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Integrated molecular and physiological mechanisms of drought tolerance in rice: linking NCED1 expression to chlorophyll and carbohydrate dynamics

Fouad Razzaq Al-Burki[1*], Maher R. Salman[1], Yahya A. Al-Ethari[2], Mohammed A. Aljaberi[3], Wafaa N. Radhi[1], Hussein M. Shamran[1]

[1]Jabir Ibn Hayyan University for Medical and Pharmaceutical Sciences - Faculty of Pharmacy.
[2] Directorate of Al-Najaf Agriculture, Al-Najaf, Iraq.
[3] Al-Muthanna University- Center of Desert Studies and Sawa Lake, Al-Muthanna University, Iraq.
*Corresponding author e-mail: fouad.razzaq@jmu.edu.iq

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Abstract

The aime of current dtuy was to analyze the productive, physiological, and molecular responses of six rice genotypes under various levels of water stress (100%, 50%, and 25% of field capacity). A field study was conducted during the summer season of 2024. The results showed a clear contrast between the genotypes, with Pokkali and genotype 13 outperforming the other genotypes, recording the highest average grain yield (522 and 547 g/m²), 1000-grain weight (27.2 and 29.4 g), and number of grains per spike (139 and 144), respectively. The results clearly demonstrated that Pokkali and Genotype 13 outperformed all other genotypes across productive, physiological, and molecular parameters. They recorded the highest grain yield, grain number, and 1000-grain weight, while maintaining stable total chlorophyll content (0.075–0.078 mg/g dry weight) and exhibiting a marked increase in total carbohydrate accumulation (21.85 and 20.07 mg/g dry weight at 25% FC). At the molecular level, both genotypes showed the highest induction of NCED1 expression under severe stress, reaching 3.90- and 4.20-fold relative to the control. These results show that the coordinated performance indicates that drought tolerance has been stimulated by an integrated regulatory mechanism combining physiological stability, metabolic modulation and activation of ABA-associated genes, making it one of the most promising drought tolerance candidates among the tested genotypes. Therefore, ABA can be used in molecular improvement programs aimed at developing high-yielding, water-efficient cultivars in water-stressed environments.

Keywords: FC, NCED1, ABA, Rice, Carbohydrate, Chlorophyll.

Introduction

Irrigated agriculture- particularly rice cultivation-is among the sectors most severely impacted by water stress, leading to reductions in rice yields by as much as

30% in recent decades [1]. The plant ability to tolerate of water shotage is very important to crop management and food security under rapid changing climate [2]. Therefore, understanding the integrated mechanisms-molecular, physiological, and productive-that enable rice cultivars to survive and produce under drought conditions is an urgent necessity. For improvement program, study of quantitatively genes linked with physiological and production patterns is very necessary to knowledge in challenges in water stress. Therefore, combining production traits such as number of grains per spike, 1000-grain weight, and grain yield with gene expression measures at the species level plays a crucial role in developing reliable predictive models [3]. In Genetic variations plays a role in determining the combinations between productivity and drought tolerance [4]. Rice exposure to water shortage, especially during sensitive stages (flowering and grain filling) cause decreased in the grains number, grain weight, and panicle filling rate which leads to a decrease in grain yield by more than 50-70% in some sensitive cultivars [5].

The NCED1 gene (9-cis-epoxycarotenoid dioxygenase 1) is associated with water deficiency mechanisms. It is a rate-limiting enzyme for abscisic acid (ABA) biosynthesis and induces the oxidative cleavage of 9-cis-violaxanthin or 9-cis-neoxanthin to produce xanthoxin in the plastids, which is key to handling water stress [6]. Drought-tolerant rice increases the expression of abscisic acid synthesis genes under stress conditions through reducing water loss by transpiration, stomatal closure and stimulating the accumulation of osmolytes [5, 7, 8], the NCED1 gene expression increased by two- to four-fold in resistance cultivars compared to sensitive cultivars, accompanied by improved water use efficiency as well as stabilization of plant tissue chlorophyll content. Also, enhancing the expression of NCED1 leads to increased ABA accumulation, which helps plants tolerate drought better, It also enhances molecular regulation during plant adaptation [9 , 10]. In addition to genetic regulation, physiological aspects play a fundamental role in maintaining plant production performance under stress. The genotypes that can tolerate drought conditions usually keep their chlorophyll levels steady, lower water loss, and help build up sugars. These sugar for energy as protectors, maintaining cellular balance and protecting vital components from damage [11,12].

