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Long-term exposure to combined treatment of elevated CO_2 and salt induces iron deficiency responses in *Porteresia coarctata*

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Plants with rising atmospheric carbon dioxide (CO_2) level in the environment may change their nutrient demands to sustain growth. The mechanisms concerning iron dynamics in plants under the interactive effect of salinity and elevated CO_2 are poorly understood. This study examines the effects of long-term as well as short-term growth at elevated CO_2 and salt on iron deficiency-associated molecular responses of *Porteresia coarctata* through analysing the transcript expression of iron deficiency-responsive genes in the leaf tissue. Plants were grown in hydroponic media at ambient or elevated atmospheric CO_2 (500 µl l^{-1}), with or without salt, and samples were analysed at three time points, on the 15th, 45th and 90th day. The semi-quantitative RT-PCR analysis showed an induced expression of iron deficiency-responsive transcription factor *PcIDEF1* and its putative targets *OsIRO2-like gene*, *OsNAAT1-like gene*, *OsNAS1-like gene*, *OsYSL2-like gene* and *PcIRT1* at elevated CO_2 with NaCl. Furthermore, a positive correlation in gene expression was observed between *PcIDEF1* and its putative targets in the 15th and 45th day samples. By contrast, in the 90th day sample, correlation in gene expression was less evident. Our findings suggest that the interactive effect of elevated CO_2 and NaCl can induce a set of molecular responses in *P. coarctata* for enhanced iron uptake and utilization, thereby reflecting an iron deficiency like stress under such conditions.

Keywords: Calcareous soil, elevated carbon dioxide, iron-responsive genes, *Porteresia coarctata*, salinity.

ATMOSPHERIC carbon dioxide (CO_2) concentration (hereafter referred to as (CO_2)) has increased from 280 µl l^{-1} in pre-industrial era to 367 µl l^{-1} at present. It is further expected to reach 550 µl l^{-1} in the coming 40–60 years[1]. As CO_2 is the main substrate for photosynthesis, its elevated level in the atmosphere has an acute impact on plant growth. The elevated CO_2 or eCO_2 increases the rate of carboxylation of ribulose 1,5-bis phosphate carboxylase/oxygenase (Rubisco) and suppresses its oxygenation particularly in C3 plants, thereby increasing the net

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photosynthesis rate and overall plant growth[2]. With increase in growth, the plant's demand for essential nutrients also increases in order to sustain its growth and optimum health. This leads to an induced nutrient uptake response by the plants when exposed to eCO_2. For example, *Arabidopsis* and durum wheat increase their P uptake from the soil when exposed to eCO_2 (refs 3 and 4). The increased demand for nutrients by plants in response to eCO_2 could be limiting over a long run considering their low bioavailability in the soil[5]. Fe is an essential microelement whose supply to the plant is often limited by edaphic factors like pH and salinity. In saline and calcareous soils which represent 8% and 30% of the total land respectively, pH ranges from 7.4 to 8.5 (refs 6 and 7). In this pH range the soluble iron concentration drops from 10^{-8} to $10^{-10.4}$ M due to over-accumulation of $Fe(OH)_3$ (ref. 7). Also, higher concentration of Na^+ in saline soil restricts the uptake of K, P, Ca, Cu, Fe and Mn ions by the plants[8,9]. Therefore, a continued increase in atmospheric CO_2 level would further aggravate the iron deficiency stress of plants. Under Fe-limiting condition, plant uses either strategy-I (reduction) or strategy-II (chelation) mechanism for iron uptake from the soil[10]. While strategy I is followed by non-graminaceous monocot and dicot species, graminaceous plants use strategy II which is mediated by natural ions chelator of mugineic acid family called phytosiderophore[11]. Till date, there are only few reports on the response of plants to iron deficiency under eCO_2 condition. In tomato grown in Fe-limited medium, the iron deficiency-induced responses like ferric chelate reducatse activity, proton extrusion and subapical root hair development were more pronounced when exposed to eCO_2 for a short duration of 2–3 days compared to the ambient CO_2 condition[12]. Also at the molecular scale, the expression of iron deficiency-responsive genes like *FER*, *FRO1* and *IRT1* was more induced under eCO_2 condition[12]. Over a long-term exposure to 550 µl l^{-1} of (CO_2) for more than one growing season, rice and legumes showed a significant drop in iron and zinc content in grains compared to ambient condition[13].

