

Effect of light stress on growth and allelopathic activity of rice in southern Thailand

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ABSTRACT: Global warming, such as rising temperature and lack of water, has effects on agriculture. Climate change can also reduce sunlight continuously for several months. This problem brings about this research to study the effect of light on growth and allelopathic activity of rice aiming at exuding allelochemicals to suppress weed growth for rice plants. Seven rice cultivars, i.e., Khao Dawk Mali 105, Phathum Thani 1, RD55, Chai Nat 1, Sang Yod Phatthalung, Leb Nok Pattani, and Cho Lung, were grown for three weeks. Two light intensities were used: 300 and 200 μ mol E/m²/s. Results showed that rice cultivars had effect on growth and allelopathic potential when tested with lettuce seedlings. Phathum Thani 1 rice cultivars had the lowest growth and the highest allelopathic potential when compared with other cultivars. Interestingly, rice cultivars that grew well, e.g., Leb Nok Pattani and Chai Nat 1, showed a low allelopathic potential. Rice plants receiving 200 μ mol E/m²/s of light grew better but had less allelopathic potential compared with those receiving 300 μ mol E/m²/s of light. This study expands the knowledge of rice allelopathy including the effect of physiological stress across rice cultivars and landraces.

KEYWORDS: rice, light stress, allelopathy, growth, southern Thailand

INTRODUCTION

Rice is an important crop with more than half of the world's population having rice as a staple food. At present, cultivated rice (*Oryza sativa* L.) has evolved from wild rice for more than 7,000 years into many rice cultivars, a result from natural adaptation and selection by farmers from past to present. Rice landraces are resources for human. They are legacy coming along with rice farming [1].

Rice has long been a staple food for Thai people. People in different areas prefer rice of different cultivars, but the generally popular one is Khao Dawk Mali 105 (KDML 105). In Southern Thailand, people prefer modern rice cultivars, such as Phathum Thani 1, Chai Nat 1, RD29, RD49, RD55, and RD57. Moreover, there are landraces favored by locals such as Sang Yod Phatthalung, Cheang Phatthalung, Leb Nok Pattani, and Hom Kradang Nga.

Climate change, either from natural variation or human activity, causes changes of average weather such as temperature, rain and wind. Global warming is a phenomenon when the earth cannot dissipate heat from sun rays as normal. This renders higher average temperature affecting living things on the earth [2, 3].

Although earth's average temperature doesn't much increase at present, it already has effects on ecosystems and general climate change, for example, melting of polar ice and glaciers, stronger storms and drought affecting plant cultivation, animal farming and fishery [3]. Moreover, global warming has affected cultivation by rising temperature, drought, and reduced sunlight from reaching the ground by small dust particles in the air. Higher number of pests, insects, and pathogens are also caused by higher temperature [3].

Allelopathy, a natural phenomenon, is biochemical reaction of plants and microbes. The product of the reaction is allelochemical, which can inhibit or stimulate chemical reactions affecting growth and development of plants and microbes [4]. For example, allelochemical exuded from a plant, a donor, can inhibit germination and growth of another plant, a recipient [5]. In general, allelopathy occurs when a plant or plant variety exudes some allelochemicals causing damages to other varieties nearby [6,7]. They can be exuded from parts of plants (volatiles, roots, leaf leachates, etc.) and from decayed materials to reduce growth of other plants nearby [8]. Important rice allelochemicals include momilactone B, 3-isopropyl-5-acetoxycyclohexene-2-one-1, and 5,7,4'-trihydroxy-3',5'-dimethoxyflavone [9]. The release of allelochemical is more or less dependable on many factors such as quality and quantity of light, nutrient, drought, temperature, chemicals, and age of plants [10]. UV and visible light intensity can affect amounts of chlorogenic acid and isochlorogenic acid. Red light can increase levels of ferulic acid and p-coumaric acid amounts compared with normal condition [11]. Relationship among light stress, allelopathy, and growth can be shown by a study on *Koeleria macrantha*. Growth of *K. macrantha*, a grass in Northern America, was suppressed by *Centaurea stoebe*, an invasive plant, in both high and low lights. However, adding activated carbon, which can absorb allelochemicals, resulted in higher growth of *Koeleria* for almost seven folds in high light environment [12].

