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Epigenetics in Plants of Agronomic Importance: Fundamentals and Applications

Transcriptional Regulation and Chromatin Remodelling in Plants

Second Edition

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Preface

The first Agricultural Revolution, that is, the initial transition from hunting and gathering to settled agriculture, is considered by many to have begun around 12,000 years ago. Since then, humans have domesticated hundreds of plant species and it is considered that the evolution of crop plants took place as human behavioral ecology changed from food gathering to farming. Domestication of wild species of plants comprises a variety of evolutionary changes (phenotypic and genetic divergence among domesticated populations) that may diminish the fitness of a plant in the wild but increase it under human exploitation. Thereafter, the selection of populations with desirable alleles, the meticulous breeding of high yielding genotypes, ease of farming and quality, and numerous technological advances have allowed crop production to increase and, in this way, supply the nutritional requirements of an ever-increasing human population.

During the last decades, and in particular as a part of the Green Revolution, modern breeding methods, novel research, development, and technology transfer initiatives have increased dramatically agriculture production worldwide. Many beneficial traits in crop species include, for example, increased yield, enhanced abiotic/biotic stress tolerance, improved nutritional quality, delayed ripening, increased post-harvest quality, and delayed senescence. However, it is still patent that if agriculture is to support human population for years to come, additional sustainable strategies for crop production must be developed (e.g., exploiting the positive associations with soil organisms while avoiding the negative ones), in concert with a profound understanding of the relationship between crop genotype and environment. Thus, it is appropriate to evaluate the mechanisms that plants may have evolved to adapt to sudden changes in the environment. Furthermore, we need to comprehend the mechanisms by which epigenetic variation may modify plant gene regulation and phenotype, and we should concentrate on how the epigenome acts as a potent new source of diversity for agronomically important traits and its potential for exploitation in crop improvement programs.

The word "epigenetics" was originally formulated by Conrad Waddington to incorporate "epi" ("above" or "on top") with the word "genetics." He took the Greek word "epigenesis," a theory of development, and changed it to epigenetics. However,

Waddington did not use a precise definition for epigenetics. It was not until 1994 that Robin Holliday broadly re-defined epigenetics as "the study of the changes in gene expression which occur in organisms with differentiated cells, and the mitotic inheritance of given patterns of gene expression." Nonetheless, the most familiar definition of epigenetics refers to changes in gene expression that do not involve changes in the DNA sequence, but that are inherited after cell divisions, even in the absence of the signal or event that initiated the change.

Nowadays, it is widely accepted that epigenetic phenomena influence gene expression at the chromatin structure and organization level, thereby modulating the access of regulatory complexes to the genome. Current research on epigenetic mechanisms suggests they are involved in almost every aspect of plant life including agronomically important traits such as flowering time, fruit development, responses to environmental factors, and plant immunity. Hence, epigenetics is a very important field in plant genetic improvement. Although fundamental epigenetic mechanisms in crops are beginning to be elucidated, we anticipate they will be extensively employed in the future for crop improvement.

The idea of publishing this new edition has arisen from the fact that epigenetics is an important player in the study of gene regulation not only in animals but also in fungi, protists, prokaryotic organisms, and plants. The inception of research in epigenetics came from the desire to understand how it affects plant development and behavior.

This book gives us comprehensive knowledge about the fundaments and applications of epigenetics in plants of agronomic importance. A total of 15 chapters (12 new and updated chapters) describe the importance of epigenetics in agriculture and highlight the applications of this field in crop plants. Topics cover from general mechanisms of epigenetic regulation, such as DNA methylation and posttranslational modifications of histones, to the smallest player with the biggest role in gene regulation, small RNAs.

We believe the information contained in this book will enhance the knowledge to develop novel approaches to manipulate and selectively activate and/or inhibit proteins and metabolic pathways to counter plant pathogens, to better cope with environmental stresses, and to increase crop productivity. In the foreseeable future there would be a strong presence of epigenetics in food production, plant fitness, and crop improvement. We hope readers of this book will find a first glance of the many contributions the field of epigenetics may bring to the table in order to help cover the food demand in the world. Finally, we would like to thank all colleagues who agreed to provide outstanding chapter contributions.

This second edition was built over the contents of the first one and has been expanded to include novel research fields on plant epigenetics. New chapters on the epigenetic regulation of biotic and abiotic stresses in plants, epigenetics of light signaling, RNA epigenetics, epigenetic reprogramming of the germline, and on the function of small RNAs in establishing cell dedifferentiation and further plant regeneration in crops have been included. Novel findings on germinally inherited

epialleles and epigenetics in forest trees have been updated. The expanded content and updated chapters reflect the rapid pace at which new discoveries in plant epigenetics are being made not only in model plants but also in agronomically important plants.

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Chapter 1
Epigenetic Mechanisms of Abiotic Stress Response and Memory in Plants

Check for
updates

Iva Mozgova, Pawel Mikulski, Ales Pecinka, and Sara Farrona

Abstract Being sessile organisms, plants are exposed to multiple stimuli without possibility for escape. Therefore, plants have evolved to be able to adapt their developmental and physiological responses to the surrounding environment. Some environmental stresses will rarely occur during the life of the plant, but others, such as seasonal drought or heat, can be recurrent. Therefore, plant responses to these stresses can be transient to provide plants with the required tools to acclimate and survive, whereas others may promote a state that we will refer to as "memory" throughout the chapter, which predisposes the plant for a more efficient stress response upon next encounter of stress. The possibility of transferring this memory to the next generation has been also proposed, which implies a lack of resetting of the priming memory during sexual reproduction. Different epigenetic and chromatin-related modifications such as DNA methylation, histone modifications, and chromatin remodeling have been associated with the memory to both biotic and abiotic stresses. This chapter reviews how and which epigenetic processes are involved in

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remembering a past abiotic stress event and also forgetting it. Contradictory arguments concerning transgenerational memory and its implications in phenotypic variation are critically discussed. In addition, the stability of epigenetic modifications during asexual propagation and its impact on clonally propagated plants is addressed. Finally, we mention possible agricultural implications of the epigenetic mechanisms involved in plant memory and propose future applications for breeding of epigenetically modified crops considering new challenges arising from climate change.

