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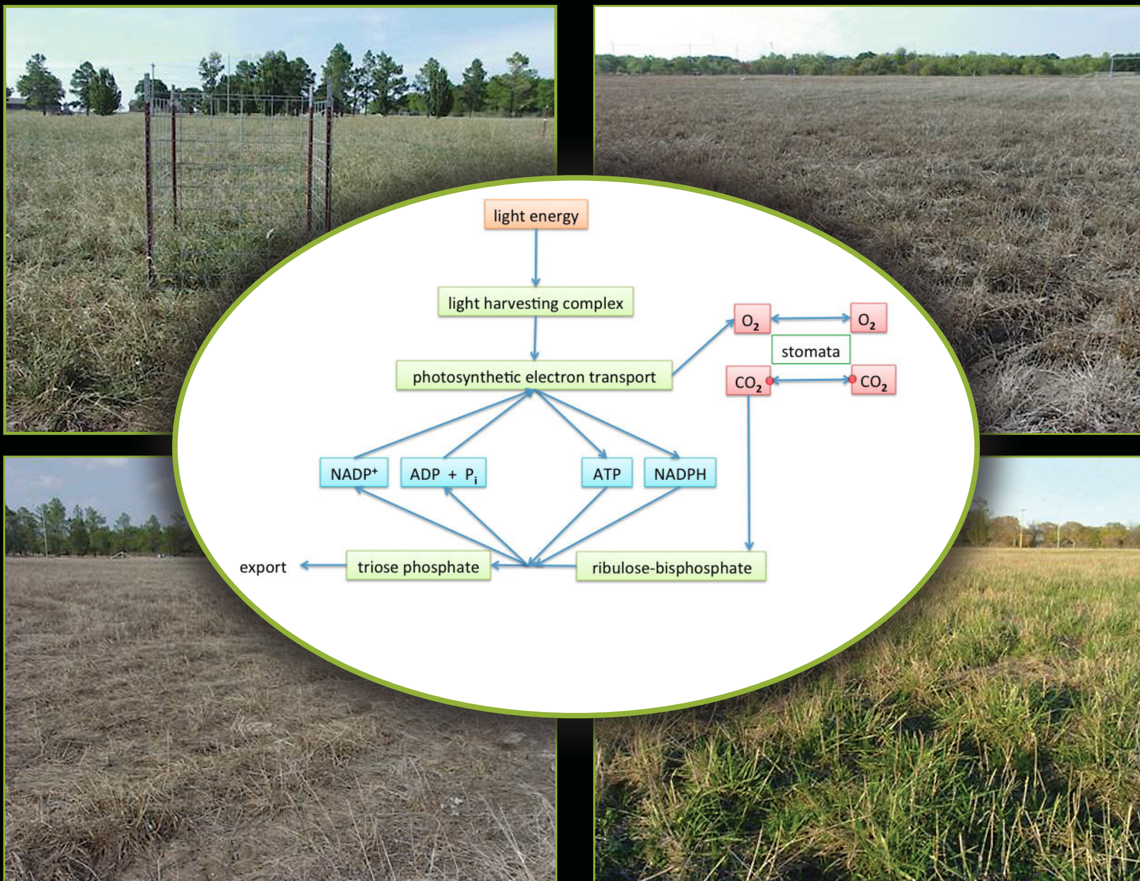

Handbook of PLANT AND CROP PHYSIOLOGY

Edited by
MOHAMMAD PESSARAKLI

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Handbook of PLANT AND CROP PHYSIOLOGY

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In memory of my beloved parents, Fatemeh and Vahab, who, regretfully, did not live to see this work and my other works, which in no small part resulted from the unconditional love that they showered on me for many years.

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Preface

Like any other area in science, both the scope and depth of our knowledge on plant and crop physiology are rapidly expanding. Plant/crop physiologists are continuously making new discoveries. This phenomenon has resulted in the compilation of a large volume of information since the second edition of the *Handbook of Plant and Crop Physiology* was published. The abundance of new data has necessitated an updated edition, which includes, as much as possible, the latest discoveries in the field. Like the first and second editions, this edition is a unique, comprehensive, and complete collection of topics in the field of plant/crop physiology.

Over 90% of the material in this edition is entirely new, and these are included in this volume under new titles. The remaining 10% have been updated and modified substantially. Therefore, overall, the material in this book is as good as new.

The *Handbook of Plant and Crop Physiology* is needed to fill the gap in the literature. It has long been recognized that physiological processes control plant growth and crop yields. This handbook will, therefore, serve as an up-to-date resource, covering the relevant information in the field.

Several decisions need to be made when compiling a handbook, such as the extent of content to include, the information to exclude, the depth to which the topics should be covered, and the organization of the selected content. In this volume, I have chosen to include information that will be beneficial to students, instructors, researchers, field specialists, and any others interested in the areas of plant and crop physiology. In order to plan, implement, and evaluate comprehensive and specific strategies for dealing with plant and crop physiology problems and issues, strategies must be based on a firm understanding of facts and principles.

The topics selected for discussion are those that I believe are relevant and in which physiology plays the dominant role. The concepts have been presented in such a manner as to give both beginning students and specialists an opportunity to expand and refine their knowledge. Certain conclusions and solutions provided throughout the text are related to the more significant and multifaceted problems of plant and crop physiology. They are presented to provide a concise guide to help students and specialists achieve their goals.

This practical and comprehensive guide has been prepared by 105 contributors from 17 countries, among which are some of the most competent and knowledgeable scientists, specialists, and researchers in agriculture, particularly in plant sciences and plant physiology. It is intended to serve as a resource for both university courses and for research. Biologists, physiologists, scientists, agriculture researchers, agriculture practitioners, and educators and students will benefit from this unique, comprehensive guide, which covers plant physiological processes from cellular aspects to whole plants.

As with other fields, accessibility of knowledge is one of the most critical factors involved in crop physiological processes and problems. Without due consideration of all the elements contributing to a specific crop physiological process and problem, it is unlikely that a permanent solution will be achieved. Therefore, this handbook includes several physiological factors. To further facilitate the accessibility of the desired information on plant/crop physiological processes covered in this collection, the volume has been divided into nine parts: Part I—Physiology of Plant/Crop Growth and Development Stages; Part II—Cellular and Molecular Aspects of Plant/Crop Physiology; Part III—Plant/Crop Physiology and Physiological Aspects of Plant/Crop Production Processes; Part IV—Physiological Responses of Plants/Crops under Stressful (Salt, Drought, Heat, Nutrient Deficiency, and Other Environmental Stresses) Conditions; Part V—Physiological Responses of Plants/Crops to Heavy Metal Concentration and Agrichemicals; Part VI—Physiology of Plant/Crop Genetics and Development; Part VII—Bioinformatics and Using Computer Modeling in Plant Physiology; Part VIII—Plant/Crop Growth Responses to Environmental Factors and Climatic Changes; and

Part IX—Future Promises: Plant and Crop Adaptation and Biotechnological Aspects of Plant/Crop Improvement. Although the parts are interrelated, each serves independently to facilitate the understanding of the material presented therein. Each part also enables the reader to acquire confidence in his or her learning and use of the information offered. Each of these parts consists of one or more chapters to discuss, independently, as many aspects of plant/crop physiology as possible.

Part I consists of eight chapters and addresses various physiological processes of plant and crop growth and development.

Part II contains four chapters and addresses the cellular and molecular aspects of plant/crop physiology, presenting the most recent information on each of these subjects.

Part III contains six chapters and presents detailed information on the physiology of production processes in plants/crops and discusses the physiology under different growth conditions.

Since plants and crops, like other living things, at one time or another during their life cycle, encounter biotic or abiotic stressful conditions, Parts IV and V are devoted to the physiological responses of plants and crops to stress. Several examples of empirical investigations of specific plants and crops grown under stressful conditions are presented in these parts. Part IV includes 14 chapters. Each of these chapters presents in-depth information on the topics covered.

Part V consists of two chapters, which discuss the interactions between heavy metals and agrichemicals and plant/crop physiological processes and the potential problems caused by the accumulation of heavy metals in soils and plant growth media and the application of agrichemicals to plants/crops.

Part VI consists of only one chapter, which presents recent findings on small RNAs in crop response to temperature stress noncoding RNAs in plants.

Part VII also consists of only one chapter, which presents information on large-scale computations and the use of bioinformatics in plant/crop physiology.

Due to recent climatic changes and increase in CO_2 levels that have had a major impact on plant/crop physiological processes, the resistance of plants to these changes must be considered for cultivation under these conditions. Part VIII, consisting of a single chapter, presents the most recent information on this subject. It deals with rising CO_2 levels and climate change (global warming) and their impacts on plant/crop growth behavior, development, and production in the twenty-first century.

Part IX presents evidence and guidance on plants and crops that can be successfully cultivated under more stressful conditions that are likely in the future. It consists of six chapters, which address alleviation of future food security problems.

Numerous tables, figures, and illustrations are included in this technical guide to facilitate comprehension of the presented materials. Thousands of words are also included in the index to further increase accessibility to the desired information.

It is hoped that an individual seeking a solution in the area of plant/crop physiology will turn to this practical and professional reference book and be able to promptly acquire the necessary assistance.

Like other fields, the area of plant/crop physiology has been growing so rapidly that all plant/crop physiologists are faced with the problem of constantly updating their knowledge. To grow in their profession, they need to extend their interests and skills. In this regard, even a casual reading of the material in this handbook will help them move ahead in the right direction.

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Acknowledgments

I would like to express my appreciation for the secretarial and the administrative assistance that I received from the staff of the School of Plant Sciences, College of Agriculture and Life Sciences, the University of Arizona. I greatly appreciate the encouragement and support that I receive from the director of the school, Dr. Karen S. Schumaker and my mentor Dr. Dennis T. Ray for my editorial work, which have been a major driving force for the successful completion of this project.

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The collective efforts and invaluable contributions of several experts in the field of plant/crop physiology made it possible to produce this unique source, which presents comprehensive information on the subject. Each and every one of these contributors and their contributions are greatly appreciated.

Last, but not least, I thank my wife, Vinca, a high school science teacher, and my son, Dr. Mahdi Pessarakli, MD, who supported me during the course of this work.

Editor

Dr. Mohammad Pessarakli, is a professor in the School of Plant Sciences, College of Agriculture and Life Sciences, at the University of Arizona, Tucson, Arizona. His work at the university includes research and extension services as well as teaching courses in turfgrass science, management, and stress physiology. He is the editor of the *Handbook of Plant and Crop Stress* and the *Handbook of Plant and Crop Physiology* (both titles published by Marcel Dekker, Inc., which has been acquired by Taylor & Francis Group, CRC Press) as well as the *Handbook of Photosynthesis* and the *Handbook of Turfgrass Management and Physiology*. He has written 18 book chapters, is an editorial board member of the *Journal of Plant Nutrition* and *Communications in Soil Science and Plant Analysis* and the *Journal of Agricultural Technology*, is a member of the Book Review Committee of the Crop Science Society of America, and is a reviewer of *Crop Science*, *Agronomy Journal*, *Soil Science Society of America Journal*, and *HortScience*. He is the author or coauthor of 135 journal articles and 55 trade magazine articles. Dr. Pessarakli is an active member of the Agronomy Society of America, Crop Science Society of America, and Soil Science Society of America, among others. He is an executive board member of the American Association of the University Professors (AAUP), Arizona Chapter. He is also a well-known, internationally recognized scientist and scholar and an esteemed member (*invited*) of *Sterling Who's Who*, *Marqueis Who's Who*, *Strathmore's Who's Who*, *Madison Who's Who*, and *Continental Who's Who* as well as numerous honor societies (i.e., Phi Kappa Phi, Gamma Sigma Delta, Pi Lambda Theta, Alpha Alpha Chapter). He is a certified professional agronomist and certified professional soil scientist (CPAg/SS), designated by the American Registry of the Certified Professionals in Agronomy, Crop Science, and Soil Science. Dr. Pessarakli is a United Nations Consultant in Agriculture for underdeveloped countries. He received his BS (1977) in environmental resources in agriculture and his MS (1978) in soil management and crop production from Arizona State University, Tempe, and his PhD (1981) in soil and water science from the University of Arizona, Tucson. Dr. Pessarakli's environmental stress research work and expertise on plants and crops are internationally recognized.

For more information about Dr. Pessarakli, please visit http://ag.arizona.edu/pls/faculty/pessarakli.htm and http://cals.arizona.edu/spls/people/faculty

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Part I

Physiology of Plant/Crop Growth and Development Stages

1 Cell Cycle Regulation and Plant Development

A Crop Production Perspective

Paolo A. Sabelli

CONTENTS

1.1 INTRODUCTION—CROP YIELD: A CELL CYCLE PERSPECTIVE

Cell number and expansion are two key parameters controlling the size of tissues, organs, and the whole plant. The cell division cycle is directly responsible for cell production (i.e., cell number), but it also influences plant shape, architecture, and morphogenesis through spatial regulation of cell wall deposition at cytokinesis, and at least in some notable cases of agricultural relevance also through cell expansion. Thus, it is intuitive that detailed understanding of the cell cycle, coupled with the ability to manipulate it, has the potential to significantly contribute to maximizing crop yield and sustaining agricultural output in the face of future depletion of resources and increased demand. Over the last 20 years or so, remarkable progress has been made in understanding how the plant cell cycle is regulated in biochemical, genetic, and physiological terms, particularly in the model species *Arabidopsis thaliana*. Key molecular players have been identified that govern the workings of the cell cycle that are highly conserved among plants and that, in some cases, have critically helped advance the understanding of the cell cycle in animals as well. However, we are currently faced with an apparent paradox where despite the advances in model plant systems, it is difficult to translate this knowledge into suitable applications for the improvement of crops, agriculture, and civilization as a whole. This is partly due, on the one hand, to the higher level of biological complexity of crop species compared to simpler model systems and, on the other hand, to the paucity of cell cycle research efforts in agriculturally important plants. As a result, our knowledge of cell cycle regulation in crops is rudimentary and rather stagnant, thereby undermining or delaying attempts aimed at transferring basic research findings into agriculture practice.

