS2023 and DS2024, respectively. In contrast, under the LL conditions, the corresponding PAR values were 322, 291 µmol/m²/s and 307 µmol/m²/s, respectively. These results indicated that the mean light intensity under the LL conditions was reduced by approximately 67% compared to the NL conditions across all three seasons. Furthermore, the average day/night canopy temperatures under the NL conditions across the three seasons were 30.34°C and 26.78°C, respectively, while those under the LL conditions were slightly lower at 29.43°C and 25.82°C, respectively, demonstrating that the LL conditions led to a reduction in canopy temperature by approximately 1°C (Fig 1B).

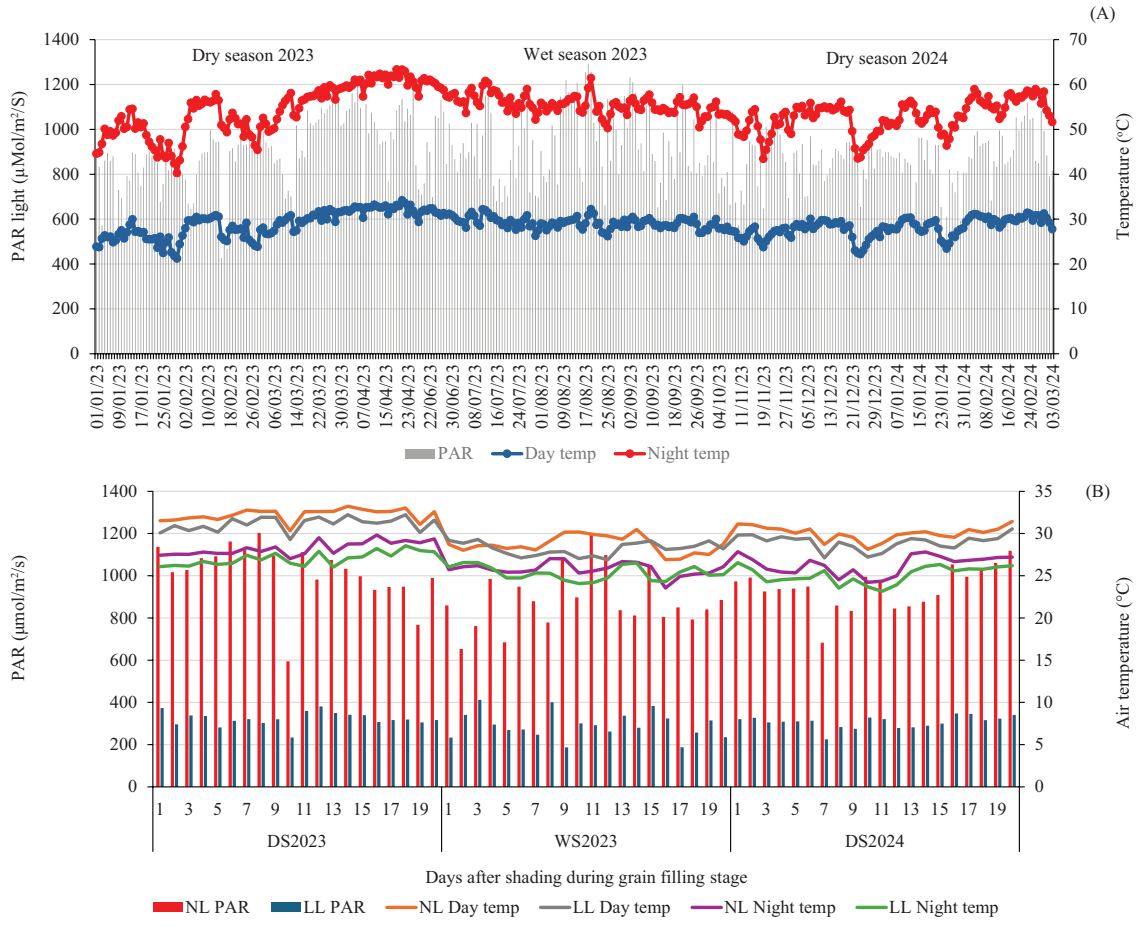


Fig. 1 Comparisons during rice cultivation across the 2023 dry season, 2023 wet season, and 2024 dry season: (A) Mean daytime temperature (temp), nighttime temperature and light intensity; (B) Mean daytime temperature, nighttime temperature and light intensity during the 20-d grain-filling stage under natural light (NL) and low light (LL) conditions across different seasons. PAR = photosynthetically active radiation.

Variance analysis of all traits

A combined analysis of variance was performed on the agronomic traits, physiological parameters, cooking quality attributes and 2AP content across the three growing seasons. The results are presented in Table 2. Both the W and L treatments significantly influenced some parameters of agronomic performance, physiological response, grain quality and 2AP accumulation ($p < 0.01$, $p < 0.05$). In addition, S had a significant impact on all measured traits.

Notably, the interaction between W × L significantly affected grain yield, grain chalkiness, 2AP content, proline accumulation, harvest index and NAR. The W × S interaction was significant for plant height, 1,000-grain weight and all the physiological traits. Similarly, L × S interaction was significant for plant height, NAR and the photosynthetic rate. Additionally, the W × L × S interaction was significant for plant height, tillers per plant and panicles per plant (Table 2).

Grain yield and agronomic traits

There was significant variation for all agronomic traits across the three growing seasons, except for days to flowering, which remained consistent throughout. The days to flowering and plant height were not significantly influenced by either W or L conditions (Table 2). Specifically, the mean of grain yield of three seasons improved from 3.31 t/ha under CF to 3.85 t/ha under AWD, reflecting a yield increase of 16.31%. Relative to the CF treatment, the AWD treatment produced significant increases in the number of tillers, number of panicles, seed set rate and 1,000-grain weight (Table 2 and Fig. 2).

The application of LL during the grain-filling stage significantly reduced the seed set rate, 1,000-grain weight and grain yield. The W × L interaction revealed that the LL conditions led to a reduction in grain yield across all three growing seasons. In the CF treatment, grain yield in the three growing seasons decreased by 11.79%, 7.05% and 23.49%, respectively, compared to the CF × NL treatment, while in the AWD treatment, there were reductions of 20.19%, 15.96% and 16.62%, respectively, relative to the AWD × NL treatment (Table 2 and Fig. 2).

