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REVIEW

Maize kernel development

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Abstract Maize (*Zea mays*) is a leading cereal crop in the world. The maize kernel is the storage organ and the harvest portion of this crop and is closely related to its yield and quality. The development of maize kernel is initiated by the double fertilization event, leading to the formation of a diploid embryo and a triploid endosperm. The embryo and endosperm are then undergone independent developmental programs, resulting in a mature maize kernel which is comprised of a persistent endosperm, a large embryo, and a maternal pericarp. Due to the well-characterized morphogenesis and powerful genetics, maize kernel has long been an excellent model for the study of cereal kernel development. In recent years, with the release of the maize reference genome and the development of new genomic technologies, there has been an explosive expansion of new knowledge for maize kernel development. In this review, we overviewed recent progress in the study of maize kernel development, with an emphasis on genetic mapping of kernel traits, transcriptome analysis during kernel development, functional gene cloning of kernel mutants, and genetic engineering of kernel traits.

Keywords Maize · Kernel development · QTL · Transcriptome · Gene cloning · Transgene

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Introduction

Maize (*Zea mays*) is one of the world's leading cereal crops along with rice and wheat, serving as a staple food, animal feed, and industrial raw materials (Troyer 2006). Since 2001, maize has become the highest tonnage crop worldwide, with the total production surpassing that of rice and wheat (UN/FAO, 2002). In 2018, the production of maize is about 1147 M tons, while 782 M and 734 M tons that of rice and wheat in the world (http://www.fao.org). Maize kernels, like in other cereal crops, are storage organ that contains essential components for plant growth and reproduction. The kernel is comprised of three distinct compartments contributing to overall energy density, including a persistent endosperm (83%), a large embryo (11%), and a maternal pericarp (6%). The kernel contains about 72% starch, 10% protein, 4% lipid, and micronutrients such as vitamins and minerals (Nuss and Tanumihardjo 2010). Maize provides an estimated 15% of the world's protein and 20% of the world's calories (Council 1988; Shiferaw et al. 2011), indicating its status as a paramount crop in the context of global nutrition.

The maize kernel development is initiated by the double fertilization event, leading to the formation of a diploid embryo and a triploid endosperm (Russell 1992). Early embryo development is marked by three major events corresponding to the acquisition of apicobasal polarity, the differentiation of epidermis, and the formation of the shoot and root meristem (Goldberg et al. 1994). Then, the embryo enters a maturation phase (Dumas and Rogowsky 2008). The development of endosperm starts with the fertilized central cells (Olsen 2001), followed by cellularization and differentiation into four main cell types, including basal endosperm transfer layer (BETL), aleurone layer (AL), starchy endosperm (SE), and embryo-surrounding region (ESR) (Consonni et al. 2005). During endosperm differentiation, mitotic cell proliferation and endoreduplication occur in endosperm cells, following by maturation (cell death, dormancy, and desiccation) (Sabelli and Larkins 2009). Although embryo and endosperm are clonally and functionally separated, genetic analyses reveal that they interact extensively throughout their development (Scanlon and Takacs 2009). With its well-characterized morphogenesis and powerful genetics, the maize kernel offers an exquisite experimental system.

The investigation of maize kernel development has a long history, starting with mutant collections in the early 1900s (Demerec 1923; Wentz 1930; Jones 1920; Mangelsdorf 1923). With the development of chemical mutagens, such as ethyl methane sulfona (EMS), mutagenesis via pollen greatly expanded the collections of maize kernel mutants (Neuffer and Coe 1978). Over 100 defective kernel (*dek*) mutants were reported with genetic, morphological, lethality, and embryo rescue studies (Neuffer and Sheridan 1980). These mutation loci are located throughout the maize chromosomes, and most of these mutants are lethal due to the failure of germination. A recent collection of EMS-mutagenized lines, which covered more than 80% of the annotated protein-coding genes in the maize genome, was generated and sequenced (Lu et al. 2018). It greatly expanded EMS induced mutant collections for potential functional analysis of genes and desirable allelic variants associated with maize kernel development.