While the effect of elevated CO_2 on C3 crops is adverse, C4 crops are marginally affected with this change due to their unique physiology, where CO_2 gets saturated around Rubisco at ambient CO_2 (ref. 14). *Porteresia coarctata* is a C4 grass which occupies a significant part of estuarine vegetation as mangrove associates in the eastern and western coasts of India. It is a wild relative of rice which can survive salinity up to 30–40 dSm (ref. 15). The natural habitats of *P. coarctata* are usually alkaline with pH ranging between 7 and 8.8 (ref. 16). High pH and salinity make *Porteresia* bed a restrictive source for bio-available iron to the plants. Yet, *P. coarctata* grows well in its natural habitat without showing any phenotypes related to iron deficiency. This makes it an ideal candidate host system to study its iron deficiency stress response. In the present study, we examine how the interactive effect to salinity and eCO_2 affects the iron deficiency response of *P. coarctata* at the molecular level. We have analysed the temporal expression pattern of key iron deficiency-responsive genes in the leaf tissue with a goal to understand the molecular responses involved in plant adaptation to these stresses.

P. coarctata plants were collected from Pichavaram mangrove wetlands, Tamil Nadu, India. They were vegetatively propagated in clayey soil in big plastic trays in open-air conditions. After one month, young plants which emerged from the rhizomes were transferred to four blocks, each containing one 1-m-diameter circular tank of 100 litres holding capacity. The plants were cultured hydroponically in half-strength Hoagland's solution at pH 5.7 in each tank[17]. The medium was changed every 14 days and 5 litres of medium was poured daily in each tank to maintain the water level lost by evapotranspiration. After four months, plants growing in two out of four tanks were acclimatized to 500 µl l^{-1} of CO_2 during daylight hours for one month and labelled as CO_2 rings. Plants from the remaining two tanks continued to grow under atmospheric air and were labelled as ambient rings. After acclimatization, 200 mM NaCl was added to one tank each from ambient and CO_2 rings with continued exposure to CO_2 in the CO_2 ring. Thus, the treatment conditions imposed were ambient control, ambient NaCl, CO_2 control and CO_2 NaCl. The treatments were given for three months. The leaf samples from each treatment were collected at three time points, i.e. on 15th, 45th and 90th day. The samples were frozen in liquid N_2 immediately after harvesting and stored at –80° until use.

Total RNA was extracted from *P. coarctata* leaf samples of ambient and CO_2 rings using a modified LiCl method[18]. The RNA sample was then treated with RQ1-RNase-free DNase (Promega, USA) at 37°C for 30 min to remove the genomic DNA. First-strand cDNA was synthesized with 2 µg total RNA from each treatment by M-MLV reverse transcriptase (Invitrogen, USA) according to the manufacturer's instructions. Transcript-level expression was analysed by semi-quantitative RT-PCR for six iron-responsive genes, *PcIDEF1* (JN615009.1), *OsIRO2-like gene*, *PcIRT1*, *OsYSL2-like gene*, *OsNAS1-like gene* and *OsNAAT1-like gene*, which are *P. coarcatata* homologs to *IDEF1* (ref. 19), *OsIRO2* (ref. 20), *OsIRT1* (ref. 21), *OsYSL2* (ref. 22), *OsNAS1* (ref. 23) and *OsNAAT1* (ref. 24) genes respectively, from rice. All the cDNA samples were normalized using *PcActin1* primers. The RT-PCR exponential phase was determined to be between 22 and 30 cycles to allow for the semi-quantitative comparison of cDNAs developed from identical reactions with ampliqon PCR master mix. Table 1 lists the gene-specific primers and endogeneous control primers used in the present study.

