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Differential role of jasmonic acid under drought and heat stress in rice (*Oryza sativa*)

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Abstract
The present study was conducted to understand the role of JA under drought and heat stress in rice during anthesis. Four contrasting rice genotypes namely N-22, N-L-44, Swarna and PS-5, were raised under normal environment and exposed to drought and heat stress at anthesis. Important physiological and biochemical traits like relative water content: RWC, membrane stability index: MSI, lipid peroxidation, H_2O_2 content and antioxidant enzyme activity (superoxide dismutase: SOD) were estimated in all the four genotypes along with endogenous level of JA and other important yield attributes. Tolerant genotypes (N-22 and N-L-44) recorded higher endogenous level of JA under drought stress and at the same time shown better RWC, MSI and SOD activity and encountered lower oxidative stress (H_2O_2 content) and lipid peroxidation. But, JA levels did not differed much under heat stress conditions and neither brought any amelioration effect in any of the above mentioned traits. Our, results clearly indicates that JA plays differential role under drought and heat stress in rice.

Keywords: Rice, Jasmonic acid, Drought, Heat stress, Pollen viability, SOD.

Introduction
Rice (*Oryza sativa*) is most important world food crop. Drought and high temperature (heat) stress are considered to be the two major environmental factors limiting crop growth and yield of rice and the situation is further going to deteriorate under the changing climate. Hormonal homeostasis, stability, content, biosynthesis and compartmentalization are altered under abiotic stress (Maestri *et al*., 2002). Various hormones have been reported to ameliorate the effect of different abiotic stresses over time. Jasmonic acid (JA) have well established role in amelioration of biotic stress. However, much study has not been done to find out the role of JA, in context to abiotic stresses.

In 1962, a floral scent compound, the methyl ester of jasmonic acid (Me JA) was isolated for the first time from the aromatic oil of *Jasminum grandiflorum* (Demole *et al*., 1962). However, the physiological effects of MeJA or its free acid (JA) were unknown until the 1980's when a senescence-promoting effect of JA (Ueda and Kato, 1980) and growth inhibition activity of Me JA to *Vicia faba* (Dathe, 1981) were observed. Now JA and derivatives (JAs) are the best characterized group of oxylipins in plants and are regarded as one of the the major hormones regulating both defense and development. JA biosynthesis and signaling pathways have been extensively investigated in dicotyledonous plants such as Arabidopsis, tobacco and tomato. In monocotyledonous species, only a scant number of JA biosynthetic enzymes have been described (Tani *et al*., 2008; Yan *et al*., 2012). Jasmonates are formed from the LOX-catalyzed peroxidation of trienoic fatty acids at carbon atom 13 to form 13-hydroperoxide, which is modified to an allene oxide fatty acid and subsequently cyclized to the compound 12-oxo-phytodienoic acid (OPDA). Jasmonic acid (JA) is synthesized from OPDA by the reduction of a double bond and three consecutive rounds of β-oxidation. The pathway can accept C18-PUFA (linolenic acid) as well as C16-PUFA (hexadecatrienoic acid), in the latter case the intermediate is the so-called dinor-OPDA that may also be metabolized to JA. JA can be further enzymatically converted into numerous derivatives or conjugates, some of which have well-described biological activity such as free JA, MeJA, cis-jasmone and JA–Ile. JA signaling pathway, the transition process of JA-Ile as a chemical signal to biological signal, was elucidated in recent years. JA initiates signalling process upon formation of a SCFCOI1-JA-Ile-JAZ ternary complex (JAZ: jasmonate ZIM-domain protein; Sheard *et al*., 2010), in which the JAZ repressors are ubiquitinated and subsequently degraded to release transcription factors, e.g., MYC2, causing downstream transcription activation of defense responses or developmental regulation (Chini *et al*., 2007; Thines *et al*., 2007). The only jasmonate receptor identified to date has been the COI1 protein (Katsir *et al*., 2008; Yan *et al*., 2009), but interestingly, only JA-Ile was found as a ligand of the SCFCOI1 E3 ubiquitin ligase complex