In addition, the LL conditions did not significantly influence tiller or panicle formation. The reductions in seed set and grain weight under the LL conditions led to a decrease in grain yield from 3.89 t/ha under NL conditions to 3.27 t/ha under LL, corresponding to a 16.0% reduction (Figs. 2A–2F). Furthermore, the combination of AWD and NL resulted in the highest grain yields across all three growing seasons, achieving 4.11 t/ha, 4.76 t/ha and 3.79 t/ha in DS2023, WS2023 and DS2024, respectively. In contrast, the combination of CF and LL produced the lowest yields of 2.99 t/ha, 3.69 t/ha and 2.54 t/ha in the respective seasons. Additionally, the average grain yield during the wet season was consistently higher than in the dry season (Fig. 2F).

Table 2 Analysis of variance of effects of water management, light intensity and season on rice agronomic traits, physiological traits, grain quality and 2-AP content

Treatment	DF[1/]	PH	TN	PN	SS	TGW	GY	Chalky	Amylose	
Water (W)	ns	ns	**	**	**	**	**	**	**	
Light (L)	ns	ns	ns	ns	**	**	**	**	**	
Season (S)	ns	**	**	**	ns	**	**	**	ns	
W × L	ns	ns	ns	ns	ns	ns	**	**	ns	
W × S	ns	**	ns	ns	ns	*	ns	ns	ns	
L × S	ns	*	ns	ns	ns	ns	ns	ns	ns	
W × L × S	ns	*	**	**	ns	ns	ns	ns	ns	
CV	1.32	4.83	14.06	15.9	4.65	3.34	8.48	12.03	3.47	
Grand Mean	80.89	90.24	15.1	12.19	83.11	30.45	3.58	8.05	17.68	
Treatment	AK	2AP	Proline	HI	NAR	Pn	Ci	Gs	E	Tleaf
Water (W)	ns	*	**	**	*	**	ns	ns	ns	**
Light (L)	ns	**	**	**	**	**	**	**	**	**
Season (S)	ns	**	**	*	**	**	**	**	**	**
W × L	ns	**	*	*	*	ns	ns	ns	ns	ns
W × S	ns	ns	ns	ns	**	**	**	*	**	*
L × S	ns	ns	ns	ns	*	**	ns	ns	ns	ns
W × L × S	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CV (%)	11.23	6.54	10.3	10.8	16.47	14.28	7.43	20.01	20.31	4.79
Grand mean	4.58	3.35	3.38	39.37	1.72	22.49	287.09	438.09	6.79	32.56

[1/]DF = days to flowering, PH = plant height, TN = number of tillers per plant, PN = number of panicles per plant, SS = seed set rate, TGW = 1,000-grain weight, GY = grain yield, AK = alkaline test, HI = harvest index, NAR = net assimilation rate, Pn = photosynthetic rate, Ci = intercellular CO_2 concentration, Gs = stomatal conductance, E = transpiration rate, Tleaf = leaf temperature; CV = coefficient of variation.

* significant difference ($p < 0.05$); ** highly significant difference ($p < 0.01$); ns = non-significant difference ($p \geq 0.05$).