The results obtained by [5] indicated that the chlorophyll content of the leaves of some plant species decreased by 45-66% when exposed to water stress, and the levels of chlorophyll-a and -b decreased at different rates depending on the plant species. This was attributed to the fact that water shortages led to the deterioration of cell walls and plant parts that contribute to photosynthesis. Carbohydrate accumulation in plants is positively correlated with the level of NCED gene expression, providing a practical link between genes and metabolic regulation [2]. This study makes a scientific contribution to exploring the dynamic relationship between NCED1 gene expression, carbohydrate accumulation, chlorophyll content stability, and productive traits such as 1000-grain weight, number of grains per spike, and grain yield under water stress. It also provides a basis for guiding molecular breeding programs toward the selection of drought-tolerant cultivars.

Materials and Methods

Location of the experiment and study factors

A field experiment was conducted in a farmer's field in the Al-Hasaniyah (Al-Mishkhab) area of Najaf Governorate during the summer growing season of 2024. The aim was to evaluate the productive characteristics of six rice (Oryza sativa L.) genotypes (Anber 33, Pokkali, Genotype 13, Genotype 16, Genotype 21, and Genotype 27) under three water stress treatments applied based on field capacity FC: regular full irrigation without stress, moderate stress (50% FC): reduced irrigation to half of field capacity, and severe stress (25% FC): reduced irrigation to one-quarter of field capacity). The seedling of the genotypes were on June 18 at 116 kg/ha in a randomized complete block design with three replicates. The experimental unit size was 2 m × 2 m, and the unit spacing was 2 m. Soil and crop management was included fertilization according to the recommendations [13]. Water stress treatments were imposed beginning at the active tillering stage, approximately 25 days after sowing, once all genotypes had established uniform stands. Three irrigation regimes were applied based on field capacity (FC): Control (100% FC): soil moisture maintained at full field capacity, moderate stress (50% FC): irrigation reduced to 50% of the water required to reach FC, and severe stress (25% FC): irrigation reduced to 25% of FC. to maintain the target FC levels, soil moisture was continuously monitored using a Time Domain Reflectometer (TDR). Irrigation volumes for each plot were measured using calibrated graduated containers, and water was supplied manually to ensure precise control of the amount applied. Irrigation was conducted whenever soil moisture dropped below the designated FC threshold for each treatment. Plants were harvested at physiological maturity on December 22, 2024. All treatments were conducted in three independent replicates to ensure statistical reliability [14]. Means ± standard error (SE) were calculated for each trait. Statistical analysis was conducted using SPSS (version 26). The data were analyzed using one-way ANOVA, and post-hoc comparisons were performed using the Least Significant Difference (LSD) test at significance levels of $p < 0.05$ and $p < 0.01$ according to the method described by [15].

Physiological Indicators

Estimation of Chlorophyll Content

Chlorophyll was extracted from rice leaves using 80% (v/v) acetone, and absorbance was measured at wavelengths of 645 and 663 nm using a UV-Visible Spectrophotometer (Shimadzu, Japan). Total chlorophyll concentrations (mg/g fresh weight) were calculated according to [16].

Second. Estimation of Total Carbohydrate Content

Leaf samples were collected at the heading stage from fully expanded upper leaves of each genotype. The samples were immediately oven-dried at 70°C for 48 hours, ground to a fine powder, and used to determine total carbohydrate content following the phenol–sulfuric acid method [17]. Absorbance was recorded at a wavelength of 490 nm, and standard glucose was used to draw a calibration curve.

A figure showing the relationship between chlorophyll and carbohydrate content was created using the Python programming language (Python, version 3.11), based on the Matplotlib library [18].