Apart from chemically induced mutations, DNA transposons, such as *Ac/Ds* (McClintock 1948), *En/Spm* (McClintock 1953; Pereira et al. 1986), and *Mutator* (Robertson 1978), were also commonly used for mutagenesis in maize. The *Mutator* system, with the advantage of a high mutation efficiency and no apparent insertion site bias (Bennetzen 1996; Walbot 2000), has been widely used for the construction of genome-wide mutation libraries in maize (May et al. 2003; McCarty et al. 2005; Liang et al. 2019; Settles et al. 2007; Clark and Sheridan 1991; Sheridan and Clark 1993b; Scanlon et al. 1994; Marcon et al. 2020). Regional transposon mutation systems were also developed using *Ac/Ds* system, based on its preferential local transposition property (Cowperthwaite et al. 2002; Vollbrecht et al. 2010). Using active Robertson's *Mutator* maize stocks (Robertson 1978), 51 embryo-specific (*emb*) mutants (Clark and Sheridan 1991; Sheridan and Clark 1993a) and 63 kernel mutants were reported (Scanlon et al. 1994). Several sequence-indexed *Mutator*-induced libraries, such as *UniformMu* (McCarty et al. 2005), *ChinaMu* (Liang et al. 2019), and *BonnMu* (Marcon et al. 2020), and Photosynthetic Mutant Library (PML) (http://pml.uoregon.edu/photosyntheticml.html) implemented a novel strategy for harnessing the power of high-copy transposons for functional analysis of maize genome. These libraries tagged more than 50% of the annotated maize genes, providing important resources for further genetic, biochemical, and molecular analysis of genes affecting kernel development.

Maize has been a leading system for molecular cloning of functional genes in plants. Among the earliest list of genetic loci in maize, storage protein genes (Geraghty et al. 1981; Burr et al. 1982; Pedersen et al. 1982), starch biosynthesis genes (Shure et al. 1983), and pigment biosynthesis genes (Fedoroff et al. 1984; O'Reilly et al. 1985) were the first batches to be molecularly cloned. With well-characterized endogenous transposon systems and the advent of transposon tagging (Wienand et al. 1982), maize led the way in gene isolation for several years. Dozens of genes affecting kernel development have been cloned from mutants isolated from different resources. For example, the first molecularly identified transcription factor (TF), OPAQUE2 (O2), was isolated by transposon tagging in 1987 (Schmidt et al. 1987). With the release of the maize reference genome (Schnable et al. 2009), as well as the success using a variety of gene cloning methods, such as positional cloning (Bortiri et al. 2006; Gallavotti and Whipple 2015), bulked-segregant analysis (BSA) (Klein et al. 2018; Dong et al. 2019; Michelmore et al. 1991), and transcription profiling (Jansen and Nap 2001; Cheung and Spielman 2002; Swanson-Wagner et al. 2006; Stupar and Springer 2006; Pea et al. 2008), the gene cloning in maize achieved a great leap in recent year. To date, a great number of maize kernel mutant genes have been cloned (Table 1), representing one of