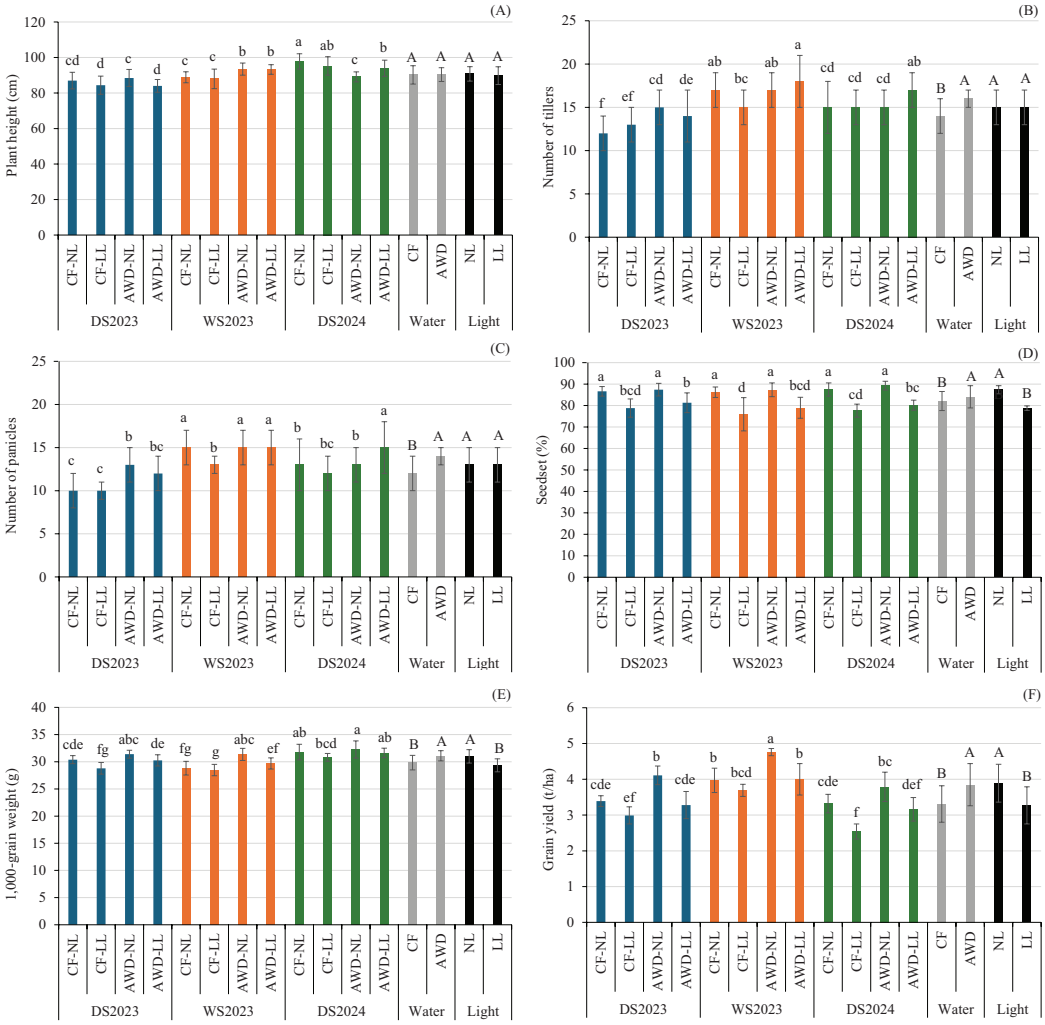


Fig. 2 Comparison of mean agronomic traits under four treatments [continuous flooding (CF), alternate wetting and drying (AWD), natural light (NL), and low light (LL)] across three consecutive seasons [dry season 2023 (DS2023), wet season 2023 (WS2023), and dry season 2024 (DS2024)]. (A) Plant height; (B) Number of tillers; (C) Number of panicles; (D) Seedset; (E) 1,000-grain weight; (F) Grain yield Different lowercase letters above columns indicate significant differences ($p < 0.05$) among treatment combinations of water management (Water) and light intensity (Light), while uppercase letters indicate significant differences ($p < 0.05$) between levels of water management or light intensity. Error bars represent ± SD.

Physiological traits

There were variations in the physiological traits, similar those in the agronomic traits, across the different growing seasons. Among the factors studied, light intensity during the 20 days grain-filling period exerted a greater effect on physiological responses than the water management practices. Compared to the NL conditions, under the LL conditions, intercellular CO_2 concentration, stomatal conductance and SPAD values increased significantly by 24.70%, 8.55% and 9.30%, respectively. In contrast, the photosynthetic rate, transpiration rate, leaf temperature (Tleaf), harvest index and NAR were significantly reduced under the LL conditions by 8.75%, 20.70%, 6.32%, 7.31% and 23.59%, respectively (Figs. 3A–3H).

No significant differences were observed between the CF and AWD treatments in terms of intercellular CO_2 concentration, stomatal conductance, transpiration rate and SPAD values. However, compared to the CF treatment, the AWD treatment significantly enhanced the photosynthetic rate, Tleaf, harvest index and NAR by 8.97%, 2.77%, 14.28% and 20.83%, respectively. Furthermore, the AWD × NL interaction consistently resulted in the highest photosynthetic rate, harvest index and NAR across all growing seasons, while the CF × LL combination produced the lowest values for these physiological parameters (Figs. 3A–3H).

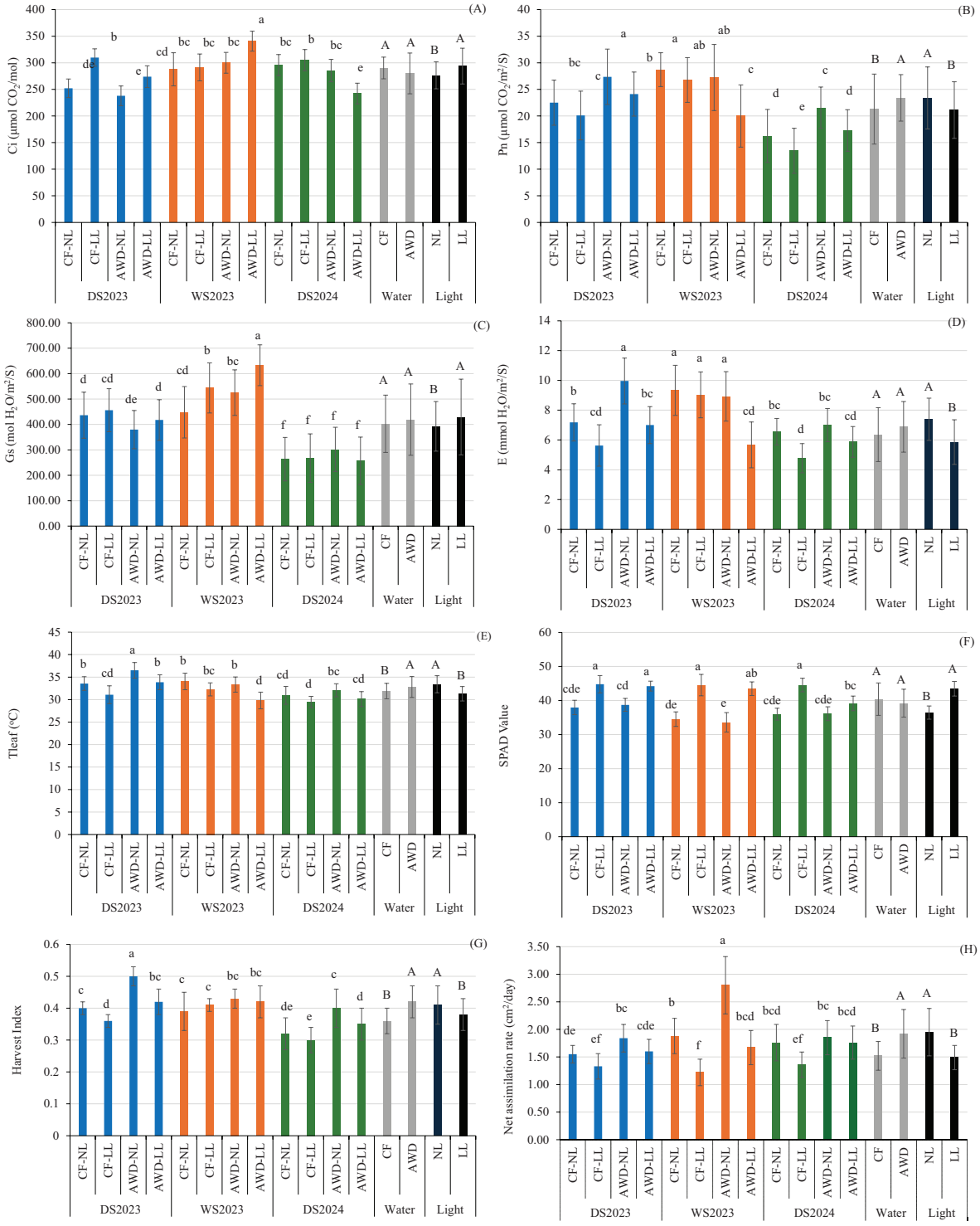


Fig. 3 Comparison of the mean physiological traits among traits of four treatments (continuous flooding = CF, alternate wetting and drying = AWD, natural light = NL, low light = LL) in three consecutive seasons (dry season 2023 = DS2023, wet season 2023 = WS2023, dry season 2024 = DS2024): (A) intercellular CO_2 concentration = Ci; (B) photosynthetic rate = Pn; (C) Stomatal conductance = Gs; (D) transpiration rate = E; (E) Leaf temperature = Tleaf; (F) SPAD value; (G) Harvest index; (H) Net assimilation rate, where different lowercase letters above columns indicate significant differences ($p < 0.05$) within treatment combinations of water management (Water) and light intensity (Light) and uppercase letters above columns indicate significant differences ($p < 0.05$) between water management or light intensity conditions and error bars indicate ± SD

