

Tackling the Heat-Stress Tolerance in Crop Plants: A Bioinformatics Approach

Palakolanu Sudhakar Reddy, Vincent Vadez,
Nese Sreenivasulu, and P.B. Kavi Kishor

Abstract

Plants are exposed to different types of environmental factors including heat stress that affect negatively various regular activities of the plant. Plants, as sessile organisms, must have developed efficient strategies of response to cope with and adapt to different types of abiotic stresses imposed by the adverse environment. Plant responses to environmental stress are complex and appear to be a difficult task to study in the classical plant-breeding program due to several technical limitations. The current knowledge of the regulatory network governing environmental stress responses is fragmentary, and an understanding of the damage caused by these environmental stresses or the plant's tolerance mechanisms to deal with stress-induced damages is far from complete. The emergence of the novel "omics" technologies from the last few years, such as genomics, proteomics, and metabolomics, is now allowing researchers to enable active analyses of regulatory networks that control abiotic stress

P.S. Reddy
International Crops Research Institute for the Semi-Arid
Tropics (ICRISAT), Patancheru, Hyderabad 502 324,
India

Leibniz Institute of Plant Genetics and Crop
Plant Research (IPK), Corrensstrasse 03,
D-06466 Gatersleben, Germany

V. Vadez
International Crops Research Institute for the Semi-Arid
Tropics (ICRISAT), Patancheru, Hyderabad 502 324,
India

N. Sreenivasulu
Leibniz Institute of Plant Genetics and Crop
Plant Research (IPK), Corrensstrasse 03,
D-06466 Gatersleben, Germany

P.B.K. Kishor (✉)
Department of Genetics, Osmania University,
Hyderabad 500 007, India
e-mail: pbkavi@yahoo.com

22 responses. Recent advances in different omics approaches have been
 23 found greatly useful in understanding plant responses to abiotic stress
 24 conditions. Such analyses increase our knowledge on plant responses and
 25 adaptation to stress conditions and allow improving crop improvement
 26 programs including plant breeding. In this chapter, recent progresses on
 27 systematic analyses of plant responses to heat stress including genomics,
 28 proteomics, metabolomics, and phenomics and transgenic-based
 29 approaches to overcome heat stress are summarized.

Keywords

30 Omics • Phenomics • Molecular regulatory networks • NGS-based
 31 transcriptome analysis • Heat-shock response • Heat-shock proteins •
 32 Heat-shock element
 33

34 Abbreviations

35	HSFs	Heat-Shock Transcription Factors
36	ROS	Reactive Oxygen Species
37	GEO	Gene Expression Omnibus
38	TAIR	The Arabidopsis Information Resource
39	NGS	Next-Generation Sequencing
40	GC-MS	Gas Chromatography Coupled to Mass Spectrometry
41		
42	LC-MS	Liquid Chromatography Coupled to Mass Spectrometry
43		
44	SGN	Sol Genomics Network

45 1 Introduction

46 Since plants are sessile in nature, they develop
 47 many physiological and molecular mechanisms
 48 to cope with different abiotic stresses. Plants
 49 started to emerge 1.5 billion years ago
 50 (Lehninger et al. 1993), and the evolutionary
 51 pressure has shaped plant responses to environ-
 52 mental fluctuations that minimize damage and
 53 ensure protection of cellular homeostasis. Heat
 54 stress is one of the main abiotic stresses that can
 55 limit the crop productivity drastically in the com-
 56 ing years due to global warming. High
 57 temperatures can be detrimental to all phases of
 58 plant development. Heat stress causes irrevers-
 59 ible damage to plant function and development
 60 (Hall 2001). Heat stress affects a broad spectrum

of cellular components and metabolism. The 61
 timing, duration, and severity of heat stress influ- 62
 ence pollen-pistil interactions in crop plants 63
 (Snider and Oosterhuis 2011). To counter the 64
 effects of heat stress on cellular metabolism, 65
 plants and other organisms respond to changes 66
 in their ambient temperature by reprogramming 67
 the composition of certain transcripts, proteins, 68
 and metabolites. Heat stress leads to a series of 69
 phenotypical and genetical changes, creates 70
 osmotic imbalances, and produces ubiquitous 71
 and evolutionarily conserved proteins known as 72
 heat-shock proteins (Hsps) (Gupta et al. 2010). 73
 Stress responses involving extreme temperature 74
 result in excess production of reactive oxygen 75
 species (ROS), leading to oxidative damage and 76
 thus limiting the growth and productivity of agri- 77
 cultural crops. Genome-wide transcriptional 78
 profiles during temperature and oxidative stress 79
 revealed coordinated expression patterns and 80
 overlapping regulons in crop plants (Mittal 81
 et al. 2012). Therefore, understanding plant 82
 responses to heat stress is now thought to be 83
 one of the hottest topics in agricultural science. 84
 Major progress in this research field has come 85
 from the application of different bioinformatics/ 86
 systems biology approaches. These high- 87
 throughput techniques have made it possible to 88
 analyze thousands of genes in one shot (Smita 89
 et al. 2013). With the introduction of bioinform- 90
 atics tools, many heat-stress-inducible genes 91
 were identified from the huge genome databases, 92

93 their promoter sequences were identified, and the
 94 putative functions of the genes were functionally
 95 characterized through transgenic approaches.
 96 This provides the information to understand the
 97 molecular mechanisms for improving heat toler-
 98 ance in crops. Availability of these data sets
 99 publicly has broadened and deepened the view
 100 of heat-stress responses and tolerance not only in
 101 model plants but also in agricultural crops.

102 **2 Bioinformatics Approaches**

103 Recent advances in functional genomics have
 104 allowed us the use of different bioinformatics
 105 approaches such as transcriptomics (global gene
 106 expression), proteomics (protein profiling/modi-
 107 fication), metabolomics (metabolite profiling),
 108 and phenomics to understand the complex
 109 molecular regulatory networks associated with
 110 stress adaptation and tolerance (Cramer et al.
 111 2011). These technologies generate enormous
 112 amounts of information which has boosted up
 113 the field of bioinformatics, with thousands of
 114 new algorithms and software published every
 115 year. System-based approaches with a combina-
 116 tion of multiple omics analyses have been an
 117 efficient tool to determine the global picture of
 118 cellular events which would increase our under-
 119 standing of the complex molecular regulatory
 120 networks and find out the interacting partners
 121 associated with heat-stress adaptation and toler-
 122 ance. The data collected from transcriptomics,
 123 proteomics, and metabolomics needs to be com-
 124 bined to achieve a better understanding of the
 125 plant as a system. In this context, different
 126 omics data should contribute greatly to the iden-
 127 tification of key regulatory steps to characterize
 128 the pathway interactions. The integration of a
 129 wide spectrum of omics data sets from various
 130 plant species facilitates to promote translational
 131 research for future biotechnological applications
 132 in crop plants and also in fruit trees. These
 133 approaches demonstrate the power of systems
 134 biology for understanding the key cellular
 135 components underlying plant functions during

temperature stress. Thus, cooperation between 136
 and beyond disciplines has a role to play in 137
 unraveling the intricacies associated with heat- 138
 stress adaptation in plants. 139

2.1 Transcriptomics 140

Transcriptomics is a powerful approach for 141
 studying the responses of plants in relation to 142
 their environment. The transcriptome consists of 143
 the entire set of transcripts that are expressed 144
 within a cell or organism at a particular develop- 145
 mental stage or under various environmental 146
 conditions. Recent transcriptomic studies have 147
 helped to provide a better understanding of plant 148
 response to different abiotic stresses like cold, high 149
 salinity, drought, high light intensity, hyper- 150
 osmolarity, and oxidative stresses (Deyholos 2010; 151
 Wang et al. 2012). The overlap of large number of 152
 genes induced by various stress conditions reveals 153
 the molecular cross talk of gene regulatory net- 154
 work responses to various abiotic stress conditions 155
 (Weston et al. 2011; Friedel et al. 2012). This 156
 contribution has enabled the discovery of novel 157
 stress-responsive genes on the basis of expression 158
 profiles in different developmental stages of the 159
 plant under stress conditions (Sreenivasulu et al. 160
 2008; Smita et al. 2013). The availability of com- 161
 plete genome sequences of *Arabidopsis* and *Oryza* 162
sativa model plants and other important crops has 163
 provided sufficient genomic information to per- 164
 form high-throughput genome-wide functional 165
 analysis. Compared to other stresses, heat-stress 166
 responses in plants have received increasing atten- 167
 tion in recent years, and accordingly global trans- 168
 criptome expression in response to heat stress has 169
 been reported in different plant species (Mang- 170
 elsen et al. 2011; Liu et al. 2012). Lim et al. 171
 (2006) found that *Arabidopsis* suspension cells at 172
 a moderate heat enhanced the expression profiling 173
 of 165 genes, with high quantity of heat-shock 174
 proteins (Hsps). Frank et al. (2009) found from 175
 the cDNA microarrays and qPCR analysis that 176
 Hsp70, Hsp90, and heat-shock transcription 177
 factors (HSF) were important to tomato 178