Table 1 List of cloned genes essential for maize kernel development

Mutant phenotype	Gene name	B73 v4 ID	Functional annotation	References
dek	*Dek1*	Zm00001d028818	Animal calpains homolog, plant signal transduction	(Lid et al. 2002; Becraft et al. 2002)
	Dek2	Zm00001d034882	PPR protein, RNA splicing	(Qi et al. 2017b)
	Dek5	Zm00001d039612	Bacterial TamB homolog, chloroplast envelope biogenesis	(Zhang et al. 2019a)
	Dek10	Zm00001d053802	PPR protein, RNA editing	(Qi et al. 2017a)
	Dek15	Zm00001d052197	SCC4, chromosome segregation	(He et al. 2019)
	Dek19	Zm00001d038257	PPR protein, unknown function	(Dong et al. 2019)
	Dek33	Zm00001d016475	Pyrimidine reductase, riboflavin biosynthesis	(Dai et al. 2019)
	Dek35	Zm00001d033749	PPR protein, RNA splicing	(Chen et al. 2017b)
	Dek36	Zm00001d013136	PPR protein, RNA editing	(Wang et al. 2017)
	Dek37	Zm00001d003543	PPR protein, RNA splicing	(Dai et al. 2018)
	Dek38	Zm00001d014595	TTI2 cochaperone, male reproductive cell development	(Garcia et al. 2017)
	Dek39	Zm00001d047013	PPR protein, RNA editing	(Li et al. 2018c)
	Dek40	Zm00001d011478	PBAC4 chaperone, 20S CP biogenesis	(Wang et al. 2019a)
	Dek41/Dek43	Zm00001d021053	PPR protein, RNA splicing	(Ren et al. 2020; Zhu et al. 2019)
	Dek42/Rbm48	Zm00001d054077	RNA-binding protein, U12-type intron splicing	(Bai et al. 2019; Zuo et al. 2019)
	Dek44	Zm00001d052865	Mitochondrial ribosomal protein L9, respiratory genes expression	(Qi et al. 2019)
	Dek45	Zm00001d023331	PPR protein, RNA editing	(Ren et al. 2019a)
	Dek46	Zm00001d043107	PPR protein, RNA editing	(Xu et al. 2020)
	Dek53	Zm00001d041326	PPR protein, RNA editing	(Dai et al. 2020)
	Dek605	Zm00001d016798	PPR protein, RNA editing	(Fan et al. 2020)
	Dek/ZmReas1*	Zm00001d038475	AAA-ATPase60S, ribosome exporting	(Qi et al. 2016)
smk	*Smk1*	Zm00001d007100	PPR protein, RNA editing	(Li et al. 2014b)
	Smk2	Zm00001d053981	Glutaminase, Vitamin B6 Biosynthesis	(Yang et al. 2017b)
	Smk3	Zm00001d041537	Mitochondrial transcription termination factor, RNA splicing	(Pan et al. 2019a)
	Smk4	Zm00001d049196	PPR protein, RNA editing	(Wang et al. 2019b)
	Smk6	Zm00001d025446	PPR protein, RNA editing	(Ding et al. 2019)
	Smk7	Zm00001d035960	Subunit of RNA polymerase III, expression of tRNAs and 5S rRNA	(Zhao et al. 2020)
	Smk9	Zm00001d000137	PPR protein, RNA splicing	(Pan et al. 2019b)
	MPPR6	Zm00001d034111	PPR protein, translation	(Manavski et al. 2012)
	Ppr78	Zm00001d034428	PPR protein, RNA stabilization	(Zhang et al. 2017c)
emp	*Emp2*	Zm00001d005675	HEAT SHOCK BINDING PROTEIN1, Heat Shock Response	(Fu et al. 2002)
	Emp4	Zm00001d033869	PPR protein, expression of mitochondrial transcripts	(Gutierrez-Marcos et al. 2007)
	Emp5	Zm00001d042039	PPR protein, RNA editing	(Liu et al. 2013)
	Emp6	Zm00001d005959	Plant organelle RNA recognition protein, BETL cell differentiation	(Chettoor et al. 2015)
	Emp7	Zm00001d008298	PPR protein, RNA editing	(Sun et al. 2015a)
	Emp8	Zm00001d049796	PPR protein, RNA splicing	(Sun et al. 2018)

Table 1 (continued)

Mutant phenotype	Gene name	B73 v4 ID	Functional annotation	References
	Emp9	Zm00001d022480	PPR protein, RNA editing	(Yang et al. 2017a)
	Emp10	Zm00001d033992	PPR protein, RNA splicing	(Cai et al. 2017)
	Emp11	Zm00001d052450	PPR protein, RNA splicing	(Ren et al. 2017)
	Emp12	Zm00001d002098	PPR protein, RNA splicing	(Sun et al. 2019)
	Emp16	Zm00001d011559	PPR protein, RNA splicing	(Xiu et al. 2016)
	Emp18	Zm00001d034253	PPR protein, RNA editing	(Li et al. 2019b)
	Emp21	Zm00001d033495	PPR protein, RNA editing	(Wang et al. 2019c)
	Emp32	Zm00001d040363	PPR protein, RNA splicing	(Yang et al. 2020c)
	Emp602	Zm00001d028046	PPR protein, RNA splicing	(Ren et al. 2019b)
	Ppr14	Zm00001d002157	PPR protein, RNA splicing	(Wang et al. 2020)
	Ppr18	Zm00001d007927	PPR protein, RNA splicing	(Liu et al. 2020c)
	Ppr27	Zm00001d029061	RNA editing, multiple sites	(Liu et al. 2020d)
	Ppr101	Zm00001d010942	PPR protein, RNA splicing	(Yang et al. 2020a)
	Ppr231	Zm00001d018219	PPR protein, RNA splicing	(Yang et al. 2020a)
	Ppr-smr	Zm00001d002345	PPR protein, RNA splicing	(Chen et al. 2019)
emb	*Emb-7L*	Zm00001d021871	Plastid PPR protein, RNA splicing	(Yuan et al. 2019)
	Emb12	Zm00001d018366	Plastid initiation factor 3, plastid protein synthesis	(Shen et al. 2013)
	Emb14	Zm00001d054079	Plastid-targeted cGTPase, 30S ribosome formation	(Li et al. 2015b)
	Emb16/Why1	Zm00001d036148	WHIRLY1 (WHY1), genome stability and ribosome formation	(Zhang et al. 2013)
	Lem1	Zm00001d034192	Plastid 30S ribosomal protein S9 (PRPS9)	(Ma and Dooner 2004)
	PPR8522	Zm00001d034962	Plastid PPR protein, chloroplast transcription	(Sosso et al. 2012a)
	ZmPRPL35-1	Zm00001d046555	L35 of the large subunit of plastid ribosomes	(Magnard et al. 2004)
opaque/floury	*DeB30*	N/A	19-kD alpha-zein protein	(Kim et al. 2004)
	Fl1	Zm00001d003398	Endoplasmic reticulum protein, zein protein body formation	(Holding et al. 2007)
	Fl2	Zm00001d049243	22-kD alpha-zein protein	(Coleman et al. 1995)
	Fl3	Zm00001d009292	PLATZ TF, tRNA and 5S rRNA transcription	(Li et al. 2017b)
	Fl4	Zm00001d048851	z1A 19-kD alpha-zein, protein body assembly	(Wang et al. 2014a)
	Mc	Zm00001d005793	16-kDa gamma-zein protein	(Kim et al. 2006)
	O1	Zm00001d052110	Myosin XI protein, endoplasmic reticulum motility and protein body formation	(Wang et al. 2012)
	O2	Zm00001d018971	bZIP TF, regulator of diverse processes in endosperm	(Schmidt et al. 1987)
	O5	Zm00001d020537	Monogalactosyldiacylglycerol synthase MGD1, galactolipids abundance	(Myers et al. 2011)
	O6/Pro1	Zm00001d010056	Δ1-Pyrroline-5- carboxylate synthetase, biosynthesis of proline	(Wang et al. 2014b)
	O7	Zm00001d026649	Acyl-activating enzyme, storage protein synthesis	(Wang et al. 2011; Miclaus et al. 2011)
	O10	Zm00001d033654	Cereal-specific PB protein, distribution of zeins	(Yao et al. 2016)
	O11/ZmZHOU	Zm00001d003677	bHLH TF, regulator of endosperm development and nutrient metabolism	(Feng et al. 2018)
	Pbf1	Zm00001d005100	Dof TF, regulator of storage protein accumulation	(Vicente-Carbajosa et al. 1997)