Grain quality and proline and 2AP contents

Both water management and light intensity significantly influenced the grain quality and aroma in rice (Figs. 4A–4D), with the exception of gelatinization temperature (data not shown). Notably, both water management and light intensity had a significant effect on the percentage of chalkiness in the grains. The combination of AWD × LL consistently resulted in the highest chalkiness across all three growing seasons, with values of 13.26%, 14.33% and 13.25% in DS2023, WS2023 and DS2024, respectively. In contrast, the CF × NL conditions produced the lowest chalkiness percentages of 3.85%, 3.38% and 3.84% across the corresponding seasons (Figs. 4D).

The AWD × LL interaction reduced amylose levels to 16.44%, 16.83% and 16.58%, whereas CF × NL treatment resulted in increased values of 18.55%, 18.99% and 18.57% in DS2023, WS2023 and DS2024, respectively (Figs. 4C). Despite these variations, the amylose content under all treatment conditions remained within the soft rice category, defined as less than 20% (Juliano, 1985).

The 2AP content in mature rice grains was significantly influenced by both water management and light intensity. The W × L interaction showed that low light conditions led to increased 2AP concentrations across all growing seasons. In the CF treatment, For the three growing seasons, the 2AP concentrations increased by 8.35%, 7.06% and 9.03%, respectively, compared to the CF × NL treatment, while in the AWD treatment, the increases were 7.60%, 12.06% and 9.69%, respectively, relative to the AWD × NL treatment (Table 2, Fig. 4A) indicating that light intensity had a greater impact on 2AP accumulation than water management. Notably, the 2AP levels varied significantly among the growing seasons, reflecting seasonal influences on aromatic compound accumulation.

The proline content measured at the soft dough stage during grain filling followed a similar trend to that observed for the 2AP accumulation in the mature grains. Specifically, the proline levels were higher under both AWD and LL conditions compared to CF and NL, respectively. Consequently, the W × L interaction indicated that low light conditions led to increased proline accumulation across all three growing seasons in both the CF and AWD treatments (Table 2, Fig. 4B). Notably, the CF × NL treatment, which represented non-stress conditions, produced the lowest proline content, although it was not significantly different from that observed under the AWD × NL treatment (Fig. 4B).

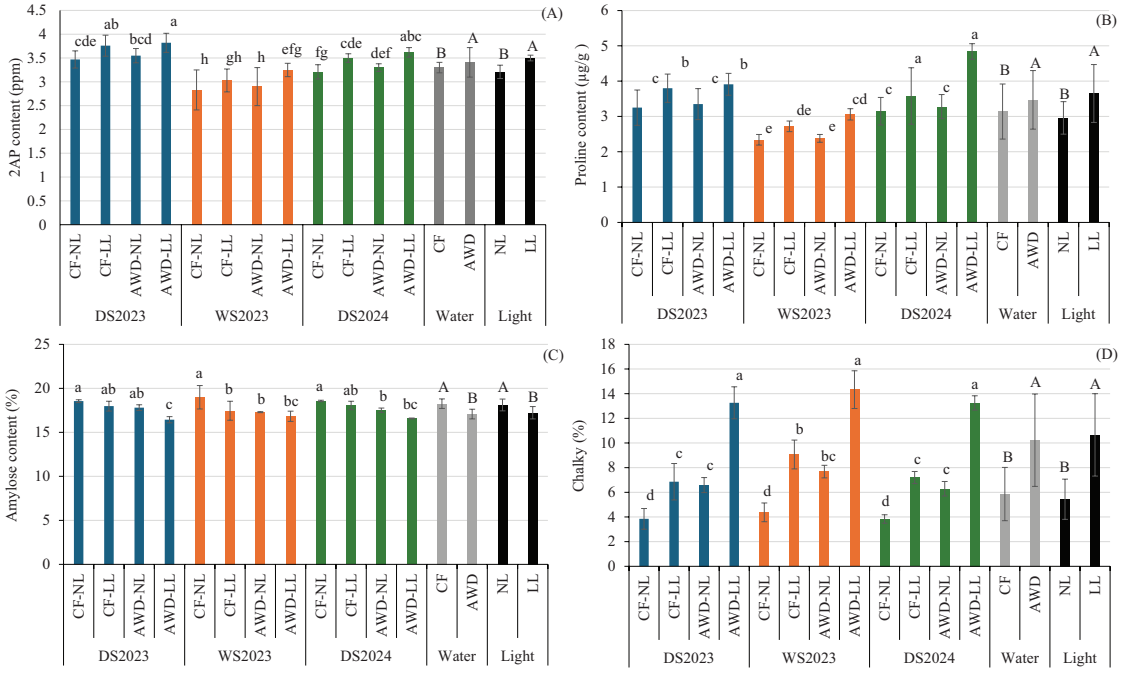


Fig. 4 Comparison of mean aroma-related traits under four treatments [continuous flooding (CF), alternate wetting and drying (AWD), natural light (NL), low light (LL)] across three consecutive seasons [dry season 2023 (DS2023), wet season 2023 (WS2023), dry season 2024 (DS2024)]: (A) 2-acetyl-1-pyrroline (2AP) content; (B) Proline content; (C) Amylose content; (D) Chalky Different lowercase letters above columns indicate significant differences ($p < 0.05$) among treatment combinations of water management (Water) and light intensity (Light) while uppercase letters indicate significant differences ($p < 0.05$) between levels of water management or light intensity. Error bars indicate ± SD. ppm = parts per million.