179 microspore resistance to heat stress. Transcrip- 227
180 ptomic data from *Triticum aestivum* and other 228
181 plants show that 5 % of the genes are significantly 229
182 affected in response to heat stress (Finka et al. 230
183 2011). But *Arabidopsis* transcriptomic data show 231
184 that 11 % of the genes expressed in response to 232
185 heat stress are encoded for heat-induced 233
186 chaperones (Qin et al. 2008). The rest of the 234
187 transcripts encode products involved in calcium 235
188 signaling, phytohormone signaling, sugar and 236
189 lipid signaling, and metabolism. Additionally, 237
190 some studies have identified various transcripts 238
191 increased during heat treatment, including 239
192 members of the *DREB2* family of transcription 240
193 factors, *AsEXPI* encoding an expand in protein, 241
194 genes encoding for galactinol synthase and 242
195 enzymes in the raffinose oligosaccharide pathway, 243
196 and antioxidant enzymes (Xu et al. 2007). Reports 244
197 exist which show decrease in transcript levels 245
198 related to programmed cell death, basic metabo- 246
199 lism, and biotic stress responses under heat-stress 247
200 conditions (Larkindale and Vierling 2008).

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199 lism, and biotic stress responses under heat-stress 247
200 conditions (Larkindale and Vierling 2008).

AU5 201 Affymetrix Grape Genome Array and qRT- 249
202 PCR techniques were used to identify the heat- 250
203 stress- and recovery-regulated genes in the grape 251
204 and found that about 8 % of total probe sets were 252
205 responsive to heat stress and subsequent recovery 253
206 in grape leaves. The responsive genes identified 254
207 in this study belong to a large number of impor- 255
208 tant factors and biological pathways, including 256
209 those for cell rescue (i.e., antioxidant enzymes), 257
210 protein fate (i.e., Hsps), primary and secondary 258
211 metabolism, transcription factors, and signal 259
212 transduction and development (Liu et al. 2012). 260
213 Wheat Genome Array was applied to measure 261
214 the transcriptome changes in response to heat 262
215 stress in the contrasting genotypes and identified 263
216 a total of 6,560 probe sets that responded to heat 264
217 stress (Qin et al. 2008). A combination of heat 265
218 and drought stresses had a significantly higher 266
219 detrimental effect on growth and productivity of 267
220 maize, barley, sorghum, and different grasses 268
221 than each of the stresses applied individually 269
222 (Abraham 2008). Nonetheless, apart from a nota- 270
223 ble study on the effects of simultaneous drought 271
224 and heat stress (Rizhsky et al. 2004), the effects 272
225 of stress combinations have been little studied 273
226 (Atkinson and Urwin 2012). Transcriptome 274

analysis has been used to investigate the expres- 227
sion in response to heat stress as well as com- 228
bined stresses in several plant species (Oshino 229
et al. 2007; Rasmussen et al. 2013). 230
Transcriptome profiling of *Arabidopsis* plants 231
during a combination of drought and heat stress 232
influences the changes in the expression pattern 233
of more than 400 transcripts (Rizhsky et al. 234
2004). Distinct responses were also observed in 235
plants exposed to a combination of heat and high 236
light intensity (Hewezi et al. 2008), heat, and 237
salinity (Keles and Oncel 2002). Their work 238
suggests that some pathways/mechanisms are 239
dependent on genotype, duration, intensity, and 240
type of abiotic stress. 241

Until now, most of the transcriptome 242
responses have focused on an improved stress 243
tolerance during the vegetative phase of plant 244
growth. Heat stress decreases the duration of 245
developmental phases leading to fewer organs, 246
smaller organs, reduced light perception over the 247
shortened life cycle, and perturbation of the pro- 248
cesses related to carbon assimilation. These 249
parameters ultimately contribute to losses in the 250
final yield of plants (Hussain and Mudasser 251
2007). But the most sensitive developmental 252
stages to heat stress are flowering and grain 253
filling (Wei et al. 2010). High temperature 254
drastically reduced both yield and quality of 255
wheat (Sharma et al. 2012). In this context, 256
recently few attempts were made to reveal the 257
transcriptome alterations in developing seeds to 258
understand the yield stability under heat stress 259
in rice (Yamakawa and Hakata 2010) and 260
barley (Mangelsen et al. 2011). Altogether, 261
transcriptome analyses provide novel insight 262
into the plant response to heat stress and have 263
great implications for further studies on gene 264
function annotation and molecular breeding. In 265
the era of post-genomics, large-scale gene 266
expression data are generated by whole-genome 267
transcriptome platforms. There are a few soft- 268
ware applications that have been developed to 269
query high-throughput microarray gene expres- 270
sion databases at the genome-wide gene content 271
level for various stress responses. The available 272
expression data are mostly deposited in online 273
repositories such as GEO (Barrett et al. 2007), 274

275 NASC Arrays (Craigon et al. 2004), PLEXdb
276 (Dash et al. 2012), and ArrayExpress
277 (Kapushesky et al. 2012). In parallel, various
278 online query-oriented tools have been developed
279 such as Genevestigator (Zimmermann et al.
280 2004), *Arabidopsis* eFP browser (Winter et al.
281 2007), RiceArrayNet (Lee et al. 2009), or
282 *Arabidopsis* and rice co-expression data mining
283 tools (Ficklin et al. 2010; Movahedi et al. 2011)
284 Gramene (Youens-Clark et al. 2011), TAIR
285 (Swarbreck et al. 2008), and MaizeGDB
286 (Schaeffer et al. 2011) to extract development-
287 and stress-specific regulons by implementing
288 global normalization and clustering algorithms
289 (Sreenivasulu et al. 2010).

290 2.1.1 NGS-Based Transcriptome 291 Analysis

292 Next-generation sequencing (NGS)-based
293 transcriptome analysis is superior to other avail-
294 able techniques since sequencing-based method
295 is digital, high throughput, highly accurate, and
296 easy to perform and is capable of identifying
297 allele-specific expression. The principal advan-
298 tage of NGS is that their throughputs are much
299 higher than that of classical sequencing. In recent
300 years, researchers have developed various
301 platforms such as the Illumina Genome Ana-
302 lyzer, the Roche/454 Genome Sequencer FLX
303 Instrument, and the ABI SOLiD System that
304 have proven to be powerful and cost-effective
305 tools for advanced research in many areas,
306 including genome sequencing, resequencing of
307 the genome, miRNA expression profiling, DNA
308 methylation analysis, and especially the de novo
309 transcriptome sequencing of non-model
310 organisms (Morozova and Marra 2008). NGS
311 transcriptome analysis is fast and simple because
312 it does not require any cloning of cDNAs and
313 generates an extraordinary depth of short reads. It
314 is a more comprehensive and efficient way to
315 measure transcriptome composition, obtain
316 transcriptome sequencing using NGS techno-
317 logies provides better alternative for the gene
318 expression studies. Application of NGS technol-
319 ogy in the plant transcriptome analysis has been
320 very limited, and only a few proof-of-concept
321 studies have been performed to reveal the

transcriptional complexity in plants. Here, we 322
provide some examples of the RNA-seq-based 323
gene expression studies performed in plants, 324
which provide novel insights into the various 325
biological aspects. The Illumina sequencing 326
analysis in maize revealed the differential 327
expression of a very high fraction of genes 328
(64.4 %) and provided the evidence for dynamic 329
reprogramming of transcriptome with transcripts 330
for basic cellular metabolism like photosynthesis 331
(Li et al. 2010). An integrated transcriptome atlas 332
of the soybean has been generated, which 333
resulted in the identification of tissue-specific 334
genes (Libault et al. 2010). Further, this expres- 335
sion data has been utilized for comparative 336
analyses of gene expression from other legumes, 337
Medicago truncatula and *Lotus japonicus*. In 338
another independent study, Severin et al. (2010) 339
identified more than 177 genes involved in the 340
agronomically important trait, like seed filling 341
process using RNA-seq in soybean. Garg et al. 342
(2011) identified the differentially expressed 343
genes in a tissue-by-tissue comparison and 344
tissue-specific transcripts in the chickpea, using 345
massively parallel pyrosequencing. The tran- 346
scriptional complexity in rice has also been 347
unraveled via sequencing of mRNA from various 348
tissues in two subspecies and identified more 349
than 15,000 novel transcriptionally active 350
regions and 3,464 differentially expressed genes 351
(Lu et al. 2010). A novel sequence-based 352
approach using Roche 454 technology focused 353
on sequencing unique 3'-UTRs of genes to dis- 354
tinguish highly conserved, related transcripts 355
such as members of same gene family and quan- 356
tify their expression (Eveland et al. 2008). 357

