REVIEW ARTICLE

Plant transcriptomics and responses to environmental stress: an overview

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Abstract

Different stresses include nutrient deficiency, pathogen attack, exposure to toxic chemicals etc. Transcriptomic studies have been mainly applied to only a few plant species including the model plant, *Arabidopsis thaliana*. These studies have provided valuable insights into the genetic networks of plant stress responses. Transcriptomics applied to cash crops including barley, rice, sugarcane, wheat and maize have further helped in understanding physiological and molecular responses in terms of genome sequence, gene regulation, gene differentiation, posttranscriptional modifications and gene splicing. On the other hand, comparative transcriptomics has provided more information about plant's response to diverse stresses. Thus, transcriptomics, together with other biotechnological approaches helps in development of stress tolerance in crops against the climate change.

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Introduction

Transcriptomes are studied for interpreting functional elements of genome and revealing molecular constituents of cells and tissues (Wang *et al.* 2009). Transcriptomics, a genomewide measurement of messenger RNA (mRNA) expression levels based on DNA micro-array technology, is a prominent field of study (Brady *et al.* 2006; Gomase and Tagore 2008). The study deals with quantification of transcriptome, complete set of transcripts in cells, and abundance of these transcripts in a specific developmental stage, physiological or pathological condition (Wang *et al.* 2009). Study of transcriptomes has a significant impact on all the facets of biological sciences as it provides the ability to analyse differences in gene expression of multiple mRNAs both quantitatively and qualitatively (Tan *et al.* 2009). The key objectives of transcriptomics are to catalogue all the transcripts including mRNAs, noncoding RNAs and small RNAs to determine transcriptional status of genes; to determine 5′end and 3′end sites of genome, posttranscriptional modifications and splicing patterns. Transcriptomics also aim to quantify the modulations in gene expression levels during different stress conditions and developmental stages (Wang *et al.* 2009).

Different technologies used for transcriptomic studies include hybridization-based approaches, sequence-based approaches and RNA sequencing (Tan *et al.* 2009; Wang *et al.* 2009), each of these has some pros and cons. Hybridization-based approaches involve incubating fluorescently-labeled cDNA with microarrays that may be custom made or commercial high-density oligo microarrays. This approach is referred as microarray technology and is used for gene expression profiling (Nowrousian 2007). Microarrays with probes spanning exon junction are also used for detection and quantification of distinct spliced isoforms (Clark *et al.* 2002). These approaches are high throughput approaches and are inexpensive, except for few approaches including high-resolution tiling arrays that are used for quantifying large genomes (Yamada *et al.* 2003; David *et al.* 2006).

Hybridization-based approaches rely upon preexisting knowledge about genome sequences and have limited dynamic range of detection for both background and saturation of signals (Okoniewski and Miller 2006; Royce *et al.* 2007). On the contrary, sequence-based approaches are used

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to determine the cDNA sequences directly. Although Sanger sequencing comes in handy, it has low throughput, high cost and low quantification (Gerhard *et al.* 2004). In view of these limitations, tag-based methods are nowadays used. These include serial analysis of gene expression (SAGE), cap analysis of gene expression (CAGE) (Kodzius *et al.* 2006) and massively parallel signature sequencing (MPSS). Tag-based methods are more reliable owing to the fact that they are high throughput and provide precise digital levels of gene expression. However, there are a few limitations of tag-based methods as only a small portion of transcript can be analysed, and the isoforms are indistinguishable from each other (Brenner *et al.* 2000).

RNA sequencing is the most recent approach used for transcriptomic studies. It does not have a reference genome to gain useful information about the transcripts (Strickler *et al.* 2012). It is a recently developed deep sequencing technology. In this approach, population of total or fractionated RNA is converted to library of cDNA with adaptors attached to both the ends. cDNA molecules are then sequenced in high throughput manner and short sequences are obtained (Holt and Jones 2008; Vera *et al.* 2008). This technology has many advantages: it is (i) not restricted for detection of transcripts that correspond to existing genomic sequence, (ii) reveals precise position of transcription boundaries, (iii) has very low background signal and (iv) does not have any upper limit of quantification. RNA sequencing is the first method that allows entire transcriptome to be surveyed in high throughput and quantitative manner (Cloonan *et al.* 2008; Mortazavi *et al.* 2008; Nagalakshmi *et al.* 2008).

Plant transcriptomics applications

Plant transcriptomics is being widely used in studying plant responses to various stresses. Transcriptomic studies have revealed many changes in expression levels of various genes during exposure to environmental extremes, e.g. cDNA isolated from leaves and roots of *Coffea arabica*, when studied with nonredundant expressed sequence tags, showed lower level of exact number of genes, however, competitive hybridization on *C. Arabica*-specific cDNA microarray treated with benzo-(1,2,3)-thiadiazole-7-carbothionic acid S-methylester (BTH) showed an increased level of overexpressed genes. This overexpression of stress responsive genes reveals a wide spectrum of defense-related response pathways against different environmental extremes. Leaf tissue metabolic pathways respond negatively in comparison to root tissues where metabolism is downregulated with subsequent increase in biosynthesis of proteins, which are involved in storage processes. BTH increases resistance of monocotyledons as well as dicotyledons against many biotic factors, such as viruses, bacteria and fungal pathogens. However, this induction of stress tolerance by BTH treatment is species-dependent (Pallavicini *et al.* 2005).

In relation to salt stress, transcriptomic analysis of plants helps in identifying important transcripts and relevant associations between various physiological processes like vascular potassium ion circulation, root–shoot translocation of calcium ions and transition metal homeostasis (Maathius 2006). Transcriptomic analysis of allopolyploid relative of soybean with the diploid species show a high degree of gene space duplication. It is also observed that the tetraploids use these redundant gene copies in novel ways (Ilut *et al.* 2012). Transcriptomic analysis of gene expression is also applied to characterize the plant responses to phloem-feeding insects (PFIs). These insects induce transcriptional reprogramming in their hosts and plant response to these insects differ from the response to other insects or pathogens. It has been suggested that these insects induce cell wall modification, reduce photosynthetic activity, manipulate source-sink relations and modify secondary metabolism in hosts (Thompson and Goggin 2006).

Transcriptomic analysis of plastid genes in *Solanum lycopersicum* have shown that most of the plastid genes are downregulated in fruits compared to leaves. These changes are more pronounced in photosynthesis-related genes than in other metabolic pathways related genes. Gene expression activity in chromoplast is regulated by plastid encoded fatty acid biosynthetic gene, *accD* (Kahlau and Bock 2008). In *Solanaceae*, there exist distinct mechanisms for synthesis of acyle sugars, as revealed through transcriptomic studies, and several convergent and divergent mechanisms leading to synthesis/production of important defensive compounds do also exist (Slocombe *et al.* 2008). In addition to its application in studying salt stress tolerance mechanisms, transcriptomics can be better employed to study cold stress responses, which is more easily and strongly made understandable as has been reported in potato. Exposure to both the stresses (cold and salinity) cause downregulation of majority of photosynthetic genes whereas cell rescue and transcription factor genes are upregulated. Salt exposure also results in downregulation of genes associated with primary metabolism, signal transduction and detoxification (Evers *et al.* 2012).

Comparative transcriptomic studies applied to tomato and its five wild species reveal footprints of positive selection in over 50 genes (Koenig *et al.* 2013). They also show shift in gene expression levels and many of which resulted from changes in selection pressure (Koenig *et al.* 2013). Most of these genes are stress responsive and are involved in imparting stress tolerance. Large-scale modifications appear in response to light in wild and cultivated species of tomato (Koenig *et al.* 2013). In tomato, majority of genes that are regulated by nitrogen enrichment show almost similar expression levels, both in mycorrhizal and nonmycorrhizal roots indicating that primary response to nitrogen enrichment is mediated by mycorrhiza-independent root processes (Ruzicka *et al.* 2012). Transcriptomic analysis of broccoli plants treated with N6-benzylaminopurine shows that genes encoding for molecular chaperones and stress-related genes are upregulated and almost similar results were

reported in plants with ipt transgenic. Both the treatments are involved in regulation of genes associated with cytokinin signalling, sugar transport, energy metabolism, carbohydrate metabolism, amino acid metabolism and lipid metabolism (Liu *et al.* 2013).

In plants having extremophile life style, e.g. mangroves, show similarities in transcriptome size, habitat, tissue type, developmental stage, biogeographic and phylogenetics in different species which results in unique life style (Dassanayake *et al.* 2009). Omrane *et al.* (2009) demonstrated that leguminous plant, *Lotus japonicas* which was incubated first in high nitrogen conditions for 10 days followed by transfer to low nitrogen conditions, and subsequently, inoculated with symbiotic fungi, showed reduced nodulation and transcriptome studies showed differential expression of genes of metabolic pathway, cell signalling, transcriptional regulation and stress response. Transcriptomic studies of oak plants subjected to long term (one year) mild drought showed upregulation of genes associated with plant cell rescue and defense. If the stress persisted longer (two years or more), the response was more vigorous. This long-term drought response triggers the adaptation process of plants to evolve these conditions and ensure the survival of the plant. But upon rewatering, the damage so caused cannot be fully recovered (Spieb *et al.* 2012).

