ASIAN CULTIVATED RICE DOMESTICATION SUPPRESSES THE EXPRESSION OF ABIOTIC STRESS- AND REACTIVE OXYGEN SPECIES SCAVENGING-RELATED GENES IN ROOTS

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Abstract

Asian cultivated rice (*Oryza sativa* L), the important cereal crop, has low resistance to numerous biotic and abiotic stresses compared to its ancestral wild rice (*Oryza rufipogon*). Although genetic studies have shown that the susceptibility of cultivated rice towards various environmental stresses is due to its narrow genetic diversity caused by domestication, whereas wild rice possesses tremendous gene pools; yet very little is known about the domestication-induced transcriptional changes in abiotic stress-related genes and/or pathways in cultivated rice. Thus, to investigate these changes, we retrieved the root transcriptome data sets of cultivated and wild rice from the GenBank of National Center for Biotechnology information. Next, we performed MapMan-based analysis of the root transcriptome data sets of cultivated and wild rice. Cellular response overview from MapMan analysis showed that key genes related to abiotic stress categories; heat stress and drought/salt stress were significantly suppressed in cultivated rice relative to wild rice. In addition, the expression level of ascorbate- and dismutase-related transcripts, which also function in abiotic stress tolerance through involvement in the detoxification of reactive oxygen species (ROS), were also down-regulated in cultivated rice compared with wild rice. In conclusion, transcriptomic-based survey of cultivated rice and wild rice reflects that domestication has significantly changed (reduced) the transcriptional level of abiotic stress and ROS-scavenging related transcripts in cultivated rice. These findings further explain the susceptibility of cultivated rice towards abiotic stresses. Thus, re-introduction of the identified desirable genes of wild rice through conventional breeding and genetic engineering may improve the abiotic stress resistance mechanisms of modern rice cultivars.

Key words: Abiotic stress, MapMan, *Oryza rufipogon*, Transcriptome analysis

Introduction

Due to ever increasing world population, the global demand for food and energy is rising (Schneider *et al.,* 2011; Foley *et al.,* 2011). In order to feed this huge population, improvement in the staple food crop production is extremely critical. *Oryza sativa* L. (Asian cultivated rice) is among the important staple food crops, which provides calories for half of the world human population (Nasir *et al.,* 2017; Zeng *et al.,* 2017). Therefore, enhancing yield of cultivated rice will be a smart move to meet the demand for food and guarantee the global food security. Unfortunately, domestication has reduced the genetic diversity of cultivated rice. As a consequence, multifarious environmental factors are easily affecting rice crop production, thereby jeopardizing food security globally (Izawa *et al.,* 2009; Nasir *et al.,* 2017). On the contrary, wild rice genotypes including, *O. rufipogon* Griff., the closest counterpart of Asian cultivated rice, possesses copious valuable traits, particularly for resistance to major biotic and abiotic stresses and has evolved to be the tremendous gene reservoir, and hence serves as a foundation for enhancing different resistance mechanisms of the modern rice cultivars (Xiao *et al.,* 1996; Brar & Khush, 1997; Tanksley & Mccouch; 1997, Xiao *et al.,* 1998; Brar *et al.,* 2002; Londo *et al.,* 2006; Wang *et al.,* 2013). Besides,

studies also demonstrated that crop domestication plays a potential role in structuring root-associated microbiomes (Zhang *et al.,* 2017; Tian *et al.,* 2017). Thus, in order to ensure global food security, better understanding of domestication-induced transcriptional changes in rice and re-introducing the set of candidate genes (of desirable traits) lost/altered during the process of domestication seems a part of solution to increase the resistance mechanism(s) of the modern rice cultivars against various environmental constrains.

Rice genome sequencing has increased our ability to understand domestication-induced changes at molecular and genetic levels (Goff *et al.,* 2002; Izawa *et al.,* 2009; Jackson, 2016; Eizenga *et al.,* 2017). In addition, the development of modern next-generation sequencing allows deep sequencing coverage in a cost-effective manner (Metzker, 2010; Quail *et al.,* 2012). Previously, the genetic basis of domestication has been studied in economically important crops such as rice, tomato and maize (Doebley *et al.,* 2006; Paran & van der Knaap, 2007; Izawa *et al.,* 2009). In addition, it has been demonstrated that domestication process continuously inducing changes in crops at transcriptional level; for instance, recent findings showed that the transcriptional network of maize, sweet potato and tomato vary greatly due to domestication (Swanson-Wagner *et al.,* 2012; Koenig *et al.,* 2013; Dai *et al.,* 2017; Ponniah *et al.,* 2017). A more recent study published from