RNA-seq is a popular approach in NGS 358
technologies to collect and quantify the large- 359
scale sequences of coding and noncoding RNAs 360
rapidly (Garber et al. 2011). NGS-based RNA- 361
seq has been used for the rapid development of 362
genomic resources in many plants (Gowik et al. 363
2011). NGS was employed to create transcrip- 364
tome databases of species without a sequenced 365
genome such as mangroves (Dassanayake et al. 366
2009), eucalyptus (Novaes et al. 2008), olive 367
(Alagna et al. 2009), and chestnut (Barakat 368
et al. 2009). For this RNA-seq approach, either 369

AU7 370 fragmented mRNA or fragmented cDNA (Wang
371 et al. 2009a, b) can be used as input, and read
372 lengths ranging from 100 to 250 nts and 500 nts
373 model length can be received depending on the
374 sequencer and sequencing kit employed. A major
375 challenge in the near future for those who like to
376 begin the work with NGS data is retooling for
377 methods to store data. This is due to the short
378 history of the technology and its continuous
379 development, and there are as yet no standard
380 methods available to detect and analyze differ-
381 entially expressed genes based on NGS data. Such
382 deep sequencing data from crop plants can help
383 to identify the candidate genes associated with
384 final yield, grain quality, disease resistance, and
385 abiotic including heat-stress tolerance. These
386 data are also useful to identify and isolate new
387 genes and promoters involved in agronomical
388 traits of economically important crops. Genera-
389 tion of such bioinformatics data would be useful
390 in crop improvement programs. NGS-based
391 sequencing applications have rapidly expanded
392 in plant genomics by browsing the Sequence
393 Read Archive (SRA) in NCBI (<http://www.ncbi.nlm.nih.gov/sra>), European Nucleotide Archive
394 (<http://www.ebi.ac.uk/ena/home>), and DDBJ
395 Sequence Read Archive (http://trace.ddbj.nig.ac.jp/dra/index_e.shtml), all of which store raw
396 sequencing data from NGS platforms; users can
397 determine how thoroughly a given species has
398 been sequenced and retrieve the publicly avail-
400 able sequencing data for further use.

402 **2.2 Proteomics**

403 Proteomics is not only a powerful molecular tool
404 used in describing complete proteomes at the
405 organelle, cell, organ, or tissue levels, but it can
406 also compare the status of protein profiling under
407 different physiological conditions, such as those
408 resulting from the exposure to stressful condi-
409 tions (Cushman and Bohnert 2000). The prote-
410 some reflects the actual state of the cell or the
411 organism and is an essential bridge between the
412 transcriptome and the metabolome (Zhu et al.
413 2003) and also acts directly on biochemical pro-
414 cesses and thus must be closer to the phenotype.

In the last decade, proteomics has been shown to 415
be a powerful tool in exploring many biological 416
mechanisms which brought much deeper insight 417
in the abiotic stress-responsive mechanisms in 418
the crop plants (Rinalducci et al. 2011; Yin 419
et al. 2012). However, the proteomic studies of 420
crop plants under heat stress are not well under- 421
stood (Neilson et al. 2010; Rinalducci et al. 422
2011). To understand the modulation mecha- 423
nisms of heat tolerance in plants, a detailed 424
study of the response to high temperature at the 425
proteomics level is essential. Thus far, there have 426
been only a few proteomic studies regarding heat 427
stress in plants (Koussevitzky et al. 2008; 428
Neilson et al. 2010). Recent developments in 429
protein analysis methods have made possible 430
the evaluation and identification of many 431
proteins and to exploit proteomic data in the 432
context of stress response particularly heat stress 433
(Nanjo et al. 2010). Proteome approach has been 434
successfully used to study the effect of heat 435
shock on wheat grain quality and to identify 436
protein markers that enable breeders to produce 437
cultivars with desired characters especially 438
cultivars that tolerate heat-stress conditions 439
(Skylas et al. 2002). The effect of heat stress in 440
the wheat endosperm by MALDI-TOF coupled 441
with 2-DE analysis identified a total of 48 differ- 442
entially expressed proteins (Majoul et al. 2003). 443
Of these, more than 37 % of the proteins have 444
been identified as Hsps that are involved in pro- 445
tein stability and folding, which suggests that 446
high temperature has severe effects on protein 447
denaturation and regulation. Rice leaf proteomic 448
analysis by 2-DE-MS method in response to heat 449
stress identified 1,000 protein spots, wherein 73 450
protein spots were differentially expressed at 451
least at one time point. These proteins were fur- 452
ther categorized into different classes related to 453
heat-shock proteins, energy and metabolism, 454
redox homeostasis, and regulatory proteins. 455

Proteomic analysis in barley cultivars under 456
heat stress identified several isoforms of sHsps 457
and S-adenosylmethionine synthetase (SAM-S) 458
and found to be upregulated (Sule et al. 2004). 459
Several studies that analyzed the proteomic 460
response to heat stress have been carried out in 461
Arabidopsis and identified 45 spots which were 462

463 unique to the combined heat and drought
464 stresses. Proteins uniquely regulated by heat in
465 *A. scabra* included sucrose synthase, superoxide
466 dismutase, glutathione S-transferase, and stress-
467 inducible Hsps. This suggests that these proteins
468 may contribute to increased survival of *A. scabra*
469 under high-temperature conditions. Using differ-
470 ential metabolic labeling, Palmblad et al. (2008)
471 identified a number of known Hsps as well as
472 other proteins previously not associated with heat
473 shock in *Arabidopsis*. Polenta et al. (2007)
474 identified the Hsps from tomato pericarp by ther-
475 mal treatment. They highlighted the importance
476 of class I sHsps that are involved in the process
477 and further characterized them by using mono-
478 specific polyclonal antiserum and MS/MS analy-
479 sis. Thus, the results of this study suggest that
480 plants cope with heat stress in a complex manner,
481 where Hsps play a pivotal role in a complex
482 cellular network. The identification of some
483 novel proteins in the heat-stress response
484 provides new insights that can lead to a better
485 understanding of the molecular basis of heat sen-
486 sitivity in plants (Lee et al. 2007).

487 Protein profiling of two ecotypes (low and high
488 elevations) of Norway spruce was investigated in
489 response to high-temperature stress using 2-DE
490 and LC-MS/MS. This analysis showed an accu-
491 mulation of sHsps during the recovery from heat
492 stress, specifically in the low-elevation ecotype
493 (higher level of thermotolerance) (Valcu et al.
494 2008). Root protein profiling under heat stress
495 identified 70 protein spots which showed differ-
496 ential accumulation in at least one species. More
497 proteins were downregulated as a result of heat
498 stress, but *A. scabra* exhibited many upregulated
499 protein spots under heat-stress regimes. The two
500 grasses displayed different proteomic profiles.
501 Some of the uniquely regulated genes by heat
502 stress in *A. scabra* included sucrose synthase,
503 superoxide dismutase, glutathione S-transferase,
504 and stress-inducible heat-shock proteins. This
505 suggests that these proteins may contribute to
506 increased survival of *A. scabra* under high-
507 temperature conditions (Xu et al. 2008). Heat-
508 stress treatment in combination with drought
509 resulted in the expression of approximately 650
510 protein spots in *C. spinarum*. Forty-nine spots

511 changed their expression levels upon heat and
512 drought treatment, and 30 proteins were identified
513 by MS and 2-D Western blot. These proteins were
514 classified into Hsps, photosynthesis-related
515 proteins, RNA-processing proteins, and proteins
516 involved in metabolism and energy production
517 (Zhang et al. 2010). Proteomic profiling of radish
518 leaves in response to high-temperature stress
519 resulted in the identification of 11 differentially
520 expressed protein spots, and they were divided
521 into four categories: Hsps, redox homeostasis-
522 related proteins, energy- and metabolism-related
523 proteins, and signal transduction-associated
524 proteins (Zhang et al. 2012). Such studies provide
525 a good starting point in understanding the overall
526 thermal responses of plants; however, further heat
527 treatments and comparative analyses should be
528 conducted in order to gain a better understanding
529 of the overall thermal responses of plants.