In this chapter, the regulation of the plant cell cycle is reviewed with an emphasis on key aspects and factors that may impact crop production and yield. Because of space limitations, however, several relevant topics are not discussed in detail here, including the regulation of the cell cycle by phytohormones (Del Pozo et al. 2005; John 2007; Dudits et al. 2011) and the role of the plant cell cycle in integrating abiotic signals with developmental programs (Granier et al. 2007; Skirycz et al. 2011; Komaki and Sugimoto 2012), which could contribute to mitigating yield losses due to environmental stresses.

For simplicity, the concept of crop yield is narrowed down to the level of the individual tissue, organ, or plant, and is not viewed in terms of a community of plants in the field. Although the latter is clearly more representative of agricultural practice, many interacting factors (e.g., the number of seeds per unit of land area, the plant's ability to intercept and harvest solar radiation, water/nutrients availability, temperature, source/sink relationships, and the ability of the plant to adapt to growing seasons of variable duration, to mention a few) contribute to determining the yield in the field (Evans 1993), which makes the evaluation of the potential of cell cycle regulation for impacting yield in agricultural settings very complicated. Notwithstanding these caveats, however, it is possible to provide an initial assessment of the role played by cell cycle regulation in crop production. Because the cell cycle is paramount for cell production, it is perhaps most obvious to consider its role in terms of biomass production, though, as described in the following text, the cell cycle can impact plants in various ways that may not be directly related to biomass, including the regulation of their architecture or their interaction with symbiotic or parasitic organisms. For example, an acceleration of growth may not modify final plant size or morphology, yet it may benefit crops in environment characterized by short growing seasons (Busov et al. 2008). In addition, several systems relevant to crop production are impacted by a cell cycle variant, known as endoreduplication, which not only does not involve cell proliferation, but also is typically mutually exclusive to it. The main goal of this chapter is to provide an overview of how cell cycle regulation can affect plant development under the perspective of crop production.

1.2 CORE MOLECULAR CONTROL OF THE CELL CYCLE: AN OVERVIEW

Cell cycle regulation in plants has been the subject of several excellent reviews (De Jager et al. 2005; Gutierrez 2005; Inze and De Veylder 2006; Francis 2007; Inagaki and Umeda 2011), and therefore only an overview of some key aspects is provided here. In plants, like in other eukaryotes, cell cycle progression is controlled by the timely activation of complexes between a cyclin-dependent kinase (CDK) and a regulatory subunit termed cyclin. In eukaryotes, the expression of the kinase component is not generally cell cycle regulated whereas that of the cyclin subunit is, and it is from these noticeable fluctuations in protein accumulation during the cell cycle that cyclin polypeptides and genes derive their name. The activity of CDK/cyclin complexes is regulated at several different levels. First, as aforementioned, the availability of cyclin subunit is paramount (Nieuwland et al. 2007).

This, in turn, is controlled at the level of gene transcription, but critically also by specific degradation of cyclin proteins by the 26S proteasome, which can be rather abrupt and is thus well suited for driving cells through unidirectional cell cycle transitions. Second, the catalytic activity of the CDK kinase moiety is subject to some exquisite protein conformation regulation, which depends in large part on the presence/absence of phosphate groups on certain amino acid residues. Thus, regulation of CDK phosphorylation/dephosphorylation is a crucial aspect of cell cycle control (Morgan 1997; Inze and De Veylder 2006; Inagaki and Umeda 2011). Third, the activity of CDK/cyclin complexes can be inhibited by the binding of specific inhibitors generally known as CKIs (Wang et al. 2008). Each of these three primary mechanisms regulating CDK activity is controlled at different levels by other factors and pathways and sometimes by CDK/CYC complexes themselves through feedback regulation, which not surprisingly results in an intricate web of protein-to-protein interactions (Van Leene et al. 2010).

1.2.1 Mitotic Cell Cycle

The standard mitotic cell cycle consists of the four canonical phases Gap1 (G1), DNA synthesis (S-phase), Gap2 (G2), and mitosis (M-phase) (Figure 1.1). Upon the orderly completion of these phases, the chromosomes are replicated as sister chromatids, which are segregated into two genetically identical daughter nuclei, within the mother cell. Subsequently, deposition of new cell wall partitions in an intervening region between the nuclei during cell division (cytokinesis) generates two daughter cells. The gap phases derive their names from early microscopic observations that could only reveal gross structural changes, which suggested that they were "resting" periods of relative cellular inactivity. We now know that a great deal of regulation occurs in G1 and G2 at the molecular level in order for subsequent S-phase or M-phase to take place.

Several classes of CDKs have been identified in plants (at least eight in *Arabidopsis*) based on amino acid sequence similarities, but it appears only four, CDKA, CDKB, CDKD, and CDKF are involved in direct cell cycle regulation (Inze and De Veylder 2006; Doonan and Kitsios 2009; Inagaki and Umeda 2011). CDKA is coded for by a single gene in *Arabidopsis* but by at least three genes in maize (Colasanti et al. 1991; Dante et al. 2013) and is believed to control the onset of the G1/S-phase transition, DNA synthesis, as well as M-phase entry and execution. B-type CDKs are unique to plants, are characterized by cell cycle–regulated pattern of accumulation from late S-phase to M-phase, and are thought to specifically regulate the G2/M-phase transition. CDKD and CDKF function upstream and regulate CDKA and CDKB through phosphorylation of specific residues and therefore are also known as CDK-activating kinases (CAKs) (Figure 1.1).

Cyclins are encoded by a larger family of genes in plants than in animals—about 50 in *Arabidopsis* and rice grouped into several different classes (Wang et al. 2004a; La et al. 2006; Nieuwland et al. 2007)—probably to facilitate the fine-tuning of cell proliferation in sessile organisms in response to changing environmental conditions (Menges et al. 2005). While for some cyclins the function is unknown, most cyclin types have been assigned at least a putative cell cycle role. A great deal is known about individual cyclins, and they display a dazzling array of cell cycle–regulated expression and protein-to-protein interaction patterns (Menges et al. 2005; Nieuwland et al. 2007; Van Leene et al. 2010). Although the following is a gross oversimplification and there are notable exceptions, CYCDs are generally involved in relying external proliferation stimuli along a pathway that leads to the onset of DNA synthesis, CYCAs are believed to regulate progression through S- and M-phases, and CYCBs are primarily required for the G2/M-phase transition (Inze and De Veylder 2006; Nieuwland et al. 2007; Inagaki and Umeda 2011) (Figure 1.1).

1.2.1.1 Regulation of the G1/S-Phase Transition

During G1, exogenous and endogenous cell proliferation stimuli, which may include sucrose as well as phytohormones such as auxin, cytokinin, and brassinosteroids (Del Pozo et al. 2005; John 2007; Dudits et al. 2011), are sensed and relayed to the core cell cycle–regulatory machinery resulting

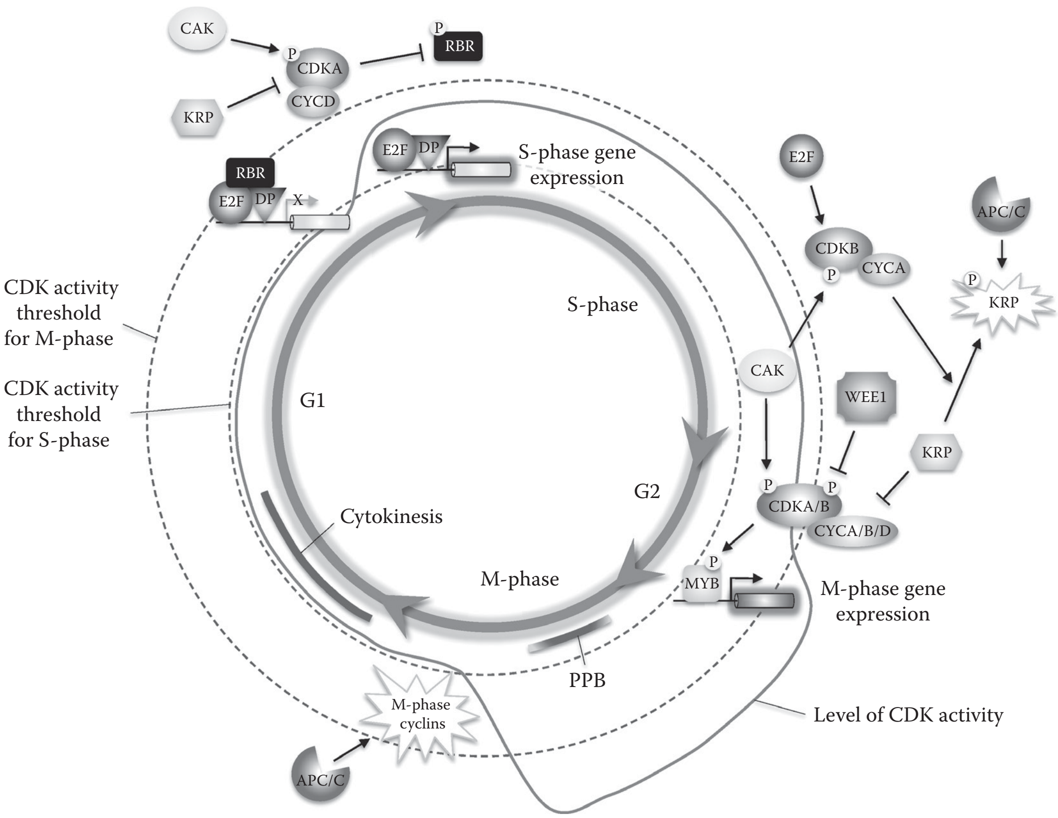

FIGURE 1.1 Schematic diagram illustrating the canonical phases during the plant cell division cycle (G1, S-phase, G2, M-phase, and cytokinesis) and, in a highly simplified fashion, the key molecular mechanisms that regulate major transitions. Fluctuations in CDK activity are paramount for cell cycle progression (solid line). CDK activity must exceed an S-phase threshold (inner broken line) for cells to transition from G1- into S-phase and replicate their DNA, while another increase during G2 above an M-phase threshold (outer broken line) drives cells into mitosis. Exit from M-phase and acquiring the competence of chromosomal replication origins for DNA synthesis (origin licensing) require a drop in CDK activity at the end of mitosis and for most of G1. At the G1/S-phase transition, a wide-ranging gene expression program dependent on heterodimeric E2F/DP transcription factors is derepressed as CDKA/CYCD complexes inactivate (through phosphorylation) RBR inhibitors. Further upstream, the activity of CDKA/CYCD is positively and negatively regulated by CAK and KRP activities, respectively. At the G2/M-phase transition, a spike in CDK activity results in the phosphorylation and activation of MYB3R transcription factors that drive M-phase-specific gene expression. This CDK activity involves specific mitotic cyclins and also is stimulated by CAK-dependent phosphorylation and is generally inhibited by WEE1-dependent phosphorylation and binding by KRP inhibitors. B-type CDKs appear to be required specifically for the execution of M-phase, in part by stimulating CDK activity through phosphorylation of KRP and targeting it for disruption by the APC/C-dependent proteasome. Degradation of mitotic cyclins by the proteasome is also key for the abrupt lowering of CDK activity that is required for M-phase exit. The cell cycle window during which the plant-specific preprophase band (PPB) is transiently formed is indicated together with postmitotic cytokinesis.

in the formation of active CDKA/CYCD complexes above a threshold required for S-phase entry (Figure 1.1). These complexes can be inhibited by specific CKIs of the ICK/KRP family (hereafter termed KRP), which, in turn, can be induced or downregulated in response to hormones such as ABA or auxin, respectively. Active CDK/CYC complexes go on to phosphorylate many substrates, which include homologs of the retinoblastoma tumor suppressor family of proteins (termed RBR, for retinoblastoma related), and proteins involved in licensing origins of DNA replication (Figure 1.1). A large number of genes need to be timely expressed at the G1/S-phase boundary and throughout S-phase in order to initiate and support chromatin replication. The expression of many of these genes requires the activity of adenovirus E2 promoter binding factor (E2F) transcription factors primarily acting in complexes with their protein dimerization partner (DP). However, regulation of E2F-dependent gene expression is complex, and the E2F protein family includes members that have primarily a repressive function and do not dimerize with DP. In G1, RBR inhibits E2F/DP-dependent gene expression by several mechanisms, which involve direct binding to the transactivation domain of E2F and the recruitment of chromatin remodeling factors at E2F-bound promoters with ensuing silencing of specific chromatin domains (Sabelli and Larkins 2009a). This block on the expression of genes required for S-phase and cell cycle progression is relieved at the G1/S-phase transition by conformational changes of RBR brought about by phosphorylation by CDK.