(Thines *et al*., 2007). JA has been reported to play role in various plant processes from time to time like cell cycle (Swiatek *et al*., 2004), Embryo development (Goetz *et al*., 2012; Wasternack *et al*., 2013), flower development (Wasternack *et al*., 2006), anther and pollen development (Mandaokar *et al*., 2009), spikelet development (Qiang *et al*., 2014), lateral root formation (Stenzel *et al*., 2012), tendril coiling (Stelmach *et al*., 1998), tuber formation (Wasternack and Hause, 2013), seed germination (Dave *et al*., 2011; Dave *et al*., 2012) and senescence (Reinbothe *et al*., 2009; Seltmann *et al*., 2010). JA plays important role in amelioration of biotic stress. Jasmonates increase upon biotic stress such as herbivory or pathogen attack and upon abiotic stress such as wounding, ozone or UV light (Wasternack *et al*., 2007). The rise in jasmonates leads to dramatic reprogramming of expression of genes involved in defense against herbivores (Devoto *et al*., 2005), formation of secondary metabolites (Pauwels *et al*., 2009) and other metabolic pathways. JA-dependent formation of secondary compounds such as anthocyanins, glycosinolates, and flavonoids, and JA dependent release of flower volatiles and nectar secretion occur. Several of these aspects are of consequence for crop quality, protection against pathogens and chilling injury as well as for harvest ability (Rohwer *et al*., 2008).

But, role of jasmonic acid in abiotic stress is still not clear. So, in our present investigation we tried to find out what happens to JA levels particularly under drought and heat stress in one of the globally most important crop rice. And how this change in JA level co-relates with various physiological and biochemical traits important for amelioration of drought and heat stress in rice during anthesis.

Material and Methods

The study was planned with four contrasting rice genotypes namely N-22, N-L-44, Swarna and PS-5, raised under normal environment and exposed to drought and heat stress at anthesis stage at Research Farm of Division of Plant Physiology, Indian Agricultural Research Institute (IARI), New Delhi during 2014-15. The plants were subjected to water stress at anthesis stage by withholding water until first symptoms of wilting was visible (-55 kPa±2.01). Similarly, heat stress was given to plants by transferring them to temperature tunnel, where the air temperature during the exposure duration was 6.87˚C±1.49 higher than ambient temperature. Panicles which emerged during stressed conditions were tagged and collected for further physiological biochemical and molecular analysis.

Physiological and biochemical parameters

All Physiological and biochemical parameters were estimated at reproductive stage (flag leaf and panicles at heading). Five replicate of plant samples (flag leaf) were collected from each treatment of all the 10 varieties. Membrane stability index (MSI) was determined according to method of Sairam and co-workers (1999). Leaf material (100mg) was taken in test tubes containing 10ml of double distilled water. Initial (C1) (40 ºC) and final (C2) (100 ºC) conductivity of the solution was recorded on a conductivity bridge (Century, Water soil analysis kit, CMK 751). MSI was calculated as: MSI = [1 – (C1/C2)] × 100. For estimating biochemical parameters samples (panicles) were collected into liquid nitrogen and stored at −80ºC until further analysis. Hydrogen peroxide (H_2O_2) content was determined spectrophotometrically with 0.2 g leaf/spikelet tissue homogenized in 2ml of 0.1% trichloroacetic acid as described by Alexieva and co-workers (2001). The amount of H_2O_2 [µmol g^{-1} fresh weight (FW)] was calculated from the standard curve plotted for H_2O_2. Lipid peroxidation was determined by measuring the amount of malondialdehyde content produced by thiobarbituric acid reaction as described by Larkindale and Knight (2002). The amount of thiobarbituric acid reactive substances (TBARS) was calculated using an extinction coefficient of 155mM cm^{-1}. Frozen panicle samples (0.5 g) were extracted with 5ml of cold extraction buffer containing 100mM potassium phosphate buffer (pH-7.0) and 0.1mM sodium ethylene diamine tetra acetic acid (EDTA). The homogenate was centrifuged at 18 400 g, 14 000 rpm for 20 min at 4 ºC. The supernatant obtained was directly used for the enzyme assay. Total soluble protein was measured from the same extract using bovine serum albumin as a standard (Lowry et al., 1951). Total superoxide dismutase activity was assayed by monitoring the inhibition of photochemical reduction of nitro blue tetrazolium (NBT) as described by Jiang and Zhang, 2001. The 3ml reaction mixture contained 50mM potassium phosphate buffer (pH-7.8), 13mM methionine, 75mM NBT, 2µM riboflavin, 0.1mM EDTA and 100µl enzyme extract. The reaction mixtures were illuminated at a light intensity of 5000 lx for 25min. One unit of SOD activity mg^{-1} protein was defined as the amount of enzyme required to cause 50% inhibition of the reduction of NBT per unit time as monitored at 560 nm.