our lab also showed significant differences at transcriptional level among cultivated rice (*Oryza sativa* L. ssp. Japonica) and wild rice (*O. rufipogon* Griff.) during rice blast disease caused by *Magnaporthe oryzae* and, these transcriptional level changes were correlated with increased susceptibility of the cultivated rice towards *M. oryzae* infection (Tian *et al.,* 2018a). As is evident that transcriptional level changes are important, there is a lack of knowledge as to which extent domestication process has altered the expression of abiotic stress-related genes in cultivated rice.

In order to gain insights into the domestication-induced transcriptional changes in abiotic stress-related genes of cultivated rice, we retrieved root transcriptome data sets of nonstressed cultivated rice (*O. sativa*) and wild rice (*O. rufipogon*) from National Center for Biotechnology Information (NCBI) GenBank, which can be accessed through the accession number (SRP111367) (Tian *et al.,* 2018a), and were analyzed by using an omics tool referred to as MapMan. The results indicated that key abiotic stress- and reactive oxygen species (ROS)-associated transcripts were suppressed in the root of cultivated rice compared with the wild rice. This transcriptome comparison will not only increase our understanding of the domestication-induced transcriptional changes in abiotic stress-related genes of cultivated rice, but the incorporation of favorable genes of the wild rice in cultivated rice via classical breeding and/or modern transgenic approaches may also improve the abiotic resistance mechanism(s) of the modern rice cultivars.

Materials and Methods

Mining of transcriptome data: The transcriptome data sets of the roots of cultivated rice, Dongdao-4 (*Oryza sativa* L. ssp. Japonica) and wild rice, Dongxiang accession (*Oryza rufipogon* Griff.) presented here were obtained from the NCBI GenBank (http://www.ncbi.nlm.nih.gov) via the accession number SRP111367 (Tian *et al.,* 2018a).

MapMan-based analysis: MapMan (http://mapman.gabipd. org/home) is a sophisticated omics tool used for in-depth survey of various functional overviews; such as biotic overview, cellular response overview, secondary metabolites overview and cell function overview, etc. (Thimm *et al.,* 2004). Aiming to study the domesticated-induced transcriptional level changes related to abiotic stress, we conducted cellular response overview analysis of the root transcriptome data sets of cultivated and wild rice by using MapMan software version 3.6 and, focused on the abiotic stress category. Besides, we also paid attention to ROS-scavenging-related transcripts, because they also act as positive regulators of abiotic stress tolerance.

Results

Transcriptome data mining: RNA-sequencing based transcriptome data of the wild and cultivated rice (Tian *et al.,* 2018a) were obtained from the NCBI GenBank and compared for understanding domestication-induced changes at transcriptional level related to abiotic stresses. Readers are referred to Tian *et al.,* (2018a), for detailed information related to transcriptome raw reads, clean reads and transcripts mapped to the reference genome. The criteria of [fold change $\geq$ 2] and false discovery rate-corrected *P*-values (*q*-values) < 0.05 was adopted in order to identify significantly expressed transcripts between cultivated and wild rice.

MapMan-based analysis of abiotic stress- and ROS-scavenging-related transcripts: In order to fully understand the domestication-induced transcriptional level changes related to abiotic stress pathways, we performed cellular response overview analysis of the root transcriptome data sets of cultivated and wild rice with the help of MapMan.

In order to combat heat stress, plants including rice induce the expression of genes coding for heat shock proteins (HSPs) during high temperature (Zou *et al.,* 2009; Jung *et al.,* 2012; Chen *et al.,* 2014). Notably, of 21 identified differentially expressed genes (DEGs) related to heat stress, 18 were highly expressed in the wild rice compared with cultivated rice, whereas 3 were down-regulated (Figs. 1A, 2A; Table 1). The highly expressed genes in wild rice includes; *Os04g0549600, Os05g0500500, Os02g0782300, Os03g0276500, Os02g0181900, Os05g0562300, Os06g0116800, Os01g0135900, Os02g0537400, Os03g0293000, Os06g0253100, Os05g0460000, Os02g0758000, Os05g0519700, Os06g0682900, Os01g0840100, Os05g0296800,* and *Os08g0500700.* It should be noted that the transcripts up-regulated in the wild type and/or down-regulated in cultivated rice mostly comprised of gene family encoding HSPs, which are involved in heat stress tolerance (Chen *et al.,* 2014).