530 Availability of proteomics data is important to
531 support published results and conclusions. Several
532 proteomics resources and repositories available
533 for plant species were updated (Schneider et al.
534 2012), e.g., Plant Proteome Database (<http://ppdb.>
535 [tc.cornell.edu/](http://ppdb.tc.cornell.edu/)) which provides information on
536 maize and *Arabidopsis* proteomes, RIKEN Plant
537 Phosphoproteome Database (RIPP-DB, <http://>
538 phosphoproteome.psc.database.riken.jp) updated
539 with a data set of large-scale identification of rice
540 phosphorylated proteins (Nakagami et al. 2012),
541 and OryzaPG-DB launched as a rice proteome
542 database based on shotgun proteomics (Helmy
543 et al. 2011). Besides those repositories, numerous
544 very valuable resources, each focused on a spe-
545 cific aspect like tandem mass spectra evidences,
546 quantitative information, and localization of phos-
547 phosphorylation sites, are available for plant proteo-
548 mics such as ProMEX (Wienkoop et al. 2012);
549 PhosPhAt, a plant phosphorylation site database
550 (Arsova and Schulze 2012); PaxDb (Wang et al.
551 2012), a meta-resource integrating information on
552 absolute protein abundance levels across different
553 organisms, including *A. thaliana*; MASCP Gator
554 (Joshi et al. 2011), an aggregation portal for the
555 visualization of *Arabidopsis* proteomics data; or
556 PPDB, the Plant Proteome Database (Sun et al.
557 2009) to cite only a few. UniProtKB is cross-
558 linked to several of those proteomics resources,

559 including PRIDE, IntAct, ProMEX, PeptideAtlas,
560 and PhosphoSite. A complete list of the cross-
561 references, with bibliographic references, is avail-
562 able at <http://www.uniprot.org/docs/dbxref>. These
563 databases help us in identifying and understanding
564 the complex protein networks associated with the
565 heat-stress tolerance and the functions of these
566 proteins during heat stress.

567 2.3 Metabolomics

568 Metabolomics is the qualitative and quantitative
569 collection of all low-molecular-weight meta-
570 bolites present in a cell that participate in general
571 metabolic reactions and are required for the main-
572 tenance, growth, and normal function of a cell
573 (Arbona et al. 2009; Jordan et al. 2009).
574 Metabolome directly influences the phenotype
575 when compared to transcriptome or proteome
576 and bridges the gap between genotype and pheno-
577 type. The study of the metabolome represents the
578 integration of the genetic background and the
579 influence of the environmental conditions, thus
580 describing more accurately the phenotype of a
581 given plant species. Metabolic regulation during
582 stressful events has been facilitated much in the
583 last decade, and the identification of metabolites
584 has been improved through mass spectrometric
585 studies (Sawada et al. 2009). More comprehensive
586 coverage can only be achieved by using several
587 extraction and detection technologies in parallel
588 and subjecting them to chemical analysis using
589 different analytical methods like gas chromatog-
590 raphy coupled to mass spectrometry (GC-MS) and
591 liquid chromatography coupled to mass spectrom-
592 etry (LC-MS) (De Vos et al. 2007). Other analyti-
593 cal techniques include liquid chromatography
594 (photodiode array detection) coupled to mass
595 spectrometry (LC-PDA/MS) (Huhman and
596 Sumner 2002), capillary electrophoresis coupled
597 to mass spectrometry (CE-MS) (Harada et al.
598 2009, Takahashi et al. 2009), Fourier transform
599 ion cyclotron resonance mass spectrometry
600 (FTICR/MS) (Oikawa et al. 2006), and NMR
601 spectroscopy (Krishnan et al. 2005). Among all
602 analyzers that can be used with the separation
603 techniques mentioned above, the most popular in

metabolomics are MS and, particularly, those 604
providing accurate mass measures (Arbona et al. 605
2013). Therefore, the future objective is the 606
standardization and annotation of data from mul- 607
tiple metabolomics technologies in public 608
databases (Castellana and Bafna 2010). The data 609
obtained can then be investigated by multivariate 610
and correlation analyses for functional genomics 611
in order to study the systems biology of plant 612
metabolism and make use of the data for crop 613
improvement (Arbona et al. 2013). From the 614
genome sequence information of the *A. thaliana* 615
and other model plants, it is evident that plants 616
reorganize their metabolic network in order to 617
adapt to such adverse conditions (Kaplan et al. 618
2004). Many plants respond to different stresses 619
by a progressive adjustment of their metabolism 620
with early and late responsive gene networks. 621
Some metabolic changes are common to salt, 622
drought, and temperature stresses, whereas others 623
are specific (Urano et al. 2009; Lugan et al. 2010). 624
Using metabolic changes as a “map” or “marker,” 625

AU9

626 factors regulating metabolic movements were 626
investigated by Saito et al. (2008) in combination 627
with other “omics” approaches. It appears, there- 628
fore, metabolomics plays a key role in understand- 629
ing cellular functions and decoding the functions 630
of genes (Hagel and Facchini 2008). 631

In plant systems, metabolomics approach has 632
already been used to study metabolomic changes 633
during a variety of stresses, for example, water and 634
salinity (Cramer et al. 2007), sulfur (Nikiforova 635
et al. 2005), phosphorus (Hernandez et al. 2007), 636
oxidative (Baxter et al. 2007), and heavy metals 637
(Le Lay et al. 2006). But, less work has been done 638
in the case of heat stress. A recent metabolome 639
analysis showed common metabolites in response 640
to cold and other stresses and demonstrated a 641
prominent role for the DREB1/CBF transcrip- 642
tional network in the cold-response pathway 643
(Maruyama et al. 2009). Comparative metabolite 644
analysis has been carried out using GC-MS 645
(Kaplan et al. 2004) and GCTOF-MS (Weinkoop 646
et al. 2008) between *Arabidopsis* plants resp- 647
onding to heat and cold shocks. Many metabolites 648
produced in response to heat shock overlapped 649
with those produced in response to cold shock 650
also. Many metabolite levels changed specifically 651

AU8

652 in response to cold than to heat. This response
653 points out a strong impact of cold stress on plant
654 metabolism. Wang et al. (2004) reported that a
655 combination of drought and heat stress results in
656 decrease of the growth and productivity of the
657 crops when compared with each of the different
658 stresses applied individually. Integrated
659 metabolome and transcriptome results were
660 applied by Yamakawa and Hakata (2010) to ana-
661 lyze rice developing caryopses under high-
662 temperature conditions. Molecular events underly-
663 ing pollination-induced and pollination-
664 independent fruit sets were carried out by Wang
665 et al. (2009a, b) and also the effects of DE-
666 ETIOLATED1 downregulation in tomato fruits
667 (Enfissi et al. 2010). Heat stress induced the accu-
668 mulation of key metabolites like alanine, allantoin,
669 arachidic acid, 2-ketoisocaproic acid, myo-
670 inositol, putrescine, and rhamnose, while it
671 decreased fructose-6-phosphate (Luengwilai et al.
672 2012). Moreover, these results suggested that a
673 metabolic network of compatible solutes including
674 proline, monosaccharides, galactinol, and raffi-
675 nose has an important role to play in temperature
676 stress tolerance (Alcazar et al. 2010).