Endogenous level of jasmonic acid (JA)

Jasmonic acid was quantified using UV-Spectrophotometer following the method of Annigeri *et al*. (2011). One g panicle tissue of all varieties were soaked in 10 ml of ethanol for 12 hrs to extract JA, contents were filtered and homogenized mixtures of 1ml were used for final loading in UV visible double beam spectrophotometer (Analyticjena, Germany). The readings were taken at 323 nm absorbance, and recorded at different concentrations of JA, standard curve was plotted to get straight line passing through the origin. From the standard curve, the concentration of jasmonic acid in the samples was calculated according to the formula y = mx + c. Jasmonic acid content was finally expressed inng g^{-1} FW.

Yield attributes: Pollen viability, spikelet fertility and panicle yield

Pollen viability was detected as per Khatun and Flowers (1995). Six fresh anthers were collected from different spots in a rice panicle from both the treatments of each variety and placed on the glass slide and smashed in 10µl of fresh MTT stain (thiazolyl blue) solution. The panthers were mixed well and 1µl of this taken was on a slide in three replicates. The pollens were counted in nine different fields of view in a Magnus compound bright-field microscope (India), three each in 1µl drop. The viable pollens reduce the MTT dye into formazon giving pink colour. The non-viable pollens were either colourless or black in colour. The viable, non-viable and total number of pollens was recorded. Spikelet fertility was estimated following Prasad *et al*. (2006). Filled and unfilled grains from 5 dried panicles of each treatment were separated and counted from all 10 varieties. The ratio of filled grains to total number of spikelets was estimated and expressed in percentage. Grains from 5 dried panicles of each treatment were separated from all 10 varieties and weighed to obtain grain yield / panicle (Panicle yield) and expressed as g/panicle (Prasad *et al*., 2006). All data were statistically analyzed using analysis of variance (ANOVA) using SPSS v.10 computer package (SPSS Inc. USA).

Relative gene expression

In order to determine the quantitative gene expression of JA biosynthesis genes *aos*, *aoc*, *opr* and JA signalling genes *coi-1*and *jaz*; isolation of total RNA was carried out by TRIzol® reagent (Invitrogen, USA) and R Nase-free DNase I (Promega, USA) was applied to remove contaminating genomic DNA at 37ºC for 1 h. Quality and integrity of total RNA were then determined by running appropriate amount in a formamide denaturing gel, and quantity of total RNA was determined using a Nano Drop™ 1000 spectrophotometer (ThermoFisher Scientific, USA). The first-strand cDNA was synthesized according to the instructions of the cDNA Synthesis Superscript® III First-Strand Synthesis System (Invitrogen, USA). Resulting cDNA was stored at -20ºC and employed as template for qPCR reactions following recommended conditions provided in user's manual. Nucleotide sequences for genes were obtained from National Center for Biotechnology Information (http:// www.ncbi.nlm.nih.gov/). The Basic Local Alignment Search Tool (http://www.ncbi.nlm.nih.gov/BLAST/) was used to identify the homologs of genes. For qPCR expression analysis the oligonucleotide primers were designed manually (Table: 1), and oligo quality (to avoid primer dimer, self dimer, etc.), GC % and Tm were analyzed by using Oligoanalyzer 3.0 tool (http://www.idtdna.com/analyzer/Applications/OligoAnalyzer , Intergrated DNA Technologies, Coralville, IA 52241, USA).

Result & Discussion

Relative water content and membrane stability index

Relative water content (RWC) is the appropriate measure of plant water status in terms of the physiological consequence of cellular water deficit (Surendar *et al*., 2013). Maintenance in RWC and MSI of cells provides desiccation resistance to leaf tissue, which can contribute to increase in total biomass. Under drought and heat stress RWC of plants decreases (Gupta *et al*., 2012). We also found that there was a decrease in RWC of all the genotypes under drought and heat stress conditions. Under drought condition RWC of tolerant genotypes N-22 and N-L-44 decreased by 7.8% and 6.2% respectively (Table: 2). Whereas, the sensitive genotypes Swarna and PS-5 shown a decrease of 12.9% and 15.9% respectively (Table: 2). Under heat stress condition there was a decrease of only 3.3% to 4.7% in RWC of all the genotypes. Decrease observed was more in drought compared to heat stress condition which is in confirmation with the results earlier reported by Ings *et al*. (2013).