In addition to heat stress, drought stress and salt stress are also the major abiotic factors, constantly negatively affecting crop productivity. As is evident that cultivated rice possesses poor resistance to drought stress and slat stress as compared to wild rice (Tian *et al.,* 2015; Zhang *et al.,* 2017). Therefore, in the present study, we also focused on drought stress and salt stress related transcripts in cellular response overview. Interestingly, 4 key drought stress- and salt stress-related transcripts were significantly down-regulated in the roots of cultivated rice relative to wild rice (Figs. 1A, 2B; Table 1). Suppressed key transcripts related to drought stress and salt stress of cultivated rice are (*BURP10, Os06g0281800*); (*BURP17, Os11g0170900*), (*BURP11, Os06g0302000*) and *Os03g0673800. BURP10, BURP11, BURP17* belong to gene family which encodes BURP domain proteins having regulatory role in drought- and salt-stress tolerance (Ding *et al.,* 2009).

A growing body of evidence supports the idea that ROS-scavenging pathway is also involved in mediation of abiotic stress tolerance through detoxification of ROS (Gill & Tuteja, 2010). Aiming to explore the domestication-induced changes in ROS scavenging-related pathway at transcriptional level, we paid attention to the relevant ROS-scavenging transcripts, most importantly ascorbate and dismutase. We observed that of 6 ascorbate and 3 dismutase DEGs, 4 ascorbate (*Os04g0533500, Os07g0694700, Os09g0538600, Os01g0151400*) and 2 dismutase (*Os02g0115700, Os07g0665200*) associated transcripts were highly up-regulated in wild rice compared with cultivated rice (Figs. 1B, 3A and B; Table 2).
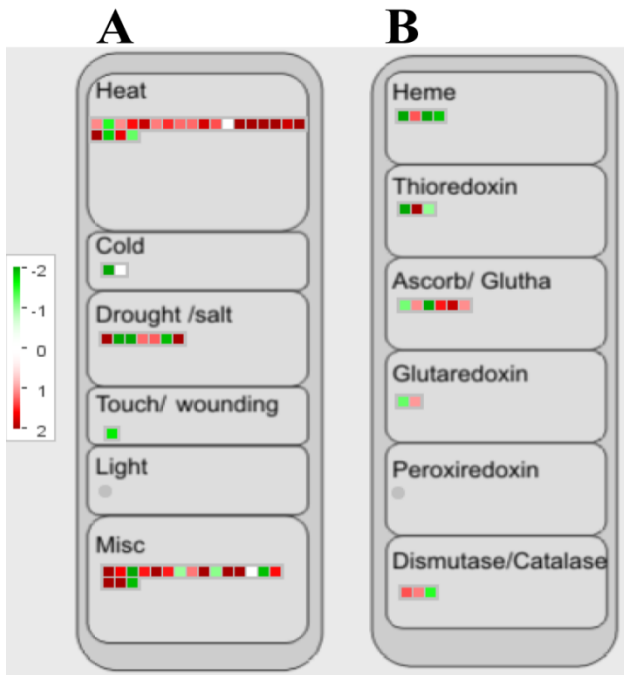
Fig. 1. MapMan analysis of differentially expressed genes related to (**A**) abiotic stress pathway and (**B**) reactive oxygen species scavenging pathway in wild rice (W) vs cultivated rice (C) comparison. Red and green colors indicate up- and down-regulated transcripts, respectively.
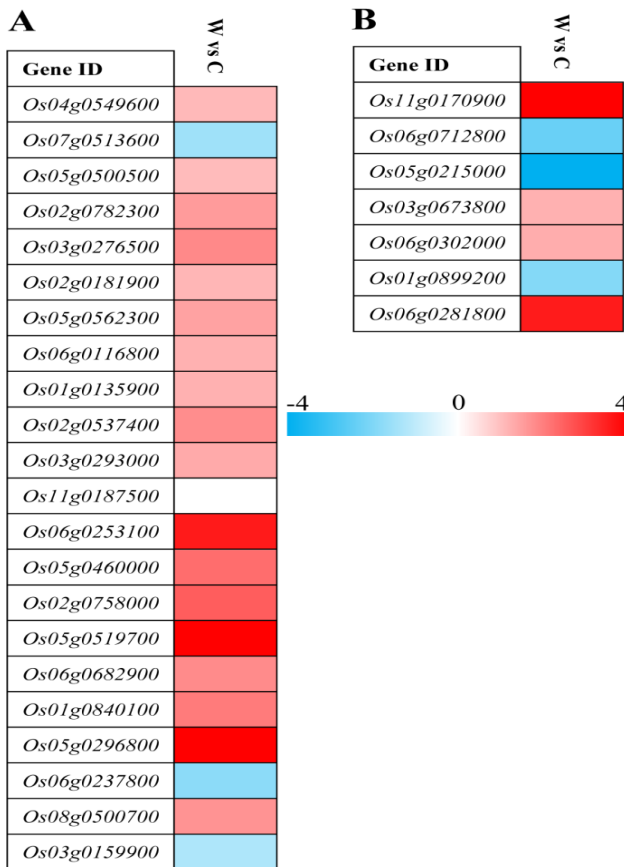