1.2.1.2 Regulation of M-Phase

As cells prepare to enter M-phase late in G2, several CDK/CYC complexes are formed and become activated above another critical threshold (Figure 1.1). These complexes include both CDKA and CDKB proteins, as well as A-, B-, and, likely, D-type cyclins (Inze and De Veylder 2006). A large number of substrates become phosphorylated as a result, and cells progress into M-phase. Several molecular mechanisms contribute to the timely activation of these complexes: gene transcription (critically regulating the availability of CDKBs and cyclins); inhibitory phosphorylation of the CDK moiety by WEE1 kinase (however, although functionally conserved in eukaryotes, there is no evidence for this mechanism in *Arabidopsis*); activating dephosphorylation that counters WEE1 (the phosphatase responsible for this reaction has not been unambiguously identified in plants, but a CDC25-like activity seems a likely candidate); and, similarly for the G1/S-phase transition, phosphorylation by CAKs. The execution of the M-phase transcriptional program seems to depend to a large extent on three-repeat MYB (MYB3R) transcription factors, which are converted from a primarily repressor to an activator type by CDK-dependent phosphorylation (Araki et al. 2004). Importantly, the 26S proteasome-dependent degradation of mitotic cyclins, such as CYCB, through polyubiquitination by the E3 ubiquitin ligase complex known as anaphase-promoting complex or cyclosome (APC/C) is key to lowering CDK activity at the end of mitosis below a critical threshold, which is required for the assembly of prereplication protein complexes at DNA replication origins (Cebolla et al. 1999; Bryant and Aves 2011; Sanchez et al. 2012). This is a key step for resetting cell cycle regulation upon mitosis completion and for ensuring the unidirectional progress of the cell cycle (Figure 1.1).

1.2.1.3 Cytokinesis

Cell division in plants initiates in late-G2 before the onset of mitosis with the formation of the so-called preprophase band (PPB), which is a transient structure consisting of microtubules and actin filaments (Figure 1.1). PPB recruits many proteins cortically in a ring-like zone and it sort of imprints the site of deposition of the future cell wall at cytokinesis (i.e., the plane of cell division), before being disassembled in late prophase/early metaphase. A second plant-specific cytoskeletal structure, the phragmoplast, forms after mitosis is completed perpendicular to the future cell division plane from the microtubule and actin microfilament remnants of the mitotic spindle and expands bidimensionally toward the so-called cortical division site (CDS) at the cell periphery through depolymerization/polymerization of microtubules and microfilaments under the apparent guidance of cortical proteins previously recruited by the PPB, which act as a beacon for the growing phragmoplast. There are a plethora of genes involved in different aspects of cytokinesis, and it is noteworthy that CDKA localizes at cell division sites (Colasanti et al. 1993), and its activity may be important for microtubule depolymerization (Rasmussen et al. 2011). The phragmoplast functions as a cytoskeletal scaffold for the deposition of golgi-derived vesicles and their fusion at its midline, which leads to the formation of the cell plate that eventually fuses with the cell wall at the CDS, effectively partitioning the mother cell into two daughter cells. The term "cytokinesis" encompasses a vastly complex set of processes that include regulation of cytoskeletal structures proper, cytoskeleton-associated structural and motor proteins, vesicular trafficking, and membrane dynamics. These processes and the many genes involved have been reviewed in detail elsewhere (Otegui and Staehelin 2000; Hong and Verma 2008; Rasmussen et al. 2011, 2013; McMichael and Bednarek 2013).

1.2.2 Alternative Cell Cycles: Asymmetric Cell Division and Endoreduplication

1.2.2.1 Asymmetric Cell Division

Generally somatic cells (typically, meristematic cells) divide symmetrically to generate similar daughter cells. However, stem cell niches, cell differentiation, and tissue patterning are often associated with the formation of unequal cells through asymmetric cell division (De Smet and Beeckman 2011; Rasmussen et al. 2011). As daughter cells remain anchored to each other by sharing a cellulosic cell wall and virtually never move relative to one another, regulation of asymmetric cell division plays a very important role in cell differentiation and plant morphogenesis. According to classical views, differential cell fates of progeny cells are specified as a result of intrinsic factors (such as in the case of asymmetric placement of the cell plate along a polarity gradient to partition cell fate determinants unevenly) or the action of positional cues (such as in the case of apparently identical daughter cells that go on to take distinct fates under the influence of specific signals from different neighboring cells). Examples of asymmetric cell divisions include (1) the first division of the zygote, (2) procambial and hypophyseal divisions in the embryo, (3) root stem cells and initials, (4) vascular initials in the procambium, (5) stomatal development, and (6) formation of trichoblasts during the development of type-2 root hairs (Datta et al. 2011; De Smet and Beeckman 2011; Rasmussen et al. 2011; Zhang et al. 2012a). While the mechanisms characterizing these instances of asymmetric cell division have not been elucidated in sufficient detail to reveal any underlying potentially common themes, core cell cycle genes are known to impact at least some of them. For example, regulation of asymmetric cell division of the root initials that generate cortex and endodermis in *Arabidopsis* involves a pathway in which SHORT ROOT (SHR) and SCARECROW (SCR) transcription factors control the expression, directly or indirectly, of *CYCD6;1* as well as B-type CDKs, which is necessary for proper tissue patterning (De Smet et al. 2008; Sozzani et al. 2010; Cruz-Ramírez et al. 2012). RBR1, in its hypophosphorylated and active forms, appears to bind and inhibit SCR, while CYCD6;1-dependent phosphorylation and consequent inactivation of RBR1 provides a positive feedforward loop potentially generating a bistable circuit. Interestingly, *CYCD6;1* expression is stimulated by auxin, which reaches a relatively high concentrations specifically in the cortex/endodermis initial cell file, thus providing an explanation for the single formative division that characterizes them. Thus, precise integration of longitudinal auxin gradients and radial distribution of transcription factors, coupled with a narrow, proteasome-dependent temporal window of activation of the CDK-RBR1 pathway, seem to ensure proper coordination of cell cycle regulation with cell differentiation and root patterning (Cruz-Ramírez et al. 2012). In both shoot and root cells of *Arabidopsis*, the decision to divide symmetrically or asymmetrically depends on the level of CDKA;1 activity (high CDKA;1 activity promotes asymmetric division while medium levels stimulate symmetric divisions) and is mediated by a transcriptional pathways controlled by RBR1, which appears to be independent from E2F. Thus, RBR1 is emerging as a central player in integrating distinct pathways and processes and gating them at the cellular level to fine-tune cell cycle activity and to coordinate it with cell differentiation and tissue/organ growth and development (Sabelli and Larkins 2009a; Gutzat et al. 2012; Weimer et al. 2012; Sabelli et al. 2013).

1.2.2.2 Endoreduplication Cell Cycle

Endoreduplication (also known as endoreplication or endocycle) is a specialized cell cycle in which iterated rounds of nuclear DNA replication occur in the absence of chromatin condensation, nuclear membrane breakdown, mitotic spindle formation, sister chromatids segregation, and cytokinesis,

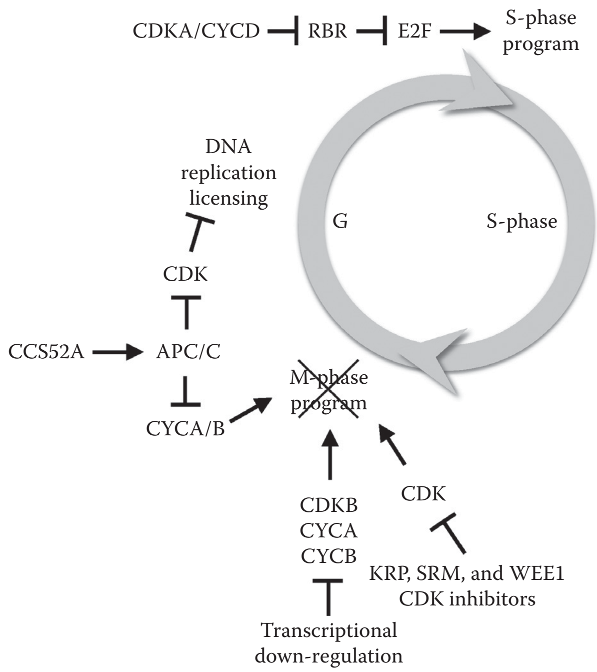

FIGURE 1.2 Schematic diagram of the regulation of the endoreduplication cell cycle, which consists of reiterated G- and S-phases in the absence of chromatin condensation, mitosis, and cytokinesis. As a result, endoreduplicated cells contain multiple genome copies (polyploidy), generally within large nuclei. During endoreduplication, a variety of mechanisms cause a downregulation of CDK activity, otherwise required for the execution of M-phase in proliferating cells. These may involve transcriptional downregulation of CDK and cyclin components, inactivation by specific inhibitors such as KRP, SRM, and WEE1, and enhanced cyclin degradation through an upregulation of APC/C by CCS52A. Decreased CDK activity may also stimulate licensing of DNA replication origins. Additionally, upregulation of the CDK–RBR–E2F pathway controlling the S-phase program may also occur during endoreduplication.

which results in endopolyploidy and usually large cells (Larkins et al. 2001; Sabelli and Larkins 2008; De Veylder et al. 2011) (Figure 1.2). Plant cells are frequently endoreduplicated, and the occurrence of this particular type of cell cycle is often associated with cell differentiation and tissue growth. Indeed, endoreduplication is the type of cell cycle that has been best characterized in agriculturally important systems such as the cereal seed endosperm (Sabelli 2012b), the symbiotic nitrogen-fixing nodules of legumes (Kondorosi and Kondorosi 2004), and the tomato fruit (Chevalier et al. 2011) (see later). Among other tissues that undergo endoreduplication, at least in certain species, are the embryo, suspensor, and cotyledons within the seed, the antipodal and synergid cells in the female gametophyte, the anther tapetum, the leaf trichomes, the epidermis of the stem and leaf, the hypocotyl, and the sites of certain biotrophic interactions (Larkins et al. 2001; Sabelli and Larkins 2008; De Veylder et al. 2011).

1.2.2.2.1 Specific Regulation of Endoreduplication

The mitotic cell cycle is characterized by exquisite coupling of chromosome segregation (M-phase) to successful execution of DNA synthesis (S-phase). Generally, a G2 DNA replication checkpoint sensing DNA integrity prevents M-phase entry until S-phase is completed. Equally important, DNA replication cannot initiate unless M-phase is completed and CDK activity drops below the threshold that prevents licensing of DNA replication origins. Together, the coordinated regulation of these two broad mechanisms is crucial for the orderly sequences of events characterizing mitotic cells, and to a large extent, it appears to depend on the timely activation and inactivation of specific

CDK/CYC complexes. Because endoreduplication consists of repeated rounds of DNA synthesis and Gap phases without intervening mitosis, it is conceivable that the regulatory programs that are responsible for mitosis are downregulated or even absent in endoreduplicating cells, while programs for S-phase are sustained or even upregulated (Figure 1.2). Indeed, the transition to the endocycle is typically characterized by the downregulation, through several distinct but likely entwined mechanisms, of CDK activity that is normally associated with and required for premitosis and M-phase in proliferating cells (Kondorosi and Kondorosi 2004; Sabelli and Larkins 2008; Chevalier et al. 2011; De Veylder et al. 2011). Generally, this involves transcriptional downregulation of B1-type CDKs and B-type and A2-type cyclins. This might result, in part, from failure to produce phosphorylated, and active, MYB3R transcription factors that control the expression of B-type cyclins (Araki et al. 2004) (Figures 1.1 and 1.2). Additionally, the levels of certain A-type and B-type cyclins, which are tightly regulated in mitotic cells by APC/C-mediated proteolysis, can be diminished in endoreduplicating cells below a critical threshold normally required for M-phase by increased proteasome activity. Indeed, the CELL CYCLE SWITCH 52A (CCS52A) protein, which is a CDH1-type activator of the APC/C involved in the degradation of mitotic B1-, A2-, and A3-type cyclins, is required for endoreduplication in a variety of plant systems and stimulates the endocycle if overexpressed (presumably by locking the APC/C in a constitutively active mode) (Cebolla et al. 1999; Vinardell et al. 2003; Larson-Rabin et al. 2009). Another mechanism for tuning down CDK activity involves the SIAMESE-RELATED (SMR) family of CKIs first identified in *Arabidopsis* but also found in rice (Peres et al. 2007). WEE1 is another well-established inhibitor of CDK activity at the G2/M-phase transition (Figure 1.2). However, it may also play important roles in the regulation of endoreduplication because its expression is associated with the endocycle in both tomato fruit and maize endosperm, and its downregulation in tomato results in lower ploidy levels and diminished fruit size (Sun et al. 1999a; Gonzalez et al. 2007). The sustained expression of WEE1 during endoreduplication in these systems, and its requirement for this type of cell cycle may be puzzling considering that, in *Arabidopsis*, WEE1 is involved in DNA damage checkpoint rather than the G2/M-phase transition. However, these proposed roles may not need to be mutually exclusive since active monitoring of DNA integrity might be integral to the regulation of the endocycle (Chevalier et al. 2011). Low CDK activity in early G1, upon completion of M-phase, is instrumental in mitotic cells for the assembly of prereplication complexes and the licensing of replication origins for DNA synthesis. Although the exact mechanisms for origin licensing during the endocycle are not clear, it is likely that they involve the general post-S-phase decrease in CDK activity that prevents M-phase. In fact, several proteins required for licensing DNA replication origin also undergo proteasome-dependent degradation through a CDK-phosphorylation-dependent mechanism (Castellano et al. 2004). Thus, low CDK activity could result in increased levels of factors required for licensing S-phase in the endocycle.

Upregulation of S-phase in endoreduplicating cells has been documented in plants, and it revolves largely around the (up)regulation of the CDK–RBR1–E2F pathway (Figure 1.2). This pathway controls the expression of many genes involved in DNA replication initiation, DNA synthesis, and S-phase. Consistent with the idea that upregulation of E2F activity leads to increased ploidy levels, endoreduplication has been stimulated by the downregulation of RBR1 in differentiating *Arabidopsis*, tobacco, and maize tissues (Park et al. 2005; Desvoyes et al. 2006; Sabelli et al. 2013), or directly by the upregulation of E2F/DP transcription factors (De Veylder et al. 2002; Kosugi and Ohashi 2003). In *Arabidopsis*, overexpression of genes involved in replication origin activation such as *CDC6* and *CDT1* stimulates endoreduplication (Castellano et al. 2001, 2004). Further upstream in the pathway, solid evidence implicates CDKA activity in inhibiting RBR-dependent suppression of S-phase (Nowack et al. 2012). In maize endosperm, downregulation of CDKA;1 inhibits endoreduplication through an RBR1-dependent pathway, though expression of specific RBR1-repressed genes is not affected (Leiva-Neto et al. 2004; Sabelli et al. 2013). Downregulation of the M-phase-specific CDK, CDKB1;1, stimulates endoreduplication (Boudolf et al. 2009), apparently because the activity of CDKB1;1/CYCA2;3 complex is needed to phosphorylate and activate MYB3R transcription factors, which are required for G2/M-phase-specific transcription (Araki et al. 2004).