P. coarctata is an iron deficiency-tolerant species as it thrives on alkaline soil in its natural habitat. Previously, we had reported that *P. coarctata* could withstand iron

Table 1. List of primers used in the present study

Gene	Primer sequences (F, forward and R, reverse)	Annealing temperature (°C)	Expected product size (bp)
PcIDEF1	F 5′-GCAAGGAGTTGACAAAGAGTGAT-3′ R 5′-TGCAGCAAAGGTGGAAGACTAG-3′	55	100
IRO2-like gene	F 5′-CGCGAGCAGCATGTCGTCGCT-3′ R 5′-GATGGATACTGTAGAATGTCCTG-3′	62	90
OsNAS1-like gene	F 5′-CTTCACAGATGGAGGCTCAGAA-3′ R 5′-GTGAACACTTCAGTACTTCACGAC-3′	55	100
OsNAAT1-like gene	F 5′-CGGTACAAGATCAGCGCCAGCG-3′ R 5′-CATATTGCTACCCAACCAAGTCGCC-3′	57	100
PcIRT1	F 5′-CAGTGTAGTTGACGAACGCAAATG-3′ R 5′-GATGACGCTGGAGACAAGGAT-3′	55	90
OsYSL2-like gene	F 5′-GACCTTGCCGCATCGACATGTG-3′ R 5′-GCTTCTGGAGAGGAACTTCATG-3′	55	200
PcActin1	F 5′-GAAAGGAAGTACAGTGTCTGGATTG-3′ R5′-AAGCATTTCCTGTGCACAATGGAT-3′	60	125

Table 2. *Porteresia coarctata* iron deficiency-responsive genes used for RT-PCR analysis

Gene from *P. coarctata*	Homologue in rice	Description	Tissue specificity
PcIDEF1	*IDEF1*[19]	ABI3/VP1 family transcription factor. Constitutive regulator of iron deficiency-responsive genes in rice	Leaf and root
IRO2-like gene	*OsIRO2*[20]	bHLH transcription factor, positive regulator of iron deficiency-responsive genes	Leaf and root
OsNAS1-like gene	*OsNAS1*[23]	Nicotinamine synthase enzyme	Leaf and root
OsNAAT1-like gene	*OsNAAT1*[24]	Nicotinamine amino transferase enzyme. Catalyses the conversion of NA to 3′-keto intermediate	Leaf and root
PcIRT1	*OsIRT1*[21]	Ferrous iron transporter	Expresses mainly in root and mildly in leaf
OsYSL2-like gene	*OsYSL2*[22]	Ferrous-NA transporter	Leaf

deficiency and salt in a hydroponic medium up to three weeks without showing any chlorotic symptoms[25]. In the present study, we examined how the short-term as well as long-term growth at eCO_2 and salt affect the iron deficiency responses of *P. coarctata* at the molecular level by analysing the mRNA expression pattern of six iron-responsive genes on the 15th, 45th and 90th days of treatment. The choice of genes for the study was based on their homology with the rice gene with a specific function in iron acquisition or utilization. The selected genes were regulators of iron deficiency-responsive genes (*PcIDEF1*[25]; *OsIRO2-like gene*), ferrous ion transporter (*PcIRT1*), metal-nicotinamine (NA) transporter (*OsYSL2-like gene*) and enzymes from mugineic acid biosynthetic pathway (*OsNAS1-like gene*, *OsNAAT1-like gene*), see Table 2. The study was conducted in the leaf tissue, as it is an important sink organ which reflects the iron status of the plants.