Allelochemicals can affect growth, physiology and biochemicals of recipient plants by damaging cell membrane. There are changes in free radicals leading to damages of plant tissue, movement of compounds out of cells, and leaf tissue wilts [13]. They can also affect cell division and expansion, nutrient absorption, photosynthesis, respiration, protein synthesis, and hormonal function [14] rendering reduced function of plants.

Generally, climate change leads to global warming, which affects agriculture including rice cultivation. However, studies on the effect of light stress on rice cultivars, especially landraces which have high genetic variation and can adapt to local environment, are still lacking. This study aimed to assess physiological relationship among light stress, rice growth, and allelopathic activity across several rice cultivars including landraces. The results would be beneficial to enhance the knowledge of rice allelopathy and physiological stress studies.

MATERIALS AND METHODS

Plant materials

The effect of light stress on allelopathic activity was studied with seven Thai rice cultivars: Khao Dawk Mali 105, Phathum Thani 1, RD55, Chai Nat 1, Sang Yod Phatthalung, Leb Nok Pattani, and Cho Lung. Khao Dawk Mali 105 (KD), an improved cultivar is generally consumed all over the country. Rice cultivars favourable in Southern Thailand are divided into modern cultivars, i.e., Phathum Thani 1 (PT), RD55 (RD), and Chai Nat 1 (CN), and popular landraces, i.e., Sang Yod Phatthalung (SY) registered as a Geographical Indication (GI) in Thailand and Malaysia, and Leb Nok Pattani (LN). These rice cultivars were compared with Cho Lung (CL), a high allelopathic cultivar [15]. Rice seeds were obtained from Phatthalung Rice Research Center, Phatthalung Province, Southern Thailand.

Rice growth

Seven rice cultivars were grown in 10 cm diameter pots filled with TIPP's All Natural Garden Soil (Songkhla, Thailand). The physico-chemical properties of the soil are 347.96 ppm total nitrogen, 72.52 ppm total P, 37.38 ppm available P, 479.34 ppm total K, and 28.48 g/kg organic matter. The soil pH and electrical conductivity were 7.08 and 0.24 ds/m, respectively [16]. The plants were grown in a plant growth cabinet (model GS–1000CH, Kinetics Corporation Ltd., Thailand) for three weeks, the age of high allelopathic

activity at seedling stage. Light intensities were set at 300 or 200 μ mol E/m²/s for 12 h per day to study the effect of low light stress. Day/night temperatures were set at 28 °C/23 °C at 60% constant humidity. Water was applied every 2–3 days. Completely randomized experimental design with 7 rice cultivars and 2 light intensities was done with ten replicates. At the end of the experiment, rice growth was measured using lengths and dry weights of shoot and root after drying at 80 °C for 48 h.

Allelopathic activity assessment

Allelopathic activity assessment was modified from a previous experiment [17]. Water extraction method from rice shoot was used at 5% (w/v) concentration testing on lettuce seeds. Rice plants were air-dried for 24 h. A total of 0.075 g rice shoot material, from 2-3 rice plants, was cut into approximately 0.5 cm pieces and submerged in 1.5 ml type III deionized water in a microcentrifuge tube and left for 24 h at room temperature to make rice water extract. Ten lettuce seeds were placed in a 3.5 cm diameter Petri dish supplied with 0.7 ml extract. The Petri dish was covered, wrapped with parafilm, and left for three days at room temperature. This is the time that seedling growth difference can be clearly distinguished among treatments. Type III deionized water was used as control. After that, germination percentage was measured. Five germinated lettuce seedlings per Petri dish were randomly selected, to measure lengths of shoot and root, and dried at 80 °C for 24 h to measure dry weight. Ten replicates were used, each one from each pot of rice plants. Inhibition percentages of germination, shoot length, root length, and dry weight of lettuce seedlings were calculated from values of (control treatment) $\times 100$ /control.

Data analysis

Data were analyzed using two-way analysis of variance (two-way ANOVA) at p = 0.05 significance level using rice cultivars and light intensities as factors. Mean differences were calculated by Tukey's test using SPSS for Windows version 29.

