

PREFACE

Over the last century, a remarkable yield increase has been achieved for many crop plants. Multiple factors have contributed to this achievement, but undoubtedly breeding has been a major driving force that has resulted in the improvement of traits of agronomical importance including growth and vigor, increased yields and better tolerance to environmental constraints and to agronomical practices. So far, crop improvement has relied on the genetic variability found within species or in wild relatives and on the introgression of traits of agronomical importance into elite crops. The recent completion of many major crop genomes has greatly facilitated precision breeding by revealing gene variants associated with specific traits. These approaches that include genome-wide association studies (GWAS), genomic selection and other genetic strategies have provided new ways to capture a substantial proportion of the sequence-based heritable variation underlying phenotypic traits (Morrell, Buckler, & Ross-Ibarra, 2012). There is still, however, a significant amount of heritability that cannot be explained by genetic methods, the “missing heritability” (Maher, 2008), that in humans can represent a substantial part of the heritability as recently shown in the case of human height (Bourrat, Lu, & Jablonka, 2017; Manolio et al., 2009; Visscher, 2008). Various mechanisms that could account for the “missing heritability” have been suggested. Possible explanations include the combination of rare alleles, variations in gene copy number or the contribution of additional gene variants that remain to be discovered and occur at very low frequency in populations (Bourrat et al., 2017; Bandyopadhyay, Chanda, & Wang, 2017).

As far as plants are concerned, GWAS appears to be a more efficient approach as illustrated by the recent demonstration that a significant proportion of flowering time variation can simply be explained by sequences diversity, however, still leaving 45% of the phenotypic diversity of this trait unexplained (Brachi, Morris, Borevitz, & Benjamin Brachi, 2011; Li, Huang, Bergelson, Nordborg, & Borevitz, 2010). This suggests that variation in gene sequences is unlikely to explain, in plants also, the complete range of the observed phenotypic diversity. This is even more true when the genetic diversity of crops is limited, for example in tomato (Lin et al., 2014), or when clonal propagation is an important method for plant multiplication (Verhoeven & Preite, 2014).

Epigenetics has been defined as the study of heritable variations of phenotypes that do not involve alterations in the genetic information (Berger et al., 2009; Dupont et al., 2009) and consequently could also be involved in determining phenotyping diversity independently of DNA sequence variations. This has been illustrated in several studies showing that epigenetic variations can lead to stable modifications of plant traits of agronomical importance, for example fruit ripening (Manning et al., 2006), plant height (Miura et al., 2009), or fruit nutrient content (Quadrana et al., 2014). In addition, an exciting aspect of epigenetic mechanisms is their potential contribution to the so-called "soft inheritance" (Richards, 2006), a term proposed by Mayr's to explain that *"the genetic basis of characters could be modified either by direct induction by the environment, or by use and disuse, or by an intrinsic failure of constancy, and that this modified genotype was then transmitted to the next generation"* (Mayr et al., 1980). Epigenetic processes could therefore contribute to the heritable phenotypic diversity through mechanisms other than DNA sequence variation (Bourrat et al., 2017). It is the focus of the present book to discuss the extent to which epigenetic diversity could contribute to stable phenotypic diversity in plants and therefore becomes part of new breeding strategies aiming at facing the numerous challenges raised by climate change and thus affecting food security in the upcoming century.

The first chapter provides an historical perspective of epigenetics that has been intensively studied over the last 20 years in plants and since 1950 in animals leading to the demonstration that they play essential functions in controlling many aspects of cell-specific gene expression programs and cell differentiation processes. In the second chapter, molecular mechanisms underlying the epigenetic processes are described highlighting the fundamental role of DNA methylation, histone posttranslational modifications (PTMs) and small noncoding RNAs in determining the conformational state of the chromatin and thereby its transcriptional state. Indeed, the heritability, stability and diversity of epigenetic marks are an essential aspect to consider for potential breeding applications. Of particular interest is the question of the relevance of locus-specific or genome-wide epigenetic diversity in determining phenotypic variations as discussed in Chapter 3. In addition, the demonstration that epigenetic recombinant-inbred *A. thaliana* lines (epiRILs) generated from isogenic parents with divergent DNA methylome segregate tens of stable parental differentially methylated regions that are stably inherited and act as epigenetic quantitative traits, highlights

the relevance of DNA methylation as a stable epigenetic mark, as discussed in Chapter 4. This chapter shows that variation in DNA methylation impacts on plant phenotypes over generations and provides a new paradigm in which DNA methylation could shape phenotypic variability, contributing to the so-called "missing heritability" and could therefore be used in breeding strategies. Indeed, a precise analysis of how epigenetic marks, including DNA methylation, histone marks and small RNAs can be transmitted through sexual and asexual plant reproduction is a central issue when considering the potential role of epigenetic heritability in breeding strategies. Chapter 5 presents the current knowledge of epigenetic marks, their stability and transmission both in sexual and asexual reproduction, and thereby provides an insight into the potentialities and limits of the use of epigenetic variability in plant improvement.

An important function of epigenetic regulation is its contribution to the stability of genomes, with a special role in the control of transposable element (TE) mobility. Indeed TEs have long been considered a major risk for genome integrity as they can generate deleterious mutations, but recent work highlights their fundamental role in plant stress responses and in crop domestication. Therefore, TEs could be important factors to consider in breeding strategies (Chapter 6). Over the last century, both grafting and heterosis have contributed to the significant increase in crop yield by improving plant vigor, yield or resistance to pathogens. Although the mechanisms underlying these processes are still far from being understood, recent work indicates that epigenetic mechanisms play an important function in these processes (Chapters 7 and 8). Chapters 9 and 10 focus on the essential roles of epigenetic mechanisms in controlling traits of agronomical importance as flowering time and bud break in perennial plants and the regulation of fleshy fruit development and quality, respectively. Finally the last chapters discuss the importance of epigenetic mechanisms in cereal yield and quality (Chapter 11) and forest tree management (Chapter 12).

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