677 Information resources related to metabolic
678 profiling are available and updated and provide
679 data archives for metabolome data sets and analyt-
680 ical platforms such as LC-MS-based metabolome
681 database ([http://appliedbioinformatics.wur.nl/
682 moto/](http://appliedbioinformatics.wur.nl/moto/)) (Moco et al. 2006), KOMICS (Iijima et al.
683 2008), Plant MetGenMAP (Joung et al. 2009),
684 Metabolome Express ([https://www.metabolome-
685 express.org/](https://www.metabolome-express.org/)) (Carroll et al. 2010; Ferry-Dumazet
686 et al. 2011), MeRy-B ([http://www.cbib.u-bor-
687 deaux2.fr/MERYB/](http://www.cbib.u-bordeaux2.fr/MERYB/)) (Ferry-Dumazet et al.
688 2011), KaPPA-View4 SOL (Sakurai et al. 2011),
689 MetaCrop 2.0 ([http://metacrop.ipk-gatersleben.
690 de](http://metacrop.ipk-gatersleben.de)) (Schreiber et al. 2012), and PRIME ([http://
691 prime.psc.riken.jp/](http://prime.psc.riken.jp/)) (Sakurai et al. 2013). Apart
692 from this, several individual species-wise
693 databases are available at Gramene database like
694 RiceCyc, MaizeCyc, BrachyCyc, SorghumCyc,
695 and Sol Genomics Network (SGN). These
696 databases play crucial roles as information
697 resources and repositories of large-scale data sets
698 and also serve as tools for further integration of
699 metabolic profiles containing comprehensive data

acquired from other omics research (Akiyama 700
et al. 2008). Following these successes, several 701
multi-omics-based systems analyses have been 702
used for understanding plant cellular systems. 703

2.4 Phenomics 704

Phenomics is the systematic study of the physical 705
and morphological properties of organism as they 706
change in response to genetic mutation and envi- 707
ronmental influences. Traditional methods of 708
measuring growth and other morphological 709
features are time consuming and costly and 710
involve many genotypes and the destructive har- 711
vest of plants. Phenomics has been considered as 712
one of the important techniques to screen the 713
germplasm and to utilize the available morpho- 714
logical variation in breeding programs aimed at 715
heat-stress tolerance. Therefore, phenomics as a 716
technique remains critical in the post-genomics 717
era. Phenomics approach also enables us to under- 718
stand the precise molecular mechanism involved 719
in conferring tolerance against different kinds of 720
abiotic stresses. This has stimulated the research 721
in several institutions to invest in developing 722
technologies and platforms able to speed up the 723
phenotyping process. The investments started ear- 724
lier in the private sectors, and more recently this 725
has been embraced by public research institutions 726
that are developing an international collaboration 727
network (www.plantphenomics.com). There are a 728
large number of initiatives launched (International 729
Plant Phenomics Network, Deutsche Plant 730
Phenomics Network, and European Plant 731
Phenomics Network) to create phenotyping 732
facilities to screen populations using high- 733
throughput methods located in Australia, 734
Germany, France, Canada, Italy, and many more 735
(Furbank 2009; Finkel 2009). Large phenotyping 736
platforms represent technologies that are mainly 737
based on nondestructive image analyses of plant 738
tissues or structural and functional features 739
obtained by advanced technologies (Nagel et al. 740
2009; Yazdanbakhsh and Fisahn 2009). In other 741
labs, glass houses and greenhouses can be fitted 742
with cameras, and plants may be carried on the 743
conveyor belts to the imaging stations. Such 744

745 facilities exist in several laboratories around the
746 world (CropDesign, Belgium; The Plant Acceler-
747 ator, Australia; PhenoPhab, Holland; Metapontum
748 Agrobios, Italy; IPK, Germany) and have the
749 advantage of acquiring 3-D images. Using high-
750 throughput phenomics platforms, various
751 parameters like water-deficit responses can be
752 studied (Sadok et al. 2007; Berger et al. 2010).
753 So far, only a handful of studies have been carried
754 out in the phenomics area in response to heat
755 stress in the crop plants (Sharma et al. 2012; Yeh
756 et al. 2012). However, the application of
757 phenomics will really become useful and impor-
758 tant if specific questions are asked to these
759 platforms.

760 Plants show numerous responses to heat stress
761 regarding carbon metabolism and water balance,
762 but unfortunately no single key physiological trait
763 that relates to a genetic base for heat-stress toler-
764 ance has been identified (Allakhverdiev et al.
765 2008; Wolkovich et al. 2012). It is known that
766 the reproductive processes are the most sensitive
767 to heat stress in many species. Heat stress signifi-
768 cantly affects cellular homeostasis including both
769 protein and membrane stability. These responses
770 include basal thermotolerance, short- and long-
771 term acquired thermotolerance, and thermo-
772 tolerance to moderately high temperatures. High
773 temperatures adversely affect the seed germina-
774 tion, growth, photosynthetic efficiency, core
775 metabolic processes, pollen viability, respiration,
776 water relations, and protein and membrane stabil-
777 ity. Different species and cultivars may vary their
778 tolerance to high temperatures with the stage of
779 development, but all vegetative and reproductive
780 stages are highly affected by heat stress (Hall
781 1992). Different phenological stages of plants dif-
782 fer in their sensitivity to high temperature. During
783 vegetative stage, high day temperature can dam-
784 age leaf gas-exchange properties. High night
785 temperatures make the pollen sterile. But this
786 depends on species and the genotype under
787 study. Sharma et al. (2012) identified 41
788 contrasting lines in terms of heat tolerance by
789 mass screening of 1,274 wheat cultivars of diverse
790 origin. This contrasting set of cultivars was then
791 used to compare the ability of chlorophyll fluores-
792 cence parameters to detect genetic difference in

heat tolerance. This identification may aid future 793
studies to understand the genetic and physiologi- 794
cal nature of heat-stress tolerance (Sharma et al. 795
2012). The temperature and duration of heat-stress 796
treatments resulting in changes in growth and 797
development of seeds, seedlings, mature leaves, 798
panicles or spikes, and fruits have been used in 799
crop thermotolerance studies (Rahman et al. 2007; 800
Seepaul et al. 2011). But, high-throughput pheno- 801
typing analyses are necessary for deepening our 802
understanding of the molecular genetics of 803
thermotolerance. 804

3 Heat-Shock Proteins

805

Heat-shock response (HSR) is a highly 806
conserved reaction caused by exposure of an 807
organism or tissue or cells to sudden high- 808
temperature stress. High-temperature stress is 809
characterized by rapid induction and transient 810
expression of conserved heat-shock transcripts 811
and other regulators. Among five conserved 812
families of Hsps (Hsp100, Hsp90, Hsp70, 813
Hsp60, and sHsp), the small heat-shock proteins 814
(sHsps) are found to be most prevalent in plants, 815
the expression of which can increase up to 200- 816
fold under heat stress. Different classes of molec- 817
ular chaperones appear to bind to specific nonna- 818
tive substrates and states. Molecular Hsps/ 819
chaperones are located in the cytoplasm and 820
cell organelles such as the nucleus, mitochondria, 821
chloroplasts, and ER (Wang et al. 2004). The 822
mechanism by which Hsps contribute to heat 823
tolerance is still enigmatic though several roles 824
have been ascribed to them. Many studies assert 825
that Hsps are molecular chaperones ensuring the 826
native configuration and functionality of cell 827
proteins under heat stress. During stress, many 828
enzymes and structural proteins undergo deleter- 829
ious structural and functional changes. There- 830
fore, it is vital to maintain proteins in their 831
functional conformations, preventing aggrega- 832
tion of nonnative proteins and refolding of dena- 833
tured proteins. It is also important to remove 834
nonfunctional and harmful polypeptides arising 835
from misfolding, denaturation, or aggregation for 836
cell survival under stress. Thus, the different 837

838 classes of Hsps/chaperones cooperate and play
839 complementary and sometimes overlapping roles
840 in the protection of proteins from stress (Bowen
841 et al. 2002). When denatured or misfolded
842 proteins form aggregates, they can be resolu-
843 bilized by Hsp100/Clp followed by refolding or
844 degraded by proteases (Schöffl et al. 1998).
845 Some Hsps/chaperones (Hsp70, Hsp90) accom-
846 pany the signal transduction and transcription
847 activation that lead to the synthesis of other
848 members of Hsps/chaperones. Similar observa-
849 tions have been reported with plant chaperones.
850 It has been shown that Hsp18.1 from *Pisum*
851 *sativum* could stably bind to heat-denatured pro-
852 tein and maintained it in a folding-competent
853 state for further refolding by Hsp70/Hsp100
854 complexes (Mogk et al. 2003). A recent study
855 has shown that Hsp70 and Hsp90 have roles to
856 play in protecting the enzymes at higher
857 temperatures (Reddy et al. 2010, 2011). HSR in
858 plants was investigated in depth, and the pres-
859 ence of multiple signaling pathways was pro-
860 posed (Kotak et al. 2007; von Koskull-Doring
861 et al. 2007). Many studies noted upregulation of
862 transcripts including high-molecular-weight
863 Hsps like Hsp101, Hsp70s, and small Hsps
864 (Sarkar et al. 2009; Mittal et al. 2009; Chauhan
865 et al. 2011) and also identified additional
866 transcripts such as DREBs, galactinol synthases
867 and other enzymes in the raffinose oligosaccha-
868 ride pathway, and oxidative stress enzymes
869 (Frank et al. 2009; Suzuki et al. 2011).
870 Genome-wide survey for Hsps and Hsfs using
871 the tools of bioinformatics helps us to find out
872 not only the number of genes present in a genome
873 but also their chromosomal location. Software
874 tools also help us to find their subcellular
875 locations and the upstream promoter sequences
876 along with their predicted functions.