Comparative transcriptomic analysis of closely-related C3 (*Cleome spinosa*) and C4 (*Cleome gynandra*) plant leaves has revealed that about 603 transcripts differ in abundance between the two leaves, out of which, 17 are transcription factors and some are important putative transport proteins (Brautigam *et al.* 2011). Comparative transcriptomics when applied to drought-stressed populus showed that activation of signalling cascades is specific to early response in leaves and general in root apices (Cohen *et al.* 2010). GS-2 mutant of *L. japonicas*, Ljgln2-2, exhibited normal sensitivity to mild water deprivation than wild type and comparative transcriptomic analysis of both the mutant and wild type revealed significant differences in expression pattern of genes involved in proline metabolism. Further, it was reported that Ljgln2-2 (mutants) showed 3-fold increase in gene regulation in response to drought as compared to wild counterparts (Diaz *et al.* 2010). Transcriptomic analysis when applied to rice oligomicroarrays revealed that there are different effects of hybridization and genome duplication in expression patterns of hybrids and allopolyploids, which is due to transcriptomic evolution in allopolyploids (Chelaifa *et al.* 2010). Comparative transcriptomics of two actinorhizal symbiotic plants, *Casuarina glauca* and *Alnus glutinous*, having association with bacteria *Frankia* revealed that there are ~14,000 unigenes present in roots and nodules of both the species. In connection with this, transcriptomic analysis showed that genes regulating carbon and nitrogen exchange, defense against pathogens and stress resistance were strongly induced. Conservation of host plant specific pathway is conserved among the plants, which showed that these plants are phylogenetically related (Hocher *et al.* 2011).

Transcriptome of *Urticuluria* (a carnivorous plant) showed its complex metabolic pathway that characterizes a minimal plant genome. The transcriptomic analysis supported the hypothesis that increased nucleotide substitution rates throughout the plant may be due to mutagenic action of amplified reactive oxygen species production (Ibarra-Laclette *et al.* 2011). Transcriptomic analysis of *Fraxinus* species revealed that there is a high occurrence of defense-related genes. Transcription factors of several defense genes are overexpressed and 1272 single nucleotide polymorphisms (SNP) as well as 980 microsatellite loci among which seven microsatellites showed polymorphism were also predicted to occur in genomes of different species of *Fraxinus* (Bai *et al.* 2011).

Transcriptomic studies on some leading plants

Arabidopsis thaliana

Transcriptome analysis of gametophyte genome of *Arabidopsis* showed 992 pollen expressed messenger RNAs out of which 40% are detectable specifically in pollen. Overexpression of mRNAs encoding proteins for cell wall metabolism, cytoskeleton and signalling can also be observed. There is extensive overlap of pollen transcriptome with that of sporophyte transcriptome (Honys and Twell 2003). Transcriptome analysis of 13,977 male gametophytes of *Arabidopsis* expressed mRNAs and 9.7% of these mRNAs are male gametophyte specific. The analysis also suggested that transition from bicellular to tricellular pollen is accompanied by decline in level of diverse mRNA species and increase in level of male gametophyte specific mRNAs. It is also observed that early synthesis of translation factors contribute to growth of pollen tube (Honys and Twell 2004). Transcriptomic studies on *Arabidopsis* reveals that HD2B histone deacetylase gene functions as a genetic factor associated with seed dormancy and its expression is upregulated by cold and after ripening treatments (Yano *et al.* 2013). Transcriptomic studies on pollen grains of *A. thaliana* revealed that they have a unique and smaller transcriptome that expresses 6587 genes with greater proportion of selectively expressed and enriched genes than any vegetative tissue. There is an accumulation of G2/M associated factors which have a role in first mitotic division. Moreover, in spite of transcription-associated transcripts which are relatively less presented, nonclassical MAD boxes are expressed as class with putative unique roles in pollen (Pina *et al.* 2005). Female gametophyte transcriptome analysis on *Arabidopsis* revealed that there are up to 225 genes that are specific to female gametophyte (Yu *et al.* 2005).

Transcriptomic studies carried on *Arabidopsis* plants grown under high carbon dioxide levels for five weeks under short days and subsequently transferred to normal conditions under short as well as long days revealed that 1549 genes were differentially expressed after the transfer from high carbon dioxide in short days (hCO_2) to normal. Among

CO_2 conditions, half of the genes were associated with redox reactions, stress and abscissic acid. Light signalling and clock genes were also differentially expressed. When the same experiment was done with hydrogen peroxide replacing carbon dioxide, the sensitive plants showed upregulation of hydrogen peroxide responsive genes indicating that carbon dioxide and hydrogen peroxide interact with day length and photoreceptor pathways, which show a close crosstalk between these three stimuli (Queval *et al.* 2012). Comparative analysis of *Arabidopsis* sperm cell transcriptome with that of representative sporophyte tissues and pollen reveals that sperm has a diverse and distinct transcriptional profile and DNA repair genes. Ubiquitin-mediated-proteolytic genes as well as cell cycle progressive genes are overexpressed in sperm cells (Borges *et al.* 2008). Transcriptomic analysis of *Arabidopsis* roots affected by sugar beet cyst nematode (a condition called Syncytia) showed that 3893 genes are upregulated and 3338 genes are downregulated. Genes that are related to high metabolic activity are upregulated (Szakasits *et al.* 2009).

Transcriptome analysis of pollen germination and tube growth in *Arabidopsis* showed high expression of genes related to cell rescue, transcription, signal transduction and cellular transport. Calmodulin, calmodulin-like proteins, cation/hydrogen exchanger and heat-shock proteins show the highest expression during tube growth and pollen germination (Wang *et al.* 2008). In *Arabidopsis*, early embryogenesis is under zygotic control which was proved by transcriptomic analysis of hybrid embryos of two polymorphic inbred lines. There are some transcripts which are inherited from either of the parents or are transcribed by imprinted loci and most of the transcripts are those produced in equal amounts by both the parents. Widespread zygotic transcription is also observed as there are some transcripts that are not expressed in sperms and eggs (Nodine and Bartel 2012).

Analysis of *Arabidopsis* transcriptome during oxidative stress revealed that there are 175 nonredundant-expressed sequence tags that are regulated by hydrogen peroxide. Out of these 175 nonredundant-expressed sequence tags, 113 were induced by hydrogen peroxide whereas 62 were repressed by it. These expressed tags have been predicted to function in cell defense and rescue processes (Desikan *et al.* 2001). Kreps *et al.* (2002) demonstrated that exposure of *Arabidopsis* to stress conditions (temperature, salt and drought), induced regulation of 30% sensitive transcriptome. They further reported that roots and leaves displayed very different changes, however, 14% of cold-specific gene expression is common in both roots and leaves. Gene (At5G52310) showed highest expression levels of 250, 40 and 57 fold in response to cold, drought and salinity, respectively in *Arabidopsis* roots (Kreps *et al.* 2002). Transcriptome profiling of *Arabidopsis* plant showed that under low temperatures, multiple regulatory pathways related to low temperature in addition to CBF (DREB1) cold response pathway exists and these pathways help in cold acclimation of the plant. A total of 306 genes are proved to be cold-responsive genes and has been reported that several genes are downregulated during cold acclimation. Out of these cold-responsive genes, 48 were putative transcription factors and two of these transcription factors were regulated by CBF expression. CBF expression in warm temperature results in repression of eight genes, which were also downregulated during the low temperatures (Fowler and Thomashow 2002).

Expression profiling analysis of Arabidopsis genome in response to cold stress showed 939 cold-regulated genes of which 655 were upregulated and 284 were downregulated. Early cold-responsive genes encode for transcription factors that control late-responsive genes and many posttranscriptional as well as chromatin level regulators. Moreover, genes important for synthesis of hormones and signalling molecules are also cold regulated (Lee *et al.* 2005). Transcriptomic analysis of Sel1, a mutant with defective sulphur transporter gene, revealed that dysfunction of sulphur transporter can mimic general sulphur symptoms. Clustering of sulphur transporter genes indicated that sulphur uptake, reductive sulphur assimilation and turnover of secondary sulphur metabolites are activated under sulphur. Profiling of sulphur-responsive genes showed that expression of sulphur-responsive genes is enhanced by decreased expression of glutathione. These sulphur-responsive genes induce high expression of genes associated with alleviation in oxidative damage (Maruyama-Nakashita *et al.* 2003). Hybridization transcript profiling of *Arabidopsis* subjected to 6, 10 and 13 days of constitutive and induced sulphur starvation revealed that 632 genes were overexpressed specifically to sulphur deficiency. The results also suggested upregulation of genes involved in flavonoid, auxin and jasmonate synthetic pathways during sulphur deficiency (Nikiforova *et al.* 2003).

To analyse the effects of 2,4,6-trinitrotoluene of *Arabidopsis* roots, transcript profiling by serial analysis of gene expression leads to the identification of 19,000 unique tags. Besides inducing expression of cytochrome P450 enzymes, ABC transporter and nitroreductases, a highly induced tag which increases upto 27-fold in response to 2,4,6-trinitrotoluene (TNT), represents glutathione *S* transferase. Unsuspected conjugation pathways are also observed (Ekman *et al.* 2003). Treatment of *Arabidopsis* seedlings with low concentration of indole acetic acid (auxin) decreases the expression levels of 23 genes and increases the expression level of 47 genes within the first 20 min of treatment and genes coding for transcription factors are expressed after 40 min of treatment. The response also revealed the presence of abscisic acid-responsive DC3 promoter-binding factor which suggest that there is a possible role of abscisic acid in regulating auxin-induced responses (Pufky *et al.* 2003). Transcriptional profiling analysis performed on *Arabidopsis* seedlings exposed to an allelochemical benzoxazolin-2(3H)-one (BOA) revealed that major responsive genes were involved in cell rescue and defense, and most of these rescue genes were associated with chemical detoxification pathways which are also induced by a variety of xenobiotic compounds (Baerson *et al.* 2005). In

wild-type *Arabidopsis*, transcript profiling showed that 262 genes were upregulated and 125 genes were downregulated by abscissic acid treatment (Xin *et al.* 2005). A genomewide analysis of transporter genes expressed in male gametophyte of *Arabidopsis* at different developmental stages was performed and it was reported that out of 1269 genes isolated from the genome encoding for classified transporters, 124 genes were preferentially expressed relative to sporophytic tissues while some genes like *COPT3*, *STP2* and *OPT9* were highly expressed in microspores and bicellular pollens, while other genes, *STP11* and *LHT7* were specifically expressed in tricellular and mature pollen (Bock *et al.* 2006).