1.1   Introduction

Crop production is deeply affected by the environmental conditions and current models for climate change indicate that future conditions will become even more challenging. Climate trends show that the Earth tends to be less cold with an increase in temperatures in every season, especially for minimal temperatures, in most of the crop producing regions, which is coupled to a major increase in the frequency of temperature extremes (Alexander et al. 2006; Lobell et al. 2011; Lobell and Gourdji 2012). Although more difficult to predict, the numbers of drought periods have shown a tendency to increase over the last 50 years in some parts of the world (i.e., Africa, southern Europe, east and south Asia, and eastern Australia) and will become much more frequent by the end of the twenty-first century, while the wet regions will become even wetter (Skliris et al. 2016). There is, therefore, a complex interconnection between climate change and food security, which is at a risk due to the effects of increasing temperatures, water-cycle changes, and higher CO_2 levels on plant yields. Indeed, a decline in the production and a subsequent price increase of important crops (i.e., wheat—*Triticum aestivum*, maize—*Zea mays*, and barley—*Hordeum vulgare*) has already been linked to global warming (Lobell et al. 2011; Lobell and Gourdji 2012; Moore and Lobell 2015). Thus, understanding the phenotypic variation of plants and how food and feed production can be secured has taken a central position in crop science.

Plants can efficiently respond to abiotic or biotic environmental conditions and modify their development and physiology accordingly. In this review, we focus on the response and memory of abiotic stresses such as extreme temperatures, drought, and salinity. Stress can be considered as any situation that can alter plant fitness and cause a substantial loss in yield. Abiotic stresses are major cause of food scarcity being responsible for estimated 50% loss in staple crops (reviewed in Boyer 1982; Bray et al. 2000). One of the main abiotic stresses that plants face are extreme temperatures, both high and low. Heat will most probably increase in the future affecting many countries, including developing countries where hunger is already an issue (reviewed in Lobell and Gourdji 2012). Increase in temperature is particularly dramatic during plant reproduction and seed filling, having a significant impact on yield (reviewed in Kosina et al. 2007). As part of global warming, heat stress usually comes in combination with water scarcity, which according to predictions will become more acute, and with higher CO_2 and UV radiation (reviewed in Williamson

et al. 2014). On the other hand, floods, which will be more recurrent in other regions of the globe, present also major agronomic constraints especially affecting yield and grazing land and, in more extreme situation, causing plant death due to hypoxia (reviewed in Jackson and Colmer 2005). Soil water content is directly linked to other main stresses including salinity and nutrient availability. Soil salinization has a strong impact on plant growth affecting the photosynthetic rate, absorbance of nutrients, and increasing senescence (reviewed in Hanin et al. 2016). Chilling temperatures also impair plant metabolism, germination, and reproduction, whereas freezing temperatures additionally cause tissue and membranes damage and cell dehydration (reviewed in Xin and Browse 2000).

An intricate network of processes involved in sensing and responding to the environment, which implies massive changes in gene expression and nuclear organization, aids the plant to cope with the stress (reviewed in Probst and Mittelsten Scheid 2015; Asensi-Fabado et al. 2017). However, plants will seldom be affected by individual conditions and, hence, they usually respond to multiple stresses at the same time. However, the challenge of simultaneously applying different stresses and analyzing their overlapping action still limits our understanding of the complexity of plant responses to abiotic stresses. Therefore, for the breeding of new crop varieties better adapted to future more severe climate conditions, multidimensional experimental approaches more closely mimicking on-field conditions will be required (reviewed in Mittler 2006; Ahuja et al. 2010; Qin et al. 2011).

Whereas some stresses occur occasionally, generating a temporal stress response in the plant, many of the abiotic changes occur as daily (e.g., day and night changes) or seasonal fluctuations (e.g., summer and winter seasons in temperate climates or dry and humid seasons in tropical areas). Recurrent stresses can therefore induce a cellular memory that poses or primes the plant for a faster and stronger response upon repeated stress exposure. This stress memory is also known as priming or, in the case of abiotic stress, as acclimation or hardening (reviewed in Bruce et al. 2007). Therefore, the priming of plants implies: (1) the action of a first stress condition that, in addition to inducing a stress response in the plant, may trigger the formation of a molecular memory, (2) the end of this first stress condition, (3) a lapse of time during which the memory can perdure in the absence of the stress that generated it, and (4) the occurrence of a second stress that will activate the recovery of the stress memory to induce a new enhanced plant response. Furthermore, an additional (5) step entails resetting the memory or maintaining it for transfer to the next generation(s) through a process usually known as inter-/transgenerational memory (Fig. 1.1 and reviewed in Bruce et al. 2007; Pecinka and Mittelsten Scheid 2012; Chen and Arora 2013; Kinoshita and Seki 2014; Avramova 2015; Crisp et al. 2016; Hilker et al. 2016; Bäurle 2017; He and Li 2018). The second stress that retrieves the memory can be of the same nature as the first one, but it seems that a different abiotic stress, or even a biotic one, can activate the priming memory, indicating a complex crosstalk between different types of stresses (reviewed in Hilker et al. 2016; Asensi-Fabado et al. 2017; Lämke and Bäurle 2017; Friedrich et al. 2018). Eventually, primed plants will be readier to respond to a second stress showing an
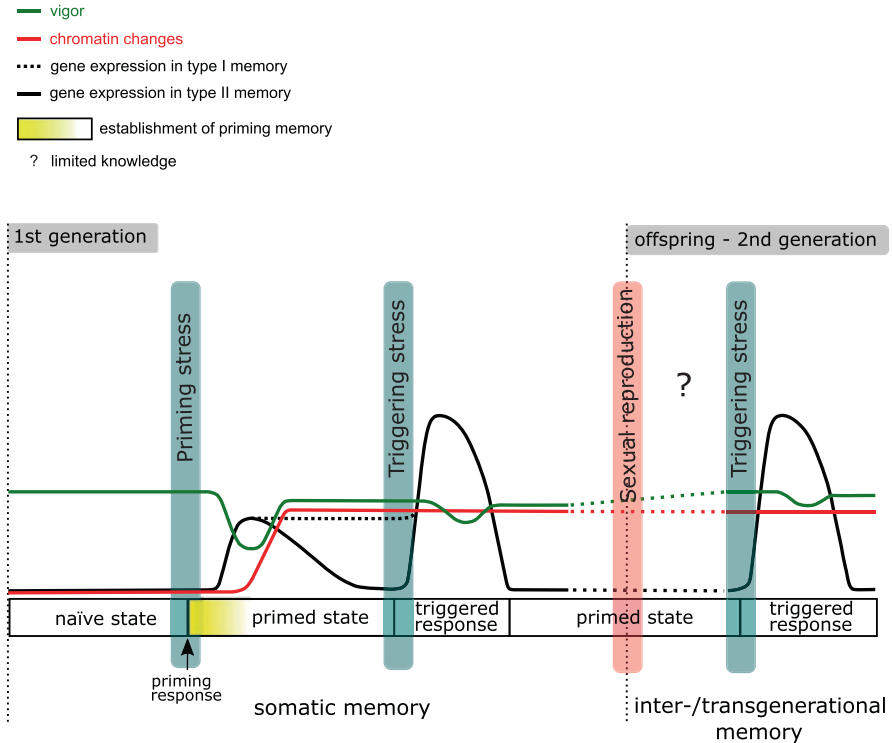
Fig. 1.1 Somatic and transgenerational memory induced by environmental stresses. Plants growing under naïve conditions can experience a first environmental stress that will promote transcriptional changes correlated with chromatin changes (i.e., DNA methylation, histone PTMs, DNA-dependent chromatin remodeling, deposition of new histone variants) of stress-responsive genes. This can result in sustained (type I) or temporal (type II) activation and/or repression of genes (Bäurle 2017) and addition and/or removal of specific chromatin modifications. However, for simplification, the figure focuses on transcriptional activation and addition of new chromatin modifications. Encountering the stress may also impair plant vigor. After the stress, the plant enters in a primed state in which transcription of stress-responsive genes may recover to original expression levels. Amplitude of the recovering phase varies depending on the environmental cue and on memory genes. Plant vigor also recovers, although a phenotypic cost may be applied. However, the new chromatin state of memory genes will be stably maintained. When the plant perceives a second stress, this triggers the response of memory genes. The triggered response can be faster, stronger, more sensitive, and/or different to the first one (Lämke and Bäurle 2017). Intensity and amplitude of the response also differs depending on experimental conditions. Although most of our current knowledge indicates that the primed state perdures for a finite period within the same generation (somatic memory) and resetting of the primed state occurs during sexual reproduction, in some cases the chromatin state linked to the stress memory may be inherited by the offspring (inter-/transgenerational memory). Although much less is known of this possibility (?), inheritance of the memory could provide the new plant generation with molecular tools to better cope with recurrent stresses