In addition to the earlier mechanisms, several additional factors have been found to be important for endoreduplication in *Arabidopsis*, including atypical E2F-like proteins and DNA topoisomerase VI, and they have been reviewed elsewhere (Sabelli and Larkins 2008; De Veylder et al. 2011; Inagaki and Umeda 2011).

1.3 ENDOREDUPLICATION AS A POTENTIAL YIELD DETERMINANT

It is interesting that some of the best-characterized systems in crop species, in terms of the relationship between cell cycle regulation and development, concern the endoreduplication cell cycle. The main reason for this is that endoreduplication is often associated with cell/tissue growth and may play a key role in the development of agriculturally important organs and structures. Examples of this are the tomato fruit, the endosperm of cereal caryopsis, and the sites of interaction between plants and several symbiotic and parasitic/pathogenic organisms.

1.3.1 Endoreduplication and Tomato Fruit Development

The fleshy fruit of tomato contains two tissues, the mesocarp and the jelly-like locular tissue, in which cells undergo endoreduplication and can reach extremely large sizes. In general, tomato fruit development is characterized by a phase of intense cell proliferation (from about 2 to 10–12 days post anthesis, dpa), which is dependent on hormones released by the embryo, coinciding with the development of the ovary into a fleshy pericarp and of the placenta into a locular tissue with a gel-like appearance enveloping the seeds. This is followed by exit from the mitotic cell cycle and a transition into the endoreduplication cell cycle, which coincides with the growth of the fruit primarily by cell expansion. The phase of endoreduplication and growth by cell expansion continues essentially until the onset of fruit maturation and can result in ploidy levels in excess of 256C (C = the haploid DNA content of a given species) (Chevalier et al. 2011). Cell proliferation following fertilization generates most of the cells comprising the fruit and therefore plays a key role in controlling fruit size, but it has been little characterized. However, it is the endoreduplication phase of fruit development that has attracted considerable interest because of its potential for impacting fruit weight. Indeed, convincing evidence indicates that endoreduplication, cell size, and fruit weight or size are positively correlated (Cheniclet et al. 2005; Nafati et al. 2011).

Investigation has focused on understanding how cell cycle genes control the switch from mitotic cell proliferation to endoreduplication, and to what extent endoreduplication affects tomato fruit development and growth. The transition from mitotic cell cycle to endoreduplication and the ensuing cell expansion phase of fruit development are characterized by downregulation of *CDKA* expression and associated kinase activity (Joubès et al. 1999). In addition, the CDK-specific inhibitory kinase WEE1 is upregulated during endoreduplication. Constitutive downregulation of *WEE1* correlates with increased CDK activity, decreased ploidy levels, and smaller cell and fruit sizes, suggesting that endogenous WEE1 is required for endoreduplication-dependent cell expansion through inhibition of CDKA activity (Gonzalez et al. 2004, 2007).

Four CDK inhibitors belonging to the *KPR* family (*KRP1–4*) have been identified in tomato. The expression of *KPR2* and *KRP4* transcripts is more closely associated with early tomato fruit development, which is characterized by cell division, whereas *KRP1* and *KRP3* mRNAs are preferentially expressed during the subsequent endoreduplication phase, suggesting specific roles for the four inhibitors in the mitotic and endoreduplication cell cycles. Overexpression of *KRP1* under the control of a promoter (*PhosphoEnolPyruvate Carboxylase 2*) that is highly active in the mesocarp during the cell expansion phase of fruit development strongly inhibited endoreduplication between 10 and 20 dpa, and had little effect thereafter (Nafati et al. 2011). Interestingly, however, cell area and fruit size were not altered (but nuclear size was reduced), effectively uncoupling cell size from endoreduplication in this *KRP1*-overexpressing mutant and resulting in fruits with altered karyoplasmic ratios.

Modulation of APC/C activity also controls endoreduplication and cell/fruit size in tomato fruit tissue. The APC/C activator *CCS52A* is normally upregulated in endoreduplicating tomato fruit pericarp. Downregulation of CCS52A by RNAi had virtually no effect on cell division, but resulted in low ploidy levels and smaller cells and fruits, apparently through enhanced stability of CYCA3;1. In *CCS52A*-overexpressing lines, however, the growth of the fruit was also transiently impaired by mid-development, whereas it fully recovered at maturity, suggesting that high levels of CCS52A protein probably interfered with other cell cycle- and tissue patterning–controlling pathways in a developmental fashion. Recently, it was shown that, in individual pericarp cells, transcription of 5.8S rRNA, the large subunit of RNA polymerase II, as well as other genes associated with endoreduplication, such as *WEE1* and *CCS52A* (but not genes associated with M-phase, such as *CDKB2*), increases according to ploidy levels. This indicates that endoreduplication may be a means to selectively upregulate gene expression (Bourdon et al. 2012). Interestingly, the topology of the nuclear membrane appears to undergo important changes in endoreduplicated cells. Large (i.e., endoreduplicated) nuclei have an invaginated and expanded surface, which contributes to maintaining the capacity of the nucleus to exchange molecules with the surrounding cytoplasm roughly constant (which would otherwise decline with increased nuclear volume if the surface were smooth). The nuclear surface invaginations are populated by relatively large numbers of active mitochondria. Together, these results support the idea that endoreduplication in tomato fruit entails larger nuclear and cell sizes, thus supporting the karyoplasmic ratio theory, and leads to specific increases in gene expression levels. Endoreduplicated nuclei are deeply grooved, thus with a relatively larger surface area available for molecular trafficking between nucleus and cytoplasm, which would be an asset for supporting increased levels of gene expression. The presence of large numbers of active mitochondria in the nuclear grooves is in agreement with the long-hypothesized role for endoreduplication in supporting high metabolic rates (Bourdon et al. 2012).

1.3.2 Endoreduplication and Cereal Endosperm Development

The starchy endosperm of cereal seeds is a key source of dietary calories and raw materials for myriad manufactured goods worldwide. The development of the endosperm has been best characterized in maize, which recapitulates well the main events also occurring in other cereals (Sabelli and Larkins 2009b,c) (Figure 1.3). Following double fertilization, endosperm development begins with a series of acytokinetic divisions of the triploid primary endosperm nucleus to give raise to a syncytium, which becomes cellularized a few days after pollination (DAP). A phase of mitotic cell division then ensues, which generates the vast majority of endosperm cells. Subsequently, in cereals, cells gradually transition to an endoreduplication phase that coincides with rapid cell expansion, the accumulation of storage compounds, and the massive growth of the endosperm and the caryopsis (Kowles and Phillips 1985; Larkins et al. 2001; Sabelli and Larkins 2009b; Sabelli 2012b). Endosperm endoreduplication, which in maize can generate ploidies in excess of 192C, appears to be ubiquitous among cereal crops but it is absent in dicots (Sabelli 2012a). Starchy maize endosperm displays a heterogeneous population of endopolyploid cells as endoreduplication begins in the center of the endosperm and spreads toward the periphery of the tissue so that inner cells are typically more highly endoreduplicated, and larger, than peripheral cells. The chromosomes in endoreduplicated cells have a loose polythenic structure and appear to be fully replicated and tightly associated at centromeric and knob regions (Kowles and Phillips 1985; Bauer and Birchler 2006). Analyses of interploidy crosses and manipulation of key cell cycle genes suggest that maize endosperm endoreduplication involves extensive reorganization of chromatin domains (Bauer and Birchler 2006; Sabelli et al. 2013).

Endoreduplication in maize endosperm appears to entail a downregulation of the M-phase program and an upregulation of the S-phase program. Several observations support this view. For example, endoreduplicated endosperm (at 16 DAP) displays a peak in S-phase-associated CDK activity, whereas mitotic endosperm (10 DAP) has a peak in M-phase-associated CDK activity (Grafi and

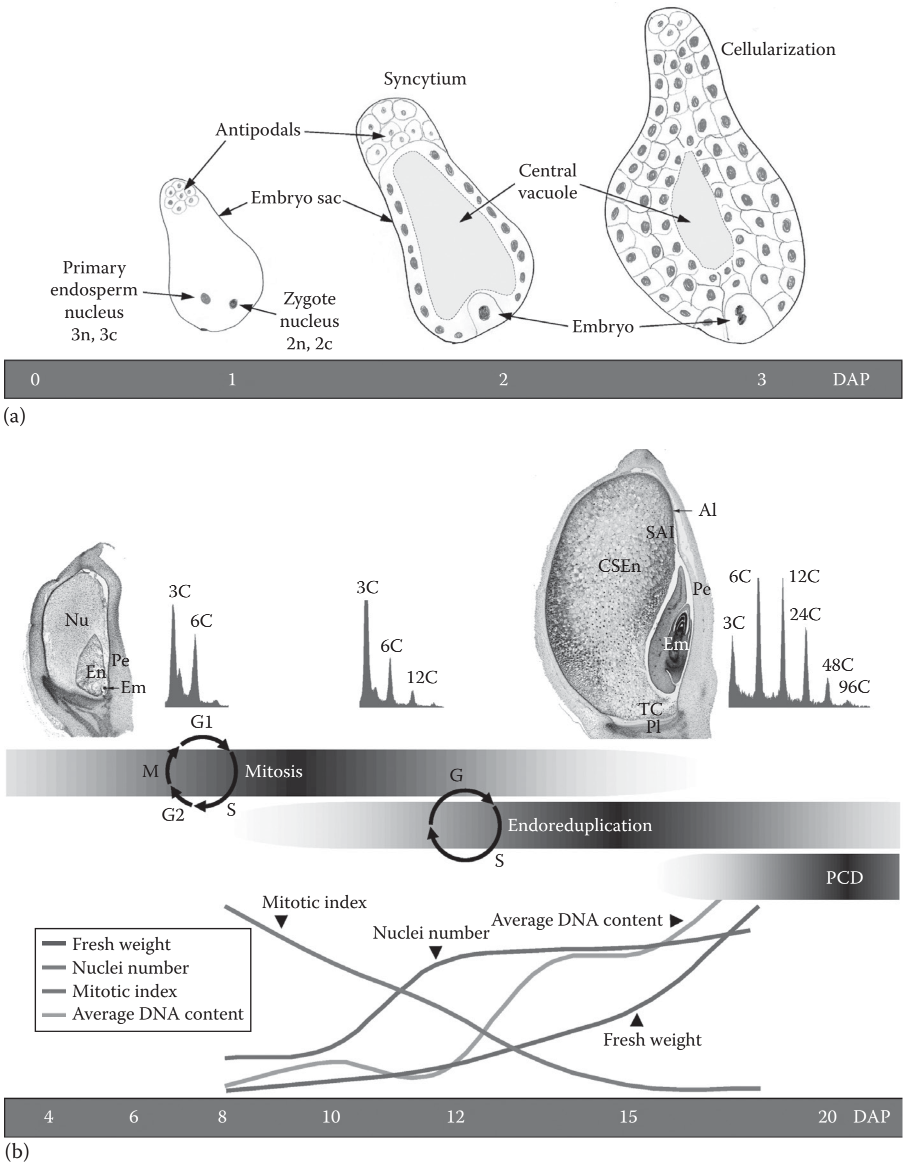

FIGURE 1.3 (**See color insert.**) Cell cycle regulation during maize endosperm development. (a) Following double fertilization, early endosperm development involves acytokinetic mitoses starting with the triploid primary endosperm nucleus, which results in a syncytium surrounding the central vacuole within the embryo sac. At around 3 days after pollination (DAP), the endosperm becomes cellularized through an open-ended alveolation process toward the central vacuole until cellularization is complete. (b) After cellularization from about 4 DAP, the endosperm develops through a phase of mitotic cell proliferation, followed (from around by 8 to 10 DAP) by endoreduplication (as shown by flow-cytometric profiles), and by programmed cell death (PCD) (starting around 16 DAP). The endoreduplication phase and the last part of the cell division phase coincide with a dramatic growth of the endosperm and the synthesis and accumulation of storage compounds. The graph at the bottom illustrates trends in endosperm fresh weight, nuclei number, mitotic index, and mean DNA content (C value). Al, Aleurone; CSEn, central starchy endosperm; Em, embryo; En, endosperm; Nu, nucellus; Pe, pericarp; Pl, placentochalaza; SAl, subaleurone layer; TC, transfer cells. (Reproduced in part from Larkins, B.A. et al., *J. Exp. Bot.*, 52, 183, 2001; Sabelli, P.A. et al., *Maydica*, 40, 485, 2005b. With permission from Oxford University Press and *Maydica*.)