Transcriptomic profiling of *Arabidopsis* suspension culture cell responses to sucrose (Suc) starvation showed that after 24 h of starvation autophagy and increased expression of vacuolar proteases is induced which contribute in degradation of cytoplasmic components delivered to the vacuole and help in nutrient recycling. Culture viability decreases after 48 h of starvation and after 72 h, substantial cell death occurs. Increase in expression levels of 343 genes after 48 h of starvation indicates the response to nutrient stress while starvation for 72 h the cells are protected from death by activation of various defense and stress response pathways regulated by specific protein kinases and transcription factors (Contento *et al.* 2004).

Armengaud *et al.* (2004) studied transcriptional responses of *Arabidopsis* seedlings to changing external supply of essential macronutrient potassium (K) and reported that genes which responded most prominently are linked to a phytohormone, jasmonic acid. Potassium starvation causes an increase in transcript levels of jasmonic acid biosynthetic enzymes lipoxygenase, allene and allene oxide synthase. Interestingly the level of these enzymes decreases as the potassium ions are resupplied. They proved a novel role of jasmonic acid in nutrient signalling and stress management through various processes, including nutrient storage, recycling and reallocation. Cell wall proteins (extensions and arabinogalactans), having putative role as calcium signalling molecule (Calmodulin) and ion transporter (high affinity potassium ion transporter HAK5) are discovered to be highly significant potassium ion responsive genes.

Transcriptome analysis of *Arabidopsis* showed that in response to phosphorus starvation 171 genes were induced and 16 genes were repressed, whereas in response to incubation with sucrose, 337 genes were induced and 307 genes were repressed. It has also been observed that several genes, which are thought to be regulated by phosphorus starvation, are also regulated by sucrose incubation and vice versa. Nearly 150 genes are responsive to both the factors antagonistically or synergistically. These genes give prominent response to these factors in combination relative when they are applied individually. These genes represent, (i) regulatory programme to increase growth when phosphorus and carbohydrates are in excess, (ii) gene set which is induced to alleviate phosphorus starvation and they are further induced by accumulation of sucrose (Muller *et al.* 2007). Hermans *et al.* (2010) studied early transcriptomic response to magnesium deprivation in *Arabidopsis* and response at whole plant level was observed after removing magnesium from the nutrients. Highest number of regulated genes was observed in roots of the plant. Major responses were perturbation of central oscillator of circardian clock and triggering of abscissic acid signals (Hermans *et al.* 2010). *Arabidopsis* infected by pathogens and insects showed a high level of transcriptional modification. Infected plants overexpressed the stress-related genes. Salicylic acid, jasmonic acid and ethylene in orchestration have been identified as key players in plant defense responses (De Vos *et al.* 2005). Silverleaf whitefly (SLWF) is phloem-feeding pest which affects *Arabidopsis* and transcript profiling of SLWF affected *Arabidopsis* revealed that 700 transcripts are upregulated and 556 transcripts are downregulated. Defense pathway of these plants showed that responses to SLWF infection are different from that of chewing insects and aphids. After SLWF feeding, jasmonic acid genes are repressed and salicylic acid genes are upregulated. Further studies showed that pathogen defense pathways are not activated (Kempema *et al.* 2007). Recent analysis on transcriptome of *Arabidopsis* showed existence of different defense systems and target overlapping gene sets. A quantitative mechanism is common to multiple defense systems and it modulates the transcript levels of these defense-associated genes (Eulgem 2004). Responses of *Arabidopsis* gene regulation to different stresses are provided in table 1.

Gossypium (cotton)

Comparative transcriptomic analysis of fibre cells of two cotton plants, wild (K101) and domesticated (Pima S-7) at three stages of elongation (early, mid and late), showed differential expression of 4200 genes between wild and domesticated accessions. In domesticated plants there is an upregulation of expression of genes for cellular redox reactions and a downregulation of genes for stress. Upregulation of signal transduction genes and hormone regulation genes result in prolonged growth of fibre (Chaudhary *et al.* 2008). Comparative transcriptomic analysis of cotton anther of wild type and genetic male sterility (GMS) mutant showed that in GMS mutant, 9595 genes are differentially expressed in meiosis, 10,407 in tetrad and 3139 genes are differentially expressed in uninucleate microspore stage of GMS mutant anther formation. Expression of genes associated with hormone synthesis, sucrose metabolism, starch metabolism, pentose phosphate pathway, glycolysis, histone protein synthesis and flavonoid metabolism is highly upregulated during tetrad stage and is downregulated during meiosis and uninucleate stage (Wei *et al.* 2013).

Cytoplasmic male sterility (CMS) is a maternally transferred trait due to which functional pollen is not produced. CMS can be restored by restorer genes. A comparative transcriptomic analysis performed to compare differentially-expressed genes between flower buds and CMS restorers in

Table 1. Responses of *Arabidopsis thaliana* to different stress conditions.

Stress condition	Response of plant by expression level of genes
Oxidative stress	113 genes upregulated, 62 genes downregulated
Cold stress	655 upregulated, 284 downregulated
Sulphur stress	632 upregulated
Indole acetic acid treatment	47 upregulated, 23 downregulated
Abscisic acid treatment	262 upregulated, 125 downregulated
Sucrose stress	343 upregulated
Phosphorus starvation	171 upregulated, 16 downregulated
Pathogen attack	700 upregulated, 556 downregulated

cotton revealed that 458 genes are differentially expressed in restorers of which 127 are upregulated and 331 are downregulated. Most differentially expressed genes encoded putative proteins which are involved in cell wall expansion, cell elongation and cell division (Suzuki *et al.* 2013). Fasciclin-like arabinogalactan (FLA) genes are expressed during the fibre development in cotton and transcriptomic studies revealed that 10 days after anthesis, three FLA were highly expressed while four genes were accumulated in fibres. The expression of these genes is also regulated by fibre development, light and sodium chloride (Huang *et al.* 2008). During fibre development, genes involved in vesicle coating and trafficking are highly upregulated, thus they have major role in maintaining growth of fibres (Hovav *et al.* 2008). Comparative transcriptomic studies on fibres of domesticated and wild cotton species showed dynamic range of differentially-expressed genes and a total of 9465 genes are differentially expressed (Rapp *et al.* 2010). Cotton transcriptome studied during water stress showed a total of 519 differentially-expressed genes, which are associated with stress, defense, metabolism and gene regulation. Moreover, pathways related to heat shock proteins and reactive oxygen species are also regulated (Park *et al.* 2012).

Transcriptomic analysis of cotton under somatic embryogenesis revealed that numerous genes are differentially expressed. The upregulated genes are associated to auxin biosynthesis, cytokinin biosynthesis and signal transduction pathways (Xu *et al.* 2013). Transcriptomic analysis under drought stress also showed number of differentially-expressed genes (Shanker *et al.* 2014). Upregulation of genes linked to pectin modification and cytoskeleton proteins is also observed. Genes encoding transcription factors, osmoprotectants, ion transporters, heat shock proteins and hormone biosynthesis are also highly upregulated. Whereas genes involved in pathways of phenylpropanoid synthesis, flavonoid biosynthesis, pentose and glucuronate interconversion, starch and sucrose metabolism are downregulated during fibre elongation (Padmalatha *et al.* 2012).

Hordeum vulgare (barley)

Comparative transcriptomics of dormant and after ripened barley embryos showed that after ripened embryos have promoted abscissic acid catabolism, reduced abscissic acid sensitivity, and 2 members of lipid phosphate phosphatase (LPP) family were differentially expressed (Barrero *et al.* 2009). Transcript profiling of steam girdled (used for carbohydrate accumulation) leaves of barley showed an increased level of aminopeptidases (cnd41), thiol and serine proteases with concomitant upregulation of SAG12, hexokinases and some other senescence specific genes (Parrott *et al.* 2007). Transcriptomic examination of barley revealed that there is six well-characterized germination stages comprising of early, late and postgermination phases. Transcription factors and signalling modification molecules are upregulated in early stage of germination, whereas histone families and metabolic pathways are upregulated in late phase. Postgermination phase refers to the upregulation of photosynthesis pathway and seed reserve mobilization pathway. Stress related and storage pathways are downregulated during whole germination process (An and Lin 2011).

RNA profiling of B trichothecene deoxynivalenol (DON) treated barley spikes showed upregulation of ABC transporters, UDP-glucosyltransferases, glutathione *S*-transferases and cytochrome P450. Moreover, cysteine synthases were largely upregulated and showed role in defense (Gardiner *et al.* 2010). Transcriptomic analysis of barley under salt stress revealed that 48 genes are highly upregulated whereas 62 genes are downregulated (Zeimann *et al.* 2013).