improved phenotypic adaptation with minor fitness cost and, hence, survival and yield. On the other hand, the priming stage increases plant sensitivity, affects development and growth, and can be more cost-effective to reset than to maintain; therefore, plants may employ mechanisms to elucidate whether to memorize or to forget (reviewed in Avramova 2015; Crisp et al. 2016; Bäurle 2017).

Transcriptional reprogramming is a common feature of the primed state. Genes that show a memory will modify their expression in response to both the first and the second stress, but expression levels will be significantly different in the second response. Considering that the primed state between the two stresses can last from days to months (as in the case of somatic memory—see Sect. 1.2), or stress can even recur in the subsequent generation(s) (as in intergenerational or transgenerational memory—see Sect. 1.2, Fig. 1.1), the transcriptional memory and molecular mechanisms that underlie it need to have the potential to be maintained and transmitted through cell division and even sexual reproduction. These criteria are met by genetic and epigenetic mechanisms. In fact, different epigenetic processes and chromatin-related mechanisms have been involved in setting memory of passed environmental events (Fig. 1.1 and reviewed in Bruce et al. 2007; Chen and Arora 2013; Kinoshita and Seki 2014; Avramova 2015; Crisp et al. 2016; Hilker et al. 2016; Bäurle 2017; He and Li 2018). Other processes, such as stability and modification of proteins, have also been involved in the priming memory (reviewed in Pastor et al. 2013).

Chromatin, the molecular complex containing DNA and nuclear proteins, mainly histones, plays an essential role in transcriptional regulation. DNA and histones can be modified by the addition of chemical groups, methyl group being by far the most common in the case of DNA and variable chemical post-translational modifications (PTMs) in case of histones (e.g., methyl, acetyl, phosphate, and ubiquitin groups being most common). The presence of these chromatin marks or their combinations acts to regulate gene expression by modifying the accessibility of DNA or the recruitment of specific proteins to chromatin. Furthermore, chromatin marks present on a gene may be stably transmitted through cell division contributing to the maintenance of its transcriptional status. In addition to primary DNA sequence, this adds a new layer of information that can be mitotically and/or meiotically transmitted and underlies epigenetic inheritance (reviewed in Zentner and Henikoff 2013; Du et al. 2015). Different pieces of evidence demonstrate that in the presence of a stress that triggers transcriptional changes, epigenetic modifications will be added/removed to/from specific key stress-response genes and create a stable chromatin environment that will perdure even once the stress that induced it has passed. This environment-triggered epigenetic memory will contribute to the phenotypic plasticity of the plant in the event of a new stress. The implication of this long-lasting chromatin-related memory has been subject of lively discussion due to the obvious potential for improving crop adaptation and its relationship to Lamarck's vision of genetic inheritance (Pecinka and Mittelsten Scheid 2012).

1.2   Somatic, Inter- and Transgenerational Memory

Memory of stress experienced by plants can be somatic (or intra-generational), lasting for a varied period of time within the exposed plant generation after the immediate stress response. Intergenerational memory persists into the next generation of progeny of the exposed plants and transgenerational memory is transmitted into further generation(s) in the absence of stress (Fig. 1.1; reviewed in Heard and Martienssen 2014; Lämke and Bäurle 2017). We will focus on the molecular mechanisms underlying stress memory and in particular on mechanisms connected to modification of chromatin structure (chromatin-based memory) in model and crop plants. At present, strong experimental support exists for somatic memory that persists in the range of days to weeks following the initial stress treatment, while less and often contradictory examples of intergenerational or transgenerational memory are available.