RESULTS

Rice growth

Two-way ANOVA results showed that rice cultivar had significant effects on shoot length, root length, shoot dry weight, and root dry weight of rice (p < 0.001 for all traits; Table 1).

Rice cultivars Leb Nok Pattani, Cho Lung, and Khao Dawk Mali 105 had high shoot lengths. Sang Yod Phatthalung, Leb Nok Pattani, and Chai Nat 1 had high root lengths. Chai Nat 1 had high shoot and root dry weights, while Phathum Thani 1 had the lowest shoot length, root length, shoot dry weight, and root dry weight (Fig. 1).

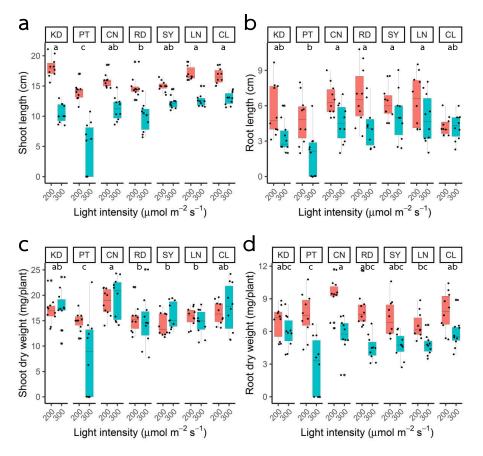


Fig. 1 Box plots showing rice growth when receiving different light intensities: (a), shoot length; (b), root length; (c), shoot dry weight; (d), root dry weight. Rice cultivars used were KD, Khao Dawk Mali 105; PT, Pathum Thani 1; CN, Chai Nat 1; RD, RD55; SY, Sang Yod Phatthalung; LN, Leb Nok Pattani; and CL, Cho Lung. Light intensities used were 200 (red bars) and 300 (green bars) μ mol E/m²/s. Different letters indicate significant differences among rice cultivars at $p \leq 0.05$.

Table 1 1	wo-way ANOVA analysis of the effect of light stress
on growth	n of rice.

Source	Dependent variable	df	F	p-value
Cultivar	Shoot length	6	21.808	< 0.001
	Root length	6	4.902	< 0.001
	Shoot DW	6	8.241	< 0.001
	Root DW	6	4.441	< 0.001
Light	Shoot length	1	294.486	< 0.001
•	Root length	1	33.882	< 0.001
	Shoot DW	1	0.988	0.322
	Root DW	1	98.071	< 0.001
Cultivar × light	Shoot length	6	7.789	< 0.001
	Root length	6	1.459	0.197
	Shoot DW	6	2.978	0.009
	Root DW	6	3.109	0.007

Light intensity had significant effects on shoot length, root length, and root dry weight of rice (p < 0.001 for all traits; Table 1). Light at 200 µmol $E/m^2/s$ resulted in higher shoot length, root length,

and root dry weight of rice than those at 300 μ mol E/m²/s (Fig. 1). However, light intensity did not have significant effect on the shoot dry weight. Interaction between rice cultivar and light intensity had significant effects on shoot length, shoot dry weight, and root dry weight of rice (Table 1).

Allelopathic activity

Rice cultivar had significant effects on inhibition percentages of germination (p = 0.021), shoot length (p = 0.019), and dry weight (p = 0.030) of lettuce seedlings (Table 2).

Rice cultivar Phathum Thani 1 showed the highest inhibition percentages of germination, shoot length, and dry weight compared with other cultivars. Leb Nok Pattani had the lowest inhibition percentages of germination and shoot length, while Chai Nat 1 had the lowest inhibition percentage of dry weight compared with other cultivars. However, inhibition percentage of root length did not show significant difference among cultivars (Fig. 2).