Water application and water use efficiency

Under AWD conditions, the water level was permitted to drop to -15 cm below the soil surface. Based on the results, at this depth, the average soil moisture tension was approximately -15 kPa during the dry seasons (DS2023 and DS2024), whereas during the wet season (WS2023), the average soil moisture tension was approximately -10 kPa at the same water level. Throughout the dry seasons, the cycle of alternate wetting and drying was applied 9–10 times from the seedling stage to the booting stage and an additional 2 applied irrigation events occurred during the grain-filling stage. In contrast, during the wet season, AWD cycles were implemented 7 times from the seedling stage to the booting stage and once during grain filling (Figs. 5A–5C).

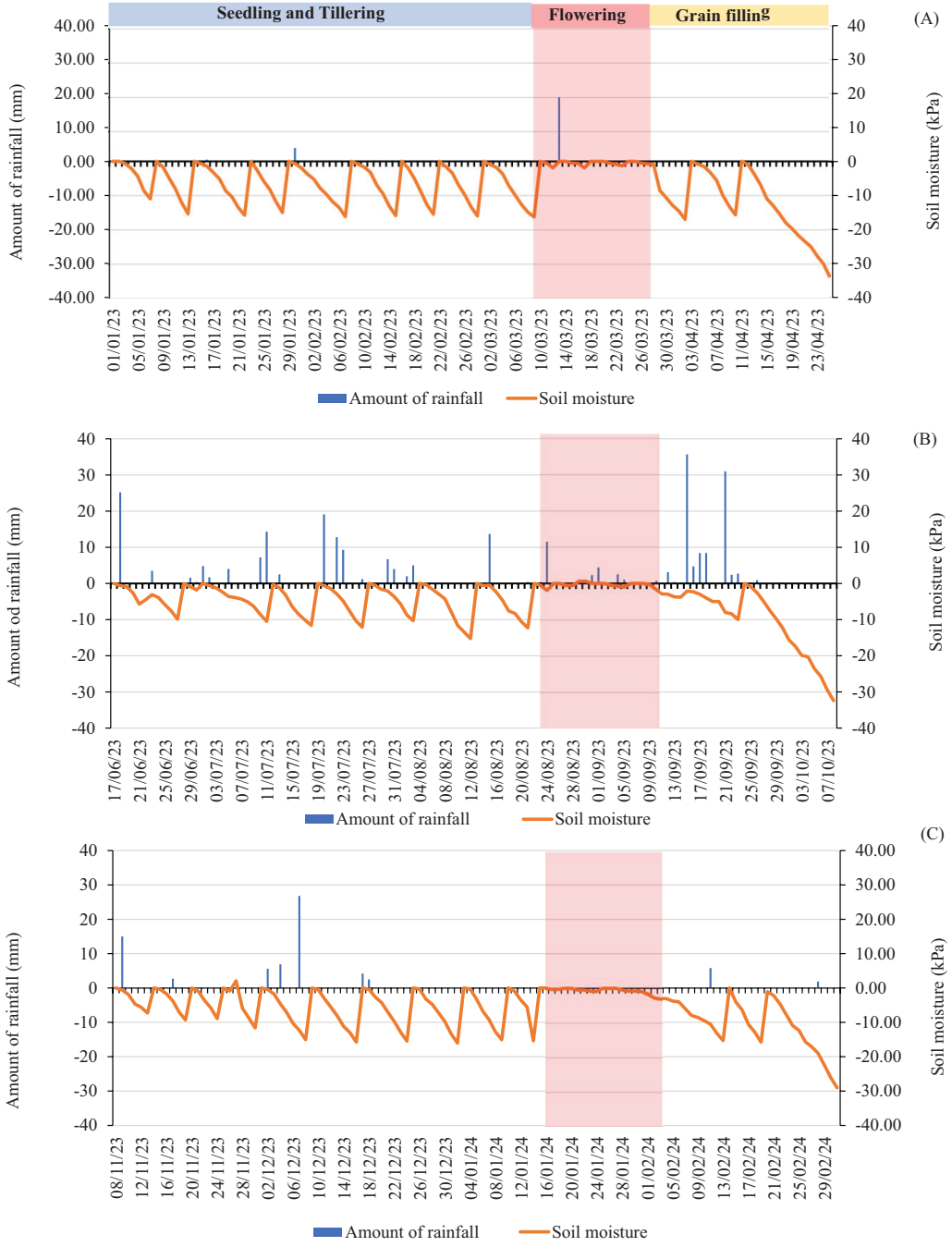


Fig. 5 Soil moisture content and amount of rainfall under alternate wetting and drying conditions in: (A) dry season 2023; (B) wet season 2023; (C) dry season 2024, where pink band indicates flowering period.

The total water input, comprising both irrigation and rainfall, was compared between the AWD and CF treatments across the dry and wet seasons. The amounts of water applied in the three growing seasons are presented in Fig. 6A. In the CF plots, the total amounts of water application during DS2023, WS2023 and DS2024 were 6,435 m³/ha, 7,175 m³/ha and 6,960 m³/ha, respectively. In contrast, the AWD plots received 5,085 m³/ha, 5,800 m³/ha and 5,785 m³/ha of water during the same respective seasons. Based on these results, AWD significantly reduced water usage compared to CF, achieving water savings of 21%, 19% and 17% in DS2023, WS2023 and DS2024, respectively.

Compared to the CF treatment, WUE was significantly higher under the AWD treatment. Additionally, WUE was greater under the NL conditions than under the LL conditions. Across all treatments in the three growing seasons, the highest WUE was in the AWD × NL combination, followed by AWD × LL, CF × NL and CF × LL (Fig. 6B).

Correlation analysis

Under the AWD conditions, the 2AP content had a significant positive correlation with proline ($p < 0.001$) and the SPAD value ($p < 0.05$), while there were significant negative correlations with intercellular CO_2 concentration ($p < 0.05$) and stomatal conductance ($p < 0.05$), as shown in Fig. 7A. The grain yield was positively correlated with seed set ($p < 0.05$), plant height ($p < 0.01$), harvest index ($p < 0.001$), biomass ($p < 0.05$) and amylose content ($p < 0.05$), whereas there was a significant negative correlation with chalkiness ($p < 0.05$), as shown in Fig. 7C.