1.2.1   Somatic Memory

Several molecular mechanisms that contribute to somatic memory of abiotic stress have been identified (reviewed in Conrath et al. 2015; Avramova 2015; Crisp et al. 2016; Bäurle 2017; Lämke and Bäurle 2017). Somatic memory has been connected to the persistence of stress-induced metabolites (Pastor et al. 2014; Balmer et al. 2015; Hu et al. 2016), to sustained expression of genes after the stress response ends (Charng et al. 2006b; Stief et al. 2014), to stalling of RNA polymerase II that potentiates transcription (Ding et al. 2012), to the accumulation of proteins (e.g., mitogen-activated protein kinases—MPKs, Beckers et al. 2009), or to mitotic stability of stress-induced chromatin changes (Ding et al. 2012; Sani et al. 2013; Singh et al. 2014; Weng et al. 2014; Lämke et al. 2016; Brzezinka et al. 2016, 2018; Feng et al. 2016; Liu et al. 2018b). Based on the transcription level of the stress-response genes, chromatin-based transcriptional memory can be separated into type I, during which transcriptional activity of stress-responsive genes persists, and type II, during which the initial stress-induced transcription ceases but a second exposure to stress can induce a modified response in comparison with the response of naïve plants (reviewed in Bäurle 2017) (Fig. 1.1). Somatic memory of abiotic stresses seems limited to several days or weeks (Bäurle 2017; Lämke and Bäurle 2017). Several chromatin-based mechanisms have been shown to contribute to somatic memory. These include nucleosome occupancy and remodeling, relative abundance of histone PTMs, cytosine (DNA) methylation, and RNA interference, and we discuss examples of the particular mechanisms in the respective sections. Although molecular aspects of somatic memory are best well studied in the short-lived annual *Arabidopsis* (*Arabidopsis thaliana*), it may be of particular importance in long-lived perennial species (Lafon-Placette et al. 2018; Le Gac et al. 2018). Its existence is suggested by maintained changes of DNA methylation in the shoot apical meristem

(SAM) of poplar (*Populus* spp.) trees that have grown under different water availability (Lafon-Placette et al. 2018). In addition, winter-dormant SAMs of trees grown at different environmental conditions retain differentially methylated regions at genes involved in abiotic stress response, SAM organization, and phytohormone metabolism and signaling (Le Gac et al. 2018) suggesting that growth conditions during vegetative phase can be reflected in cells that will produce organs in the next vegetative season and may potentially influence performance and growth. It is of note, however, that global DNA methylation level changes occur during bud dormancy and break that are mediated by DNA demethylases (Conde et al. 2017), suggesting that active reprogramming occurs. Whether environmentally induced epialleles can escape the global DNA methylation reprogramming remains to be addressed.

1.2.2 Inter- and Transgenerational Memory

Transgenerational stress memory can be in principle mediated by transmission of structural variation in the genome, inheritance of chromatin states (or epialleles), and/or seed provisioning (or maternal effect) whereby different level of resources such as mRNA, hormones, proteins, starch, lipids, or other reserve molecules are stored in the seed based on the environmental conditions during growth of the maternal plant (reviewed in Herman and Sultan 2011; Pecinka and Mittelsten Scheid 2012; Pecinka et al. 2013; Heard and Martienssen 2014). Due to the difficulty in separating maternal effects from heritability of epialleles, transgenerational inheritance of acquired epialleles as means of environmental memory and its adaptive value has been debated (Boyko and Kovalchuk 2011; Mirouze and Paszkowski 2011; Paszkowski and Grossniklaus 2011; Pecinka and Mittelsten Scheid 2012; Ganguly et al. 2017). Taking into consideration also maternal effects or possible induced structural variation, intergenerational memory mechanisms can nevertheless contribute to adaptive transgenerational plasticity (Herman and Sultan 2011) and to rapid environmental adaptation in plants (Franks and Hoffmann 2012).

Transmission of acquired epialleles between generations is prevented by active resetting of chromatin states during sexual reproduction (reviewed in Paszkowski and Grossniklaus 2011; Heard and Martienssen 2014; Kawashima and Berger 2014; Iwasaki 2015). In mammals, extensive epigenetic reprogramming occurs during germline formation and early embryogenesis during which DNA methylation and histone PTMs are erased and thus examples of transgenerational inheritance of epialleles are rare (reviewed in Heard and Martienssen 2014). On the contrary, several features of plant development make plants more prone to transgenerational inheritance of acquired epialleles. First is the late developmental origin of the germline that forms from stem cells within the SAM, in which exposure of the somatic tissue to environmental conditions can be reflected. Nevertheless, it needs to be considered that mechanisms which restrict responses affecting genome and epigenome stability may operate with higher stringency in stem cells that give rise to the

germline than in vegetative tissue (Yadav 2009; Baubec et al. 2014). Second, stress-induced epigenetic changes have a chance to be copied and maintained during plant sexual reproduction. In plants, reprogramming (reduction) of DNA methylation mainly occurs in the companion cells, the vegetative cell nucleus in pollen and the central cell nucleus in the ovule, rather than in the nuclei (sperm cell and egg cell) that will fuse to form the zygote during fertilization (reviewed in Kawashima and Berger 2014). Still, considerable global epigenetic reprogramming does take place during gametogenesis, connected to histone replacement (Ingouff et al. 2007; Schoft et al. 2009; She et al. 2013; She and Baroux 2015) and DNA demethylation (Calarco et al. 2012). Despite the constraint imposed by epigenetic reprogramming during sexual reproduction for the transmission of acquired epialleles, examples of sexual transmission of epialleles are more abundant in plants than in mammals suggesting a higher potential for transgenerational epiallele inheritance (reviewed in Heard and Martienssen 2014). Finally, it is important to note that plants possess an immense capability of vegetative reproduction, which may increase the probability of epiallele retention and its later outgrowth into a sexually propagating individual.

1.2.2.1   Memory During Sexual Reproduction

Despite sexual reprogramming and other mechanisms that actively limit transgenerational inheritance of epialleles (Iwasaki 2015), natural epialleles that can be stable over sexual plant generations exist in plants (Cubas et al. 1999; Manning et al. 2006; Martin et al. 2009; Stam 2009). Much information on the inheritance of acquired and existing epialleles has been provided by genome-wide studies employing DNA methylation variation in natural accessions (ecotypes) (Dubin et al. 2015; Kawakatsu et al. 2016), in mutation accumulation lines (Becker et al. 2011; Schmitz et al. 2011), recombinant inbred lines (RILs) (Eichten et al. 2013; Schmitz et al. 2013), or the epigenetic RILs (epi-RILs) (Reinders et al. 2009; Teixeira et al. 2009; Johannes et al. 2009). These studies demonstrated that natural as well as some newly acquired DNA methylation epialleles can be inherited over several sexual generations and that DNA methylation at some loci can be re-established in the epiRILs to resemble the ancestral epiallelic states (Reinders et al. 2009; Teixeira et al. 2009). Hence, DNA methylation-based epialleles can be stably inherited mitotically and meiotically but are often reversible, especially if located close to TEs and small RNA-producing loci (Becker et al. 2011).