Larkins 1995). Downregulation of CDKA;1 activity, through ectopic expression of a dominant-negative *CDKA;1* allele, resulted in an approximately 50% decrease in ploidy levels, indicating that this CDK is necessary for S-phase in endoreduplicating endosperm cells (Leiva-Neto et al. 2004) (Table 1.1). Further analyses of a double *CDKA;1/RBR1* mutant revealed that CDKA;1 controls endoreduplication through an RBR1-dependent pathway, most likely by targeting RBR1 for inhibitory phosphorylation at the G/S-phase transition (Sabelli et al. 2013). The pattern of *CYCB1;3* RNA accumulation shows a dramatic decline at the mitosis–endoreduplication transition during endosperm development, which suggested a specific involvement for this cyclin in M-phase and supported the idea that the M-phase program is downregulated in endoreduplicating endosperm (Sun et al. 1999b). Consistent with this interpretation, the expression of the M-phase CDK-specific inhibitor *WEE1* peaks in endoreduplicated cells (Sun et al. 1999a). CYCA1;3-associated kinase activity was present in 9-DAP endosperm, and it phosphorylates RBR substrates in vitro (Sabelli et al. 2005a), which suggests that CYCA1;3 could be a component of S-phase CDK activity at least in mitotic endosperm. Two CDK inhibitors belonging to the KRP family have been characterized during endosperm development, *KRP1* and *KRP2*, and although they appear to have similar activities toward CDK complexes containing CYCA1;3, CYCD5;1, and CYCB1;3, they have been shown to have different patterns of protein accumulation. Whereas KRP1 protein is expressed at a roughly constant level, KRP2 declines substantially in endoreduplicated endosperm cells, which may indicate preferential roles for these two CKIs in regulating the oscillation of CDK activity in the endocycle and mitotic cell cycle (Coelho et al. 2005). Another key factor controlling S-phase entry is *RBR1*. In maize, the RBR family of genes comprise at least four members, *RBR1–4*, organized into two closely related groups: *RBR1*-type (comprising also *RBR2*) and *RBR3*-type (comprising also *RBR4*) (Sabelli et al. 2005a, 2013; Sabelli and Larkins 2006, 2009a). Within each group, RBR genes have similar expression patterns, but while *RBR3*-type genes are preferentially expressed during the mitotic phase of endosperm development, the expression of *RBR1*-type genes is sustained during the endoreduplication phase. *RBR1* represses the expression of *RBR3* in endoreduplicated endosperm just like it does other E2F targets required for DNA replication. *CDKA;1* and *RBR1* are epistatic with regard to endoreduplication, but it is intriguing that they are uncoupled in the control of downstream gene expression. This is in contrast with the situation in *Arabidopsis* where *CDKA;1* and *RBR1* are tightly coupled (Nowack et al. 2012). Both CDKA and RBR activities are encoded by multiple genes in maize compared to a single gene in *Arabidopsis*. Thus, CDKA- and RBR-dependent pathways in maize appear to be considerably more complex than their counterparts in *Arabidopsis*. Importantly, downregulation of RBR1 activity in maize endosperm stimulates S-phase gene expression and endoreduplication, but the increase in nuclear DNA content does not result in proportionally more active chromatin or increases in nuclear size, cell size, or mature kernel weight (Sabelli et al. 2013). Collectively, these studies suggest that *RBR1* controls important aspects concerning epigenetic mechanisms, chromatin structure and organization, and the coupling of cell size to DNA content. In maize, the role of the APC/C in endoreduplication and endosperm development has not been investigated, but recent work in rice suggests that the APC/C activator *CCS52A* homolog plays an important positive role in these processes (Su'udi et al. 2012), consistent with other systems.

In spite of a large of body of correlative evidence linking endoreduplication to the expansion of endosperm cells, the accumulation of storage compounds, and the growth of the whole tissue, definite proof that it controls seed size and yield remains elusive (Sabelli 2012b). This is believed to be partly due to the difficulty to disentangling cell cycle regulation from cell differentiation during seed development.

1.3.3 Endoreduplication and Biotrophic Interactions

Interactions between plants and other organisms are often agriculturally very important. In certain cases, both symbiotic and parasitic interactions involve and require endoreduplication of the affected plant tissue, probably as part of a metabolic strategy enabling and supporting the relationship (Kondorosi and Kondorosi 2004; Wildermuth 2010).

TABLE 1.1
List of Genes and QTLs Controlling the Cell Cycle That May Impact Crop Yield

Crop	Gene/QTL	Encoded Product	(Putative) Function	Phenotype (Gene Up- or Downregulation)[a]	References
Wheat	*Ph1*	CDK2-like kinase	Prevents homeologous chromosome pairing	Down: Homeologous pairing and stability of polyploidy genome	Griffiths et al. (2006)
Barrel medic	*CCS52A*	CCS52A, a CDH1-type activator of the APC/C	Positive regulator of mitotic cycle/endocycle transition	Down: Decreased endoreduplication, cell size and development of root nodules. Increased lethality	Vinardell et al. (2003)
	CDC16	Component of APC/C	Positive regulator of APC/C-dependent degradation of mitotic cyclins	Down: Decreased sensitivity to auxin, reduced root apparatus, and increased number of root nodules	Kuppusamy et al. (2009)
Tomato	*FW2.2*	Transmembrane protein	Repression of cell proliferation during fruit development	Down: Increased fruit size/fresh weight	Frary et al. (2000); Cong and Tanksley (2006)
	SlCCS52A	CDH1-type activator of the APC/C. Ortholog of *Medicago* CCS52A	Positive regulator of mitotic cycle/endocycle transition	Down: Decreased endoreduplication, cell size, and fruit size	Mathieu-Rivet et al. (2010)
Maize	*tb1*	Class II TCP transcription factor	Negative regulator of cell cycle–dependent gene expression	Up: Reduced branching/Increased grain yield	Studer et al. (2011)
	CNR1 and *CNR2*	Related proteins to FW2.2 from tomato	Negative regulator of cell proliferation	Up or down: Negatively correlated with organ size	Guo et al. (2010b)
	CDKA;1	CDKA;1 cell cycle–controlling kinase	Regulator of G1/S-phase and G2/M-phase transitions during mitotic cycle	Down: Decreased endosperm endoreduplication. No effect on kernel size	Leiva-Neto et al. (2004)
	RBR1	RBR1 protein	Negative regulator of E2F-dependent gene expression and cell cycle progression	Down: Increased endosperm endoreduplication and cell number. No effect on kernel size/weight	Sabelli et al. (2013)
Rice	*KRP1*	CDK/CYC specific inhibitor	Regulator of mitotic cycle/endocycle transition in endosperm	Up: Decreased endosperm endoreduplication, seed-filling rate and weight	Barrôco et al. (2006)
	CYCB1;1	B-type cyclin	Positive regulator of mitotic cell cycle in syncytial endosperm	Down: Abortive endosperm due to abnormal cellularization	Guo et al. (2010a)

(*continued*)

TABLE 1.1 (continued)
List of Genes and QTLs Controlling the Cell Cycle That May Impact Crop Yield

Crop	Gene/QTL	Encoded Product	(Putative) Function	Phenotype (Gene Up- or Downregulation)[a]	References
	CYCB2;2	B-type cyclin	Positive regulator of M-phase	Up: Increased root cell number and growth	Lee et al. (2003)
	TE/TAD1/ OsCCS52A	CDH1-type activator of the APC/C. Ortholog of *Medicago* CCS52A	Positive regulator of APC/C-dependent degradation of MOC1 and mitotic cycle/endocycle transition	Down: Increased axillary meristem activation and tillering. Decreased endosperm endoreduplication, cell size, and seed size (width) and fertility	Lin et al. (2012); Su'udi et al. (2012); Xu et al. (2012)
	GW2	RING-type E3 ubiquitin ligase	Negative regulator of cell proliferation in spikelet hull	Down: Increased grain width/weight	Song et al. (2007)
	GS3	Transmembrane protein	Negative regulator of ovule development/ grain length	Down: Increased grain length/size	Fan et al. (2006); Takano-Kai et al. (2009)
	GS5	Serine carboxypeptidase	Positive regulator of cell proliferation in palea/lemma	Up: Increased seed size (width) and weight	Li et al. (2011)
	qSW5/GW5	Nuclear protein interacting with polyubiquitin	Negative regulator of cell number in outer glume	Up: Increased seed size	Shomura et al. (2008); Weng et al. (2008)
	GW8	OsSPL16 transcription factor	Positive regulator of *CDKA1*, *CYCD3* and *E2F2* expression, and cell proliferation in spikelet hull	Up: Increased grain width, filling, and yield	Wang et al. (2012)
	TGW6	IAA-glucose hydrolase	Positive regulator of *CYCB2;2* and *E2F1* expression in syncytial endosperm	Down: Delayed endosperm cellularization; Increased endosperm cell number, grain length, and weight	Ishimaru et al. (2013)
	qGL3	OsPPKL1 type 2A phosphatase	Negative regulator of cell proliferation in spikelet hull	Down: Increased grain length, weight, and yield	Zhang et al. (2012b)
	SG1	Novel protein	Negative regulator of cell number	Up: small seed size (length)	Nakagawa et al. (2012)
	HGW	Novel ubiquitin-associated (UBA) domain protein	Positive regulator of cell number in spikelet hull	Down: Decreased seed size (width)	Li et al. (2012)
	RSS1	Novel interactor of protein phosphatase 1, and substrate of APC/C	Positive regulator of meristem cell proliferation under salt stress	Down: Decreased SAM size, dwarfism, and short root under salt stress	Ogawa et al. (2011)

[a] Gene up- or downregulation may refer to mutant loss of function, RNAi downregulation, overexpression, or gain of function.

1.3.3.1 Endoreduplication and Symbiotic Interactions

One of the best characterized symbiotic interactions occurs between legumes, such as *Medicago truncatula* or *sativa* with endosymbiotic, nitrogen-fixing bacteria, such as *Sinorhizobium meliloti*, which results in the formation of specialized lateral root organs known as root nodules that provide nitrogen to the plant. These nodules, which are characterized by indeterminate development, are induced in the root cortex by infective threads and typically consist of an apical meristematic zone, an infection zone, a symbiotic zone, and a senescent zone sequentially distributed according to the longitudinal axis of the growing nodule. Root nodule cells exit the mitotic cell cycle and undergo endoreduplication below the meristematic zone, particularly in the infection zone and the symbiotic zone, the latter becoming populated with N-fixing bacteroids (Kondorosi and Kondorosi 2004). Endoreduplication is a requirement for the development of functional root nodules and is achieved primarily by enhanced APC/C-dependent proteolysis of mitotic cyclins. Integral to this process is the upregulation of the activator of APC/C, *CCS52A* (Cebolla et al. 1999; Vinardell et al. 2003). As a result, the mitotic program is skipped (Figure 1.2), and cells continue to replicate their DNA (up to 64C) without cell division, dramatically enlarging in the process.

Endoreduplication is also involved in the establishment of arbuscular mycorrhizal symbiosis (AMS), where the fungus provides the plant with the majority of its phosphorus requirements. Here, too, there is evidence that not only chromatin decondensation and nuclear enlargement of host root cells, typical of endoreduplication, are associated with AMS, but also their onset precedes and may be required for fungal infection (Genre et al. 2008; Wildermuth 2010).

1.3.3.2 Endoreduplication and Parasitic/Pathogenic Interactions

Powdery mildews (PMs) are obligate biotrophic ascomycetes that cause widespread disease to thousand of angiosperms, including important crops such as wheat, barley, and grape (Glawe 2008). PMs establish feeding sinks in the plant host by infecting cells with haustorial complexes, which acquire nutrient resources from the plant. In the case of *Arabidopsis* leaves infected with *Golovinomyces orontii*, the haustorial complexes infect epidermal cells, and this is associated with endoreduplication (resulting in a mean ploidy of 32C) in the underlying mesophyll cells, with their concomitant increases in nuclear and cell volumes. Transcript and genetic analyses identified one member of the MYB3R family of transcription factors associated with M-phase (*MYB3R4*) as a key factor for PM-induced host cell endoreduplication (Chandran et al. 2010). Because MYB3R transcription factors may inhibit transcription when hypophosphorylated and appear to be activated by CDK-dependent phosphorylation (Figure 1.1), a variety of mechanisms impinging on CDK activity could contribute to regulating *MYB3R4*-dependent gene expression in this system. Additionally, three other *Arabidopsis* genes (*PUX2*, *PMR5*, and *PMR6*), which are also suspected to be involved in the regulation of M-phase, have recently been involved in control of PM-associated mesophyll cell endoreduplication. The evidence obtained so far indicates that endoreduplication in specific mesophyll cells underlying infected epidermal cells coincides with a shift in carbohydrate metabolism toward fermentation, which could favor the metabolic requirements of PM. Endoreduplication of host cells associated with infection sites has recently been established as a determinant of susceptibility to PM infection (Chandran et al. 2013).

Nematode infections in the root apparatus cause large losses in many crops, such as tomato, soybean, and potato. Two main infection types are relevant to the present discussion; those caused by cyst nematodes, which include the genera Heterodera and Globodera, and those caused by root-knot nematodes (genus *Meloidogyne*) (Williamson and Hussey 1996). These obligate sedentary parasites typically penetrate the root and migrate toward the vascular tissue where they establish so-called nematode feeding sites (NFS), causing distinct responses in the affected cells of the procambium. In the case of cyst nematodes, a procambium cell develops into a multinucleate, metabolically active feeding site by incorporating adjoining cells through cell wall dissolution and protoplast fusion. In root-knot nematode infections, instead, feeding sites consist of small groups of giant cells with multiple (up to 100) enlarged nuclei, resulting from acytokinetic mitoses and endoreduplication. Eventually, reactivation of cell division in the cell layers surrounding the feeding sites results in tissue enlargement and the formation of galls (Williamson and Hussey 1996; Wildermuth 2010; de Almeida Engler et al. 2012).

Thus, stimulation of root cells associated with the vascular tissue to reenter the cell cycle as well as activation of the endoreduplication program are common themes in both types of nematode infections (De Almeida Engler and Gheysen 2013). Recently, functional genetic analyses of NFS utilizing *Arabidopsis* lines with altered expression of several genes known to impact the G2/M-phase transition and endoreduplication (i.e., *CCS52A*, *CCS52B*, *DEL1*, and *RHL1*) have suggested that coordination of mitotic with endoreduplication cell cycle is important for the establishment and the expansion of functional feeding sites both for root-knot and cyst nematodes (De Almeida Engler et al. 2012).