Transcriptomic analysis of barley roots subjected to low temperature (4°C) for four weeks showed that 2577 genes were found to be cold responsive as revealed by their two-fold increase. Among these, 185 genes showed increase in expression levels upto 10-fold. AGL19 is considered as most important regulator in vernalization response. FAD7 is proved to be active against many cold stress pathways (Wu 2010). Through transcriptome profiling, 11 genes have been reported to be upregulated in barley exposed to salinity (Lee *et al.* 2009). Further, the transcriptomic analysis also showed upregulation of genes like leucine-rich repeat transmembrane protein kinases, glycine-rich RNA-binding protein involved in leaf senescence. Accelerated leaf senescence is also associated with upregulation of plastidial and extra plastidial proteases in the germplasm (Jukanti *et al.* 2008).

Oryza sativa (rice)

Transcriptomic analysis of mature rice embryos showed differentially-expressed genes that are involved in stress

tolerance. There are 191 differentially-expressed genes between LYP9 and its parents. These differential genes represent overdominance, high parent dominance, low parent dominance, additivity and underdominance (Ge *et al.* 2008). Transcriptomic studies of rice genome showed a total of 3646 tandem repeats and 3633 pairs of segmental genes which together make up about 30% of total annotated rice genes, excluding transposons, and share different physical locations and exhibit biased subset of functions. Their regulation depends upon tissues and existing environmental conditions. Divergence in their expression is also related to promoter differentiation and DNA methylation status (Jiang *et al.* 2013).

Transcriptomic studies of rice panicle and grains under ozone stress revealed regulation of 620 genes in panicle and 130 genes in grains. In panicles, 176 genes are upregulated and 444 genes are downregulated, whereas in grains, 24 genes are upregulated and 106 genes are downregulated. Among these differentially-expressed genes majority are involved in processes like cell signalling, hormone synthesis, cell wall formation, transcription, proteolysis and defense (Cho *et al.* 2013).

Transcriptomic profiling of rice roots, grown in phosphorus deficient conditions, confirmed upregulation of certain genes involved in responses to phosphorous starvation. Changes in expression of genes involved in response to metal stress like aluminum, iron and zinc are also observed (Wasaki *et al.* 2003; Li *et al.* 2010). *Ospl1* gene is the most differentially-expressed gene in phosphorus stress. Starch metabolic genes and inorganic phosphorus liberating genes are also upregulated (Wasaki *et al.* 2006). Two-week-old rice plants subjected to ozone stress, when analysed transcriptomically showed five-fold increase in expression of 135 genes. These genes belong to eight major families, which are involved in storage, cellular processing, as transcriptional factor, in signal transduction and metabolism (Cho *et al.* 2008). Transcriptomic analysis of rice plants subjected to oxygen availability showed 730 genes are anaerobic responders and are upregulated in the absence of oxygen (Narsai *et al.* 2009). Transcriptomic analysis of arsenate tolerant rice plants exposed to sodium arsenate showed two-fold increase in upregulation of 576 genes and downregulation of 622 genes with concomitant expression of transcription factors, transporters and stress protein genes (Norton *et al.* 2008). Moreover, genes involved in glutathione synthesis, metabolism and transport were majorly affected by the arsenate treatment (Norton *et al.* 2008). Sucrose-starved rice plants upon transcriptomic analysis showed that hydrogen pyrophosphatases are upregulated and most of the upregulated genes are involved in degradation pathways, whereas the downregulated genes are involved in biosynthetic pathways (Wang *et al.* 2007). Jasmonic acid-treated rice seedlings when subjected to transcriptomic analysis showed that genes involved in photosynthesis, cellular respiration and protein modification were highly upregulated in the shoots whereas, genes representing antioxidants and defense molecules are upregulated in roots. Overall, 107 genes were upregulated and 34 genes were downregulated in shoots; and 325 genes were upregulated and 213 genes were suppressed in roots (Cho *et al.* 2007). Transcriptomic analysis of transgenic rice overexpressing *TERF1* revealed increased tolerance to high salt and drought stress. *TERF1* is shown to regulate the expression of other stress-related functional genes including *Lip5*, *Wcor413-l*, *OsPrx* and *OsABA2* (Gao *et al.* 2008). Transcriptomic analysis of rice exposed to oxidative stress revealed that seven mRNA families are differentially expressed and these families include genes for transcriptional regulation, nutrient transport, auxin homeostasis, programmed cell death and cell proliferation (Li *et al.* 2010).

Saccharum (sugarcane)

Saccharum transcriptome reflects that *Saccharum* constitutes a highly polyploid genome (Manners and Casu 2011) and two-third of its genome is approximately same as that of Arabidopsis as shown by comparative transcriptomic studies. In sugarcane, 3500 genes are reported to be involved in signal transduction including genes coding for 600 transcription factors, 510 protein kinases, 477 receptors, 114 calcium and inositol metabolism proteins, 107 protein phosphatases, 75 small GTPases and 17 G proteins (Papini-Terzi *et al.* 2005). Regulation of signal transduction genes of sugarcane is provided in table 2. Transcriptomic studies of signal transduction pathways involved in sucrose synthesis in sugarcane (both low and high sucrose producing cultivars) had revealed differential expression of 24 genes and of them 19 were reported in low sucrose producing plants. Three of these genes are involved in reducing sucrose phosphate synthase (Felix *et al.* 2009). Expression of 165 genes has been reported in tolerant sugarcane through transcriptomic studies (Rodrigues *et al.* 2009).

Transcriptomic analysis of plants subjected to polyethylene glycol (PEG) stress for 2–4 h showed upregulation of sodium proton antiporter, sucrose transporter 1, proline dehydrogenase and catalase-2. When these plants were subjected to salt stress, they showed a decrease in expression

Table 2. Transcriptome profiling for signal transduction in *Saccharum*.

Gene name	Number
Transcription factors	600
Protein kinases	510
Receptors	477
Calcium/inositol metabolism proteins	114
Protein phosphatases	107
GTPases	75
G proteins	17
Others	1600
Total genes involved in signal transduction	3500

of sodium proton antiporter, proline dehydrogenase and catalase-2. The results indicate differential expression of sugarcane genes to different types of stress (Patade *et al.* 2012). Drought-stressed sugarcane plants showed differential expression of 987 genes of these 928 were sense transcripts and 59 were antisense transcripts (Lembke *et al.* 2012). Osmoprotectants accumulation increases on exposure to stress and transcriptomic studies of sugarcane plants reported upregulation of 56 clusters of osmoprotectant candidate genes (Dos Santos *et al.* 2011). Sugarcane plant infected by *Leifsonia xyli* when subjected to transcriptome profiling showed differential expression of 49 genes and of these 44 were expressed in tolerant variety while five in susceptible variety. Genes expressed in tolerant variety are related to pathogen resistance, protein phosphorylation, cellulose synthesis, cell division, saline stress, RNA cleavage and transcription factors (Barros *et al.* 2004). Expression profile of nodulin genes when examined using transcriptomics showed existence of 129 clusters of nodulin genes and their expression is higher in flowers, roots and mixed tissues which uncovered their multiple functions (Vieira-de-Melo *et al.* 2011).

Triticum (wheat)

Transcriptome studies of developing caryopses in wheat showed 14,550 genes that are differentially expressed between 6 and 42 days after anthesis (Wan *et al.* 2008). In wheat plant, transcriptomic analysis during early stages of meiosis showed 1350 transcripts that are regulated on temporary basis. These temporarily expressing transcripts belong to chromatin condensation, synaptonemal complex formation, recombination and fertility (Crismani *et al.* 2006). There are a total of 129 genes which are shown to have meiotic roles (Crismani *et al.* 2011). Studies on gene expression during cold acclimation of two wheat cultivars showed that expression levels of more than 300 genes are altered by freezing temperatures. These genes include protein kinases, putative transcription factors, calcium-binding proteins, inorganic pyrophosphatase, Golgi-localized proteins, proteins involved in photosynthesis and cell wall hydrolase (Gulick *et al.* 2005).

Comparative transcriptomic analysis of wheat cultivars, Shanrong no. 3 (SR3) and Jinan 177 (JN177), under salt and polyethylene glycol stress showed genes responsive to stress are more highly expressed in SR3 as compared to JN177 (Liu *et al.* 2012). In SR3, unsaturated fatty acid content and flavonoid synthesis are also enhanced and there is an increase in pentose phosphate metabolism (Liu *et al.* 2012). Transcriptomic analysis of sense and antisense strands of wheat showed 110 sense to antisense transcripts pairs and 80 antisense-specific transcripts. It is also shown that antisense transcription is tissue specific (Coram *et al.* 2009). Transcriptomic profiling of dormant wheat seeds revealed that the genes which are expressed in these seeds are extremely related to maintenance of seed dormancy. Analysis of after ripened seeds showed activation of biological processes which include, DNA replication, nitrogen metabolism, jasmonate biosynthesis, cytoplasmic membrane bound vesicle and cell wall modification. These after ripened responses are due to epigenetic factors (Gao *et al.* 2012). Tricothecene deoxynivalenol (DON) treated wheat (Remus variety) when subjected to transcriptome profiling showed that expression of genes involved in metabolite transformation, metabolite detoxification, phenylpropanoid biosynthesis, carbohydrate metabolism, jasmonate biosynthesis and signalling and ubiquitin proteasome proteolytic pathway are highly upregulated (Walter and Doohan 2011). Transcriptomic analysis of embryo at postanthesis developmental stage (21 and 40 days postanthesis.) revealed that 392 genes are upregulated by two-fold including genes for ribosomal composition, initiation of translation, initiation of transcription, respiration, protein turnover, energy production, lipid metabolism, signal transduction, cell development, cell division, amino acid biosynthesis and metabolism. It is also observed that 163 genes are downregulated by at least two-fold (Wilson *et al.* 2005). Transcriptomic analysis of developing starchy endosperm of wheat revealed that 124 glucosyltransferases and 72 glucosylhydralses are associated with cell wall. Most highly expressed glucosyltransferase is GT47 followed by GT61. Genes related to glucomannan, pectin, cellulose and callose are also highly upregulated in endosperm (Pellny *et al.* 2012).