Alternative epialleles could serve as a source of variation for breeding purposes (Hofmeister et al. 2017). Indeed, epialleles can confer alternative transcription of their respective gene loci (Becker et al. 2011; Schmitz et al. 2011) and alter phenotypic traits of plants (Roux et al. 2011; Zhang et al. 2013b; Cortijo et al. 2014). Phenotypes associated with changes in chromatin states also affect traits that are of potential agronomic importance, including stress tolerance (Kooke et al. 2015; Verkest et al. 2015), disease resistance (Akimoto et al. 2007; Reinders et al. 2009), plant stature (Miura et al. 2009; Reinders et al. 2009; Johannes et al. 2009), root length (Soppe et al. 2000; Reinders et al. 2009; Johannes et al. 2009; Cortijo et al.

2014), transition to flowering (Soppe et al. 2000; Reinders et al. 2009; Johannes et al. 2009; Cortijo et al. 2014), senescence (He et al. 2018), flower sex determination (Martin et al. 2009), genetic incompatibility (Durand et al. 2012), fruit ripening (Manning et al. 2006), or yield (Hauben et al. 2009; Ong-Abdullah et al. 2015). However, the extent of purely epigenetic contribution to the observed phenotypes must be interpreted with care as the studied plant lines are not completely isogenic and genetic changes may accompany chromatin states connected to a particular epiallele (Pecinka et al. 2013). In some cases, structural changes to the genome can be induced by strong selective pressure imposed by stress (e.g., by chemical treatment, as is frequent during evolution of herbicide resistance—reviewed in Markus et al. 2018) or by activation of transposable elements (TEs) (discussed in Sect. 1.4.2). Even though combined effect of genetic and epigenetic change contributing to the desired phenotypic traits is not necessarily an obstacle and may be exploited for agricultural purposes (Yasuda et al. 2013), the nature of stress-induced epigenetic changes may be stochastic (Eichten and Springer 2015) and present an impediment to targeted crop improvement.

Transgenerational memory of abiotic stress observed in subsequent sexual generations of stress-exposed plants seems limited to one to two generations of unstressed sexual progeny of stressed plants. Activation of TEs induced by heat stress was only retained for maximum of several weeks in the treated plants but was not observed in the progeny (Pecinka et al. 2010). In a more extensive study the effect of several abiotic stress treatments was seen in the first or second generation after the treatment, but the appearance was stochastic and could represent experimental variation (Pecinka et al. 2009). Similarly, the resistance to several stresses (including heat, cold, flood, and UV-C) was elevated in the progeny of plants when both generations were subjected to stress but the effect was diminished in unstressed progeny (Boyko et al. 2010). Recently, Wibowo et al. (2016) observed enhanced resistance to hyperosmotic stress in the progeny of plants exposed to the stress for at least two consecutive generations. In the absence of the stress, however, the enhanced resistance was lost within two sexual generations (Wibowo et al. 2016), demonstrating transient retention of stress memory. Interestingly, repetitive stress over several generations does not always seem to correlate with improved phenotypic performance under stress. *Arabidopsis* plants subjected to drought conditions during five generations did not show any growth advantage to control plants (Ganguly et al. 2017). The only trait that showed significant memory through generations and perdured one generation after the stress was seed dormancy that was increased by drought (Ganguly et al. 2017).

1.2.2.2 Memory During Vegetative Reproduction

Epialleles can also be transmitted during vegetative propagation in vitro. Multiple economically important species are propagated vegetatively, producing large numbers of clonal progeny. Despite clonal origin, phenotypic variability occurs among individuals of the progeny, a phenomenon called somaclonal variation. Even though

somaclonal variation can in principle contribute to the emergence of advantageous traits and progeny improvement, it often leads to reduced plant vigor, and substantial quality and yield losses (reviewed in Miguel and Marum 2011). Somaclonal variation can be caused by different chromatin states, often associated with differences in DNA methylation (reviewed in Miguel and Marum 2011). Somaclonal variation may also be connected to genome structural rearrangements, as tissue culture in several crop species including rice (*Oryza sativa*) or maize may promote mobilization of TEs (reviewed in Negi et al. 2016), and other types of structural changes including polyploidization, aneuploidy, chromosomal mutations or DNA mutations (reviewed in Neelakandan and Wang 2012).

Three recent studies show that DNA methylation patterns can be maintained in plants regenerated from tissue culture in *Arabidopsis* (Wibowo et al. 2018), rice (Stroud et al. 2013), or maize (Stelpflug et al. 2014; Han et al. 2018). Importantly, the altered epiallelic states were retained in sexual progeny of plants obtained from these tissue cultures and DNA methylation changes were reflected in gene expression changes (Stroud et al. 2013; Han et al. 2018; Wibowo et al. 2018). In *Arabidopsis*, plants were regenerated from somatic embryos induced from either root or leaf and the original tissue-specific DNA methylation patterns persisted for two generations of sexual progeny of the regenerated plants. Especially the leaf of root-derived plants retained DNA methylation pattern of the original root tissue (Wibowo et al. 2018). These results suggest that DNA methylation epialleles established during tissue culture can be retained during regeneration and sexual propagation and that tissue of origin can be reflected in the regenerated plants and their sexual progeny. Although it remains unclear to what extent the changes in DNA methylation may be associated with genomic structural changes, these findings raise important considerations for massive clonal propagation of plants.

Information regarding inheritance of other than DNA-methylation dependent epialleles during vegetative propagation is scarce. Nevertheless, environmentally induced epialleles that are known to be stable somatically, such as the repressed form of the *FLOWERING LOCUS C* (*FLC*) (which will be discussed later in the chapter), can be maintained during vegetative propagation in vitro, changing the phenotypic traits of the regenerated plants by promoting early flowering (Nakamura and Hennig 2017). It is therefore possible that asexual propagation in tissue culture may allow for retention of histone PTMs but much more work is required in the future to gain more global insights.

In summary, epialleles (especially connected to alternative DNA methylation states) can be transmitted over generations both during sexual and vegetative plant propagation and can have an impact on plant phenotypes. The adaptive value of purely epigenetic, but not structural, variation and its contribution to evolution of populations under changing environmental conditions however remains to be determined (De Waele 2005; Franks and Hoffmann 2012).

1.3 Abiotic Stresses: Physiological Perspective

Although environmental stresses are usually combined in nature, most research so far has focused on application of a particular stress type. A compilation of major abiotic stresses and plant responses in relation to plant memory is summarized in the following section.