Thus, the alteration of plant cell cycle regulation by other organisms appears to be key both in the case of symbiotic (i.e., N-fixing root nodules, AMS) and pathogenic/parasitic (i.e., PM/nematode infections) relationships. Endoreduplication, in particular, may be a strategy to increase the metabolism of plant cells to support symbiotic or parasitic organisms alike (Wildermuth 2010). Thus, targeted regulation of the cell cycle may be a valuable strategy to control these biotrophic associations in agricultural settings.

1.4 REGULATION OF PLANT BIOMASS AND ARCHITECTURE

1.4.1 Reproductive Development

1.4.1.1 Gametogenesis

A notable involvement of core cell cycle genes in cell fate- and cell differentiation-related decisions occurs during male gametogenesis in *Arabidopsis* (Iwakawa et al. 2006; Borg et al. 2009). Following asymmetric division of the microspore at pollen mitosis I into one large vegetative and one small generative cell, proper differentiation of sperm cells depends on selective proliferation of the generative cell, while the vegetative cell exits the cell cycle. *RBR1* is essential in restricting cell cycle activity in both cell types. Correct regulation of cell proliferation of the generative cell requires *CDKA;1* and is specifically sustained through FBL17-dependent degradation of KRP inhibitors by the proteasome. Interestingly, FBL17 is a direct transcriptional target of RBR1 and E2F, which closes the negative KRP ┤ CDKA;1 ┤ RBR1 ┤ E2F → FBL17 ┤ KRP feedback loop and essentially provides a bistable switch predicted to be heavily dependent on the levels of KRP activity. This module has been proposed as a general controlling mechanism for the G1/S-phase transition in *Arabidopsis* and elements of it have been shown also to control the first two divisions during female gametophyte development (Zhao et al. 2012). Moreover, recent results in maize endosperm where downregulation of *RBR1* results in increased CDKA;1 activity (Sabelli et al. 2013) suggest that this pathway may regulate S-phase entry also in monocots. In addition to the module described earlier, high levels of expression of CYCB1;1 appear to contribute to maintaining CDKA;1 activity high, which is necessary for the formation of two sperm cells (Brownfield et al. 2009). Additional factors are important for pollen microspore cell divisions, such as *SAMBA*, a component of the APC/C, which is involved in the proteolysis of CYCA2;3 and in maintaining the ratio of M-phase-related transcripts versus those of CDK inhibitors relatively high (Eloy et al. 2012).

Besides the regulation of cell division during male gametogenesis, cell cycle genes are also important for other steps in reproductive development. Examples of this are *CYCA1;2*, which is required for the correct execution of metaphase at meiosis during female gametophyte development (Wang et al. 2004b); *MCM7*, which is required for cell divisions in the female gametophyte (Springer et al. 2000); and *RBR1*, which is required also for female gametophyte development (Ebel et al. 2004) and for the control of key epigenetic mechanisms during sexual reproduction (Sabelli and Larkins 2009c). Additionally, R2R3 MYB transcription factors, known to control M-phase-related cell cycle genes (Figure 1.1), are important for embryo sac development (Makkena et al. 2012). A number of cell cycle gametophytic mutants have been reviewed elsewhere (Liu and Qu 2008).

1.4.1.2 Seed Development

The production of vast amount of grain is one of the most outstanding outcomes of modern agriculture. One monocot family (Poaceae) and one dicot family (Leguminosae or Fabaceae) contribute the species that are responsible for the vast majority of grain production worldwide. At the individual seed level, yield is given by two major components: the seed growth rate (SGR) and the seed-filling duration (SFD), which have been thoroughly discussed by Egli (1998, 2006). Seed development generally comprises three phases: A first formative phase (phase I), which begins at fertilization and is characterized by rapid cell division; a middle phase (phase II), during which economically and nutritionally valuable compounds are accumulated and stored; and a third maturation phase (phase III), which begins with a decrease in the accumulation of storage metabolites, includes physiological maturity (i.e., maximum seed dry weight), and finally involves dehydration (Sabelli and Larkins 2009b,c). During phase I, rapid cell division is responsible for creating most of all the cells that will make up the storage structures of the seed or fruit. In the Poaceae, these are primarily the endosperm but also, in some cases, the embryo, whereas in the Fabaceae, it is (mostly) the cotyledons (Sabelli 2012a). During this phase, the domains of the seed that are important for establishing transfer cells, as a specialized link with the mother plant's vascular tissue for the uptake of metabolic precursors by the seed, are also specified. This phase is characterized by sucrose uptake that is quickly metabolized to glucose and fructose by cell wall–bound invertase to support intense cell division activity. Although this phase is critical for seed development and grain yield, the resulting cells generated are very small, and overall the direct contribution of this phase to seed biomass is rather minor. Phase II is characterized by the deposition of storage reserves according to a linear pattern in which the accumulation of dry matter is constant with time. This phase is characterized by cell expansion resulting, in part, from an initial increase in seed water content, so that seed size throughout phase II and at maturity reflects almost entirely cell volume. This phase is characterized in cereals by endoreduplication, discussed earlier, which is associated with the sizes of the cell and the storage compartment (Sabelli and Larkins 2009b,c) (Figure 1.3). During phase III, the seeds reaches its physiological maturity, which represents the end of the seed-filling period. At this stage, the seed becomes functionally severed from the vascular system of the mother plant and begins to lose moisture at a rate that is species-specific for a given environment. Seed size is closely associated not only with SGR ($r = 0.81$) but also, to a lesser extent, with SFD ($r = 0.5$) (Egli 1998; Sabelli and Larkins 2009c). SGR is determined largely by genetic control, and it is possibly influenced by the flux of assimilates from the mother plant as well as by intrinsic mechanisms to the seed. A number of studies indicate that there is a positive correlation between SGR and the number of cells of the storage tissues within the seed: the cotyledons or the endosperm. Regulation of the cell cycle contributes to seed development in several important ways: In both monocots and dicots, the first zygotic division is asymmetric, generating a cytoplasmic-dense apical cell projected toward the chalaza and a large vacuolated basal cell toward the micropylar end of the embryo sac. This asymmetric division leads to the establishment of embryo bipolarity and patterning. Subsequent intense cell proliferation coupled to cell differentiation essentially produces all embryo structures including the cotyledon(s) and the suspensor (Sabelli 2012a). In *Arabidopsis*, embryo development and seed size are negatively affected by SAMBA, a negative regulator of the APC/C (Eloy et al. 2012). Additionally, a recent comprehensive investigation on D-type cyclins highlighted the importance of proper spatiotemporal regulation of CYCD expression for embryo cell division, patterning, and seed development (Collins et al. 2012). *DEL1* is known to inhibit the endocycle, and loss of its function results in a small but significant increase in *Arabidopsis* seed size, though the underlying mechanism is not known (Van Daele et al. 2012). Moreover, there is evidence that the coordination of cell proliferation with tissue patterning during *Arabidopsis* seed development depends on a signaling pathway that involves the peptide ligand

CLAVATA3/EMBRYO SURROUNDING REGION-RELATED8 (CLE8) and the transcription factor WUSCHEL-LIKE HOME-OBOX8 (WOX8) (Fiume and Fletcher 2012).

The endosperm develops most often through the so-called nuclear type pattern of development, which involves early acytokinetic divisions of the primary endosperm nucleus that generate a syncytium. Subsequent cellularization of nuclear domains results in a cellular endosperm that goes on to proliferate by standard mitosis coupled to cell divisions. However, while the endosperm is absorbed by the growing embryo in nonendospermic species such as *Arabidopsis*, in cereals, endosperm cells exit the mitotic cell cycle and engage in reiterated rounds of genome replication, known as endoreduplication, which is associated with cell expansion and accumulation of storage compounds (see Section 1.3.2). While endoreduplication correlates with cell and endosperm sizes in cereals, the rate and potential of grain filling correlate with the number of starch granules, which, in turn, depends on cell number and therefore the extent of the cell proliferation phase (Brocklehurst 1977; Reddy and Daynard 1983; Chojecki et al. 1986a,b; Jones et al. 1996; Sabelli and Larkins 2009b). A number of endosperm mutants in *Arabidopsis* resulting in small or aborted seeds display cell cycle defects during the syncytium and cellularization phases of endosperm development, indicating that correct regulation of early nuclear proliferation and the timing of the transition to cellularized endosperm are important for the attainment of proper seed size (Sabelli and Larkins 2009c). In rice, *TGW6*, encoding an IAA-glucose hydrolase, appears to stimulate the expression of *CYCB2;2* and *E2F1* during the first 3 days after fertilization and to hasten early endosperm nuclear proliferation leading to premature cellularization, which reduces endosperm cell number, length, and grain weight significantly (Ishimaru et al. 2013). This indicates that regulation of the duration of the syncytium period is also important for the development and the yield of cereal grain. Interestingly, the same investigation suggested that downregulation of *TGW6* may play an important role in mitigating yield losses due to climate warming. Supporting the view that proper syncytium development and endosperm cellularization are crucial, conserved aspects of seed development, knockdown of *OsCYCB1;1* interfered with cellularization, caused aborted endosperm, enlargement of the embryo, and overall abnormal seed development (Guo et al. 2010a). Also, the role of *KRP3* may be key in specifically inhibiting CDKA activity during syncytial endosperm proliferation in rice (Mizutani et al. 2010).

Besides playing an important role in controlling the number of cells in the main seed storage tissue, cell proliferation must be coordinated between endosperm and seed coat for proper seed development (Ingouff et al. 2006; Li and Berger 2012). In addition, there is increasing evidence indicating that factors controlling the cell cycle and regulation of epigenetic mechanisms during seed development are intertwined and that the RBR pathway may be central to their integration (Sabelli and Larkins 2009c).

1.4.2 Shoot Branching

Following embryonic development, where the apical–basal body axis is established with the formation of the two apical meristems, the architecture of the aboveground plant structures, which is extremely diverse, is largely due to the regulation of shoot branching, which depends on the development of secondary growth axes. These axes ultimately derive from the shoot apical meristem, through the iterated formation of axillary meristems, which may develop into buds, stems, leaves, and reproductive structures (Müller and Leyser 2011). Shoot branching (known as tillering in grasses) may negatively affect grain yield, because often branches and the reproductive organs they bear compete for limited resources. Thus, reduction in tillering has been one of the key traits that has been selected during the domestication of several cereal crop species, such as maize and millet (Studer et al. 2011; Kebrom et al. 2013). However, increased shoot branching may be a desirable trait for some cereal crops, such as rice. Axillary meristem development and activity are controlled by phytohormones as part of a complex regulatory web of genetic information and external stimuli. Generally, it is repressed by auxin and strigolactones and stimulated by cytokinin.

The cell cycle plays an important role in branching. Bud activation and outgrowth in pea correlate with cell cycle entry as revealed by increased expression of several cell cycle genes, such as *PCNA*, which is involved in the regulation of DNA synthesis, *CYCD3*, and *CYCB1;2* (Shimizu and Mori 1998). Expression of cell cycle genes and bud outgrowth are inhibited by the *TCP* (for *TEOSINTE BRANCHED, CYCLOIDEA, PROLIFERATING CELL FACTORS 1 and 2*) family of transcription factors (Müller and Leyser 2011). TCP transcription factors are stimulated further upstream by strigolactone and inhibited by cytokinin. Although this pathway linking transactivation of cell cycle genes, cell proliferation, and bud outgrowth with phytohormones, centered on TCP transcription factors, is conserved in monocots and dicots, there may exist important differences between the two phyla in its fine-tuning (Kebrom et al. 2013). With regard to the role of cell cycle regulation in controlling shoot branching, there is evidence to suggest that while increased expression of certain cell cycle genes (such as D-type cyclins) can enhance bud outgrowth, it is not sufficient to activate buds or stimulate shoot branching. Conversely, upregulation of cytokinin results in increased bud activation and branching, while it has little effect on bud growth rate. In summary, the cytokinin-TCP cell cycle pathway appears to play an important role in plant branching and architecture, though several important aspects concerning its regulation remain to be understood in more detail (Müller and Leyser 2011). Recent evidence also implicates CCS52A in the regulation of tillering in rice through proteolysis of MONOCULM1 (Lin et al. 2012; Xu et al. 2012).