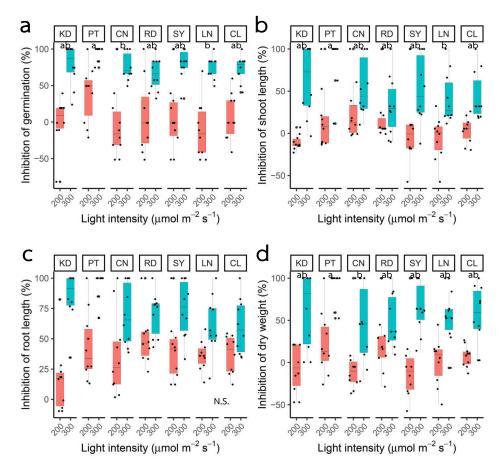


Fig. 2 Box plots showing inhibition percentages of lettuce seedlings applied with extracts from rice receiving different light intensities: (a), germination inhibition percentage; (b), shoot length inhibition percentage; (c), root length inhibition percentage; and (d), dry weight inhibition percentage. Rice cultivars used were KD, Khao Dawk Mali 105; PT, Pathum Thani 1; CN, Chai Nat 1; RD, RD55; SY, Sang Yod Phatthalung; LN, Leb Nok Pattani; and CL, Cho Lung. Light intensities used were 200 (red bars) and 300 (green bars) µmol $E/m^2/s$. Different letters indicate significant differences among rice cultivars at $p \le 0.05$. N.S. = non-significant.

Table 2 Two-way ANOVA analy	sis of the effect of light stress
on allelopathic activity of rice.	

Source	Dependent variable	df	F	<i>p</i> -value
Cultivar	Germination inhibition	6	2.596	0.021
	Shoot length inhibition	6	2.641	0.019
	Root length inhibition	6	2.182	0.049
	Dry weight inhibition	6	2.417	0.030
Light	Germination inhibition	1	173.029	< 0.001
	Shoot length inhibition	1	75.618	< 0.001
	Root length inhibition	1	89.335	< 0.001
	Dry weight inhibition	1	90.077	< 0.001
Cultivar × light	Germination inhibition	6	0.602	0.728
	Shoot length inhibition	6	2.177	0.049
	Root length inhibition	6	2.886	0.011
	Dry weight inhibition	6	1.047	0.398

Light intensity had significant effects on all traits of rice allelopathy (p < 0.001 for all traits; Table 2). Light at 300 µmol E/m²/s resulted in higher inhibition of rice extracts on lettuce seedlings than 200 µmol E/m²/s (Fig. 2). Interaction between rice cultivar and light intensity had significant effects on rice allelopathy for the inhibition percentages of shoot length (p = 0.049) and root length (p = 0.011; Table 2).

DISCUSSION

Different rice cultivars have different growth rates which affect allelopathic activity. For example, Phathum Thani 1 had the lowest growth compared with other cultivars with the lowest shoot length, root length, shoot dry weight, and root dry weight (Fig. 1a–d) but had the highest allelopathic activity with the highest inhibition percentages of germination, shoot length, and dry weight of lettuce seedlings

(Fig. 2a,b,d). This is an addition to our previous knowledge of high allelopathic Thai rice cultivars, such as Cho Lung. In contrast, rice cultivars that grew well such as Leb Nok Pattani that had high shoot length (Fig. 1a) and Chai Nat 1 that had high root length, shoot dry weight, and root dry weight (Fig. 1b,c,d) had low allelopathic activity. Leb Nok Pattani had significantly lower inhibition percentages of germination and shoot length of lettuce seedlings compared with other rice cultivars, and Chai Nat 1 had significantly lower inhibition percentage of lettuce seedlings dry weight compared with other cultivars (Fig. 2a,b,d). High allelopathic rice cultivars have advantage in rice cultivation as these cultivars can suppress the growth of weed in the rice field, rendering less use of herbicide which is harmful to both farmers and environment. Different rice cultivars behave differently in their growth potential due to their different genetic potential and parental background. This also influences their response to light stress. A study on nutrient stress of 3 rice cultivars showed that when nutrient concentrations were changed from high to low, rice growth decreased while allelopathic potential increased with different rates of the 3 cultivars [18]. This is in accordance with a theory that plants allocate nutrients to balance between growth and pathogen defense which is a type of stress following the growth-differentiation balance theory (GDB) [19]. Plants use primary metabolites such as proteins, lipids, nucleic acids, and carbohydrates for growth while secondary metabolites are not directly related to plant growth but help in other functions such as defense against pathogens. Allelochemicals released from plants are secondary metabolites [4]. Therefore, rice cultivars that allocate high amount of resources such as nutrients and energy for growth, e.g. Leb Nok Pattani and Chai Nat 1 may allocate lower amount of resources for defense including allelochemical production. In contrast, rice cultivars that grew slowly such as Phathum Thani 1 might allocate high amount of resources for secondary metabolite production including allelochemicals rendering high allelopathic activity. Growth-defense trade-off also depends on biotic and abiotic factors such as light, circadian clock, carbon dioxide, temperature, humidity, water, nutrient, and soil microbes. Activation of defense network has a substantial demand for resources, and an inverse relationship between defense and growth indicates resource redistribution under a fixed total resource budget [20].