877 The regulation of heat-shock gene expression
878 in eukaryotes is mediated by the heat-shock tran-
879 scription factors (Hsfs), which are highly
880 conserved throughout the eukaryotic kingdom
881 (Scharf et al. 2012). Plant *Hsfs* have unique
882 characteristics and the existence of heat-stress-
883 induced *Hsf* genes might have a major role to
884 play in the modulation of transcription during
885 long-term heat-shock response (Chauhan et al.

2011). Temperature stress-response signal 886
transduction pathways and defense mechanisms 887
involving Hsfs and Hsps are thought to be inti- 888
mately associated with reactive oxygen species 889
(ROS) production (Frank et al. 2009). Heat- 890
shock transcription factor-dependent expression 891
of antioxidant enzymes such as ascorbate 892
peroxidases in *Arabidopsis* (Frank et al. 2009) 893
suggested that Hsfs might be involved not only in 894
Hsp regulation but also in the regulation of oxi- 895
dative stress (Reddy et al. 2009). Recent research 896
revealed the involvement of noncanonical tran- 897
scription factors in HSR; for instance, bZip28, a 898
gene-encoding membrane, tethered TF, which 899
was induced by HS, and the bzip28 null mutant 900
became hypersensitive to HS (Gao et al. 2008). 901
Besides Hsps, there are other plant proteins 902
including ubiquitin, LEA proteins, and cytosolic 903
Cu/Zn-SOD and Mn-SOD whose expressions are 904
stimulated upon heat stress. A number of 905
osmotin-like proteins induced by heat and nitro- 906
gen stresses, collectively called Pir proteins, have 907
also been found to be overexpressed in many 908
plant cells under heat stress conferring them 909
resistance. Microarray expression data in 910
Hordeum vulgare revealed that most of the 911
sHsp and *Hsf* genes are differentially regulated 912
during drought and temperature stresses at differ- 913
ent plant developmental stages suggesting con- 914
siderable cross talk between stress and non-stress 915
regulatory networks. In silico *cis*-regulatory 916
motif analysis of *Hsf* promoters showed an 917
enrichment with abscisic acid-responsive *cis*- 918
elements (ABREs), implying regulatory role of 919
ABA in mediating transcriptional response of 920
HvsHsf genes. 921

4 Heat-Shock Promoters 922

The need for inducible or specific promoters can 923
be a key tool in plant biotechnology, and their need 924
will increase as we attempt to transfer and validate 925
genes associated with abiotic stress tolerance. In 926
the last decade, several candidate genes, pathways, 927
and strategies have been identified by various 928
groups across the globe and provided insights in 929
plant heat-stress adaptation. Strong constitutive 930

931 promoters are routinely used in plant transforma- 980
932 tion with a regulated expression of heat-stress- 981
933 responsive genes. But such use of constitutive 982
934 promoters is resulting in serious penalties on 983
935 plant growth and development with overall nega- 984
936 tive performance of transgenics (Sakuma et al. 985
937 2006a, b). Since constitutive promoters are ham- 986
938 pering the final productivity, it is important for us 987
939 to identify and isolate heat-stress-inducible 988
940 promoters and use them while developing trans- 989
941 genic crops. However, the regulated expression of 990
942 transgenes in plants in a tissue-specific manner and 991
943 at a specific developmental stage remains a chal- 992
944 lenging task. The isolation and characterization of 993
945 heat-stress-responsive promoters and their regu- 994
946 latory regions will have more biotechnological 995
947 applications as these promoters could be used to 996
948 engineer the target genes to express only at the site 997
949 of stress. A powerful approach for measuring the 998
950 activity of any heat-shock promoter is by fusing 999
951 the promoter of heat-shock gene to reporter genes 1000
952 such as GFP or GUS. This allows measuring the 1001
953 developmental and tissue-specific expression of 1002
954 genes with or without heat stress (Khurana et al. 1003
955 2013). It has been found that while some 1004
956 transcripts exhibit translational repression, others 1005
957 escape such repression and remain actively trans- 1006
958 lated. But the underlying mechanisms that mediate 1007
959 this control especially the identities of the regu- 1008
960 latory RNA elements involved were poorly under- 1009
961 stood. Using a computational and experimental 1010
962 approach, Matsuura et al. (2013) identified a 1011
963 novel *cis*-regulatory element in the 5'-UTR that 1012
964 affects differential translation and has a *cis*-regu- 1013
965 latory signature responsible for heat-stress-regu- 1014
966 lated mRNA translation in *Arabidopsis*. A 1015
967 comprehensive transcriptome analysis by using 1016
968 microarrays revealed the relationships among 1017
969 stress-regulated transcripts and enabled the predic- 1018
970 tion of their *cis*-regulatory elements in temperature 1019
971 stress-inducible genes (Weston et al. 2008). In 1020
972 addition, characterization of the transcriptional 1021
973 dynamics during seed development under different 1022
974 stress conditions enabled the prediction of their 1023
975 *cis*-regulatory elements (Weston et al. 2008). Ma 1024
976 and Bohnert (2007) showed a clear correlation 1025
977 between expression profiles and the 5'*cis*-regu- 1026
978 latory motifs of stress-regulated genes. These 1027
979 analyses indicated that stress-regulated genes are

controlled by a complicated regulatory network 980
and cross talk between pathways. This type of 981
network has been proposed based on 982
transcriptome data using different bioinformatics 983
approaches (Long et al. 2008). The basic structure 984
and promoter recognition of Hsfs are highly 985
conserved throughout the eukaryotic kingdom 986
(Scharf et al. 2012). Expression of *cis*-motifs 987
containing these *Hsf* genes might be regulated 988
by *Hsfs* themselves, via formation of a regulatory 989
network as proposed by Nover et al. (2001). The 990
expression of *Hsps* during stress treatments and 991
different developmental stages will depend on the 992
cis-motifs present in the respective *Hsp* and *Hsf* 993
promoters which will subsequently bind to differ- 994
ent transcription factors particularly *Hsfs* as 995
demonstrated by transient reporter assays in 996
sunflower embryos (Almoguera et al. 2002). 997
Hsp18.2 promoter fused to the *GUS* gene trans- 998
genic *Arabidopsis* plants showed that heat stress 999
induced the *GUS* gene activity in almost all the 1000
organs of the plant (Takahashi et al. 1992). Simi- 1001
larly, heat-shock-induced GUS activity was 1002
observed in transgenic *Arabidopsis* when the pro- 1003
moter of *Hsp81* gene was used (Yabe et al. 1994). 1004
Crone et al. (2001) did a detailed analysis of the 1005
expression of the GmHsp17.5E promoter in all 1006
the organs and tissues of the flower and found that 1007
promoter is differentially expressed after heat 1008
shock in different floral tissues. Hsfs bind to 1009
heat-stress elements (HSEs) with the core 1010
sequence nGAAnnTTCn or nTTCnnGAAn and 1011
form trimers, thereby regulate downstream gene 1012
expression (Wu 1995). Despite the occurrence of 1013
heat-shock elements in the promoters of heat- 1014
stress-inducible genes, a set of *Hsp* genes are 1015
expressed during seed development (Kotak et al. 1016
2007). Atsp90-1 promoter region contributes in a 1017
combinatorial manner to regulate the expression 1018
in development and stress conditions (Harala- 1019
mpidis et al. 2002). The heat-stress induction of 1020
Arabidopsis HsfA3 is regulated directly by 1021
DREB2A, a transcription factor functioning in 1022
drought stress responses (Sakuma et al. 2006a, 1023
b). Accordingly, the DRE has been identified in 1024
the promoters of a cluster of heat-inducible genes 1025
(Larkindale and Vierling 2008). 1026

Promoters of heat-shock protein (*Hsp*) genes 1027
are good candidates for inducible expression, 1028