1.3.1 Drought and Desiccation

Drought is one of the factors limiting agricultural output that will be increasingly important due to the predicted climate change in next decades (reviewed in IPCC 2013). Therefore, drought-induced responses and stress memory in crops attract considerable attention in tackling negative effects of global warming.

In *Arabidopsis*, drought memory was studied by single or multiple desiccation stress treatments, followed by recovery (re-watering) periods of varying duration. In the seminal works from Avramova group (Ding et al. 2012, 2013; Liu et al. 2014a), *Arabidopsis* seedlings were treated with air-dry desiccation/rehydration cycles repeated up to four times. The samples were collected at pre-stress, stress, and recovery phases and subjected to gene expression and chromatin analyses. As a result, the group identified desiccation-responsive genes whose transcriptional and chromatin status is changed by the stress. Importantly, a subset of drought-responsive targets exhibited stress memory pattern, where response to subsequent stresses was altered in relation to the priming stress (Ding et al. 2012). Interestingly, categorized by the function, the biggest fraction of drought-memory genes is implicated also in response to salt, cold/heat, light, and abscisic acid (ABA) (Ding et al. 2013), highlighting a crosstalk between different stress signaling pathways. Another example of desiccation memory in *Arabidopsis* concerns drought tolerance induced at the seed stage. Imbibed seeds were treated with polyethylene glycol (PEG) at different developmental stages, followed by rehydration and growth/survival assessment during post-germination development. Strikingly, improved survival in PEG-treated plants was still present for at least 5–10 days after rehydration. A microarray experiment revealed significant subset of genes related to temperature- and hormone-response upregulated 3 days after PEG-treatment demonstrating continuous transcriptional response (Maia et al. 2011).

In crops, drought leads to morphological (e.g., reduced germination, plant height, plant biomass), physiological (e.g., reduced water content, photosynthetic activity, pigment content, membrane integrity), biochemical (e.g., accumulation of osmo-protectants like proline, sugars, antioxidants), and molecular (e.g., altered expression of stress-related genes) changes (reviewed in Farooq et al. 2012; Fahad et al. 2017). Rice, as submerged crop, is one of the most drought-sensitive species (Jaleel and Llorente 2009), in which drought-induced yield losses can amount even to 92% (Lafitte et al. 2007). Intermediate drought stress applied to rice seedlings causes

dehydration-induced oxidative cellular damage symptoms (Li et al. 2011). However, rice seedlings pre-treated with mild drought and re-watered before intermediate stress exhibited less pronounced oxidative damage as assessed by the levels of lipid peroxidation and selective antioxidants (Li et al. 2011). The beneficial effect of pre-treatment of rice seedlings suggests existence of drought memory mechanisms protecting against oxidative-stress caused by subsequently applied stronger drought. Wheat seedlings acclimated by dehydration, re-watered, and exposed to further water deficit showed limited membrane damage, retained water content, decreased accumulation of reactive oxygen species (ROS), compared to non-acclimated controls (Selote et al. 2004; Selote and Khanna-Chopra 2006, 2010). The authors correlated drought acclimation with levels of antioxidant enzymes that were induced by pre-treatment and maintained over re-watering period and triggering stress event (Selote and Khanna-Chopra 2006, 2010). In maize, drought memory was assessed by studying response to repetitive dehydration/rehydration cycles in seedlings. Plants exposed to multiple stress cycles exhibited improved water content in leaves as compared to single-stress controls. By comparing transcriptomic responses in maize and *Arabidopsis*, the authors identified not only conserved acclimation features, but also species-specific gene regulation patterns, indicating not only evolutionarily conservation but also divergence in drought stress response and memory (Ding et al. 2014). In potato (*Solanum tuberosum*), drought stress acclimation was shown to have positive effect on yield and overall plant growth. Plants exposed to two mild dehydration cycles before two complete soil dehydration showed reduced leaf wilting, cuticle accumulation, greater stem number and more open stomata under stress, compared to non-acclimated controls. In contrast, the authors did not observe acclimation effect on tuber weight and number under severe drought (Banik et al. 2016).

1.3.2   Osmotic Stress and Salinity

High salinity is one of the most detrimental factors for agricultural production on both, naturally saline soils and irrigated lands with high level of evaporation or insufficient water management. Salt-induced osmotic stress impairs plant growth by reduction of water uptake, stomatal closure, and decline in photosynthetic activity. In turn, ionic stress caused by specific salts taken up at above-optimum concentrations influences the homeostasis of essential ions, metabolic activity, and integrity of plasma membranes (reviewed in Sudhir and Murthy 2004; Rasool et al. 2012). Priming with mild salt treatment can increase the tolerance of model plants and different crop species to subsequent salt stress, improving the physiological and growth parameters connected to plant vigor and fitness.

Memory in salinity and osmotic stress responses in *Arabidopsis* were studied at both, somatic and *trans*-generational level. Regarding the somatic memory, Sani et al. (2013) reported that plants primed with low NaCl concentration accumulate less sodium in their shoots, have higher biomass and better survival after triggering

stress than control plants. The memory of initial stress was retained for at least 10 days and salinity-primed plants acquired tolerance also to drought, highlighting the crosstalk between the two stresses. Importantly for biotechnology applications, the plants did not exhibit obvious growth retardation effects after the priming stress, suggesting that memory did not come with a cost of overall plant vigor (Sani et al. 2013). Response to salinity stress in *Arabidopsis* was also related to proline content (Feng et al. 2016). Proline is an amino acid implicated in metal chelation, antioxidation and signaling, and its accumulation is positively correlated with tolerance to various stresses (Hayat et al. 2012). *Arabidopsis* plants primed by salt (NaCl) exhibited increased proline content upon subsequent stresses than non-primed controls. The effect was dependent on the transcription of the gene encoding the enzyme Δ1-pyrroline-5-carboxylate synthetase 1 (P5CS1) that mediates the rate-limiting step of proline biosynthesis pathway (Feng et al. 2016).