Under the LL conditions, 2AP content was significantly and positively correlated with proline ($p < 0.001$) and Tleaf ($p < 0.01$) and significantly negatively correlated with intercellular CO_2 concentration ($p < 0.001$) and stomatal conductance ($p < 0.001$), as shown in Fig. 7B. Grain yield under the LL conditions has a significant positive correlation with harvest index ($p < 0.01$) and a significant negative correlation with amylose content ($p < 0.05$), as shown in Fig. 7D.

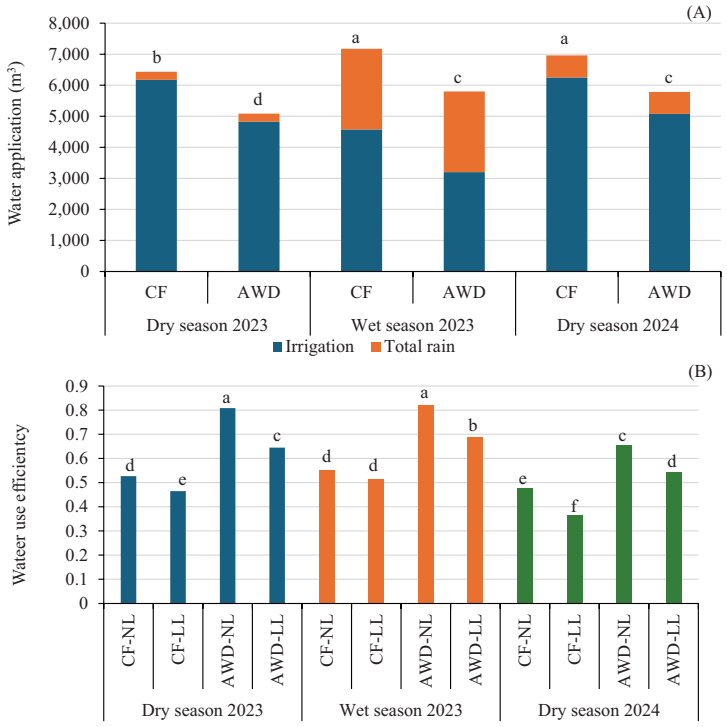


Fig. 6 Comparison of treatments (continuous flooding = CF, alternate wetting and drying = AWD, natural light = NL, low light = LL) in three consecutive seasons: (A) total water use in rice field (irrigation, rainfall = Total rain); (B) water use efficiency, where different lowercase letters above columns indicate significant differences ($p < 0.05$)

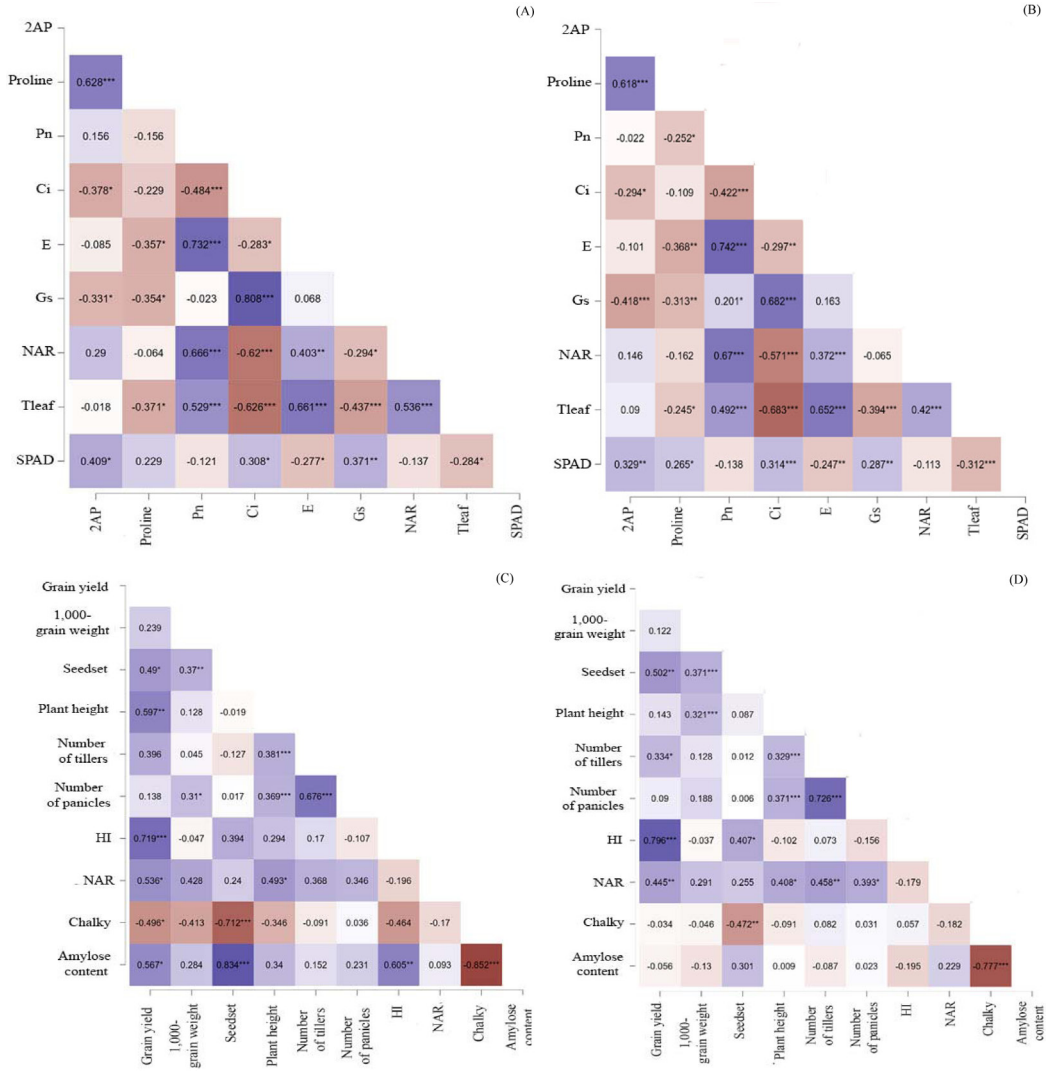


Fig. 7 Pearson's correlation heatmap indicating relationships between 2-acetyl-1-pyrroline (2AP), proline and physiological traits: (A) under alternate wetting and drying (AWD); (B) low light intensity (LL), (C) between grain yield, agronomic traits and grain quality under AWD (C); (D) between grain yield, agronomic traits and grain quality under LL from 3 growing seasons