Gene Expression Analysis

Gene expression analysis of the NCED1 (9-cis-epoxycarotenoid dioxygenase 1) gene was performed, using the following steps:

First. Total RNA Extraction

Young leaf samples were collected 7 days after water stress was applied, and RNA was extracted using the TRIzol™ reagent kit (Invitrogen, USA) according to the manufacturer's instructions. RNA purity and concentration were verified using a NanoDrop™ Spectrophotometer (Thermo Scientific, USA) at 260/280 nm.

cDNA Synthesis

1µg of total RNA was used to synthesize cDNA using the RevertAid First Strand cDNA Synthesis Kit (Thermo Fisher Scientific) according to the manufacturer's protocol. Primers for the NCED1 and Actin genes were designed using Primer3Plus software based on published gene sequences of Oryza sativa, deposited in the GenBank database under the numbers LOC_Os07g05940 and LOC_Os03g50885, respectively. The specificity of the primers was verified using the NCBI-BLAST tool to ensure amplification of a specific single amplicon. The expected size of the amplified fragments was 148 base pairs for the NCED1 gene and 132 base pairs for the Actin gene. All primers were synthesized by Bioneer (South Korea), as shown in (Table 1).

Table (1): Primer sequences used for qRT–PCR analysis

Gene	Primer name	Sequence (5' – 3')	Product size (bp)	Tm (°C)
NCED1	Forward	AGCTTCTTCCTCCACCTTCTC	148	60 °C
	Reverse	TGCTTGATCTCCACGTTGTC		
Actin (Reference gene)	Forward	GCTGCTGACCGTATGAGCAA	132	59 °C
	Reverse	AGCAAGGTCGAGACGAAGGA		

Gene expression analysis by RT-qPCR

Gene expression was performed using qRT-PCR analysis according to the steps using a StepOnePlus™ Real-Time PCR System (Applied Biosystems) with SYBR™ Green Master Mix reagents. The Actin gene was used as a reference gene for data normalization. The relative expression level of the NCED1 gene was calculated using Livak method (2^-ΔΔCt) [19].

Results and Discussion

Productive traits under water stress

The results in Table (2) revealed the presence of highly significant differences in the studied production traits of rice genotypes under different water stress levels. The values of all studied traits gradually decreased with increasing drought severity, however, the decline in performance was limited in some genotypes. The Pokkali genotype showed high stability in performance, recording average grain yields of 524, 522, and 520 g/m^2 at 100%, 50%, and 25% FC treatments, respectively. While genotype 13 gave the highest averages for production traits, with 1000-grain weight reaching 29.4 g, number of grains/spike 144, and total yield 547 g/m^2, with a highly significant difference ($p < 0.01$). As for the remaining genotypes, they showed a significant decrease in studied traits under severe stress, such as Anber 33 and Genotypes 21 and 27. Obtained results indicate that Pokkali and genotype 13 are characterized by high physiological efficiency and productive stability under drought conditions compared to the other genotypes.

These results were achieved these genotypes efficiently regulate cellular water balance and utilize water effectively. Also, they induce the expression of the NCED1 gene , which is related to the production of abscisic acid (ABA). ABA is super important for how plants deal with not getting enough water by contributing to controlling the closure of stomata and reducing water loss from tissues [20, 21]. Our findings line up with what [9,22] found - drought-resistant types tend to produce consistently, even under high water deficit conditions, It is a result of the integration of molecular and physiological responses [21].

Table (2): Productivity traits of genotypes under different levels of stress.

Genotype	Trait	Treatment			Average	p-value
		(100% FC)	(50% FC)	(25% FC)		
Anber 33	1000-Grain Weight (g)	21.9	21.6	20.3	21.6	0.047 *
	No. of Grains per Panicle	99.4	99.2	96.0	98.2	0.047 *
	Grain Yield (g/m^2)	385	381	377	381	0.047 *
Pokkali	1000-Grain Weight (g)	27.6	27.2	26.8	27.2	0.008 **
	No. of Grains per Panicle	141	139	137	139	0.008 **
	Grain Yield (g/m^2)	524	522	520	522	0.008 **
Genotype 13	1000-Grain Weight (g)	29.6	29.4	29.2	29.4	0.004 **
	No. of Grains	146	144	142	144	0.004 **