Fig. 2. Heatmap of differentially expressed genes related to (**A**) heat stress and (**B**) drought/salt stress in wild rice (W) vs cultivated rice (C) comparison using log2 fold change values. Red and blue colors indicate up- and down-regulated transcripts, respectively.
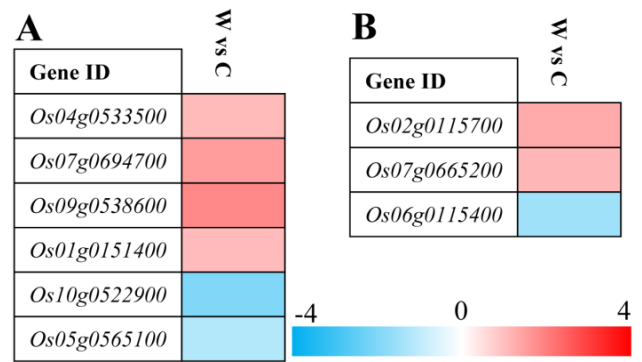

Fig. 3. Heatmap of differentially expressed genes related to (**A**) ascorbate and (**B**) dismutase in wild rice (W) vs cultivated rice (C) comparison using log2 fold change values. Red and blue colors indicate up- and down-regulated transcripts, respectively.
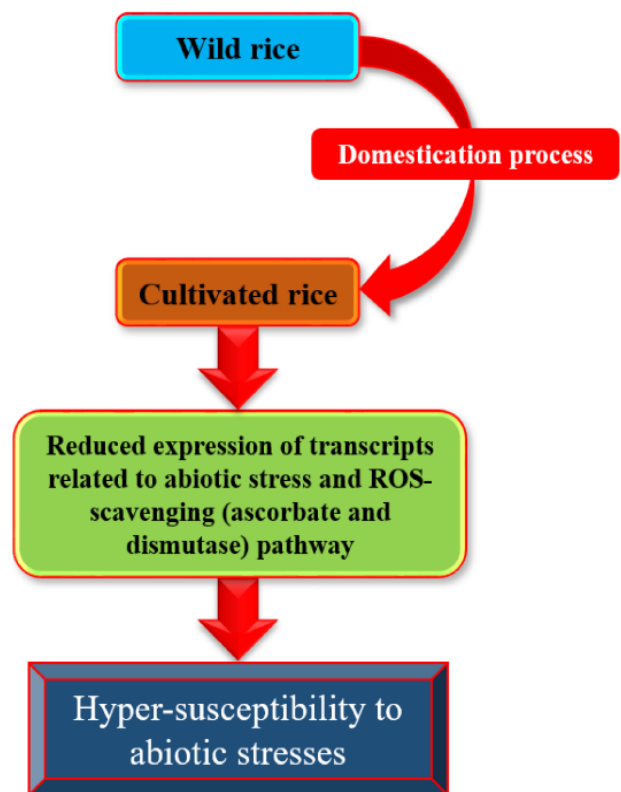

Fig. 4. Model illustrating domestication-induced transcriptional level changes in rice. Rice domestication suppressed the expression of genes related to abiotic stress and reactive oxygen species (ROS)-scavenging pathway, resulting hyper-susceptibility of cultivated rice towards various abiotic stresses.