Cellular membrane dysfunction due to stress is well expressed in increasing permeability and leakage of ions which can readily be measured by the efflux of electrolytes. Estimation of membrane dysfunction under stress by measuring cellular electrolytes leakage from stressed leaf tissues into an aqueous medium is finding a growing use as a measure of MSI and as a screen for stress resistance (Surendar *et al*., 2013). In the present investigation, MSI of tolerant genotypes N-22 and N-L-44 decreased by 11.6% and 12.5% respectively (Table: 2) under heat stress. Whereas, the sensitive genotypes Swarna and PS-5 shown a decrease of 15.3% and 14.8% respectively (Table: 2). Under drought condition also MSI of all the genotypes decreased but the decrease was less compared to heat stress. Similar results were also observed by Kebede *et al*. (2012).

Oxidative stress and antioxidant enzymes

When plant experiences any kind of stress various Reactive Oxygen Species (ROS) are generated like Superoxide radicals, Hydroxyl ions etc. which damages the functioning of various organelles mainly Chloroplast and Mitochondria thus affecting the two most important functions Photosynthesis and Respiration in plant. In the present investigation it was found that under heat stress condition H_2O_2 level of tolerant genotypes N-22 and N-L-44 increased by 23.4% and 31.6% respectively (Table: 2) and in the sensitive genotypes Swarna and PS-5 increase was even higher (54.5% and 56.5% respectively). Similar results (Table: 2) were also observed under drought stress (N22: 49.5%, N-L-44: 54.8%, Swarna: 89.6% and PS-5: 76.7% increase over control). Ali *et al*. (2013) and Naji *et al*. (2011) also reported that both H_2O_2 and TBARS elevates under heat and drought stress and so considered to be reliable biochemical indicators for abiotic stress severity. TBARS (Thiobarbituric acid reactive substances) determines the malondialdehyde (MDA) as an end product of lipid peroxidation in the plant parts. Lipid peroxidation is the system most commonly ascertained to oxidative damage and hence is regarded as an indicator of stress. Under heat stress condition TBARS content of N-22, N-L-44, Swarna and PS-5 increased by 46.9%, 49.8%, 92.3% and 99.3%, respectively (Table: 2). Under drought condition there was an increase of 31.5% in N22 and 29.8% in N-L-44 (Table: 2). Whereas, the sensitive genotypes Swarna and PS-5 shown an increase of 57.1% and 64.0% respectively (Table: 2). To overcome the problem of oxidative stress plants have an inherent mechanism of producing various antioxidant enzymes which encounters different ROS. Superoxide dismutase (SOD) is the first enzyme produced in plant system to curb ROS. The extent of the increase in SOD differs among rice among genotypes and is associated with tolerance to abiotic stress (Zhao *et al*., 2014). SOD Content of tolerant genotypes N-22 and N-L-44 increased by 12.3% under heat stress. Whereas, the sensitive genotypes Swarna and PS-5 shown an increase of 26% and 20% respectively (Table: 2). Under drought condition there was an increase of 17% in N22, 21.8% in N-L-44, 33% in Swarna and 35.3% in PS-5 respectively (Table: 2). Stress induced, enhanced activity of superoxide dismutase in rice has been also reported by Mafakheri *et al*. (2011).

Yield attributes

The most susceptible stages in rice for development to temperature is flowering (i.e. anthesis and fertilization), and to a lesser extent booting (micro-sporogenesis) (Farrell *et al*. 2006; Manigbas *et al*., 2014; Kim *et al*., 2014). We also found that heat stress caused a significant decrease in the viability of the pollens leading to less fertile spikelets, which ultimately resulted in reduced grain yield per panicle in all the varieties. We also found that pollen viability, spikelet fertility and panicle grain weight decreased drastically under drought and heat stress. Reduction under drought was even higher than heat stress. Tolerant genotypes encountered a decrease in panicle grain weight of around 30%. Whereas, sensitive genotypes a reduction of around 50% (Table: 3).

Endogenous level of jasmonic acid (JA)

The endogenous JA content was increased markedly under drought and cold stresses, but it was reduced by heat stress (Du *et al*., 2013). Similar result was observed in our investigation where we found that JA content of all the genotypes increases under drought conditions but not under heat stress. Under drought condition JA Content of tolerant genotypes N-22 and N-L-44 increased by 57.3% and 85.7% respectively. Whereas, the sensitive genotypes Swarna and

PS-5 shown an increase of 42% and 32.7% respectively (Fig. 1).