1.4.3 Leaf Development

Development and growth of leaves depend on several cell-autonomous and cell-nonautonomous pathways impinging on cell division and expansion (Fleming 2007; Gonzalez et al. 2012; Nelissen et al. 2012; Powell and Lenhard 2012). In both monocots and dicots, intense cell proliferation characterizes the growth of the leaf primordium, which is followed by a transition from the mitotic into the endoreduplication cell cycle that coincides with the onset of cell expansion and differentiation. Leaf size in *Arabidopsis* is determined to a large extent by cell number, which appears to be a common denominator in several mutants seemingly affecting different pathways (Gonzalez et al. 2010). The RBR1–E2F pathway plays a central role in linking the cell cycle to leaf development, but its influence is mostly context dependent. Upregulation of E2F activity results in increased cell proliferation or endoreduplication, depending on whether cells are undifferentiated within immature leaves or differentiated (Kosugi and Ohashi 2003). Accordingly, *RBR1* is involved in restricting progression of the mitotic or endoreduplication cycle based on context (Desvoyes et al. 2006). Upregulation of the E2F pathway, with prolongation of the cell division phase and hyperproliferation of leaves, is also obtained by overexpression of *CYCD3;1* (Dewitte et al. 2003). However, the situation is probably more complex, and it has recently been proposed that the effect on leaf shape upon downregulation of *RBR1* is primarily due to smaller cell size rather than increased cell division rates (Kuwabara et al. 2011). Although changes in the duration of the proliferation phase strongly correlate with final leaf size (Mizukami and Fischer 2000; Li et al. 2008; Dhondt et al. 2010; Nelissen et al. 2012), not necessarily increased cell division through the modification of core cell cycle genes results in larger leaves, often because of compensatory effects on cell size that offset cell proliferation changes (Powell and Lenhard 2012). Indeed, leaf development is commonly regarded as one of the best examples of the dependence of (cell-autonomous) cell division activity on higher-order control at the tissue or organ levels (see later). However, reduced cell proliferation and leaf size in *scr* and *shr* mutants have been linked to E2F-dependent cell cycle defects (Dhondt et al. 2010), suggesting that the *SCR–RBR1* pathway works similarly in leaves and roots, although only in the latter system, there is an obvious stem cell population, where these two genes are known to play key roles. Additionally, there is evidence that other genes such as *APC10*, *CDC27a*, and *SAMBA*, which control different components of the APC/C, play important roles in controlling mitotic activity, cell number, and leaf growth (Rojas et al. 2009; Eloy et al. 2011, 2012). Development of the leaf in cereals involves transitioning between a basal division zone, an expansion zone, and an apical zone along the longitudinal leaf axis. The boundary between the division and the expansion zones is characterized by a downregulation of genes involved in M-phase, such as *CYCB* and *CDKB;1*, and a switch to the endoreduplication cycle. Although there is a paucity of functional studies on the role of the cell cycle in cereal leaf growth and development, recent results in maize indicate that the positioning of the boundary between the division zone and expansion zone largely depends on a peak of bioactive gibberellins and that this affects cell proliferation patterns, cell expansion, and the size of the leaf (Nelissen et al. 2012).

1.4.4 Root Development and Architecture

The root system plays fundamental roles in crop production, including the physical anchoring and support of the plant, the uptake of water and nutrients from the soil, the storage of metabolites, and the interaction with a range of biotic and abiotic factors. Root growth is controlled in part by the availability of some of these factors but also by endogenous plant genes. For example, overexpression of *CYCB2;2* in rice resulted in increased root cell number and growth, probably by stimulating CDKB2 activity (Lee et al. 2003).

Manipulation of root growth and architecture is increasingly recognized as an important strategy to potentially maximize the utilization of decreasing resources and mitigate potential yield losses. The architecture and organization of the root apparatus is markedly different in *Arabidopsis* and cereal crops, the latter being characterized by a higher complexity, a more fibrous appearance, and comprising, in addition to lateral roots, crown roots and, often, seminal roots as well. In both monocots and dicots, activation of the cell cycle at the pericycle (and in cereals also at the endodermis) near the vascular system is a conserved hallmark of the initial stages of lateral root development (Casero et al. 1995; Dubrovsky et al. 2001; Smith and De Smet 2012). Several core cell cycle genes play important roles in lateral root formation. In *Arabidopsis*, *KRP2* is downregulated during cell cycle reentry in the pericycle, and there is genetic evidence that it antagonizes lateral root initiation and density by inhibiting CDKA/CYCD2;1 (Sanz et al. 2011). Additionally, *E2Fa* has been shown to be rate limiting for the initiation of lateral root primordia (Berckmans et al. 2011). However, it is currently not clear whether *KRP2* and *E2Fa* control later root formation through the same or distinct pathways. Although cell cycle regulation is important for later root primordium formation, it does not appear to be sufficient, and a paramount role is played by auxin-dependent signaling pathways that specify lateral root cell founder fate (Vanneste et al. 2005; Dubrovsky et al. 2008; De Smet et al. 2010). The understanding of root architecture control in cereals is very limited at present, due primarily to a lack of suitable mutants.

Manipulation of root hair density could conceivably enhance the ability of roots to uptake water and nutrients from their surroundings and to impact a range of plant/soil interactions. In many plants, regulation of asymmetric, formative cell division of specific epidermal cells in the root differentiation zone is critical for specifying root hair cell fate. CDT1, a DNA replication factor, has been implicated in root hair cell differentiation in *Arabidopsis* through a pathway that appears to coordinate cell division with modification of histone chromatin marks and cell fate decisions (Caro et al. 2007). Although this highlights the role of certain cell cycle genes in coordinating cell division with differentiation, it is not clear whether the role of CDT1 is conserved in other plants, given that root hair specification in angiosperms involves distinct cell division patterns, and this process is clearly different in monocots compared to *Arabidopsis* (Datta et al. 2011).

1.5 PLANT TISSUE CULTURE

The culturing of cells and tissue in vitro is integral to many processes in plant biotechnology, such as micropropagation, transgenic plant production, and culturing plant and algal cells in bioreactors for the production of many different compounds including pharmaceuticals and biofuels.

Space limitations prevent a detailed description of cell cycle control in plant tissue culture in this chapter. However, it is worth mentioning that tissue culture has been deployed extensively as a tool to unravel important aspects of cell cycle regulation in plants, while, at the same time, the modification of cell cycle parameters has been pursued to improve plant tissue culture technology. The importance of an appropriate hormonal input (primarily auxin and cytokinin) for plant tissue culture is well known (Del Pozo et al. 2005; John 2007; Dudits et al. 2011), and there is substantial evidence to indicate that modulation of cell cycle regulation mediates the action of hormones. For example, overexpression of *E2Fb/DPa* transcription factors stimulate proliferation of tobacco BY-2 cells in the absence of auxin, which is otherwise necessary, and supplementing the medium with auxin increases the levels of E2Fb protein by enhancing its stability (Magyar et al. 2005). Thus, auxin apparently stimulates the cell cycle by upregulating the E2F pathway. In addition, during the culturing of *Arabidopsis* explants, cytokinin stimulates the cell cycle and induces callus formation by upregulating the expression of D3-type cyclins (Riou-Khamlichi et al. 1999). Likewise, sucrose signaling stimulates cell cycle progression by upregulating both *CYCD2* and *CYCD3* (Riou-Khamlichi et al. 2000). In maize, a key role has been established for the RBR pathway in controlling callus growth and plant regeneration. *RBR1* inhibits these processes, and its inactivation by ectopic expression of RepA from wheat dwarf virus (an RBR-binding protein) stimulates callus formation and regeneration of transgenic plants (Gordon-Kamm et al. 2002). Interestingly, expression of *RBR3* is also repressed by *RBR1* and appears to be required for the transcription of several E2F target genes and for S-phase, although it is not sufficient for upregulation of cell proliferation (Sabelli et al. 2009). Thus, appropriate control of the RBR–E2F pathway is required in cell and tissue culture, and the upregulation of this pathway generally is associated with or required for increased cell cycle activity in vitro. This is consistent with the observation that the RBR-homolog *MAT3* gene is important for cell cycle progression in the unicellular alga *Chlamydomonas reinhardtii* (Umen and Goodenough 2001).

1.6 CONTRIBUTION OF CELL CYCLE MANIPULATION TO CROP EVOLUTION AND BREEDING

A central question concerning the role of cell cycle regulation in plant development is whether and to what extent it has been a factor in the evolution and breeding of crops and whether its manipulation has potential for future crop improvement. This is a topic under constant development as information gained from model plants such as *Arabidopsis* is slowly but gradually being applied to crop plants. A number of genes or quantitative trait loci (QTLs) impacting the cell cycle and yield parameters have already been identified in important crops and characterized to some extent (Table 1.1). Many of the underlying pathways remain to be characterized, and it is possible that these genes may control the cell cycle in rather indirect ways. However, they may reveal key aspects of how the cell cycle regulatory engine is linked to plant growth and development.

Several important crop species that sustain human civilization are allopolyploid, such as wheat, oats, canola, cotton, and sugarcane. Their genomes contain sets of related homeologous chromosomes in addition to the homologous chromosomes that are also present in diploid species. The fertility and genetic stability of allopolyploids generally depend on preventing the exchange of genetic material between homeologous chromosomes at meiosis during gametogenesis. As a result, allopolyploids behave as diploids at meiosis, with chromatin exchanges limited to true homologous chromosomes. Although allopolyploid crops are highly productive, they suffer from the problem that their breeding is generally rather inefficient because the block on homeologous recombination in a polyploidy hybrid essentially precludes introgression of desirable alleles from other species such as wild relatives. Homeologous chromosome pairing has been investigated in durum (*Triticum turgidum*) and bread (*Triticum aestivum*) wheats, which are tetraploid and hexaploid, respectively. A major repressor of homeologous chromosome pairing in these species is the *Ph1* locus, which probably arose after the polyploidization events that generated these species.

The *Ph1* locus contains a defective cluster of seven genes related to mammalian *CDK2* on chromosome 5B (Griffiths et al. 2006). Although this locus additionally presented evidence of insertion of etherochromatic DNA sequences, recent analyses indicated that the *CDK2*-like genes on chromosome 5B are the most likely candidates for *Ph1* locus activity (Yousafzai et al. 2010a,b). Although these *CDK2*-like genes are divergent from the *CDKA* and *CDKB* genes (which are more closely related to mammalian CDK1) commonly believed to control the cell cycle in plants, they appear to share several properties with *CDK2* concerning the control of premeiotic DNA replication, chromatin condensation at meiosis, the phosphorylation pattern of histone H1, and chromosome pairing. Deletion of the *Ph1* locus allows homeologous pairing, which is associated with upregulated expression of related *CDK2*-like genes at the *Ph1* homeologous loci on chromosomes 5A and 5D. Thus, it would appear that low CDK2-like activity prevents homeologous pairing whereas increased activity allows it (Greer et al. 2012). While the precise mechanism of action of *CDK2*-like genes at the *Ph1* loci remain to be unraveled, this insight illustrates the importance of CDK genes in shaping and maintaining the allopolyploid genome of wheat and offers an opportunity to improve, through strategies targeted at relieving the inhibition on homeologous pairing, the breeding of allopolyploid crops and increase their genetic diversity.

Maize *teosinte branched 1* (*tb1*) is a classic example of a gene with a paramount role in the domestication of a major crop species, such as maize from its wild ancestor (teosinte, *Zea mays* ssp. *parviglumis*) (Studer et al. 2011). The TB1 protein belongs to the class II of TCP family of transcription factors and inhibits axillary bud outgrowth, thereby contributing to apical dominance. *tb1* is bud specific and is expressed at higher levels in modern maize than teosinte, resulting in reduced shoot branching, reduced development of the branches compared to the main stalk, reduced number of ears, and increased grain yield. *tb1* is conserved in both monocots and dicots, with a similar negative function on branching. It appears to inhibit axillary bud outgrowth by negatively regulating cell proliferation. Although the exact role of *tb1* in cell cycle regulation remains to be clarified, possible TB1 targets are *PCNA*, *CYCB1;1* and *PROLIFERATION FACTOR 1* and *2* (*PCF1* and *PCF2*) (Müller and Leyser 2011). Thus, specific inhibition of the cell cycle during axillary bud activation appears to have been a key event in the domestication of maize and contributing to its high grain yield.

An additional example of the importance of modulating cell proliferation during domestication of a major crop comes from tomato. The *fw2.2* QTL is responsible for up to 30% of the difference in fresh fruit weight between domesticated tomato and its smaller wild relatives (Frary et al. 2000). It encodes a putative transmembrane protein believed to be involved together with CKII kinase in a signaling pathway that represses the mitotic cell cycle early in fruit development (Cong and Tanksley 2006). In domesticated tomato fruit, *FW2.2* is expressed at lower levels than its wild relatives, and this correlates with more cells and a larger fruit size. In addition, FW2.2 appears to be conserved in plants, with related genes in maize (*CNR1* and *CNR2*) (Guo et al. 2010b) and avocado (*PaFW2.2*) (Dahan et al. 2010) that display similar roles in restricting cell proliferation and organ size. A related gene in soybean (*GmFWL1*) also controls nodule number and nuclear size, potentially also impacting chromatin structure (Libault et al. 2010).

Regulation of ubiquitination-dependent proteolysis, such as by the APC/C, appears to be a central theme in the developmental control of the cell cycle. Factors that control APC/C activity, such as the activator CCS52A, play important roles in the developmental regulation of the endocycle and other processes, thereby affecting yield parameters, in different crop systems such as barrel medic (*Medicago truncatula*) (Vinardell et al. 2003; Kuppusamy et al. 2009), tomato (Mathieu-Rivet et al. 2010; Chevalier et al. 2011), and rice (Lin et al. 2012; Su'udi et al. 2012; Xu et al. 2012). Additionally, other agriculturally important genes and QTLs involved in ubiquitination- and proteasome-dependent proteolysis have been identified in rice (Song et al. 2007; Shomura et al. 2008; Weng et al. 2008; Ogawa et al. 2011; Li et al. 2012).

As mentioned earlier, regulation of the cell cycle during syncytial proliferation and endosperm cellularization is another important theme with potential implications for grain yield in cereal crops, which has been shown to be impacted by *KRP1*, *CYCB1;1*, and *CCS52A* in rice (Barrôco et al. 2006; Guo et al. 2010a; Su'udi et al. 2012; Ishimaru et al. 2013). However, cereal seeds appear to be more resilient to alteration of core cell cycle gene activity occurring later in development (Leiva-Neto et al. 2004; Sabelli et al. 2013).

Regulation of cell proliferation in maternal reproductive structures, such as the palea/lemma during early spikelet hull development, is emerging as an important grain size and yield determinant in rice, and several key genes have been identified: *GW2* (Song et al. 2007), *GS3* (Fan et al. 2006; Takano-Kai et al. 2009), *GS5* (Li et al. 2011), *qSW5/GW5* (Shomura et al. 2008; Weng et al. 2008), *GW8* (Wang et al. 2012), *qGL3* (Zhang et al. 2012b), and *HGW* (Li et al. 2012). Intriguingly, evidence is emerging that *HGW*, *GW2*, *qSW5/GW5*, and *GS3* may function in the same ubiquitination pathways to regulate grain size and weight (Li et al. 2012).