Contrary to animals, plants are sessile in nature and are unable to avoid various environmental stresses including abiotic and biotic stresses. Thus to confront these environmental stresses, plants have evolved a sophisticated innate resistance mechanisms at molecular, biochemical and physiological levels (Wahid *et al.,* 2007; Shanker *et al.,* 2014). Due to rapid and continues climate changes, heat stress and drought/salt stress are becoming the major abiotic threats to rice production globally. Besides, domestication has reduced the genetic diversity of cultivated rice, thus various biotic and abiotic factors are easily affecting rice crop production globally. In this

context, a recently published report has shown that domestication reduced the transcriptional network of cultivated rice and thus became more susceptible to rice blast disease (Tian *et al.,* 2018a). The author conducted the genome-wide transcriptome analysis of cultivated and wild rice during *M. oryzae* inoculated and non-inoculated conditions and, focused on biotic stress-related pathways, but the abiotic stress-related pathways remained untapped. Thus, we were interested to unravel that to which extent domestication has affected abiotic stress-related pathways at transcriptional level. To achieve this, we obtained the recently deposited root transcriptome data sets of cultivated and wild rice (Tian *et al.,* 2018a) from NCBI GenBank and analyzed the cellular response overview (including abiotic stress and reactive oxygen species-scavenging pathway related genes) through MapMan.

Discussion

MapMan-based analysis of the cellular response pathway analysis of the root transcriptome data sets of cultivated and wild rice revealed that candidate transcripts associated with abiotic stress especially related to heat stress and drought/salt stress were down-regulated in cultivated rice relative to wild rice (Figs. 1A, 2A and B; Table 1). In addition, we also found a significant reduction in the expression levels of ROS-scavenging related transcripts in cultivated rice compared with wild rice (Figs. 1B, 3; Table 2). This could explain the domestication-induced susceptibility of cultivated rice to numerous abiotic factors relative to ancestral wild genotypes.

Previously it has been demonstrated that upon perception of heat stress by rice, as an adaptive strategy rice triggers the expression of key transcripts encoding HSPs (Zou *et al.,* 2009; Jung *et al.,* 2012; Chen *et al.,* 2014). It must be noted that among the 21 identified DEGs related to heat stress pathway, 18 were significantly (fold changes $\geq$ 2, *q*-values < 0.05) induced in the wild rice relative to that cultivated rice, whereas the expression levels of 3 transcripts were suppressed (Fig. 2A). Here, the abiotic stress related transcripts up-regulated in wild rice are listed in Table 1. Strikingly, most of the transcripts up-regulated in the wild type and/or down-regulated in cultivated rice comprised of gene family coding for HSPs, which are well-known for their adaptive role in heat stress tolerance (Chen *et al.,* 2014). Given the importance of HSP genes in heat stress resilience, it has been shown that overexpressing the *HSP101* in transgenic plants increased tolerance of the rice towards heat stress (Katiyar-agarwal *et al.,* 2003). It is worth noting that the expression level of *HSP101*, *Os05g0519700* gene was 22.9 fold higher in wild rice compared with the cultivated rice. These results clearly indicate that domestication suppressed the heat stress tolerance pathway at transcriptional level and this can be correlated with the lower tolerance of cultivated rice to heat stress.

Drought stress and salt stress are also among the main abiotic factors, which adversely affect both crop development and yield. Recent studies have shown that cultivated rice has low resistance to drought stress as compared to wild rice (Tian *et al.,* 2015; Zhang *et al.,* 2017). Thus, here, we paid closed attention to the drought- and salt-stress related transcripts in abiotic stress overview. Notably, we observed that in the abiotic stress pathway, 4 key drought stress- and salt stress-related transcripts were suppressed in the roots of cultivated rice compared to wild rice (Fig. 2B; Table 1), proposing that cultivated rice has poor transcriptional network to combat these stresses. Drought stress- and salt-stress-related transcripts which were down-regulated in cultivated rice were (*BURP10, Os06g0281800*); (*BURP17, Os11g0170900*), (*BURP11, Os06g0302000*) and *Os03g0673800*. Earlier reports have shown that *BURP10, BURP11* and *BURP17* belong to a gene family coding for proteins having BURP domains and are involved in abiotic stress tolerance including drought- and salt-stress tolerance (Ding *et al.,* 2009). Here, we observed that the expression of *BURP10, BURP11* and *BURP17* genes were 12, 2.4 and 78.24 fold higher in the root of wild rice with respect to cultivated rice, providing ample evidence that the wild rice possess strong drought- and salt-stress tolerance mechanism at genetic level as compared with cultivated rice.

Table 1. Tabular representation of differentially expressed genes (DEGs) related to heat stress and drought/salt stress in wild rice (W) vs cultivated rice (C) comparison.