In wheat, priming of seedlings with low NaCl concentration led to increased tolerance to subsequent treatment with high NaCl concentrations. Specifically, primed plants exhibited efficiently reduced chlorotic symptoms, undisturbed photosynthetic activity, and improved osmotic potential upon high salt stress than non-primed controls (Janda et al. 2016). Higher tolerance to salinity stress was achieved in rice by pre-treatment of seedlings with sublethal NaCl dose. Primed plants showed better control of ion absorption, improved ion transport to leaves, less affected photosynthesis activity, and enhanced accumulation of osmolytes for osmotic adjustment than non-pre-treated controls (Djanaguiraman et al. 2006). In sorghum (*Sorghum bicolor*), priming of seedlings with NaCl led to improved growth upon severe salt treatment (Amzallag et al. 1990). In maize, priming treatment with low salt significantly reduced the detrimental effect of high salt stress manifested by less decreased chlorophyll concentration, water content, and stomatal conductance in comparison with non-primed plants (Pandolfi et al. 2016). Salt priming effect was also observed in other crops like pea (*Pisum sativum*—Pandolfi et al. 2012), potato (Etehadnia et al. 2010), or olive (*Olea europaea*—Pandolfi et al. 2017). In potato and olive, salt tolerance and priming effect were related also to cultivar type. In potato, the biggest effect of priming was seen for relatively salt-sensitive cultivars (Etehadnia et al. 2010), while in olive, priming had overall similar effect in improving salt tolerance, but affected plant organs to different extent, depending on the cultivar (Pandolfi et al. 2017).

1.3.3 Heat

Increase in temperatures is one of the major predictions from climate change models that will likely deeply impact on food security as it impairs plant growth, affects plant reproduction and, therefore, final yield (reviewed in Bäurle 2016).

In *Arabidopsis*, heat stress memory was studied mostly at the seedling stage. Current evidence suggests that heat stress memory in *Arabidopsis* seedlings can be kept up to 3 days after initial stress (Lämke et al. 2016; Brzezinka et al. 2016).

However, the memory strength may decay within hours of recovery (Charng et al. 2006b).

Works on heat stress memory in *Arabidopsis* served as an aid for similar studies in agronomic plant species. For example, an experimental setup established for *Arabidopsis* (Charng et al. 2006a, b) was applied to rice seedlings where the duration of the memory differed between cultivars (Lin et al. 2014).

The crosstalk between different stress types in crops was studied for heat, as priming stress, and cold or salinity as triggering stress. For example, barley plants subjected to high salt stress exhibit impaired growth, as measured by root elongation (Faralli et al. 2015). However, this response can be prevented by acute heat shock priming (Faralli et al. 2015). The beneficial effect of heat shock priming in protection against cold stress-mediated damage was observed in tomato (*Lycopersicon esculentum*). Harvested tomato fruits exposed to non-freezing cold conditions exhibit signatures of chilling injury, i.e. aroma loss, electrolyte leakage, failure to ripen, and oxidative stress (Malacrida et al. 2006; Biswas et al. 2016). However, post-harvest treatment of tomato fruits with higher temperature results in decreased chilling injury upon subsequent cold stress (Saltveit 1991; Zhang et al. 2013a).

Heat-stress memory has been frequently linked also to the tolerance to subsequent heavy metal exposure in crops. In wheat, priming heat shock was shown to mediate higher viability rate of seedlings upon subsequent injection of iron and cadmium salts to leaf segments (Orzech and Burke 1988). In wild tomato (*Lycopersicon peruvianum* L.) cell suspension cultures, acute heat shock prevented cell membrane leakage upon treatment with cadmium (Neumann et al. 1994). In rice, short-term heat pre-treatment led to reduced cadmium-induced chlorosis in seedlings (Hsu and Kao 2007; Chao et al. 2009; Chao and Kao 2010; Chou et al. 2012). Heat-shock-induced accumulation of antioxidative compounds is suggested to play a prominent role in protection against subsequent exposure to cadmium (Hsu and Kao 2007; Chao et al. 2009; Chao and Kao 2010; Chou et al. 2012). These studies indicate that heat pre-treatment can be efficient for priming against heat but also heavy metal, cold or salt stresses.

1.3.4   Cold

Low temperature is also one of the major factors determining locations of crop production and is periodically responsible for losses in crop yields (reviewed in Thomashow 1999). Exposure to low temperatures causes various phenotypic symptoms such as poor germination rate, chlorosis, reduced organ expansion, wilting, and inhibited reproductive development (reviewed in Yadav 2009). Cold memory in *Arabidopsis* can be triggered by persisting or oscillating low temperature stress (reviewed in Thomashow 1999; Markovskaya et al. 2008), both of which have an immense impact on plant fitness to seasonal and daily temperature changes in the environment.

Arabidopsis response to triggering cold stress was assessed after two different priming stress types, short-term cold stress (STC) or long-term cold stress (LTC), both followed by a 5 day-long recovery phase. Only LTC plants showed higher effective quantum yields of photosystem II and higher photochemical quenching after triggering stress, in contrast to STC plants (van Buer et al. 2016). The results indicate that long-term, but not short-term, priming allows better energy dissipation through photosystem II in response to cold.

Cold stress memory was studied in a number of chilling-sensitive agronomic species. Here, exposure to moderate temperatures before cold alleviates cold-induced negative effects on plant growth and development. For example, in rice, cold-priming prevents cold-induced impaired water uptake in roots, leaf wilting, and color bleaching (Ahamed et al. 2012). Priming of maize was shown to protect the photosynthetic apparatus from cold-induced damage. The authors used maize inbred lines of different cold-sensitivity to demonstrate a crucial role of cold priming in chilling-resistant high cold-tolerant varieties (Sobkowiak et al. 2016). Cold priming effect on different varieties was also studied in wheat (Charest and Ton Phan 1990). Cold treatment led to increased soluble protein content, decreased water content, and accumulation of proline even 30 days after cold. Most importantly, such cold memory effect was more pronounced in winter than in spring wheat cultivars. Cold priming has an effect in tolerance to subsequent exposure to freezing temperatures in winter wheat and also in winter and spring cultivars of canola (Trischuk et al. 2014).

Similar to heat priming, cold priming treatment was shown to increase resistance to further exposure to stress of other types. For example, cold priming results in better survival and growth of mustard seedlings exposed to salt and drought (Hossain et al. 2013), in alleviated photoinhibition and oxidative cellular damage caused by cadmium, copper or high light intensity in pea (Streb et al. 2008) and in increasing resistance to heat stress (Zhang et al. 2006a; Wan et al. 2009).