1.7 DOES THE CELL CYCLE DETERMINE YIELD? CONCLUDING REMARKS

The cell cycle is directly responsible for the number of cells, which together with cell expansion determines overall tissue/organ size. There are documented cases in which stimulation of cell division results in increased tissue growth (Lee et al. 2003; Li et al. 2008; Guo et al. 2010b) (Table 1.1). However, it has long been recognized that even a severe defect in cell proliferation may not impair plant development in a dramatic fashion (Haber 1962). This is because cell division frequently appears to be inversely correlated with cell expansion. A larger number of cells resulting from increased cell division activity may be compensated for by a smaller cell size, leaving the tissue/organ as a whole largely unaffected. One of the most convincing examples of compensatory regulation between cell division activity and cell size is represented by the development of the leaf in *Arabidopsis* (Inze and De Veylder 2006; John and Qi 2008; Massonnet et al. 2011; Powell and Lenhard 2012). This kind of compensatory effect brings into question the basic role of cell cycle regulation in driving plant growth and raises concerns about designing strategies for plant improvement through the manipulation of cell cycle–controlling genes (Inze and De Veylder 2006; John and Qi 2008; Sabelli et al. 2013). If cell-autonomous effects, based on the alteration of cell cycle regulation, can be dampened or even entirely swamped by counteracting tissue/organ-wide changes in cell size, should we expect to modify yield parameters, such as those impacting biomass production, by manipulating genes controlling the cell cycle? The debate between the so-called cellular theory (cell-autonomous role of the cell cycle in driving growth) and the organismal theory (cell proliferation follows a developmental plan) is still largely unresolved, and it seems sensible that this view represents too a polarized way of framing the central question concerning the role of the cell cycle in growth and development (Beemster et al. 2003). In this chapter, several examples have been provided that illustrate how manipulation of the cell division cycle in crop plants can impact yield components, such as seed and fruit development, plant architecture and size, and the interaction with symbiotic and parasitic organisms. Regulation of the cell cycle is fundamental for many developmental programs, and there is the growing realization that, far from strictly representing the mechanism for producing cells, it is embedded in a highly complex web of context-specific pathways that spans metabolism, physiology, and genetic and epigenetic processes, to mention just a few. Thus, it would be sensible to assess the impact of the cell cycle on crop production on a case-by-case basis, relying on detailed knowledge of the specific system under consideration.

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2 Chapter 2: Seed Dormancy, Germination, and Seedling Recruitment in Weedy Setaria

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3 Chapter 3: Alterations in Structural Organization Affect the Functional Ability of Photosynthetic Apparatus

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5 Chapter 5: Role of Alternative Respiratory Pathway in Plants: Some Metabolic and Physiological Aspects

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8 Chapter 8: Evaluating and Managing Crops Water Requirement

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Part II

Cellular and Molecular Aspects

of Plant/Crop Physiology

9 Chapter 9: Biochemistry and Physiology of Carbon Partitioning in Crop Plants

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12 Chapter 12: Signaling Molecules Involved in the Postharvest Stress Response of Plants: Quality Changes and Synthesis of Secondary Metabolites

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Part III

Plant/Crop Physiology and Physiological Aspects of Plant/Crop Production Processes

13 Chapter 13: Quantifying Immediate Carbon Export from Leaves Predicts Source Strength

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Part IV

Physiological Responses of Plants/Crops under Stressful (Salt, Drought, Heat, Nutrient Deficiency, and Other Environmental Stresses) Conditions

19 Chapter 19: Role of Polyamines in Plant Abiotic Stress Responses

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31 Chapter 31: Physiological Responses of Cotton (Gossypium hirsutum L.) to Salt Stress

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Part V

Physiological Responses of Plants/Crops to Heavy Metal Concentration and Agrichemicals

33 Chapter 33: Metal Nanoparticles in Plants: Formation and Action

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Part VI

Physiology of Plant/Crop

Genetics and Development

35 Chapter 35: Small RNAs in Crop Response to Temperature Stress Noncoding RNAs in Plants

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TABLE 35.1 (continued)

Appendix

Species miRNA Organ specifciity (Putative)Target Reference

Low-temperature stress miR393 ↓ Transport inhibitor response 1-like protein miR396 ↓ GRF miR444 ↓ –

Manihot

esculenta miR156 a ; miR159 a ; miR160 a ; miR162 a ; miR165/ miR166 a ; miR167 a ; miR170/ miR171 a ; miR395 a ; miR396 a ; miR397 a – – Zeng et al., 2010

High-temperature stress

Triticum

aestivum miR172 ↓ miR156 ↑ miR159 ↑ miR160 ↑ miR166 ↑ miR168 ↑ miR169 ↑ miR827 ↑ miR2005 ↑ – – Xin at al., 2010

Brassicarapa miR156h ↑ miR5714 ↑ miR5718 ↑ miR5726 ↑ miR398a ↓ miR398b ↓ miR399b ↓ miR827 ↓ miR5716 ↓ miR1885b.3 ↓ BracPAP10. BracCSD1 – Yu et al., 2012

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Part VII

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Part VIII

Plants/Crops Growth Responses to Environmental Factors

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Part IX

Future Promises: Plants and Crops

Adaptation and Biotechnological

Aspects of Plants/Crops Improvement

38 Chapter 38: CAM Plants as Crops: Adaptable, Metabolically Flexible, and Highly Productive Cultivars

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FIGURE 1.3 Cell cycle regulation during maize endosperm development. (a) Following double fertilization,

early endosperm development involves acytokinetic mitoses starting with the triploid primary endosperm

nucleus, which results in a syncytium surrounding the central vacuole within the embryo sac. At around 3

days after pollination (DAP), the endosperm becomes cellularized through an open-ended alveolation process

toward the central vacuole until cellularization is complete. (b) After cellularization from about 4 DAP, the

endosperm develops through a phase of mitotic cell proliferation, followed (from around by 8 to 10 DAP)

by endoreduplication (as shown by flow-cytometric profiles), and by programmed cell death (PCD) (starting

around 16 DAP). The endoreduplication phase and the last part of the cell division phase coincide with a

dramatic growth of the endosperm and the synthesis and accumulation of storage compounds. The graph at

the bottom illustrates trends in endosperm fresh weight, nuclei number, mitotic index, and mean DNA content

(C value). Al, Aleurone; CSEn, central starchy endosperm; Em, embryo; En, endosperm; Nu, nucellus; Pe,

pericarp; Pl, placentochalaza; SAl, subaleurone layer; TC, transfer cells. (Reproduced in part from Larkins,

B.A. et al., J. Exp. Bot., 52, 183, 2001; Sabelli, P.A. et al., Maydica, 40, 485, 2005b. With permission from

Oxford University Press and Maydica.) A c r e s o f N o n F
e d e r a l G r a z i n g L a n d , 2 0 0 7 e r e w e r e a
p p r o x i m a t e l y 5 8 3 . 9 m i l l i o n a c r e s o
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i n c l u d e s a p p r o x i m a t e l y 4 0 9 . 1 m i l l
i o n a c r e s o f r a n g e l a n d , 1 1 8 . 6 m i l l i
o n a c r e s o f P a s t u r e l a n d , a n d 5 6 . 1 m i
l l i o n a c r e s o f g r a z e d f o r e s t l a n d . E
a c h d o t r e p r e s e n t s 2 5 , 0 0 0 a c r e s P a s
t u r e l a n d R a n g e l a n d G r a z e d F o r e s t L
a n d F e d e r a l L a n d N o t e t h a t t h e d o t s d
o n o t r e p r e s e n t a c t u a l f e a t u r e l o c a
t i o n s o r p o i n t s . e d o t s a r e d i s t r i b u
t e d r a n d o m l y w i t h i n e a c h a r e a — i n t h
i s m a p s t a t e a n d 8 d i g i t h y d r o l o g i c u
n i t . P u e r t o R i c o a n d U S V i r g i n I s l a n
d s (n o d a t a) A l a s k a (n o d a t a) M a p I D :
1 1 0 3 9 D a t a S o u r c e : 2 0 0 7 N a t i o n a l R e
s o u r c e s I n v e n t o r y U S D e p a r t m e n t o f
A g r i c u l t u r e , N a t u r a l R e s o u r c e s C o
n s e r v a t i o n S e r v i c e M a p S o u r c e : U S D
e p a r t m e n t o f A g r i c u l t u r e , N a t u r a l
R e s o u r c e s C o n s e r v a t i o n S e r v i c e R e
s o u r c e s I n v e n t o r y a n d A s s e s s m e n t D
i v i s i o n , W a s h i n g t o n , D C , D e c e m b e r
2 0 0 9 H a w a i i (n o d a t a) P a c i � c B a s i n (
n o d a t a) N o r t h e r n M a r i a n a s G u a m A m e
r i c a n S a m o a F I G U R E 2 2 . 1 D i s t r i b u t i
o n o f p a s t u r e l a n d a c r o s s t h e U n i t e d
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r a l d e , R . C . e t a l . , A g r o n . J . , 1 0 3 (
2) , 3 7 1 , 2 0 1 1 .) Tall fescue in June Tall fescue
in August Tall fescue in November Tall fescue in September

FIGURE 22.2 Tall fescue grazing plots at the Samuel Roberts Noble Foundation, Ardmore, Oklahoma,

in 2006. Grasses went to complete dormant in August and September during hot and dry weather and returned to

full green growth in November. Through dormancy, forage grasses can escape drought stress by reducing water

need until soil water is replenished through irrigation or precipitation. (Pictures taken by M. Anowarul Islam.)

FIGURE 30.1 Damage to structures caused by salinity.

FIGURE 30.6 Necrotic leaves of Alstonia scholaris due to salinity.

(a) (b)

FIGURE 30.7 C. decidua (a) and S. fruticosa (b) are widely grown in salt-affected landscapes in Pakistan. S c a o l d _ 9 S c a o l d _ 8 S c a o l d _ 7 S c a o l d _ 6 S c a o l d _ 5 S c a o l d _ 4 S c a o l d _ 3 S c a o l d _ 2 S c a o l d _ 1 S c a o l d _ 1 S c a o l d _ 2 S c a o l d _ 3 S c a o l d _ 4 S c a o l d _ 5 S c a o l d _ 6 S c a o l d _ 7 S c a o l d _ 8 S c a o l d _ 9 x-axis: Setaria italica (foxtail millet) (v2.1) y-axis organism: Setaria italica (foxtail millet) (v2.1)

FIGURE 36.3 Syntenic dotplot of a self-self analysis of foxtail millet using SynMap. Green dots are syn

tenic gene pairs identi�ed through a collinear arrangement. These are derived from the most recent whole

genome duplication event in this lineage. Analysis may be regenerated at http://genomevolution.org/r/8m4c. 2 0 0 0 M e a n : 0 . 0 0 4 8 m e d i a n - 0 . 2 2 8 4 1 8 0 0 1 6 0 0 1 4 0 0 1 2 0 0 1 0 0 0 8 0 0 C o u n t s 6 0 0 4 0 0 2 0 0 0 - 1 . 2 4 9 8 7 - 1 . 0 7 2 5 2 - 0 . 8 9 5 1 7 - 0 . 7 1 7 8 3 - 0 . 5 4 0 4 8 - 0 . 3 6 3 1 3 - 0 . 1 8 5 7 8 - 0 . 0 0 8 4 3 0 . 1 6 8 9 2 0 . 3 4 6 2 7 0 . 5 2 3 6 1 0 . 7 0 0 9 6 O u t p a r a l o g s (a) (b) N o i s e O r t h o l o g s Y o u n g e r < - - > O l d e r 0 . 8 7 8 3 1 1 . 0 5 6 1 . 2 3 3 1 . 4 1 0 1 . 5 8 8 1 . 7 6 5 1 . 9 4 2 2 . 1 2 0 2 . 2 6 2 1 0 9 8 7 6 5 4 3 2 1 1 0 9 8 7 6 5 4 3 2 1 S c a o l d _ 1 S c a o l d _ 2 S c a o l d _ 3 S c a o l d _ 4 S c a o l d _ 5 S c a o l d _ 6 S c a o l d _ 7 S c a o l d _ 8 S c a o l d _ 9 S c a o l d _ 1 S c a o l d _ 2 S c a o l d _ 3 S c a o l d _ 4 S c a o l d _ 5 S c a o l d _ 6 S c a o l d _ 7 S c a o l d _ 8 S c a o l d _ 9 x-axis: Setaria italica (foxtail millet) (v2.1) y-axis organism: Sorghum bicolor (v1.4) y-axis organism: Sorghum bicolor (v1.4) x-axis: Setaria italica (foxtail millet) (v2.1) l o g 1 0 ( ) s u b s t i t u t i o n p e r s i t e f o r K s (c)

FIGURE 36.4 Syntenic dotplots of a foxtail millet (x-axis) versus sorghum (y-axis) using SynMap. (a)

Syntenic gene pairs are colored green. Note that a given region of either genome is syntenic to two regions

in the other genome (red dashed line). This is due to one syntenic region being orthologous and one being

out-paralogous. Note the large gaps in some syntenic regions (blue arrow). This is a centromere in sorghum.

Results may be regenerated here: http://genomevolution.org/r/8m2u. (b) Syntenic gene pairs are colored by their

synonymous mutation values (Ks). Purple gene pairs are younger than cyan gene pairs and represent ortholo

gous and out-paralogous relationships, respectively. Results may be regenerated here: http://genomevolution.

org/r/8m2v. (c) Histogram of Ks values shown used in the dotplot from (b).