Genotype	Trait	Treatment			Average	p-value
		(100% FC)	(50% FC)	(25% FC)		
	per Panicle					
	Grain Yield (g/m^2)	549.2	547.3	545.1	547.2	0.004 **
Genotype 16	1000-Grain Weight (g)	25.3	25.1	24.9	25.1	0.011 *
	No. of Grains per Panicle	129.4	129.2	129.0	129.2	0.011 *
	Grain Yield (g/m^2)	508	506	504	506	0.011 *
Genotype 21	1000-Grain Weight (g)	24.0	23.0	22.0	23.0	0.042 *
	No. of Grains per Panicle	115	116	114	115	0.042 *
	Grain Yield (g/m^2)	416	414	412	414	0.042 *
Genotype 27	1000-Grain Weight (g)	23.8	23.4	23.0	23.4	0.038 *
	No. of Grains per Panicle	120	119	118	119	0.038 *
	Grain Yield (g/m^2)	435	433	431	433	0.038 *

Note: Data are means ± SE of three biological replicates. Treatments correspond to 100%, 50%, and 25% field capacity (FC). Pokkali and Genotype 13 showed superior performance in yield attributes, consistent with higher NCED1 gene expression and physiological stability under water stress. * $p < 0.05$ = significant; ** $p < 0.01$ = highly significant.

Carbohydrate and Chlorophyll analysis

The results in Table (3) and Figure (1) indicate the effect of stress levels on total carbohydrate content, which significantly increased under severe stress (25% FC), particularly in the Pokkali genotype , which showed an accumulation of 21.85, 20.07, and 25.12, compared to the control strains (14.55, 17.65, and 10.13, respectively). In contrast, it was observed that total chlorophyll content was not significantly affected by stress levels, with averages values for all genotypes ranging from 0.073 to 0.080. This demonstrates the ability of these genotypes to adapt to water stress and irrigation shortages by maintaining a constant level of chlorophyll content in plant tissues while increasing carbohydrate accumulation. This stability in chlorophyll content is relatively due to enhanced antioxidant defense systems that reduce chlorophyll oxidation and decomposition under water stress conditions [11], as well as to the work of abscisic acid and its regulatory role by closing the stomata and reducing water loss, it also plays a role in maintaining the metabolic activity of the plant [21]. These results suggest that the two superior genotypes (Pokkali and genotype 13) have a dual mechanism of adaptation to water scarcity, increased accumulation of protective carbohydrates and maintenance of photosynthetic efficiency, making them promising candidates for breeding programs in arid regions.

Table (3): Effect of water stress on chlorophyll and carbohydrate contents in different rice cultivars.

Genotype	Trait	0%	50%	25%	Average	L.S.D
Anber 33	Chlorophyll	0.076	0.080	0.078	0.078	N
	Carbohydrate	14.010	10.090	14.380	12.827	N
Pokkali	Chlorophyll	0.073	0.077	0.077	0.0757	N.S
	Carbohydrate	14.550	15.760	21.850	17.387	0.01725
Genotype 13	Chlorophyll	0.078	0.077	0.077	0.0773	V
	Carbohydrate	17.650	11.600	20.070	16.440	V
Genotype 16	Chlorophyll	0.074	0.078	0.078	0.0767	N.S
	Carbohydrate	10.130	13.820	25.120	16.357	0.02440
Genotype 21	Chlorophyll	0.076	0.076	0.076	0.0760	N*V
	Carbohydrate	11.390	10.860	17.690	13.313	N*V
Genotype 27	Chlorophyll	0.077	0.077	0.076	0.0767	N.S
	Carbohydrate	13.220	15.100	18.140	15.487	0.04226
Average	Chlorophyll	0.0757	0.0775	0.0770		
Average	Carbohydrate	13.492	12.872	19.542		

NCED1 Gene Expression and ABA Regulation

The results in Table (4) and Figure (2) show that NCED1 gene expression increases under water deficit conditions . Pokkali and Genotype 13 showed the highest expression at 25% FC. They went up 3.90 and 4.20 times compared to the control. This increase shows that the NCED1 gene is important in how ABA is made. ABA is a main hormone that helps plants deal with not having enough water [23].