Light at 200 µmol $E/m^2/s$ resulted in higher rice shoot length, root length, and root dry weight than 300 µmol $E/m^2/s$ (Fig. 1). It could be that 300 µmol $E/m^2/s$ light is too high for rice growth in this experiment rendering stress and less growth with yellow leaves. Light at 200 µmol $E/m^2/s$ could be suitable for rice growth. Light intensity in the field of Thailand ranges approximately between 200–1,000 µmol $E/m^2/s$. Light intensities used to grow rice in growth chamber are between 70–700 μ mol E/m²/s [21–23]. Light at 300 μ mol E/m²/s resulted in higher inhibition of rice extract on lettuce seedlings growth than 200 μ mol E/m²/s for all traits (Fig. 2). This suggested that stress from too high light intensity could result in higher allelochemical production thus higher allelopathic activity. Plants receiving stress allocate more resources for growth to produce defense compounds [24]. Some rice cultivars are sensitive to photoperiod, i.e., Khao Dawk Mali 105, Sang Yod Phatthalung, Leb Nok Pattani and Cho Lung. They flower in winter when the photoperiod is less than 12 h per day. Other rice cultivars, i.e., Phathum Thani 1, RD55 and Chai Nat 1 are non-photosensitive to photoperiod. However, this might not affect their response to light intensity stress as the results did not form 2 distinct groups of rice to growth and allelopathic activity responses.

Many enzymes and metabolites are involved in rice allelochemical production under stress. Flavones, phenolic acids, fatty acids, terpenoids, and steroids are rice allelochemicals [22, 25, 26]. Some enzymes such as cytochrome P450 (P450s) are involved in diverse biochemical pathway to produce primary and secondary metabolites such as phenylpropanoids, lipids, alkaloids, and terpenoids [27]. Glutathione S-transferase (GST) is essential in protecting cells from abiotic and biotic stresses, including oxidative stress, xenobiotic stress, and pathogen stress in plants [28, 29]. Rice allelopathy is connected with molecular mediation of secondary metabolic pathways [30, 31]. Genes involved in various secondary metabolic pathways, including phenylpropanoids, terpenoids, lignin and lignans, simple phenols, and different flavonoid pathways, are up-regulated when rice is stressed in interaction with barnyardgrass [32]. There have been several other reports concerning the effect of light on allelopathy. Increasing temperature and day length resulted in higher allelopathic effects of allelopathic rice accessions initially, decreasing at 2-3 leaf stage and continuously increasing again at 4-5 and 7-8 leaf stages. Factor affecting allelopathic potential the most is temperature, followed by growth stage and light [33]. The effect of light on growth, allelochemical production, and native plants of garlic mustard (Alliaria petiolata) under extended shade, natural shade, and no-shade was studied. Garlic mustard biomass was the highest under natural shade and the lowest under noshade. Garlic mustard reduced growth of native plants (Blephilia hirsuta and Ageratina altissima) the highest under natural shade. Considering whole community, the invasion reduced growth of native species the most under no-shade, having the least invasive species biomass with highest allelochemical production [34]. Moreover, Guinea grass reduced invasion and growth in height and weight of four other plant species in the same area under shade better than full sunlight [35].