Zea mays (maize)

Comparative transcriptomic analysis of two transgenic maize lines showed that the environment plays a very important role in controlling the gene expression of maize samples. Environmental variations caused change in expression of 65 genes (Barros *et al.* 2010). Pericycle cell transcriptomic analysis of B73 inbred maize lines revealed that 32 genes preferentially expressed in pericycle as compared to all other root cells. Transcriptomic analysis of nitrogen-deficient maize plants showed that a number of genes are either upregulated or downregulated by nitrogen deficiency, which mainly effects photosynthesis, carbon metabolism and downstream metabolic pathways (Amiour *et al.* 2012).

Transcriptomic studies on maize diurnal rhythms, reveal that 23% of total expressed transcripts exhibit diurnal cycling pattern (Hayes *et al.* 2010). Transcript profiling of maize exposed that canonical mRNAs and endogenous small interfering RNAs are organ specific, i.e. they are involved in tissue-specific biogenesis. Further studies revealed that decreasing levels of mop1 leads to a concomitant decrease of 21 nucleotide small interfering RNAs relative to 21 nucleotide miRNAs in tissue-specific manner (Wang *et al.* 2009). Transcriptomic profiling of maize cells to study the regulatory and functional differentiation of mesophyll and bundle sheath cells showed that the genes which are expressed in mesophyll cells include 53 mesophyll-enriched transcription factors, whereas bundle sheath cells express 214 enriched

transcription factor genes. Further analysis revealed that mesophyll plays major role in light reactions, protein synthesis, protein folding, tetra pyrole synthesis and RNA binding. Bundle sheath cells play a role in transport, signalling protein degradation and posttranslational modifications (Chang *et al.* 2012).

Two maize inbred lines, Huangzao (HZ4) and Chang 7-2 (C7-2), were subjected to comparative transcriptomic studies and showed that C7-2 seedlings are more tolerant towards progressive water deficit than HZ4 since C7-2 seedlings have large stomatal resistance, stronger water holding capacity in leaf, and timely increase in activities of antioxidant enzymes in roots. The reason behind high water deficit tolerance is fine transcriptional coordination between maize leaves and roots (Li *et al.* 2009). Transcriptome studies of maize (inbred lines HZ32) roots at late stage of water logging revealed that a large number of genes are upregulated which are involved in signal transduction, transcriptional regulation, protein degradation, translational regulation, ion transport and amino acid metabolism (Zou *et al.* 2010).

Exposure to UV-B light alters the transcriptome of irradiated organs. There are some phenyl propanoid pathway genes that are expressed only in irradiated leaves (Casati *et al.* 2011a) and moreover number of UV-B regulated transcripts increases with the exposure length (Casati *et al.* 2011b). Comparative transcriptomic analyses of maize embryos exposed to camptothecin, a chemical which inhibits activity of topoisomerase showed that camptothecin effects the expression of genes involved in stress responses and calcium-dependent nucleases (Sanchez-Pons *et al.* 2011). Expression of posttranslational regulatory genes is also observed (Sanchez-Pons *et al.* 2011). By comparing the transcriptomes of mature silk, mature pollen, mature ovary and seedlings of maize, it was observed that there are 1427 genes which are preferentially expressed in maize silk. These genes encode peptide and oligo-peptide transporters, amino acid transporters and cysteine-rich receptor-like kinases. These genes are potentially involved in stigma-mediated reproductive process (Xu *et al.* 2012).

Microarray analysis of maize dwarf mutant dwarf11 (D11) showed upregulation of transcripts encoding for giberellic acid biosynthetic as well as catabolic enzymes (Wang *et al.* 2013). Aluminum sensitive genotype (S1587-17) when subjected to transcriptome profiling at toxic levels of aluminum showed that a large number of genes are differentially expressed. Root growth inhibition was seen as a result of upregulation of genes for biosynthesis of auxin, ethylene and lignin (Mattiello *et al.* 2010).

Future prospects

Plant transcriptomics is an integral component of systems biology and is widely applied in plant sciences in both model as well as crop plants. Transcriptomic analysis is expected to flourish in near future with the development of new technologies in systems biology. Plant transcriptomics can be applied widely to improve marker discovery, relevance of resources developed for related species and characterize the genes associated with different functions in different varieties of plants (Casu *et al.* 2010). Transcriptomic analysis is widely used in comparing wild relatives of crops and hence helps in improvement of domesticated crops (Xu *et al.* 2012). Emerging area of multispecies transcriptomics holds promise to provide knowledge for the understanding of complex plant microbe interactions (Schenk *et al.* 2012). Future development in plant molecular biology, computational biology and systems biology is based on plant transcriptomics for several aspects, thus, this field is expected to play a major role in future research on plant sciences.

References

Amiour N., Imbaud S., Clement G., Agier N., Zivy M., Valot B. *et al.* 2012 The use of metabolomics integrated with transcriptomic and proteomic studies for identifying key steps involved in the control of nitrogen metabolism in crops such as maize. *J. Exp. Bot.* **63**, 5017–5033.

An Y. and Lin L. 2011 Transcriptional regulatory programs underlying barley germination and regulatory functions of gibberellin and abscisic acid. *BMC Plant Biol.* **11**, 105.

Armengaud P., Breitling R. and Amtmann A. 2004 The potassium-dependent transcriptome of *Arabidopsis* reveals a prominent role of jasmonic acid in nutrient signaling. *Plant Physiol.* **136**, 2556–2576.

Baerson S. R., Sanchez-Moreiras A., Pedrol-Bonjoch N., Schulz M., Kagan I. A., Agarwal A. K. *et al.* 2005 Detoxification and transcriptome response in *Arabidopsis* seedlings exposed to the allelochemical benzoxazolin-2(3H)-one. *J. Biol. Chem.* **280**, 21867–21881.

Bai X., Rivera-Vega L., Mamidala P., Bonello P., Herms D. A. and Mittapalli O. 2011 Transcriptomic signatures of Ash (*Fraxinus* spp.) phloem. *PLoS One* **6**, e16368.

Barrero J. M., Talbot M. J., White R. G., Jacobsen J. V. and Gubler F. 2009 Anatomical and transcriptomic studies of the coleorhiza reveal the importance of this tissue in regulating dormancy in barley. *Plant Physiol.* **150**, 1006–1021.

Barros E., Lezar S., Anttonen M. J., Van Dijk J. P., Rohlig R. M., Kok E. J. *et al.* 2010 Comparison of two GM maize varieties with a near-isogenic non-GM variety using transcriptomics, proteomics and metabolomics. *Plant Biotechnol. J.* **8**, 436–451.

Barros N. M., Mauro S. M. Z., di Laia M. L., de Dabbas K. M., Ferro J. A. and Ferro M. I. T. 2004 Differential expression pattern in sugar cane varieties infected with *Leifsonia xyli* subsp xyli. The international conference on the status of plant and animal genome research, 12, Jan.10–14. San Diego, USA.

Bock K. W., Honys D., Ward J. M., Padmanaban S., Nawrocki E. P., Hirschi K. D. *et al.* 2006 Integrating membrane transport with male gametophyte development and function through transcriptomics. *Plant Physiol.* **140**, 1151–1168.

Borges F., Gomes G., Gardner R., Moreno N., McCormick S., Feijo J. A. *et al.* 2008 Comparative transcriptomics of *Arabidopsis* sperm Cells. *Plant Physiol.* **148**, 1168–1181.

Brady S. M., Long T. A. and Benfey P. N. 2006 Unraveling the dynamic transcriptome. *Plant Cell* **18**, 2101–2111.

Brautigam A., Kajala K., Wullenweber J., Sommer M., Gagneul D., Weber K. L. *et al.* 2011 An mRNA blueprint for C4 photosynthesis derived from comparative transcriptomics of closely related C3 and C4 species. *Plant Physiol.* **155**, 142–156.

Brenner S., Johnson M., Bridgham J., Golda G., Lloyd D. H., Johnson D. *et al.* 2000 Gene expression analysis by massively parallel signature sequencing (MPSS) on microbead arrays. *Nat. Biotechnol.* **18**, 630–634.

Casati P., Campi M., Morrow D. J., Fernandes J. F. and Walbot V. 2011a Transcriptomic, proteomic and metabolomic analysis of UV-B signaling in maize. *BMC Genomics* **12**, 321.

Casati P., Morrow D. J., Fernandes J. and Walbot V. 2011b UV-B signaling in maize: transcriptomic and metabolomic studies at different irradiation times. *Plant Signal Behav.* **6**, 1926–1931.

Casu R. E., Hotta C. T. and Souza G. M. 2010 Functional genomics: transcriptomics of sugarcane–current status and future prospects. In *Genetics genomics and breeding of sugarcane* (ed. R. J. Henry and C. Kole), pp. 167–191. Science Publishers, Enfield, USA.

Chang Y. M., Liu W. Y., Shih A. C., Shen M. N., Lu C. H., Lu M. Y. *et al.* 2012 Characterizing regulatory and functional differentiation between maize mesophyll and bundle sheath cells by transcriptomic analysis. *Plant Physiol.* **160**, 165–177.

Chaudhary B., Hovav R., Rapp R., Verma N., Udall J. A. and Wendel J. F. 2008 Global analysis of gene expression in cotton fibers from wild and domesticated *Gossypium barbadense*. *Evol. Dev.* **10**, 567–582.