1029 since they are rapidly and highly induced under
1030 heat-stress conditions. Besides, their induction can
1031 be accurately controlled by varying the tempera-
1032 ture and duration of induction. Several detailed
1033 studies have been performed using the reporter
1034 gene expression driven by plant small Hsp
1035 promoters in different hosts. The AtHsp18.2 pro-
1036 moter has been successfully used in *Arabidopsis*
1037 (Takahashi et al. 1992) and in other species, such
1038 as *N. plumbaginifolia* (Moriwaki et al. 1999) and
1039 *N. tabacum* hairy roots (Lee et al. 2007). Besides,
1040 the inducibility of soybean GmHsp17.3B pro-
1041 moter was studied in the moss *Physcomitrella*
1042 *patens* (Saidi et al. 2007). *Arabidopsis* Hsp18.2
1043 promoter was used to drive the expression of
1044 GUS gene in *N. tabacum* BY-2 cells, and maxi-
1045 mum activity of protein was obtained under the
1046 heat stress (Shinmyo et al. 1998). Khurana et al.
1047 (2013) studied the wheat sHsp26 promoter activity
1048 in transgenic *Arabidopsis* and observed consis-
1049 tently high levels of *GUS* gene expression under
1050 different abiotic stress conditions especially in
1051 heat stress. However, the mechanisms that regulate
1052 Hsp expression during seed maturation remain
1053 largely unknown. In addition to their direct
1054 functions in acquired stress tolerance and develop-
1055 ment, Hsps/chaperones function synergistically
1056 with other components, thus help in decreasing
1057 cellular damage. If the range of promoters is
1058 wide, then it is possible to introduce multiple
1059 transgenes into plants that are expressed differen-
1060 tially in response to various environmental
1061 stresses. Identification of heat-stress-inducible
1062 promoters from crop plants would be of immense
1063 help in generating transgenic plants with improved
1064 agronomic performance.

1065 **5 Heat-Stress-Tolerant**
1066 **Transgenic Crops Generated**
1067 **Through Expression of Hsps**

1068 Most crops are affected by daily/seasonal
1069 fluctuations in day and/or night temperatures.
1070 Conventional breeding for high-temperature
1071 stress tolerance has not been successful so far.
1072 This could be due to lack of our understanding on
1073 the genetic mechanisms associated with heat

stress, suitable source of genes, and complex 1074
nature of the HS trait. This complexity is now 1075
being dissected out including features like heat- 1076
shock elements (HSEs), heat-shock factors 1077
(HSFs), possible receptors of the heat-shock 1078
response, signaling components, and chromatin 1079
remodeling aspects (Proveniers and van Zanten 1080
2013). Several groups have altered the levels of 1081
sHsps in bacterial systems and shown that when 1082
overexpressed in bacterial cells, Hsps have a role 1083
in conferring thermotolerance. The overexp- 1084
ression of *OsHsp16.9* in *E. coli* conferred 1085
thermotolerance. Yeh et al. (2012) constructed 1086
deletion mutants of this sHsp to find out the 1087
regions associated with heat-stress tolerance. 1088
They overexpressed the constructs in *E. coli* 1089
(Yeh et al. 2012) and found out that the deletion 1090
of amino acid residues 30–36 (PATSDND) in the 1091
N-terminal domain or 73–78 (EEGNVL) in the 1092
consensus-II domain of *OsHsp16.9* caused the 1093
loss of chaperone activities and also rendered 1094
the *E. coli* incapable of surviving at 47.5 °C. 1095
When three sHsps were introduced into *E. coli*, 1096
they acquired thermotolerance and were able to 1097
protect malate dehydrogenase (MDH) from 1098
in vitro thermal aggregation (Pike et al. 2001). 1099
The survivability of *E. coli* B121 (DE3) cells 1100
transformed with a recombinant plasmid 1101
containing different Hsps was compared with 1102
the control *E. coli* cells (transformed with the 1103
PET28a vector) under heat and different abiotic 1104
stresses. The PgHsp transformed cells showed 1105
thermotolerance at 47.5 °C, a treatment that 1106
was lethal to the untransformed bacterial cells. 1107
When the cell lysates from transformed and 1108
untransformed were heated at 55 °C, the amount 1109
of protein denatured in the PgHsps-B121 DE3 1110
cells was 50 % less than that of the PET28a 1111
vector (control) cells (Reddy et al. 2010, 2011). 1112
Furthermore, genetically modified *E. coli* 1113
expressing DcHsp17.7 exhibited a higher salt 1114
stress tolerance than control *E. coli* (Song and 1115
Ahn 2011). These results suggest that expression 1116
of Hsps confers abiotic stress tolerance to *E. coli* 1117
cells and may play a role in the plant's adaptation 1118
to harsh environments. 1119

The involvement of Hsps in regulating thermo- 1120
tolerance has been further carried out in higher 1121

1122 plants by downregulating their expression levels
1123 using either antisense or RNAi approach. Mutants
1124 of *Zea mays* and *A. thaliana* plants under-
1125 expressing their respective Hsp100 proteins were
1126 observed to lack both basal and induced
1127 thermotolerance (Hong and Vierling 2000, Nieto-
1128 Sotelo et al. 2002). Yang et al. (2006) showed that
1129 the tomato plants silenced for Hsp100/ClpB protein
1130 were impaired in thermotolerance. Acquisition of
1131 thermotolerance has been found to be negatively
1132 affected in Hsp70 antisense *A. thaliana* plants (Lee
1133 and Schoffl 1996). Mutants of *Zea mays* and
1134 *Arabidopsis* with low levels of their respective
1135 Hsp100 proteins were observed to lack both basal
1136 and induced thermotolerance. Plants lacking Hsa32
1137 do not survive HS treatment even after a
1138 pretreatment at a sublethal temperature (Chang
1139 et al. 2006). Heat-inducible transactivator HsfA2
1140 with low levels of expression results in an increased
1141 sensitivity of the mutant plants to heat stress
1142 (Chang et al. 2007). Genome-wide transcriptome
1143 analysis of HsfA1a, A1b, and A2 knockout mutants
1144 in *Arabidopsis* suggests that HsfA1a and A1b play
1145 important roles in the initial phase of heat-stress
1146 response, but HsfA2 functions under prolonged
1147 heat-stress conditions and during the recovery
1148 phase (Schramm et al. 2006; Nishizawa et al.
1149 2006). The heat-stress-induced expression of
1150 HsfA2 in *Arabidopsis* is not influenced by
1151 HsfA1a or HsfA1b (Busch et al. 2005). The
1152 *HsfA2* gene is also induced by high light intensity
1153 and H₂O₂ (Nishizawa et al. 2007). It is also closely
1154 related to the regulation of *ASCORBATE PEROX-*
1155 *IDASE 2 (APX2)* encoding a key enzyme in oxida-
1156 tive stress response, indicating that HsfA2 plays
1157 diverse roles under various environmental stresses.
1158 Conversely, upregulation of Hsps has been
1159 achieved in a large number of plant species. Trans-
1160 genic carrot cell lines and plants in which carrot
1161 *sHsp17.7* was overexpressed resulted in enhanced
1162 survival of transgenic tissues at high temperature
1163 (Malik et al. 1999). Transgenic tobacco plants
1164 overexpressing tobacco sHsps result in higher cot-
1165 yledon opening rate (Park and Hong 2002). Simi-
1166 larly, transgenic tomato plants overexpressing
1167 tomato *HsfA1* gene showed increased thermo-
1168 tolerance. Tomato mitochondrial *Hsp* gene
1169 overexpressed in tobacco showed that transgenics

were more thermotolerant at 48 °C than the 1170
transgenics produced with the antisense construct 1171
of the same gene (Sanmiya et al. 2004). Transgenic 1172
rice overexpressing *OsHsp17.7* gene showed 1173
increased thermotolerance and greater resistance 1174
to UV-B stress than untransformed control plants 1175
(Murakami et al. 2004). Constitutive expression of 1176
RcHsp17.8 in transgenic *Arabidopsis* conferred 1177
higher thermotolerance and resistance to salt, 1178
drought, and osmotic stresses (Jiang et al. 2009). 1179
Overexpression of *CaHsp26* in transgenic tobacco 1180
protected PSII and PSI during chilling stress under 1181
low irradiance (Guo et al. 2007). When transgenic 1182
A. thaliana plants were generated with overexp- 1183
ression of high-molecular-weight Hsps, trans- 1184
genics survived at temperatures as high as 45 °C 1185
(1 h) and they showed vigorous growth after 1186
relieving the plants from stress, while vector- 1187
transformed control plants could not regain growth 1188
during the post-stress recovery period (Queitsch 1189
et al. 2000). Similarly, transgenic rice lines 1190
overexpressing *AtHsp100* exhibited regrowth in 1191
the post-high-temperature-stress recovery phase, 1192
while the untransformed plants could not recover 1193
to the similar extents (Katiyar-Agarwal et al. 1194
2003). Recent study in maize demonstrated that 1195
small *Hsp* gene, *ZmsHsp*, might have a function in 1196
cytokinin response (Cao et al. 2010). Also, 1197
MsHsp23 gene in the tall fescue (*Festuca* 1198
arundinacea) transgenics protected the leaves 1199
from oxidative damage through chaperon and anti- 1200
oxidant activities. These results suggest that 1201
MsHsp23 confers abiotic stress tolerance in trans- 1202
genic tall fescue and may be useful in developing 1203
stress tolerance in other crops also (Lee et al. 1204
2012). Overexpression of *ZmHSP16.9* in trans- 1205
genic tobacco conferred tolerance to both heat 1206
and oxidative stresses and increased the seed ger- 1207
mination rate, root length, and antioxidant enzyme 1208
activities when compared with wild-type plants 1209
(Sun et al. 2012). Transgenic *Arabidopsis* plants 1210
overexpressed with *WsHsp26* were tolerant under 1211
continuous high temperature and produced bold 1212
seeds under high temperature, having higher ger- 1213
mination rate than wild type (Chauhan et al. 1214
2012). The list of transgenic plants raised for high- 1215
temperature tolerance using Hsps is shown in the 1216
Table 1. 1217