In the 15th day leaves, *PcIDEF1* expression was strongly induced in ambient control, but only moderately in 200 mM NaCl-treated sample (Figure 1; Table 3). Corroborating the *PcIDEF1* induction, the expression of its putative targets *OsIRO2-like gene*, *OsNAAT1-like gene*, *OsYSL2-like gene*, *PcIRT1* and *OsNAS1-like gene* was also increased in ambient control compared to the 200 mM NaCl condition. The decrease in transcript level at 200 mM NaCl was more evident for *OsNAAT1-like gene* and *PcIRT1* in particular (Figure 1). The induced expression of iron-responsive genes in leaves had been earlier seen in rice in response to Fe deficiency stress, where the *OsIRO2* and *OsNAAT1* transcripts were upregulated in the leaf tissue[20,24]. Furthermore, the transcript accumulation of metal-NA transporter gene *OsYSL2* was specific to leaf tissue upon Fe deficiency stress in rice[22]. The correlation between *PcIRT1* with *PcIDEF1* gene expressions was consistent with the earlier observation in *P. coarctata* leaves, where the *PcIRT1* transcripts paralleled the *PcIDEF1* mRNA accumulation pattern over Fe deficiency and 150 mM NaCl stresses[25]. The induced expression of iron responsive genes at ambient control is also reflective of a probable iron deficiency condition experienced by *P. coarctata*. At CO_2 control, there was a

Table 3. Relative transcript levels of six *P. coarctata* iron deficiency-responsive genes on 15th, 45th and 90th day of ambient control (AC), ambient 200 mM NaCl (AN), CO_2 control (CC) and CO_2 200 mM NaCl (CN) treatment conditions in leaves. Gene expression at AC is set to 1

	15th day				45th day				90th day			
Gene	AC	AN	CC	CN	AC	AN	CC	CN	AC	AN	CC	CN
PcIDEF1	1	↓	↓	↑	1	=	↓	↑	1	=	=	=
OsIRO2-like gene	1	↓	↓	↑	1	=	↑	↓	1	↓	=	=
OsNAAT1-like gene	1	↓	↓	↑	1	=	↓	↑	1	↓	=	=
OsNAS1-like gene	1	↓	↓	↓	1	=	=	↑	1	↓	=	=
OsYSL2-like gene	1	↓	↓	↑	1	=	↓	↑	1	↓	↑	↑
PcIRT1	1	↓	↓	↑	↑	=	↓	↑	1	↑	↑	↓
PcActin1	1	=	=	=	1	=	=	=	1	=	=	=

'↑' denotes up-regulation, '↓' denotes down-regulation and '=' denotes equal expression of genes relative to AC.

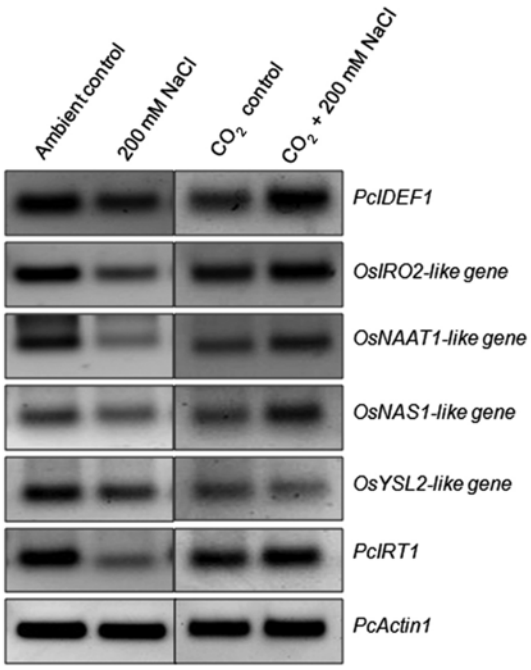

Figure 1. Effect of elevated CO_2 and salt on the transcript accumulation of iron-responsive genes on the 15th day of treatment by semi-quantitative RT-PCR. *PcActin 1* was used as endogeneous control.