Chelaifa H., Monnier A. and Ainouche M. 2010 Transcriptomic changes following recent natural hybridization and allopolyploidy in the salt marsh species Spartina × townsendii and *Spartina anglica* (Poaceae). *New Phytol.* **186**, 161–174.

Cho K., Agrawal G. K., Shibato J., Jung Y. H., Kim Y. K., Nahm B. H. *et al.* 2007 Survey of differentially expressed proteins and genes in jasmonic acid treated rice seedling shoot and root at the proteomics and transcriptomics levels. *J. Proteomics Res.* **6**, 3581–3603.

Cho K., Shibato J., Agrawal G. K., Jung Y. H., Kubo A., Jwa N. S. *et al.* 2008 Integrated transcriptomics, proteomics, and metabolomics analyses to survey ozone responses in the leaves of rice seedling. *J. Proteom. Res.* **7**, 2980–2998.

Cho K., Shibato J., Kubo A., Kohno Y., Satoh K., Kikuchi S. *et al.* 2013 Genome-wide mapping of the ozone-responsive transcriptomes in rice panicle and seed tissues reveals novel insight into their regulatory events. *Biotechnol. Lett.* **35**, 647–656.

Clark T. A., Sugnet C. W. and Ares Jr M. 2002 Genome wide analysis of mRNA processing in yeast using splicing specific microarrays. *Science* **296**, 907–910.

Cloonan N., Forrest A. R., Kolle G., Gardiner B. B., Faulkner G. J., Brown M. K. *et al.* 2008 Stem cell transcriptome profiling via massive scale mRNA sequencing. *Nat. Methods* **5**, 613–619.

Cohen D., Bogeat-Triboulot M. B., Tisserant E., Balzergue S., Martin-Magniette M. L., Lelandais G. *et al.* 2010 Comparative transcriptomics of drought responses in *Populus*: a meta-analysis of genome-wide expression profiling in mature leaves and root apices across two genotypes. *BMC Genome* **11**, 630.

Contento A. L., Kim S. J. and Bassham D. C. 2004 Transcriptome profiling of the response of *Arabidopsis* suspension culture cells to suc starvation. *Plant Physiol.* **135**, 2330–2347.

Coram T. E., Settles M. L. and Chen X. 2009 Large-scale analysis of antisense transcription in wheat using the Affymetrix Gene Chip Wheat Genome Array. *BMC Genome* **10**, 253.

Crismani W., Baumann U., Sutton T., Shirley N., Webster T., Spangenberg G. *et al.* 2006 Microarray expression analysis of meiosis and microsporogenesis in hexaploid bread wheat. *BMC Genome* **7**, 267.

Crismani W., Kapoor S. and Able J. A. 2011 Comparative transcriptomics reveals 129 transcripts that are temporally regulated during anther development and meiotic progression in both bread wheat (*Triticum aestivum*) and rice (*Oryza sativa*). *Int. J. Plant Genome* (article ID 931898).

Dassanayake M., Haas J. S., Bohnert H. J. and Cheeseman J. M. 2009 Shedding light on an extremophile lifestyle through transcriptomics. *New Phytol.* **183**, 764–775.

David L., Huber W., Granovskaia M., Toedling J., Palm C. J., Bofkin L. *et al.* 2006 A high-resolution map of transcription in the yeast genome. *Proc. Natl. Acad. Sci. USA* **103**, 5320–5325.

De Vos M., Van Oosten V. R., Van Poecke R. M., Van Pelt J. A., Pozo M. J., Mueller M. J. *et al.* 2005 Signal signature and transcriptome changes of *Arabidopsis* during pathogen and insect attack. *Mol. Plant Microbe Interact.* **18**, 923–937.

Desikan R., Mackerness S. A. H., Hancock J. T. and Neill S. J. 2001 Regulation of *Arabidopsis* transcriptome by oxidative stress. *Plant Physiol.* **127**, 159–172.

Diaz P., Betti M., Sanchez D. H., Udvardi M. K., Monza J. and Marquez A. J. 2010 Deficiency in plastidic glutamine synthetase alters proline metabolism and transcriptomic response in *Lotus japonicus* under drought stress. *New Phytol.* **188**, 1001–1013.

Dos Santos P. B., Soares-Cavalcanti N. M., Vieira-de-Melo G. S. and Benko-Iseppon A. M. 2011 Osmoprotectants in the sugarcane (*Saccharum* spp.) transcriptome revealed by in silico evaluation. *Comput. Intel. Meth. Bioinfo. Biostat.* **6685**, 44–58.

Ekman D. R., Lorenz W. W., Przybyla A. E., Wolfe N. L. and Dean J. F. D. 2003 SAGE analysis of transcriptome responses in *Arabidopsis* roots exposed to 2,4,6-trinitrotoluene. *Plant Physiol.* **133**, 1397–1406.

Eulgem T. 2004 Regulation of the Arabidopsis defense transcriptome. *Trends Plant Sci.* **10**, 71–78.

Evers D., Legay S., Lamoreux D., Hausman J. F., Hoffmann L. and Renaut J. 2012 Towards a synthetic view of potato cold and salt stress response by transcriptomic and proteomic analyses. *Plant Mol. Biol.* **78**, 503–514.

Felix J. M., Papini-Terzi F. S., Rocha F. R., Vencio R. Z. N., Vicentini R., Nishiyama Jr M. Y. *et al.* 2009 Expression profile of signal transduction components in a sugarcane population segregating for sugar content. *Tropic Plant Biol.* **2**, 98–109.

Fowler S. and Thomashow M. F. 2002 *Arabidopsis* transcriptome profiling indicates that multiple regulatory pathways are activated during cold acclimation in addition to the CBF cold response pathway. *Plant Cell* **14**, 1675–1690.

Gao F., Jordan M. C. and Ayele B. T. 2012 Transcriptional programs regulating seed dormancy and its release by after-ripening in common wheat (*Triticum aestivum* L.) *Plant Biotechnol. J.* **10**, 465–476.

Gao S., Zhang H., Tian Y., Li F., Zhang Z., Lu X. *et al.* 2008 Expression of TERF1 in rice regulates expression of stress-responsive genes and enhances tolerance to drought and high-salinity. *Plant Cell Rep.* **27**, 1787–1795.

Gardiner S. A., Boddu J., Berthiller F., Hametner C., Stupar R. M., Adam G. *et al.* 2010 Transcriptome analysis of the barley–deoxynivalenol interaction: evidence for a role of glutathione in deoxynivalenol detoxification. *Mol. Plant Microbe Interact.* **23**, 962–976.

Ge X., Chen W., Song S., Wang W., Hu S. and Yu J. 2008 Transcriptomic profiling of mature embryo from an elite super-hybrid rice LYP9 and its parental lines. *BMC Plant Biol.* **8**, 114.

Gerhard D. S., Wagner L., Feingold E. A., Shenmen C. M., Grouse L. H., Schuler G. *et al.* 2004 The status, quality, and expansion of NIH full length cDNA project: the mammalian gene collection. *Genome Res.* **14**, 2121–2127.

Gomase V. S. and Tagore S. 2008 Transcriptomics. *Curr. Drug Metabol.* **9**, 245–249.

Gulick P. J., Drouin S., Yu Z., Danyluk J., Poisson G., Monroy A. F. *et al.* 2005 Transcriptome comparison of winter and spring wheat responding to low temperature. *Genome* **48**, 913–923.

Hayes K. R., Beatty M., Meng X., Simmons C. R., Habben J. E. and Danilevskaya O. N. 2010 Maize global transcriptomics reveals pervasive leaf diurnal rhythms but rhythms in developing ears are largely limited to the core oscillator. *PLoS One* **5**, e12887.

Hermans C., Vuylsteke M., Coppens F., Craciun A., Inze D. and Verbruggen N. 2010 Early transcriptomic changes induced by magnesium deficiency in *Arabidopsis thaliana* reveal the alteration of circadian clock gene expression in roots and the triggering of abscisic acid-responsive genes. *New Phytol.* **187**, 119–131.

Hocher V., Alloisio N., Auguy F., Fournier P., Doumas P., Pujic P. *et al.* 2011 Transcriptomics of actinorhizal symbioses reveals homologs of the whole common symbiotic signaling cascade. *Plant Physiol.* **156**, 700–711.

Holt R. A. and Jones S. J. 2008 The new paradigm of flow cell sequencing. *Genome Res.* **18**, 839–846.

Honys D. and Twell D. 2003 Comparative analysis of the *arabidopsis* pollen transcriptome. *Plant Physiol.* **132**, 640–652.

Honys D. and Twell D. 2004 Transcriptome analysis of haploid male gametophyte development in Arabidopsis. *Genome Biol.* **5**, R85.

Hovav R., Udall J. A., Hovav E., Rapp R., Flagel L. and Wendel J. F. 2008 A majority of cotton genes are expressed in single-celled fiber. *Planta* **227**, 319–329.

Huang G., Xu W., Gong S., Li B., Wang X., Xu D. *et al.* 2008 Characterization of 19 novel cotton FLA genes and their expression profiling in fiber development and in response to phytohormones and salt stress. *Physiol. Plant.* **134**, 348–359.

Ibarra-Laclette E., Albert V. A., Perez-Torres C. A., Zamudio-Hernandez F., Ortega-Estrada M. J., Herrera-Estrella A. *et al.* 2011 Transcriptomics and molecular evolutionary rate analysis of the bladderwort (*Utricularia*), a carnivorous plant with a minimal genome. *BMC Plant Biol.* **11**, 101.