Discussion

This study examined the impacts of water management and light intensity during the grain-filling stage. Based on the results, there were significant alterations in the yield and quality traits, particularly under the AWD and LL treatments, which exerted the greatest influence on grain yield and 2AP content. Seasonal variation also contributed to differences in all evaluated traits, with inconsistent temperature patterns observed across dry seasons, in contrast to the relatively stable temperatures recorded during the wet season. Furthermore, the rainy season had higher relative humidity compared to the dry seasons, while light intensity in DS2024 was lower than that in DS2023 and WS2023.

Under varying seasonal conditions, the AWD treatment reduced water use by approximately 17–21%, aligning with the findings by Bouman et al. (2007) and Carrijo et al. (2017), who reported water savings of 30% and 23%, respectively. In addition to conserving water, AWD in the present study significantly enhanced WUE, corroborating the results of Anapalli et al. (2023). In addition, AWD promoted agronomic traits, such as increased tillers per plant, panicles per plant, seed set rate and 1,000-grain weight, collectively contributing to a higher grain yield compared to the CF condition. These findings were consistent with those reported by Yang et al. (2017) and Song et al. (2021).

Lampayan et al. (2015) noted that implementing AWD with a threshold of -15 cm (the approach also adopted in the current study) did not negatively affect yield, as rice roots

could continue to access water from saturated soil layers. Furthermore, rhizosphere drying induced by AWD has been reported to enhance root-zone oxygenation and modulate plant hormone signaling, thereby improving grain-filling rates (Zhang et al., 2012; Yang et al., 2017). The increase in grain yield under AWD observed in the current study was further supported by the significantly higher photosynthetic rate, NAR and harvest index under AWD relative to CF. These physiological improvements suggested that the enhanced yield under moderate AWD conditions may be attributed to sustained water uptake under mild stress, improved photosynthetic efficiency and greater biomass accumulation, ultimately leading to an increased harvest index (Lampayan et al., 2015; Yang et al., 2017).

At a water level of -15 cm below the soil surface, the corresponding soil moisture tension was approximately -15 kPa. According to Bao et al. (2018), this level is classified as moderate soil drying. In contrast, Anapalli et al. (2023) reported that soil water tensions ranging from 0 to -10 kPa generally do not result in yield reductions. Nevertheless, a meta-analysis conducted by Gao et al. (2024), which synthesized data from 437 AWD-related studies, indicated an average yield reduction of approximately 1.56% under AWD conditions. Therefore, in the current study, the water level was maintained at -15 cm below the soil surface, which could increase not only the WUE but also the grain yield of rice.

Water management practices influenced the accumulation of 2AP, the key aromatic compound in fragrant rice. Numerous studies have demonstrated that AWD (typically characterized by soil water tension ranging from -15 to -25 kPa during the booting or grain-filling stages) can effectively enhance 2AP concentration in rice grains (Bao et al., 2018; Deng et al., 2018; Mo et al., 2019). In the current study, AWD resulted in a 3.22% increase in 2AP content compared to CF. Although this increase was modest, other reports have shown that AWD enhanced 2AP levels by 5–45% depending on various factors (Bao et al., 2018; Ashraf et al., 2022; Zhang et al., 2023). Therefore, Kongpun et al. (2024) indicated that the optimal soil moisture content should be considered and that the increase in 2AP content may vary among fragrant rice varieties, soil types and climates. Furthermore, they recommended that water management strategies should be specifically tailored to the fragrant rice cultivar, local soil properties and regional agroecological conditions to achieve optimal aroma expression.

In the current study, the AWD treatment during both the vegetative and reproductive stages increased the levels of endogenous proline, a precursor for the biosynthesis of 2AP in rice grains. According to Bradbury et al. (2008), amino acids (glutamate, proline and ornithine) are converted into Δ^1-pyrroline-5-carboxylate (P5C) through the catalytic actions of enzymes such as proline dehydrogenase (PRODH), Δ^1-pyrroline-5-carboxylate synthetase (P5CS) and ornithine aminotransferase (OAT). P5C, or Δ^1-pyrroline, can then react non-enzymatically with methylglyoxal to form 2AP. Dien et al. (2019) confirmed that a considerable amount of proline was accumulated under drought stress. Therefore, the elevated proline content observed under AWD in the current study may represent a key factor contributing to the increased 2AP concentration in rice grains (Fig. 8). However, notably, other components involved in the 2AP biosynthetic pathway were not analyzed in the current experiment. Nevertheless, similar trends have been reported by Bao et al. (2018) and Ashraf et al. (2022), supporting the proposed relationship between water stress-induced proline accumulation and 2AP enhancement.

In addition, the AWD treatment in the current study resulted in a reduction in the amylose content and a concurrent increase in the proportion of chalky grains. These findings were consistent with those reported by Hou et al. (2023), who observed that AWD conditions decreased amylose levels while increasing grain chalkiness. Fofana et al. (2010) and Yang et al. (2019) suggested that drought stress may suppress amylose synthesis by downregulating the expression of the *Wx* gene, which is responsible for amylose biosynthesis.