CONCLUSION

Rice cultivars had effects on growth and allelopathic activity of rice. Rice cultivar Phathum Thani 1 had the lowest growth but highest allelopathic activity compared with other cultivars. In contrast, rice cultivars that grew well such as Leb Nok Pattani and Chai Nat 1 had low allelopathic activity. This could be because plants allocate nutrients to balance between growth and defense following growth-differentiation balance theory. Light at 200 μ mol E/m²/s resulted in higher rice growth than 300 μ mol E/m²/s. Light intensity at 300 μ mol E/m²/s might be too high for rice growth in this experiment rendering stress and less growth. Light at 300 μ mol E/m²/s resulted in higher inhibition of rice extract on lettuce seedlings growth than 200 µmol $E/m^2/s$. Rice plants receiving too high light intensity, which is 300 μ mol E/m²/s in this experiment, might be stressed resulting in higher allelochemical production and higher allelopathic activity. Results from this study could be used to estimate the effects of light stress on growth and allelopathic activity of rice cultivation as climate change also affects growth of plants and rice cultivation worldwide. Low light intensity from reduced sunlight could prevail occasionally for several months affecting photosynthesis and growth of rice including its allelopathic activity to weed in the rice field.

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REFERENCES

- Saeton S, Preecha R, Kotchapakdee K, Vaewsak A, Seethongkaew P, Khamprasert A, Nounong N (2007) Southern Rice Landraces, vol 1, Phatthalung Rice Research Center, Division of Rice Research and Development, Rice Department, Ministry of Agriculture and Cooperatives, Thailand.
- Climate Center (2023) Climate Change, Meteorological Department, Ministry of Digital Economy and Society, Thailand. Available at: http://climate.tmd.go.th/ content/article/9. [in Thai].
- Climate Center (2023b) Global Warming, Meteorological Department, Ministry of Digital Economy and Society, Thailand. Available at: http://climate.tmd.go.th/ content/file/11. [in Thai].
- 4. Rice EL (1984) *Allelopathy*, 2nd edn, Academic Press, Orlando, Florida.
- Putnam AR (1985) Weed allelopathy. In: Duke SO (ed) Weed Physiology. Reproduction and Ecophysiology, CRC Press, Flolida, pp 131–155.

- An M, Pratley E, Haig T (1998) Allelopathy from Concept to Reality, Environmental and Analytical Laboratories and Farrer Centre for Conservation Farming, Charles Sturt University, Wagga, NSW.
- Bhowmik PC, Inderjit (2003) Challenges and opportunities in implementing allelopathy. Crop Prot 22, 661–671.
- Koocheki A, Lalegani B, Hosseini SA (2013) Ecological consequences of allelopathy. In: Cheema ZA, Farooq M, Wahid A (eds) Allelopathy – Current Trends and Future Applications, Springer, pp 23–38.
- 9. Kong CH, Li HB, Hu F, Xu XH, Wang P (2006) Allelochemicals released by rice roots and residues in soil. *Plant Soil* **288**, 47–56.
- 10. Rongsa K (2008) Study on the allelopathic potential in *Limnophila aromatica* and *Otacanthus azureus*. MSc thesis, Srinakharinwirot University, Thailand.
- 11. Rizvi SJH, Rizvi V (1992) Allelopathy Basic and Applied Aspects, Springer Dordrecht.
- 12. Chen S, Xiao S, Callaway RM (2012) Light intensity alters the allelopathic effects of an exotic invader. *Plant Ecol Divers* **5**, 521–526.
- Patsai S (2011) Allelopathic effect of *Praxelis clematidea* (Griseb.) R.M.King & H.Rob on germination and growth of some crops. MEd thesis, Srinakharinwirot University, Thailand.
- 14. Sawatdikarn S, Tientong S (2008) Allelopathy between crops and weeds. *J Appl Sci* **7**, 95–105.
- 15. Sudprang J (2015) Comparison of allelopathic activity between local rice cultivars of southern Thailand and improved cultivars. BSc thesis, Prince of Songkla University, Thailand.
- Nopphakat K, Runsaeng P, Klinnawee L (2022) Acaulospora as the dominant arbuscular mycorrhizal fungi in organic lowland rice paddies improves phosphorus availability in soils. Sustainability 14, 31.
- Klinnawee L, Kaewchumnong K, Nualtem K (2023) Effect of phosphorus deficiency on allelopathic activity of lowland *indica* rice. *ScienceAsia* 49, 184–191.
- Sarsutham K (2018) Relationship between allelopathic potential and growth of rice (*Oryza sativa* L.) under stress condition. MSc thesis, Prince of Songkla University, Thailand.
- 19. Le Bot J, Benard C, Robin C, Bourgaud F, Adamowicz S (2009) The 'trade-off' between synthesis of primary and secondary compounds in young tomato leaves is altered by nitrate nutrition: Experimental evidence and model consistency. *J Exp Bot* **60**, 4301–4314.
- He Z, Webster S, He SY (2022) Growth-defense tradeoffs in plants. *Curr Biol* 32, R589–R683.
- Mahmood K, Khan MB, Song YY, Ijaz M, Luo SM, Zeng, RS (2013) UV-irradiation enhances rice allelopathic potential in rhizosphere soil. *Plant Growth Regul* 71, 21–29.
- Zhang Q, Li L, Li J, Wang H, Fang C, Yang X, He H (2018) Increasing rice allelopathy by induction of barnyard grass (*Echinochloa crus-galli*) root exudates. J Plant Growth Regul 37, 745–754.
- Stuerz S, Asch F (2021) Responses of rice growth to day and night temperature and relative air humidity– leaf elongation and assimilation. *Plants* 10, 134.
- 24. Gawronska H, Golisz A (2006) Allelopathy and biotic stresses. In: Reigosa MJ, Pedrol N, Gonzalez L (eds) Allelopathy: A Physiological Process with Ecological Implications, Springer, Dordrecht, The Netherlands, pp