Ilut D. C., Coate J. E., Luciano A. K., Owens T. G., May G. D., Farmer A. *et al.* 2012 A comparative transcriptomic study of an allotetraploid and its diploid progenitors illustrates the unique advantages and challenges of RNA-seq in plant species. *Am. J. Bot.* **99**, 383–396.

Jiang S. Y., González J. M. and Ramachandran S. 2013 Comparative genomic and transcriptomic analysis of tandemly and segmentally duplicated genes in rice. *PLoS One* **8**, e63551.

Jukanti A. K., Heidlebaugh N. M., Parrott D. L., Fischer I. A., Mclnnerney K. and Fischer A. M. 2008 Comparative transcriptome profiling of near-isogenic barley (*Hordeum vulgare*) lines differing in the allelic state of a major grain protein content locus identifies genes with possible roles in leaf senescence and nitrogen reallocation. *New Phytol.* **177**, 333–349.

Kahlau S. and Bock R. 2008 Plastid transcriptomics and translatomics of tomato fruit development and chloroplast to chromoplast differentiation: chromoplast gene expression largely serves the production of a single protein. *Plant Physiol.* **20**, 856–874.

Kempema L. A., Cui X., Holzer F. M. and Walling L. L. 2007 *Arabidopsis* transcriptome changes in response to phloem-feeding silverleaf whitefly nymphs. Similarities and distinctions in response to aphids. *Plant Physiol.* **143**, 849–865.

Kodzius R., Kojima M., Nishiyori H., Nakamura M., Fukuda S., Taqami M. *et al.* 2006 CAGE: cap analysis of gene expression. *Nat. Methods* **3**, 211–222.

Koenig D., Jiménez-Gómez J. M., Kimura S., Fulop D., Chitwood D. H., Headland L. R. *et al.* 2013 Comparative transcriptomics reveal patterns of selection in domesticated and wild tomato. *Proc. Natl. Acad. Sci. USA* **110**, E2655–E2662.

Kreps J. A., Wu Y., Chang H. S., Zhu T., Wang X. and Harper J. F. 2002 Transcriptome changes for *Arabidopsis* in response to salt, osmotic, and cold stress. *Plant Physiol.* **130**, 2129–2141.

Lee B., Henderson D. A. and Zhu J. K. 2005 The *Arabidopsis* cold-responsive transcriptome and its regulation by ICE1. *Plant Cell* **17**, 3155–3175.

Lee S., Lee K., Kim K., Choi G. J., Yoon S. H., Ji H. C. *et al.* 2009 Identification of salt-stress induced differentially expressed genes in barley leaves using the annealing control-primer-based GeneFishing technique. *Afr. J. Biotechnol.* **8**, 1326–1331.

Lembke C. G., Nishiyama Jr. M. Y., Sato P. M., de Andrade R. F. and Souza G. M. 2012 Identification of sense and antisense transcripts regulated by drought in sugarcane. *Plant Mol. Biol.* **79**, 461–477.

Li L., Qiu X., Li X., Wang S., Zhang Q. and Lian X. 2010 Transcriptomic analysis of rice responses to low phosphorus stress. *Chinese Sci. Bull.* **55**, 251–258.

Li T., Li H., Zhang Y. and Liu J. 2010 Identification and analysis of seven H_2O_2-responsive miRNAs and 32 new miRNAs in the seedlings of rice (*Oryza sativa* L. ssp. indica). *Nucleic Acid Res.* **39**, 2821–2833.

Li Y., Sun C., Huang C., Pan J., Wang L. and Fan X. 2009 Mechanisms of progressive water deficit tolerance and growth recovery of chinese maize foundation genotypes Huangzao 4 and Chang 7-2, which are proposed on the basis of comparison of physiological and transcriptomic responses. *Plant Cell Physiol.* **50**, 2092–2111.

Liu C., Li S., Wang M. and Xia G. 2012 A transcriptomic analysis reveals the nature of salinity tolerance of a wheat introgression line. *Plant Mol. Biol.* **78**, 159–169.

Liu M. S., Li H. C., Lai Y. M., Lo H. F. and Chen L. F. 2013 Proteomics and transcriptomics of broccoli subjected to exogenously supplied and transgenic senescence-induced cytokinin for amelioration of postharvest yellowing. *J. Proteom.* **93**, 133–144.

Maathius F. J. M. 2006 The role of monovalent cation transporters in plant responses to salinity. *J. Exp. Bot.* **57**, 1137–1147.

Manners J. M. and Casu R. E. 2011 Transcriptome analysis and functional genomics of sugarcane. *Tropic Plant Biol.* **4**, 9–21.

Maruyama-Nakashita A., Inoue E., Watanabe-Takahashi A., Yamaya T. and Takahashi H. 2003 Transcriptome profiling of sulfur-responsive genes in *Arabidopsis* reveals global effects of sulfur nutrition on multiple metabolic pathways. *Plant Physiol.* **132**, 597–605.

Mattiello L., Kirst M., Da Silva F. R., Jorge R. A. and Menossi M. 2010 Transcriptional profile of maize roots under acid soil growth. *BMC Plant Biol.* **10**, 196.

Mortazavi A., Williams B. A., McCue K., Schaeffer L. and Wold B. 2008 Mapping and quantifying mammalian transcriptomes by RNA-Seq. *Nat. Methods* **5**, 621–628.

Muller R., Morant M., Jarmer H., Nilsson L. and Neilson T. H. 2007 Genome-wide analysis of the *Arabidopsis* leaf transcriptome reveals interaction of phosphate and sugar metabolism. *Plant Physiol.* **143**, 156–171.

Nagalakshmi U., Wang Z., Waern K., Shou C., Raha D., Gerstein M. *et al.* 2008 The transcriptional landscape of the yeast genome defined by RNA sequencing. *Science* **320**, 1344–1349.

Narsai R., Howell K. A., Carroll A., Ivanova A., Millar A. H. and Whelan J. 2009 Defining core metabolic and transcriptomic responses to oxygen availability in rice embryos and young seedlings. *Plant Physiol.* **151**, 306–322.

Nikiforova V., Freitag J., Kempa S., Adamik M., Hesse H. and Hoefgen R. 2003 Transcriptome analysis of sulfur depletion in *Arabidopsis thaliana*: interlacing of biosynthetic pathways provides response specificity. *Plant J.* **33**, 633–650.

Nodine M. D. and Bartel D. P. 2012 Maternal and paternal genomes contribute equally to the transcriptome of early plant embryos. *Nature* **482**, 94–97.

Norton G. J., Lou-Hing D. E., Meharg A. A. and Price A. H. 2008 Rice–arsenate interactions in hydrophonics: whole genome transcriptional analysis. *J. Exp. Bot.* **59**, 2267–2276.

Nowrousian M. 2007 Of patterns and pathways: microarray technologies for the analysis of filamentous fungi. *Fungal Biol. Rev.* **21**, 171–178.

Okoniewski M. J. and Miller C. J. 2006 Hybridization interactions between probesets in short oligo microarrays lead to spurious correlations. *BMC Bioinformatics* **7**, 276.

Omrane S., Ferrarini A., D'Apuzzo E., Rogato A., Delledonne M. and Chiurazzi M. 2009 Symbiotic competence in *Lotus japonicus* is affected by plant nitrogen status: transcriptomic identification of genes affected by a new signalling pathway. *New Phytol.* **183**, 380–394.

Padmalatha K. V., Dhandapani G., Kanakachari M., Kumar S., Dass A., Patil D. P. *et al.* 2012 Genome-wide transcriptomic analysis of cotton under drought stress reveal significant down-regulation of genes and pathways involved in fibre elongation and up-regulation of defense responsive genes. *Plant Mol. Biol.* **78**, 223–246.

Pallavicini A., Del Terra L., Sondhal M. R., Guerreiro-Filho O., Asquini E., Martellosi C. *et al.* 2005 Transcriptomics of resistance response in *Coffea arabica* L. In *Proceedings of the ASIC 2004*, pp. 584–590. 20th International Conference on Coffee Science, Bangalore, India.

Papini-Terzi F. S., Rocha F. R., Vêncio R. Z., Oliveira K. C., Felix Jde M., Vicentini R. *et al.* 2005 Transcription profiling of signal transduction related genes in sugarcane tissues. *DNA Res.* **12**, 27–38.

Park W., Scheffler B. E., Bauer P. J. and Campbell B. T. 2012 Genome-wide identification of differentially expressed genes under water deficit stress in upland cotton (*Gossypium hirsutum* L.). *BMC Plant Biol.* **12**, 90.

Parrott D. L., Mclnnerney K., Feller U. and Fischer A. M. 2007 Steam-girdling of barley (*Hordeum vulgare*) leaves leads to carbohydrate accumulation and accelerated leaf senescence, facilitating transcriptomic analysis of senescence-associated genes. *New Phytol.* **176**, 56–69.

Patade V. Y., Bhargava S. and Suprasanna P. 2012 Transcript expression profiling of stress responsive genes in response to short-term salt or PEG stress in sugarcane leaves. *Mol. Biol. Rep.* **39**, 3311–3318.

Pellny T. K., Lovegrove A., Freeman J., Tosi P., Love C. G., Knox P. *et al.* 2012 Cell walls of developing wheat starchy endosperm: comparison of composition and RNA-seq transcriptome. *Plant Physiol.* **158**, 612–627.

Pina C., Pinto F., Feijo J. A. and Becker J. D. 2005 Gene family analysis of the *Arabidopsis* pollen transcriptome reveals biological implications for cell growth, division control, and gene expression regulation. *Plant Physiol.* **138**, 744–756.