Relative expression of genes involved in JA synthesis and signalling

Many genes involved in JA biosynthesis and signalling were induced by drought and cold treatment but these genes were significantly suppressed by heat stress (Du *et al*., 2013). In our study too we found that expression of genes involved in JA synthesis and regulation increased under drought stress but decreased under heat stress or showed no change. Under drought, expression of *aos* (allene oxide synthase) was 4.62 times higher in N-22 and 3.43 times higher in PS-5. Expression of *aoc* (allene oxide cyclase) was almost 3-5 times higher under drought. Expression of *opr* (oxo phytodienoic acid reductase) and *coi-1* (Coronatine insensitive-1: JA receptor) also showed similar trend whereas *jaz* (JA ZIM domain protein), a repressor of JA signalling shown completely reverse trend (Fig. 2).

The findings of the study conclude that JA plays differential roles under drought and heat stress. On the one hand, where, JA shows ameliorative effect on Rice under drought stress as evident by an increase in their endogenous level coinciding with better physiological and biochemical adaptations in the plant. At the same time, it does not seem to bring any amelioration under heat stress.

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Table 1: Oligonucleotide primer sequence details

Genes	Primer sequence
AOS1_F	GCT GGT GAA GAA GGA CTA CGA C
AOS1_R	CGT CGG GAA CAG GAT CTT CAT C
AOC4_F	CCA ACA AGC TGT ACA GCG GAA G
AOC4_R	GGA CTC CTC GTA GGT CAG GTA C
OPR_F	CCT CTA CTG CCA CAT GGT GGA G
OPR_R	GGA GAC AAG ATC AGT GTA GCC AT
COI1_F	CCT GAA CCC TGA TCA GTC TAT CAG
COI1_R	CTC ACT CGA CGA ACT TCT CCT CAG C
JAZ_F	TTC ACC GGT TCC TCG AGA AAA G
JAZ_R	GCA TTG ATT CAT TGG CTC GAT TCC

Table 2: Physiological and biochemical traits

		RWC	MSI	H_2O_2	TBARS	SOD
		(%)	(%)	(µ mol gm^{-1} FW)	(µ mol gm^{-1} FW)	(µ mol min^{-1} mg^{-1} protein)
N-22	C	89.1±2.58	81.4±1.2	3.17±0.26	10.52±0.47	2.30±0.09
	D	82.0±1.31	73.3±1.04	4.75±0.07	13.84±1.03	2.70±0.15
	H	84.9±1.32	71.9±1.30	3.92±0.25	15.46±0.71	2.59±0.16
N-L-44	C	90.7±1.00	79.5±1.04	2.85±0.18	7.98±0.41	2.31±0.12
	D	85.0±2.02	70.6±0.83	4.42±0.16	10.36±0.53	2.82±0.11
	H	87.7±2.09	69.5±1.70	3.75±0.26	11.96±0.83	2.60±0.15
Swarna	C	86.5± 1.35	77.9±1.75	4.55±0.20	13.12±0.81	1.74±0.10
	D	75.3±2.22	67.4±1.91	8.63±0.22	20.62±0.57	2.32±0.22
	H	82.4±1.00	65.9±1.47	7.03±0.31	25.23±1.43	2.20±0.15
PS-5	C	84.1±1.35	73.1±0.78	5.35±0.28	14.98±0.68	1.69±0.09
	D	70.6±1.28	65.8±1.55	9.45±0.31	24.57±1.22	2.29±0.16
	H	83.1±1.54	62.2±1.70	8.37±0.24	29.85±0.92	2.03±0.14
Factor A	CD at 5%	2.714	2.323	0.399	1.408	0.24
	SE(m)	0.952	0.815	0.14	0.494	0.084
Factor B	CD at 5%	2.35	2.012	0.346	1.219	0.208
	SE(m)	0.824	0.705	0.121	0.427	0.073
Factor A×B	CD at 5%	ns	ns	0.692	2.438	ns
	SE(m)	1.648	1.411	0.242	0.855	0.146
Factor A : Genotype						
Factor B: Treatment						