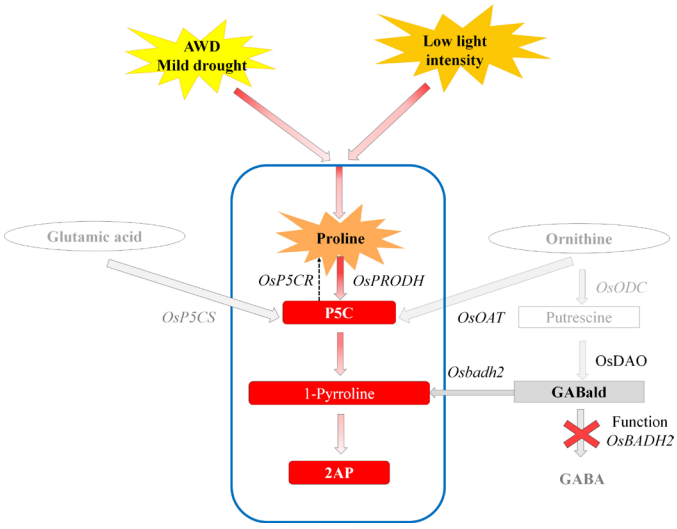


Fig. 8 Proposed regulatory effects of alternate wetting and drying (AWD) and low light intensity on the biosynthesis of 2-acetyl-1-pyrroline (2AP) in Hom Malaiman aromatic rice. The increased 2AP content is suggested to occur via the proline pathway, involving Δ^1-pyrroline-5-carboxylate (P5C) and 1-pyrroline as intermediates. PRODH = proline dehydrogenase, P5CS = Δ^1-pyrroline-5-carboxylate synthetase, OAT= ornithine aminotransferase. (Modified from Bao et al., 2018)

Furthermore, drought stress has been shown to impair the starch synthesis capacity in the endosperm during the grain-filling period, attributed to a decline in the activity of key enzymes involved in sucrose-to-starch conversion, ultimately leading to inhibited grain growth and increased chalkiness (Yang et al., 2019)).

Photosynthetically active radiation (PAR), in the range 400–700 nm, is the portion of solar radiation utilized by plants for photosynthesis (McCree, 1981). The field-level PAR readings in the current study were consistent with other studies (Mo et al., 2015; Chen et al., 2021), with the current study confirming that LL conditions during grain filling significantly reduced seed set and 1,000-grain weight, leading to a 16.0% decrease in grain yield compared to the NL conditions. LL also altered physiological traits by increasing intercellular CO_2 concentration, stomatal conductance and SPAD values, while decreasing photosynthetic rate, transpiration rate and Tleaf. These findings aligned with another report by Pan et al. (2016), indicating that LL reduces photosynthetic performance. Reduced light-harvesting efficiency under LL likely impairs photochemistry, thus limiting overall photosynthetic productivity (Panda et al., 2019). In terms of grain quality, LL conditions increased the percentage of chalky grains. According to Li et al. (2022), LL reduced the activities of granule-bound starch synthase and starch branching enzyme during grain filling, which along with mild drought stress, delays endosperm development, leading to loosely packed amyloplasts and increased grain chalkiness.

The light intensity reduction in the current study (a 67% decrease from natural levels), was consistent with the findings of Mo et al. (2015), Li et al. (2020) and Xie et al. (2021). Ganguly et al. (2024) reported a similar reduction in the wet season, with light intensity decreasing from 1,400 µmol/m²/s in the dry season to approximately 500 µmol/m²/s (a 64% reduction). This aligned with Murchie et al. (2002), who noted that rice grown in the rainy season typically received less than 500 µmol/m²/s due to overcast conditions, while optimal net photosynthesis occurred at 800–1000 µmol/m²/s. Thus, the low light intensity applied in the current study mirrored cloudy weather conditions, which significantly impaired photosynthesis and may ultimately reduce rice yield.

In contrast, LL conditions during grain filling significantly increased both the 2AP and proline concentrations in the rice grains. The 2AP increase under LL conditions aligned with the findings from Mo et al. (2015), Li et al. (2020) and Chen et al. (2021). In the current study, there was a positive correlation between 2AP and proline accumulation, indicating that under LL conditions, plant stress induced 2AP biosynthesis via the proline pathway, as for drought and salinity stress (Fig. 8). Mo et al. (2015) suggested that increased 2AP under LL was attributable to higher gamma-aminobutyric acid (GABA) levels; however, the current study did not measure GABA content. GABA is known to act as a growth promoter under stress (Kinnersley et al., 2000). While Mo et al. (2015) also observed an increase in proline at the early grain-filling stage under LL, its effect on 2AP accumulation was not clear. Therefore, further research is needed to explore the relationship between GABA:2AP and proline:2AP under LL conditions and their impacts on aroma enhancement. There should be additional study on the differences due to growth stage, treatment duration and rice variety under LL conditions to optimize aroma enhancement strategies.

In the current study, the average Tleaf at 20 d under LL conditions was 2.0°C lower than under NL conditions and the canopy temperature decreased by 1.0°C. This finding aligned with Prodhan et al. (2017), who reported that lower temperatures during the grain-filling stage under LL conditions enhanced the 2AP content in aromatic rice. One hypothesis could be that the enzymes involved in the 2AP biosynthesis pathway are more active under LL conditions. Therefore, LL conditions during grain filling may reduce Tleaf and canopy temperatures, thereby increasing enzyme activities related to 2AP biosynthesis.

The interaction between water management and light intensity showed that AWD × NL resulted in the highest yield, while CF × LL led to the lowest yield. Similarly, Li et al. (2020) reported yield reductions under LL conditions in aromatic rice. The interaction between AWD and LL had the greatest impact on the 2AP content, while CF × NL had the least effect. Li et al. (2020) observed increased 2AP under LL but a decrease under water stress. However, their study applied more severe water stress conditions than were used in the current study. Therefore, a 67% reduction in light intensity for 20 d during grain filling negatively impacted grain yield but positively affected 2AP synthesis, more so than mild drought under AWD (-15 kPa) management throughout the growing season.

Conclusion

AWD management was confirmed as an effective tool for efficient water use in rice fields without compromising yield, while also slightly increasing the 2AP content. In contrast, LL, although possibly enhancing the 2AP content, was not suitable for maximizing yield. However,

variability between the current results and other studies could be attributed to factors such as rice variety, climate and soil properties. Therefore, further research is needed on aromatic rice varieties, soil properties and the optimal soil moisture content (-15 to -25 kPa) under AWD, along with an appropriate light intensity reduction (30–60%) for each growing season, to enhance the 2AP content without negatively impacting yield or other grain qualities.

Conflict of Interest Statement

There are no conflicts of interest.

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