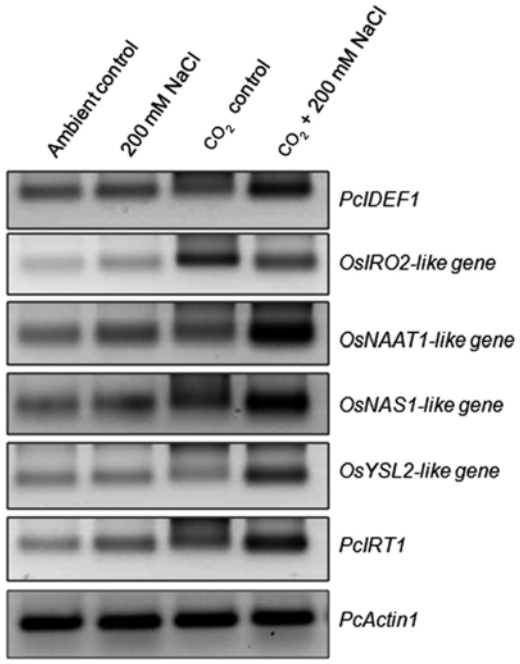

Figure 2. Effect of elevated CO_2 and salt on the transcript accumulation of iron-responsive genes on the 45th day of treatment by semi-quantitative RT-PCR. *PcActin 1* was used as endogeneous control.

slight reduction in transcript level of all the genes compared to ambient control. This finding is similar to an earlier observation in tomato, where elevated CO_2 did not induce the expression of iron deficiency-responsive genes *LeIRT1*, *LeFRO1* and *FER* in Fe-sufficient roots[12]. Interestingly, however, with 200 mM NaCl at eCO_2, transcripts level increased for all the genes except for *OsYSL2-like gene*. The increase in expression could be attributed to the presence of salt in the medium, which limits access to bio-available iron to the plants[26]. For example, in *P. coarctata* total Fe content in leaf and root tissues reduced after growth in 150 mM NaCl-containing medium for three weeks[25]. Similarly, rice plants grown in salt-containing medium showed decreased Fe content in root and shoot tissues with chlorotic leaves[26]. Therefore, it is possible that the interactive effect of salt and elevated CO_2 imposes an iron deficiency-like condition in the growth medium, which results in Fe-deficiency-induced responses like increased expression of iron deficiency-responsive genes in plants.

In the 45th day sample, the expressions of all the genes were weak under ambient condition, either with or without salt (Figure 2). In contrast, under elevated CO_2, the expressions of *PcIDEF1*, *OsNAAT1-like gene*, *OsNAS1-like gene*, *OsYSL2-like gene* as well as *PcIRT1* were induced in 200 mM NaCl-treated leaves, whereas the expression of *OsIRO2-like gene* was decreased. However, in CO_2 control the *OsIRO2-like gene* expression was

high, thereby following a reverse transcript accumulation pattern similar to that of *PcIDEF1* (Figure 2; Table 3). The internal control gene *PcActin1* showed a constitutive expression and the transcript abundance was not affected by the treatment conditions imposed.

In the 90th day sample, *PcIDEF1* expression was strongly induced across all the treatments. By contrast, the expression of putative targets like *OsNAAT1-like gene*, *OsNAS1-like gene* and *PcIRT1* was substantially repressed both under ambient and elevated CO_2 conditions (Figure 3; Table 3). For *OsIRO2-like gene* and *OsYSL2-like gene*, transcript accumulation was repressed at 200 mM NaCl-treated sample, though it remained high for ambient control, CO_2 control and CO_2 NaCl treatments (Figure 3). Notably, the expression profiles of the downstream genes were markedly different from that of *PcIDEF1*, whereas target genes like *OsYSL2-like gene* and *OsNAAT1-like gene* shared a similar expression pattern with *OsIRO2-like gene*. In rice, IDEF1 is involved in the regulation of iron uptake/utilization-related genes during the early stage of iron deficiency while in subsequent stages it employs a different set of genes for regulation[27]. Also in leaves the effect of IDEF1 on target genes is less coordinated and more divergent[27]. Alternatively, OsIRO2 induces the expression of iron deficiency-responsive genes during the subsequent stages of Fe deficiency in rice[27]. Also, rice plants over-expressing *OsIRO2* were tolerant to long-term Fe deficiency in both hydroponic medium and calcareous soils[28]. Therefore, it is possible that in response to a prolonged eCO_2 exposure-mediated Fe deficiency-like situation, the expression of iron uptake/utilization-related genes is independent of *PcIDEF1* regulation, but is otherwise regulated by *OsIRO2-like gene*-encoded protein in *P. coarctata*.