Abiotic stress	W vs C	
	Gene ID	**Log2 fold change**
Heat stress	*Os04g0549600*	1.103
	Os07g0513600	-1.504
	Os05g0500500	1.082
	Os02g0782300	1.583
	Os03g0276500	1.862
	Os02g0181900	1.155
	Os05g0562300	1.472
	Os06g0116800	1.232
	Os01g0135900	1.237
	Os02g0537400	1.803
	Os03g0293000	1.343
	Os06g0253100	3.607
	Os05g0460000	2.303
	Os02g0758000	2.554
	Os05g0519700	4.517
	Os06g0682900	1.834
	Os01g0840100	2.071
	Os05g0296800	5.293
	Os06g0237800	-1.8
	Os08g0500700	1.708
	Os03g0159900	-1.257
Drought/salt stress	*Os11g0170900*	6.29
	Os06g0712800	-2.338
	Os05g0215000	-4.244
	Os03g0673800	1.237
	Os06g0302000	1.288
	Os01g0899200	-1.916
	Os06g0281800	3.583

*Log2 fold change values of DEGs of W vs C comparison were obtained by Tian and co-workers (2018b). The criteria for significantly expressed genes was [fold change $\geq$2] and *q*-values < 0.05

Table 2. Tabular representation of differentially expressed genes (DEGs) related to ascorbate and dismutase in wild (W) vs cultivated rice (C) comparison.

ROS-scavengers	W vs C	
	Gene ID	**Log2 fold change**
Ascorbate	*Os05g0565100*	1.083
	Os04g0533500	1.549
	Os10g0522900	1.872
	Os07g0694700	1.074
	Os09g0538600	-1.992
	Os01g0151400	-1.19
Dismutase	*Os02g0115700*	1.333
	Os07g0665200	1.156
	Os06g0115400	-1.493

*Log2 fold change values of DEGs of W vs C comparison were obtained by Tian and co-workers (2018b). The criteria for significantly expressed genes was [fold change ≥ 2] and q-values < 0.05

It is well-established that abiotic stresses trigger the production of ROS, which is lethal for plants (Gill & Tuteja, 2010). On the contrary, plants possess ROS-scavenging machinery, which acts as antioxidants and, remove and/or detoxify ROS (Gill & Tuteja, 2010). Compelling evidence suggested that ROS-scavenging-related genes are critical for positive regulation of abiotic constrains (Pandey *et al.*, 2017). With the aim to study the domestication-induced changes in ROS scavenging-related pathway at transcriptional level, we also focused on the expression of ROS-scavenging-related transcripts, most importantly ascorbate and dismutase. Notably, 4 ascorbate (*Os04g0533500, Os07g0694700, Os09g0538600, Os01g0151400*) and 2 dismutase (*Os02g0115700, Os07g0665200*) transcripts were significantly induced in wild rice relative to cultivated rice (Figs. 3A and B; Table 2). In this context, a recent study has shown that *ascorbate peroxidase 2, Os07g0694700* gene mediates the abiotic stress tolerance including drought- and salt-stress tolerance, accompanied with the enhanced ascorbate peroxidase activity (Zhang *et al.*, 2013). As is evident that ROS-scavenging pathway is also involved in abiotic stress tolerance through removal of ROS, thus our results further explain that cultivated rice is less resistant abiotic stress than wild rice. Taken together, we conclude that domestication-induced changes (suppression) of transcripts related to heat stress- and drought/salt stress-related pathways as well as ROS-scavenging pathway may contribute to reduce resistance and/or tolerance of cultivated rice to abiotic stresses (Fig. 4).

Conclusion

In the present study, we used MapMan omic tool to explore the transcriptional level changes in the cellular response overview, induced by domestication in *O. sativa* (a cultivated rice) compared to its progenitor *O. rufipogon* (a wild rice). The transcripts related to cellular response overview, which includes heat stress, drought/salt stress and ROS-scavenging pathways were significantly induced in wild rice and/or suppressed in the roots of cultivated rice during nonstressed condition. Our findings further confirmed that cultivated rice possesses low tolerance and/or resistance to confront abiotic stress especially heat stress and drought/salt stress. The DEGs identified in this study will be important for understanding the molecular mechanisms related to abiotic stress tolerance in wild rice. Moreover, abiotic stress resistance and/or tolerance mechanism of the cultivated rice maybe improved by the introgression of the identified desirable genes of the wild genotype using conventional breeding and modern transgenic approaches.

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