211-227.

- 25. Kong C, Xu X, Liang W, Zhou Y, Hu F (2004) Nonphenolic allelochemicals in root exudates of an allelopathic rice variety and their identification and weedsuppressive activity. *Acta Ecologica Sin* 24, 1317–1322.
- Seal AN, Pratley JE, Haig T, An M (2004) Identification and quantitation of compounds in a series of allelopathic and non-allelopathic rice root exudates. *J Chem Ecol* 30, 1647–1662.
- Mizutani M, Ohta D (2010) Diversification of P450 genes during land plant evolution. *Annu Rev Plant Biol* 61, 291–315.
- Soranzo N, Gorla MS, Mizzi L, De Toma G, Frova C (2004) Organisation and structural evolution of the rice glutathione s-transferase gene family. *Mol Genet Genomics* 271, 511–521.
- 29. Peng X, Wang N, Sun S, Geng L, Guo N, Liu A, Chen S, Ahammed GJ (2023) Reactive oxygen species signaling is involved in melatonin-induced reduction of chlorothalonil residue in tomato leaves. *J Hazard Mater* 443, 130212.
- 30. Bi HH, Zeng RS, Su LM, An M, Luo SM (2007) Rice allelopathy induced by methyl jasmonate and methyl

salicylate. J Chem Ecol 33, 1089-1103.

- Fang C-X, Xiong J, Qiu L, Wang H-B, Song B-Q, He H-B, Lin R-Y, Lin W-X (2009) Analysis of gene expressions associated with increased allelopathy in rice (*Oryza sativa* L.) induced by exogenous salicylic acid. *Plant Growth Regul* 57, 163.
- 32. Sultana MH, Alamin M, Qiu J, Fan L, Ye C (2023) Transcriptomic profiling reveals candidate allelopathic genes in rice responsible for interactions with barnyardgrass. *Front Plant Sci* **14**, 1104951.
- 33. Xu G, Shen S, Zhang F, Zhang Y, Kato-Noguchi H, Clements DR (2018) Relationship between allelopathic effects and functional traits of different allelopathic potential rice accessions at different growth stages. *Rice Sci* 25, 32–41.
- Smith LM, Reynolds HL (2014) Light, allelopathy, and post-mortem invasive impact on native forest understory species. *Biol Invasions* 16, 1131–1144.
- 35. Morrison CR, Rhodes AC, Bowman EA, Plowes RM, Sedio BE, Gilbert LE (2023) Adding insult to injury: Light competition and allelochemical weapons interact to facilitate grass invasion. *Ecosphere* **14**, e4438.