Table 3: Yield attributes

		PV	SF	Grain weight $panicle^{-1}$
		(%)	(%)	(g)
N-22	C	89.1±2.58	81.4±1.2	3.17±0.26
	D	82.0±1.31	73.3±1.04	4.75±0.07
	H	84.9±1.32	71.9±1.30	3.92±0.25
N-L-44	C	90.7±1.00	79.5±1.04	2.85±0.18
	D	85.0±2.02	70.6±0.83	4.42±0.16
	H	87.7±2.09	69.5±1.70	3.75±0.26
Swarna	C	86.5± 1.35	77.9±1.75	4.55±0.20
	D	75.3±2.22	67.4±1.91	8.63±0.22
	H	82.4±1.00	65.9±1.47	7.03±0.31
PS-5	C	84.1±1.35	73.1±0.78	5.35±0.28
	D	70.6±1.28	65.8±1.55	9.45±0.31
	H	83.1±1.54	62.2±1.70	8.37±0.24
Factor A	CD at 5%	4.757	4.094	0.402
	SE(m)	1.692	1.435	0.141
Factor B	CD at 5%	4.12	3.545	0.348
	SE(m)	1.465	1.243	0.122
Factor A×B	CD at 5%	ns	ns	0.695
	SE(m)	2.93	2.486	0.244
Factor A : Genotype				
Factor B: Treatment				

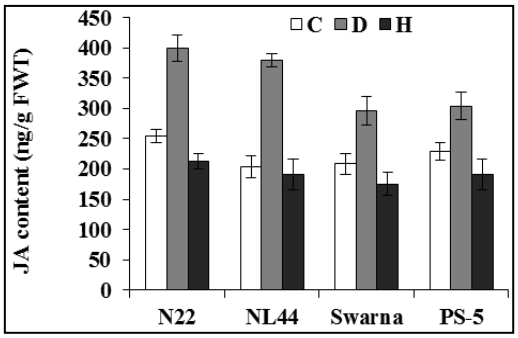

Fig 1: JA content

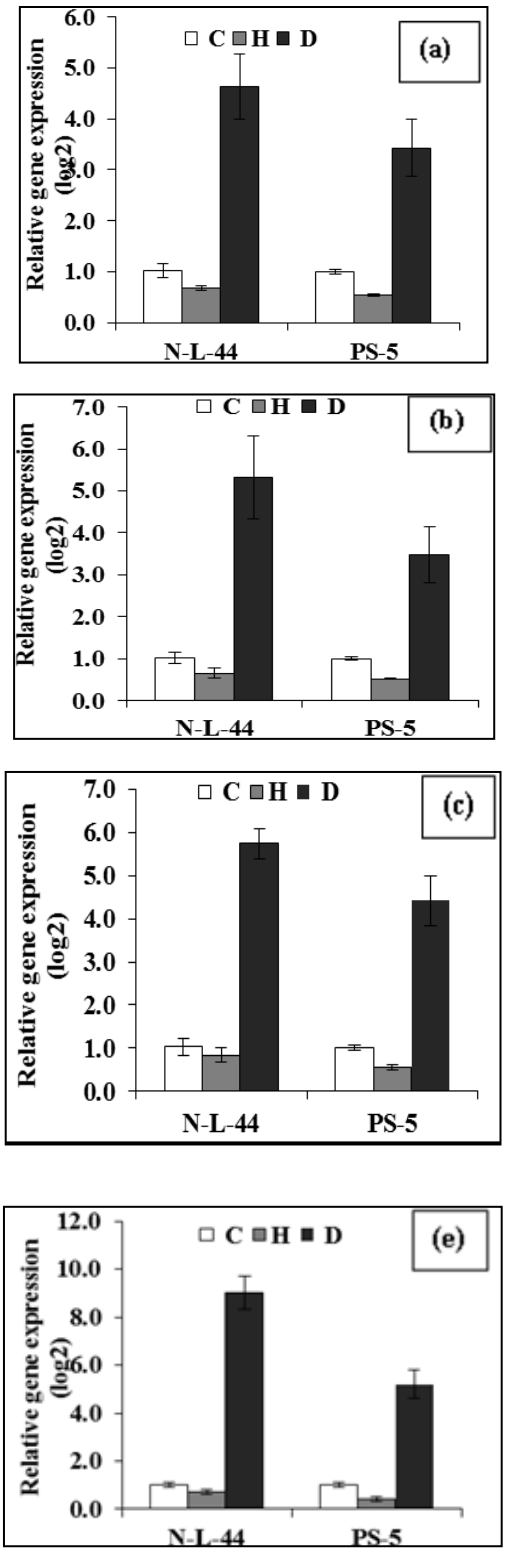

Fig. 2: Relative gene expression of (a) *aos*, (b) *aoc*, (c) *opr*, (d) *coi-1* & (e) *jaz*

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