Table 1 Comprehensive details on plant transgenics raised by using Hsp genes for high-temperature tolerance

Gene	Protein	Source	Target plant	Function	Reference
<i>Hsf1</i>	Hsf	<i>A. thaliana</i>	<i>A. thaliana</i>	Thermotolerance and also constitutive expression of the Hsp genes	Lee et al. (1995)
<i>Hsf3</i>	Hsf	<i>A. thaliana</i>	<i>A. thaliana</i>	Increase in basal thermotolerance and thermoprotective processes	Prandl et al. (1998)
<i>HsfA1</i>	Hsf	<i>S. lycopersicon</i>	<i>S. lycopersicon</i>	Advantage for growth and fruit ripening processes under high temperature	Mishra et al. (2002)
<i>Hsf3</i>	Hsf	<i>A. thaliana</i>	<i>A. thaliana</i>	Lower threshold temperature	Panchuk et al. (2002)
<i>HsfA2</i>	Hsf	<i>A. thaliana</i>	<i>A. thaliana</i>	Mutants displayed reduced basal and acquired thermotolerance, while the overexpression lines displayed increased tolerance	Li et al. (2005)
<i>HsfA2e</i>	Hsf	<i>O. sativa</i>	<i>A. thaliana</i>	Enhanced thermotolerance	Yokotani et al. (2005)
<i>HsfA2</i>	Hsf	<i>A. thaliana</i>	<i>A. thaliana</i>	Increased thermotolerance but also salt/osmotic stress tolerance and enhanced callus growth	Ogawa et al. (2007)
<i>HsfA2e</i>	Hsf	<i>O. sativa</i>	<i>A. thaliana</i>	Enhances tolerance to environmental stresses	Yokotani et al. (2008)
<i>Hsf7</i>	Hsf	<i>O. sativa</i>	<i>A. thaliana</i>	Response to high temperature	Liu et al. (2009)
<i>HsfC1b</i>	Hsf	<i>O. sativa</i>	<i>O. Sativa</i>	Osmotic stress and is required for plant growth under non-stress conditions	Schmidt et al. (2012)
<i>DnaK</i>	Hsp70	<i>Aphanothece halophytica</i>	<i>O. sativa</i> and <i>N. tabacum</i>	Increased seed yield and total plant biomass in high temperature and salt stress	Uchida et al. (2008)
<i>Hsp70</i>	Hsp70	<i>Trichoderma harzianum</i>	<i>A. thaliana</i>	Enhanced tolerance to heat stress	Montero-Barrientos et al. (2010)
<i>mtHsp70</i>	Hsp70	<i>O. sativa</i>	<i>O. Sativa</i>	Suppresses programmed cell death	Qi et al. (2011)
<i>Hsc70-1</i>	Hsp70	<i>A. thaliana</i>	<i>A. thaliana</i>	More tolerant to heat shock	Sung and Guy (2003)
<i>Hsp101</i>	HSP100	<i>A. thaliana</i>	<i>A. thaliana</i>	Sudden shifts to extreme temperature better than the controls	Quietsch et al. (2000)
<i>Hsp101</i>	Hsp100	<i>A. thaliana</i>	<i>O. sativa</i>	Enhanced tolerance to high temperature	Katiyar-Agarwal et al. (2003)
<i>Hsp17.7</i>	Hsp17.7	<i>D. carota</i>	<i>D. carota</i>	Increased thermotolerance	Malik et al. (1999)
<i>mtsHsp</i>	sHsp	<i>S. lycopersicon</i>	<i>N. tabacum</i>	Thermotolerance	Sanmiya et al. (2004)
<i>Hsp21</i>	sHsp	<i>S. lycopersicon</i>	<i>S. lycopersicon</i>	Temperature-dependent oxidative stress	Neta-Sharir et al. (2005)
		<i>sHsp17.7</i>	sHsp	<i>O. sativa</i>	<i>O. Sativa</i>
Drought		tolerance in transgenic rice seedlings	Sato and Yokoya (2008)		
<i>Hsp16.9</i>	sHsp	<i>Zea mays L.</i>	<i>N. tabacum</i>	Enhanced tolerance to heat and oxidative stress	Sun et al. (2012)
<i>Hsp17.5</i>	sHsp	<i>Nelumbo nucifera</i>	<i>A. thaliana</i>	Improved basal thermotolerance	Zhou et al. (2012)
<i>Hsp26</i>	sHsp	<i>Capsicum annuum</i>	<i>N. tabacum</i>	Protection of PSII and PSI during chilling stress under low irradiance	Guo et al. 2007

(continued)

t.26 **Table 1** (continued)

t.27	Gene	Protein	Source	Target plant	Function	Reference
t.28	<i>Hsp17.8</i>	sHsp	<i>Rosa chinensis</i>	<i>A. thaliana</i>	Increased tolerance to heat, salt, osmotic, and drought stresses	Jiang et al. (2009)
t.29			<i>sHsp17.7</i>	sHsp	<i>O. sativa</i>	<i>O. sativa</i>
			Increased	thermotolerance	Murakami et al. (2004)	
	<i>sHsp26</i>	sHsp	<i>Triticum</i>	<i>A. thaliana</i>	Seed maturation and germination and imparts tolerance to heat stress	Chauhan et al. (2012)
	<i>sHsp18</i>	sHsp	<i>Opuntia streptacantha</i>	<i>A. thaliana</i>	Increased the seed germination rate under salt, osmotic, and ABA treatments	Salas-Muñoz et al. (2012)

1218 **6 Conclusions**

1219 It appears that a wide range of “omics” studies are
 1220 currently in progress using numerous methodo-
 1221 logies, plant species, and stress conditions. As
 1222 more results are published, it is becoming increas-
 1223 ingly clear that high-temperature stress causes dis-
 1224 tinct molecular responses in plant tissues. As more
 1225 data are generated in such studies, it provides
 1226 suitable candidates for selective breeding prog-
 1227 rams aimed at enhancing stress tolerance in
 1228 ecologically and economically important plant
 1229 species. Plant cells are fundamentally different to
 1230 those of mammalian species, and these biological
 1231 differences cause inherent difficulties in plant
 1232 functional genomic studies. Advances in techni-
 1233 ques and approaches will change the way plant
 1234 heat-stress omics studies are conducted in future.
 1235 Genomics, transcriptomics, proteomics, and
 1236 metabolomics investigate different facets of a
 1237 given scientific issue, such as heat-stress tolerance,
 1238 but complement each other. Integration of pheno-
 1239 typic, genetic, transcriptomic, proteomic, and
 1240 metabolomic data will enable accurate and
 1241 detailed gene network reconstruction. This will
 1242 ultimately result in the elucidation of the molecu-
 1243 lar pathways involved in complex phenotypic
 1244 traits. A better understanding of genetic and cellu-
 1245 lar mechanisms behind heat-stress tolerance would
 1246 facilitate generation of transgenic plants with
 1247 desired traits with little or no undesired/unforeseen
 1248 effects. Bioinformatics tools are also helping us to
 1249 obtain genome-wide data on the number of Hsps
 1250 and Hsfs and their regulations. Taken together, the
 1251 omics data and the information generated using

the tools of bioinformatics would help us to
 understand better about heat-stress tolerance in
 crop plants. Future knowledge of tolerance compo-
 nents and the identification of QTLs and cloning
 of responsible genes may allow transformation of
 plants with multiple genes and production of highly
 stress-tolerant transgenic crop plants.

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