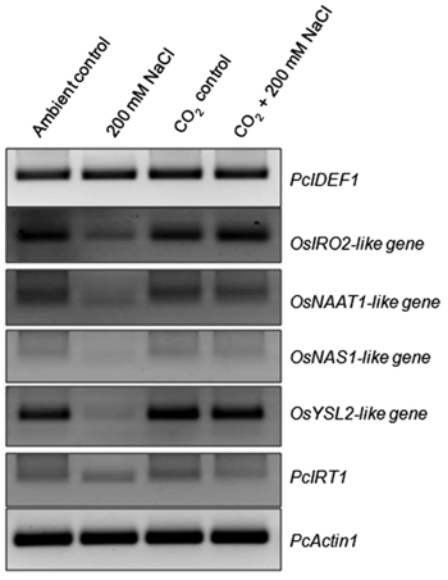

Figure 3. Effect of elevated CO_2 and salt on the transcript accumulation of iron-responsive genes on the 90th day of treatment by semi-quantitative RT-PCR. *PcActin 1* was used as endogeneous control.

Our findings support the hypothesis that interactive effect of elevated CO_2 and salinity can impose an iron deficiency-like condition in the soil as evidenced by induced iron deficiency-associated molecular responses in *P. coarctata* under such conditions. Also, the long-term exposure of plants to elevated CO_2 and salinity resulted in a smooth and pronounced change in gene expression patterns, which would allow appropriate physiological and metabolic adjustments in the plants under the prevailing conditions. The time-dependent differential gene expression in leaves at elevated CO_2 could be advantageous for sustainable iron efficiency in *P. coarctata*. The difference in temporal gene expression pattern can also be used as an indicator to study the role of individual genes in *P. coarctata* under the combined treatment of iron deficiency, salinity and eCO_2 for breeding programmes designed to reduce the vulnerability of crop plants to elevated CO_2.

Conflict of interest: The authors declare that they have no conflict of interest.

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Petrographic texture of sediments vis-à-vis aquifer characteristics from WGAMG′0 watershed, Chandrapur district, Maharashtra, India

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The present study deciphers the interrelationship between petrography and texture of sediments with aquifer characteristics. Sandstones representing the aquifers around Minjhari–Murpar village (lat. 20°34′05″N: long. 79°18′05″E), Chimur Tahsil, Chandrapur district, Maharashtra, India corresponding to the watershed WGAMG′ have been selected for the study. These sandstones are grouped as arenites and wackes to unravel the aquifer distinctiveness. The values of transmissivity from 102.28 to 450.42 m^2/day, and for wackes from 58 to 165.59 m^2/day. The values of specific yield (storativity) for arenites range from 20% to 35% and for wackes from 10% to 17%. The computed values of transmissivity as well as specific yield are attributed to the petrographic texture of the rocks. It is propounded that the percentage of detrital grains and matrix is the prime factor that governs the characteristic of aquifers. In addition, it is also found that the sorting of rocks also influences the aquifer performance. The high values of transmissivity and specific yield in arenite aquifer are accountable for higher percentage of detrital grains, lesser amount of matrix and moderate sorting of the grains. Conversely, the lower percentage of detrital grains, higher amount of matrix and poor sorting of the grains are responsible for low values of transmissivity and specific yield in the wacke aquifer.

Keywords: Aquifer characteristics, petrography, texture of sediments, watershed.

IT is now an established fact that the inherent properties of aquifers govern the occurrence and movement of groundwater. These inherent properties in hard-rock aquifers encompass the presence of primary and secondary interconnected conduits and post-emplacement/depositional physical activities like weathering, fracturing, jointing, etc. Extensive work has been carried out on the relationship between occurrence and movement of groundwater, and the above-mentioned inherent hard-rock aquifer properties[1–4]. In sedimentary rocks, the occurrence and movement of groundwater is primarily governed by the grain-to-grain relationship[5–9]. The sedimentological properties govern the movement of groundwater and such well-penetrating aquifers have good yielding capacities[10]. The individual particles of the geological formation are

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