1.3.5 Ultraviolet (UV-B) Radiation

UV-B is one of the types of ultraviolet light and a natural component of solar radiation. Increased UV-B intensities are especially detrimental for plants due to their sessile lifestyle and obligatory requirement for sunlight. UV-B stress can be divided into low- and high-dose, and short-term (acute, seconds to hours) or long-term (chronic, hours to days) exposure (reviewed in Brown and Jenkins 2007; Lang-Mladek et al. 2012; Hideg et al. 2013). Whereas acute, high dose radiation causes severe detrimental effects and results ultimately in programmed cell death, chronic, low-dose UV-B causes effective activation of defense mechanisms and acclimation to UV stress (reviewed in Hideg et al. 2013).

Arabidopsis plants exposed to long-term low-dose UV-B exhibited stress memory even after 9 days of recovery period and showed morphological changes such as decreased rosette diameter, reduced inflorescence height, increased number of flow-

ering stems, and stimulated axillary branching (Hectors et al. 2007). However, such stress did not affect photosynthesis efficiency—increased pigment content compensated reduced leaf area, preventing substantial growth impairment (Hectors et al. 2007). *Arabidopsis* plants treated with a 2-h pulse for several days showed increased flavonoid content that eventually reaches a steady-state (Hectors et al. 2014). Such result suggests a role of flavonoids in long-term UV memory and acclimation.

The response to low-dose UV treatment and the UV stress memory was studied also in crops. Beneficial effect of low-dose UV-B was observed on morphological, physiological, and metabolic levels. Plant species showing long-term beneficial effect after UV-B stress range from crops (wheat, maize, rice) to commonly cultivated Brassicaceae (cabbage—*Brassica oleracea*, rapeseed—*B. napus*) and legumes (mungo bean—*Vigna radiata*, kidney bean—*Phaseolus vulgaris*, cowpea—*Vigna unguiculata*, soybean—*Glycine max*) (Thomas and Puthur 2017). Crop seeds treated with UV-B exhibit, i.e. increased germination, faster growth rate, elevated pigment content, and increased tolerance to other stresses (i.e., salinity, pathogens). For example, increased germination rate as a result of UV-B treatment was seen for maize (Wang et al. 2010); increased content of pigments for cabbage, beet (*Beta vulgaris*), kidney bean (Kacharava et al. 2009), soybean (Yanqun et al. 2003), mash bean (*Vigna mungo*—Shaukat et al. 2013), and rice (Olsson et al. 1998); and increased biomass for tartary buckwheat (*Fagopyrum tataricum Gaertn.*—Yao et al. 2007). Increased chlorophyll or carotenoid content was reported for UV-treated seedlings of rice (Xu and Qiu 2007), cowpea (Mishra et al. 2008), and bitter gourd (*Momordica charantia* L.—Mishra et al. 2009).

1.3.6   Chemical Agents

Instead of applying initial mild abiotic stress, stress memory in plants can be also induced by treatment with chemical compounds in a process called chemical priming. Such chemicals can be synthetic or of natural origin and include, i.e. amino acids, hormones, nutrients, pesticides, reactive oxygen-nitrogen-sulfur species (RONSS) (reviewed in Jisha et al. 2013; Savvides et al. 2016; Antoniou et al. 2016; Lutts et al. 2016). One of the advantages of using chemical agents to prime plants against environmental stresses is the robustness, enhancing plant resilience against many different stress types.

Chemical priming on *Arabidopsis* was assessed in a number of studies. Pretreatment of *Arabidopsis* seedlings with the non-protein amino acid β-aminobutyric acid (BABA) 1 day before, either high salt or drought treatment showed improved tolerance to subsequent stresses—lower wilting rate and water loss (Jakab et al. 2005). Interestingly, BABA is also a commonly used agent enhancing systemic acquired resistance (SAR) for pathogen protection, indicating that the compound triggers activation of a pathway common for biotic and abiotic stresses. *Arabidopsis* plants pre-treated with melatonin showed better growth following cold stress, manifested in fresh weight, root length and shoot length increase (Bajwa et al. 2014).

Melatonin increased expression of cold-inducible genes at different timepoints during stress (Bajwa et al. 2014), suggesting that the compound triggered a similar primed state at the transcriptomic level as a mild cold pre-treatment (van Buer et al. 2016).

Spermine is a natural polyamine synthesized in eukaryotic cells and it was reported to accumulate, along with the other polyamines, under abiotic stress conditions (reviewed in Rhee et al. 2007). Pre-treated *Arabidopsis* seedlings with exogenously applied spermine exhibited attenuated chlorosis in cotyledons compared to controls. The crucial impact of spermine on heat acclimation was also confirmed by genetic approaches—transgenic plants overexpressing spermine biosynthetic genes showed less inhibited growth upon heat shock, whereas knock-out mutants were hypersensitive to a high temperature (Sagor et al. 2013).

The exogenous application of chemical compounds on crops has frequently been used for seed priming, because seeds can be more easily treated and with a minor cost than the adult plants (reviewed in Jisha et al. 2013; Savvides et al. 2016; Lutts et al. 2016). Confirmed for a big range of various agronomic plants, chemical pre-treatment of seeds can increase the rate and percentage of seed germination. In addition, it can have a beneficial effect in the longer term by improving seedling vigor, especially during growth under stress conditions (reviewed in Savvides et al. 2016; Lutts et al. 2016). However, there are also reports showing priming effect of chemicals, when applied at later developmental stages. The application of the chemical on a specific organ, for instance roots, leaves, or stems, or at specific developmental stage, such as seedlings, promoted a systemic response that will spread to protect other parts of the plant and not only the organs that were treated in different crops such as wheat (Hasanuzzaman et al. 2011; Shan et al. 2011; Turk et al. 2014), rice (Uchida et al. 2002; Saleethong et al. 2013; Mostofa et al. 2014), maize (Li et al. 2013), tomato (İşeri et al. 2013; Amooaghaie and Nikzad 2013), strawberry (*Fragaria* sp.—Christou et al. 2013, 2014a, b), oil rapeseed (Yıldız et al. 2013; Xiong et al. 2018), or tangerine (*Citrus* sp.—Shi et al. 2010).

1.4 Epigenetic Mechanisms of Abiotic Stress Response and Memory

Responses to stress result in genome-wide changes to chromatin structure and gene transcription or can be even associated with modifications to genomic sequence. Exposure to stress induces alterations at all levels of chromatin structure, including DNA methylation, nucleosome occupancy and composition, presence of histone variants as well as histone PTMs and global chromatin arrangement. Uncoupling the direct effects of stress on chromatin structure and nuclear architecture from its effects on gene transcription is very challenging, making a large part of evidence describing mechanisms of stress-induced changes correlative. In addition, even though the connections between chromatin rearrangement and response to various