These findings are attributed to the potential activity of abscisic acid, which has been shown to be linked to NCED1 gene expression [8, 22]. The genotypes that showed the highest gene expression (Pokkali and Genotype 13) are the same ones with the most carbohydrates and the most stable chlorophyll (see Table 3). This suggests that how active the NCED1 gene is directly ties into how well the plant can handle dry conditions. NCED1 gene plays a dual role: it helps plants defend themselves and the continuation of its physiological functions when they don't have enough water to survive, and it was clear that stress affected how genes behaved differently in each genotype. This shows that their genes respond to dryness in different ways.

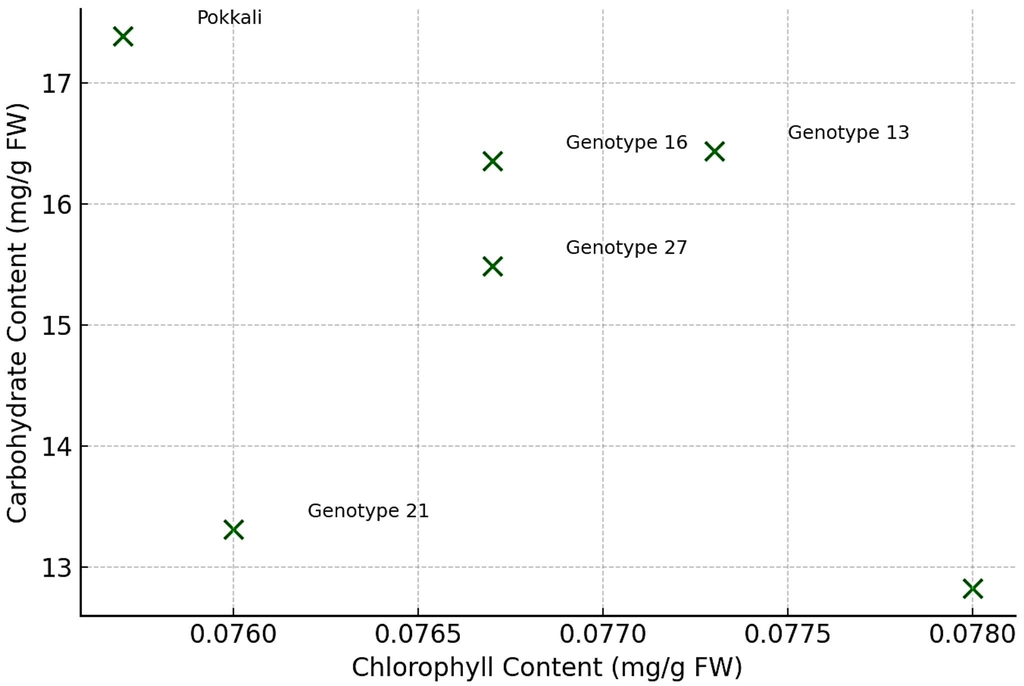

Figure (1): Shows the relationship between chlorophyll and carbohydrate content in different rice genotypes under water stress

Table (4): Gene expression of NCED1 in studied genotypes under applied water stress.

Variety	(100% FC)	(50% FC)	(25% FC)	Fold Change	p-value
Anber 33	1.00 ± 0.05	1.20 ± 0.06	1.60 ± 0.8	1.32	0.042 *
Pokkali	1.00 ± 0.04	2.10 ± 0.8	3.90 ± 0.16	2.40	0.009 **
Genotype 13	1.00 ± 0.05	2.50 ± 0.10	4.20 ± 0.18	2.52	0.006 **
Genotype 16	1.00 ± 0.05	1.80 ± 0.11	3.10 ± 0.12	2.05	0.014 **
Genotype 21	1.00 ± 0.06	1.40 ± 0.09	2.10 ± 0.13	1.50	0.046 *
Genotype 27	1.00 ± 0.05	1.55 ± 0.7	2.20 ± 0.12	1.62	0.035 *

Note: The results represent the relative expression levels of NCED1 normalized to the reference gene (Actin). Data are means ± SE of three biological replicates. Treatments correspond to 100%, 50%, and 25% field capacity (FC).