Pufky J., Qiu Y., Rao M. V., Hurban P. and Jones A. M. 2003 The auxin-induced transcriptome for etiolated *Arabidopsis* seedlings using a structure/function approach. *Funct. Integr. Genomics* **3**, 135–143.

Queval G., Neukermans J., Vanderauwera S., Van Breusegem F. and Noctor G. 2012 Day length is a key regulator of transcriptomic responses to both CO_2 and H_2O_2 in *Arabidopsis*. *Plant Cell Environ.* **35**, 374–387.

Rapp R. A., Haigler C. H., Flagel L., Hovav R. H., Udall J. A. and Wendel J. F. 2010 Gene expression in developing fibres of upland cotton (*Gossypium hirsutum* L.) was massively altered by domestication. *BMC Biol.* **8**, 139.

Rodrigues F. A., De Laia M. L. and Zingaretti S. M. 2009 Analysis of gene expression profiles under water stress in tolerant and sensitive sugarcane plants. *Plant Sci.* **176**, 286–302.

Royce T. E., Rozowsky J. S. and Gerstein M. B. 2007 Toward a universal microarray: prediction of gene expression through nearest neighbor probe sequence identification. *Nucleic Acid Res.* **35**, e99.

Ruzicka D. R., Hausmann N. T., Barrios-Masias F. H., Jackson L. E. and Schachtman D. P. 2012 Transcriptomic and metabolic responses of mycorrhizal roots to nitrogen patches under field conditions. *Plant Soil* **350**, 145–162.

Sanchez-Pons N., Irar S., Garcia-Muniz N. and Vicient C. M. 2011 Transcriptomic and proteomic profiling of maize embryos exposed to camptothecin. *BMC Plant Biol.* **11**, 91.

Schenk P. M., Carvalhais L. C. and Kazan K. 2012 Unraveling plant–microbe interactions: can multi-species transcriptomics help? *Trend Biotechnol.* **30**, 177–184.

Shanker A. K., Maheswari M., Yadav S. K., Desai S., Bhanu D., Attal N. B. *et al.* 2014 Drought stress responses in crops. *Funct. Integr. Genom.* **14**, 11–22.

Slocombe S. P., Schauvinhold I., McQuinn R. P., Besser K., Welsby N. A., Harper A. *et al.* 2008 Transcriptomic and reverse genetic analyses of branched chain fatty acid and acyl sugar production in *Solanum pennellii* and *Nicotiana benthamiana*. *Plant Physiol.* **148**, 1830–1846.

Spieb N., Oufir M., Matusikova I., Stierschneider M., Kopecky D., Homolka A. *et al.* 2012 Ecophysiological and transcriptomic responses of oak (*Quercus robur*) to long-term drought exposure and rewatering. *Environ. Exp. Bot.* **77**, 117–126.

Strickler S. R., Bombarely A. and Mueller L. A. 2012 Designing a transcriptome next-generation sequencing project for a nonmodel plant species. *Am. J. Bot.* **99**, 257–266.

Suzuki H., Rodriguez-Uribe L., Xu J. and Zhang J. 2013 Transcriptome analysis of cytoplasmic male sterility and restoration in CMS-D8 cotton. *Plant Cell Rep.* **32**, 1531–1542.

Szakasits D., Heinen P., Weiczorek K., Hofmann J., Wagner F., Kreil D. P. *et al.* 2009 The transcriptome of syncytia induced by the cyst nematode *Heterodera schachtii* in *Arabidopsis* roots. *Plant J.* **57**, 771–784.

Tan K. C., Ipcho S. V. S., Trengove R. D., Oliver R. P. and Solomon P. S. 2009 Assessing the impact of transcriptomics, proteomics and metabolomics on fungal phytopathology. *Mol. Plant Pathol.* **10**, 703–715.

Thompson G. A. and Goggin F. L. 2006 Transcriptomics and functional genomics of plant defence induction by phloem feeding insects. *J. Exp. Biol.* **57**, 755–766.

Vera J. C., Wheat C. W., Fescemyer H. W., Frilander M. J., Crawford D. L., Hanski I. *et al.* 2008 Rapid transcriptome characterization for a nonmodel organism using 454 pyrosequencing. *Mol. Encol.* **17**, 1636–1647.

Vieira-de-Melo G. S., dos Santos P. B., Soares-Cavalcanti N. M. and Benko-Iseppon A. M. 2011 Identification and expression of early nodulin in sugarcane transcriptome revealed by *in silico* analysis. *Comput. Intel. Meth. Bioinfo. Biostat.* **6685**, 72–85.

Walter S. and Doohan F. 2011 Transcript profiling of the phytotoxic response of wheat to the *Fusarium* mycotoxin deoxynivalenol. *Mycotoxin Res.* **27**, 221–230.

Wan Y., Poole R. L., Huttly A. K., Toscano-Underwood C., Feeney K., Welham S. *et al.* 2008 Transcriptome analysis of grain development in hexaploid wheat. *BMC Genomics* **9**, 121.

Wang H., Wan A., Hsu C., Lee K., Yu S. and Jauh G. 2007 Transcriptomic adaptations in rice suspension cells under sucrose starvation. *Plant Mol. Biol.* **63**, 441–463.

Wang X., Elling A. A., Li X., Li N., Peng Z., He G. *et al.* 2009 Genome-wide and organ-specific landscapes of epigenetic modifications and their relationships to mRNA and small RNA transcriptomes in maize. *Plant Cell* **21**, 1053–1069.

Wang Y., Deng D., Ding H., Xu X., Zhang R., Wang S. *et al.* 2013 Gibberellin biosynthetic deficiency is responsible for maize dominant dwarf11 (d11) mutant phenotype: physiological and transcriptomic evidence. *PLoS One* **8**, e66466.

Wang Y., Zhang W., Song L., Zou J., Su Z. and Wu W. 2008 Transcriptome analyses show changes in gene expression to accompany pollen germination and tube growth in *Arabidopsis*. *Plant Physiol.* **148**, 1201–1211.

Wang Z., Gerstein M. and Snyder M. 2009 RNA-Seq: a revolutionary tool for transcriptomics. *Nat. Rev. Genet.* **10**, 57–63.

Wasaki J., Shinano T., Onishi K., Yonetani R., Yazaki J., Fujii F. *et al.* 2006 Transcriptomic analysis indicates putative metabolic changes caused by manipulation of phosphorus availability in rice leaves. *J. Exp. Bot.* **57**, 2049–2059.

Wasaki J., Yonetani R., Kuroda S., Shinano T., Yazaki J., Fujii F. *et al.* 2003 Transcriptomic analysis of metabolic changes by phosphorus stress in rice plant roots. *Plant Cell Environ.* **26**, 1515–1523.

Wei M., Song M., Fan S. and Yu S. 2013 Transcriptomic analysis of differentially expressed genes during anther development in genetic male sterile and wild type cotton by digital gene-expression profiling. *BMC Genomics* **14**, 97.

Wilson I. D., Barker G. L. A., Lu C., Coghill J. A., Beswick R. W., Lenton J. R. *et al.* 2005 Alteration of the embryo transcriptome of hexaploid winter wheat (*Triticum aestivum* cv. Mercia) during maturation and germination. *Func. Integr. Genomics.* **5**, 144–154.

Wu J. 2010 Transcriptomic analysis of barley plant responses to cold stress. Dissertation submitted in partial fulfillment of the Master of Research (MRes) in advanced genomic and proteomic sciences, School of Biosciences, The University of Nottingham.

Xin Z., Zhao Y. and Zheng Z. 2005 Transcriptome analysis reveals specific modulation of abscisic acid signaling by ROP10 small GTPase in *Arabidopsis*. *Plant Physiol.* **139**, 1350–1365.

Xu X. H., Chen H., Sang Y. L., Wang F., Ma J. P., Gao X. *et al.* 2012 Identification of genes specifically or preferentially expressed in maize silk reveals similarity and diversity in transcript abundance of different dry stigmas. *BMC Genomics* **13**, 294.

Xu Z., Zhang C., Zhang X., Liu C., Wu X., Yang Z. *et al.* 2013 Transcriptome profiling reveals auxin and cytokinin regulating somatic embryogenesis in different sister lines of cotton cultivar CCRI24. *J. Integr. Plant Biol.* **55**, 631–642.

Yamada K., Lim J., Dale J. M., Chen H., Shinn P., Palm C. J. *et al.* 2003 Emperical analysis of transcriptional activity in the *Arabidopsis* genome. *Science* **302**, 842–846.

Yano R., Takebayashi Y., Nambara E., Kamiya Y. and Seo M. 2013 Combining association mapping and transcriptomics identify HD2B histone deacetylase as a genetic factor associated with seed dormancy in *Arabidopsis thaliana*. *Plant J.* **74**, 815–828.

Yu H., Hogan P. and Sundaresan V. 2005 Analysis of the female gametophyte transcriptome of *Arabidopsis* by comparative expression profiling. *Plant Physiol.* **139**, 1853–1869.

Zeimann M., Kamboj A., Hove R. M., Loveridge S., El-Osta A. and Bhave M. 2013 Analysis of the barley leaf transcriptome under salinity stress using mRNA-Seq. *Acta Physiol. Plant.* **35**, 1915–1924.

Zou X., Jiang Y., Liu L., Zhang Z. and Zheng Y. 2010 Identification of transcriptome induced in roots of maize seedlings at the late stage of waterlogging. *BMC Plant Biol.* **10**, 189.

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