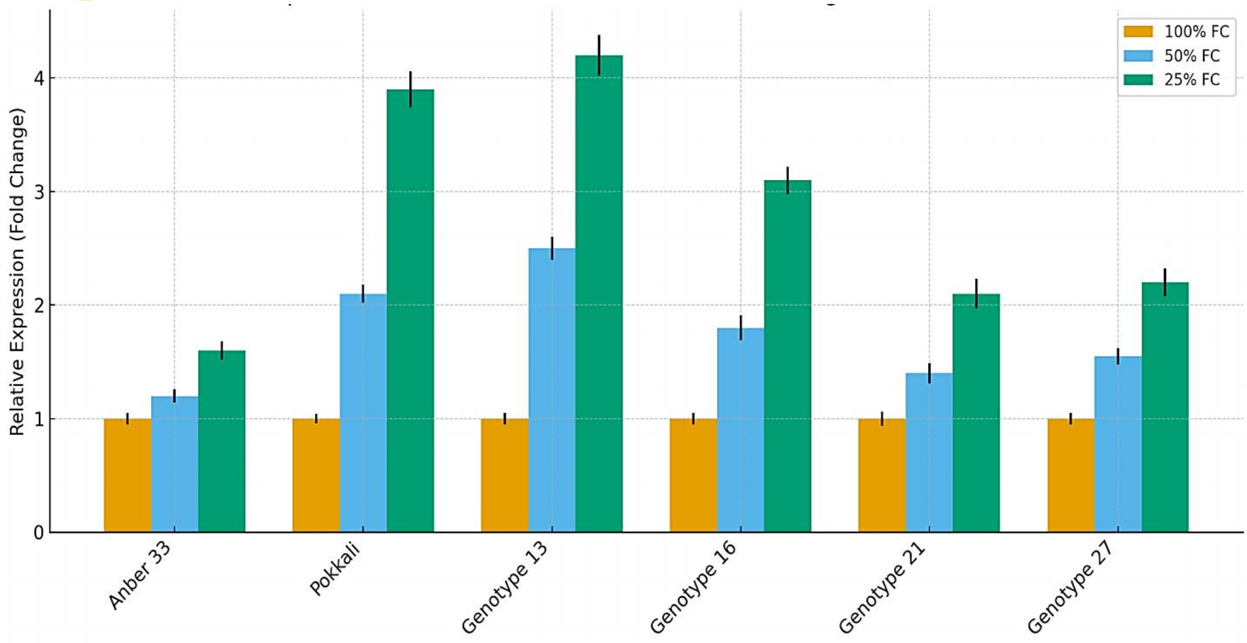

Figure (2): The relative expression of NCED1 gene in genotypes of rice under water stress

From the results in Tables (2), (3) and (4), it is clear that there is a relationship between the productive, physiological and molecular responses of rice genotypes under water stress conditions. The Pokkali and Genotype 13 genotypes demonstrated superior performance in production traits (thousand-grain weight, number of grains per spike, and grain yield), along with higher carbohydrate levels and stable chlorophyll content. This is consistent with a significant increase in the expression of the NCED1 gene. This helps them store sugars and keeps their photosynthetic parts from breaking down and this keeps them producing even under drought conditions [24, 25, 8].

In Pokkali and Genotype 13, chlorophyll remained stable, indicating the effectiveness of their antioxidant defenses, as well as the accumulation of carbohydrates to protect proteins and cell membranes when facing harsh stress conditions [26, 27].

These results demonstrate that rice's drought tolerance is due to a three-level integration: (1) Genetic regulation via stimulation of the NCED1 and ABA pathways.
(2) Metabolic response to sugar accumulation.
(3) Physiological balance maintains photosynthetic efficiency.

Thus, Pokkali and Genotype 13 represent promising genetic resources that can be exploited in genetic improvement programs aimed at developing water stress-resistant cultivars.

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