Table 1 (continued)

Mutant phenotype	Gene name	B73 v4 ID	Functional annotation	References
	Ocd1	Zm00001d008739	Oxalyl-CoA Decarboxylase 1, catalyzes oxalyl-CoA into formyl-CoA and CO2	(Yang et al. 2018)
	Os1/Shai1	Zm00001d002661	RWP-RK domain TF, regulator of nutrient allocation and embryonic patterning	(Song et al. 2019; Mimura et al. 2018)
	Pdk1	Zm00001d038163	Pyruvate phosphate dikinase (PPDK), energy charge and storage protein gene expression	(Lappe et al. 2018)
	Pdk2	Zm00001d010321	Pyruvate phosphate dikinase (PPDK), energy charge and storage protein gene expression	(Lappe et al. 2018)
	ZmNAC128	Zm00001d040189	NAC TF, starch and zein accumulation	(Zhang et al. 2019d)
	ZmNAC130	Zm00001d008403	NAC TF, starch and zein accumulation	(Zhang et al. 2019d)
shrunken (Starch related genes)	*Ae1*	Zm00001d016684	Starch branching enzyme IIB, starch biosynthesis	(Fisher et al. 1996; Kim et al. 1998)
	Bt2	Zm00001d050032	ADP-glucose pyrophosphorylase (AGPase), starch biosynthesis	(Preiss et al. 1990)
	Se1	Zm00001d007657	FANTASTIC FOUR (FAF) domain protein, starch biosynthesis	(Zhang et al. 2019c)
	Sh1	Zm00001d045042	Sucrose synthase, starch biosynthesis	(Chourey and Nelson 1976)
	Sh2	Zm00001d044129	Large subunit of AGPase, starch biosynthesis	(Bhave et al. 1990)
	Su1	Zm00001d049753	Isoamylase-type DBE, starch biosynthesis	(James et al. 1995)
	Wx1	Zm00001d045462	Granule-bound starch synthase, starch biosynthesis	(Shure et al. 1983)
Others	*Bige1*	Zm00001d012883	MATE transporter	(Suzuki et al. 2015)
	Cr4	Zm00001d023425	TNFR-like receptor kinase, BETL differentiation	(Becraft et al. 1996)
	de18	Zm00001d023718	Yucca1, IAA biosynthesis	(Bernardi et al. 2012)
	hda101	Zm00001d053595	Histone deacetylase	(Rossi et al. 2007)
	Mn1	Zm00001d003776	Cell Wall Invertase CWI-2, BETL differentiation	(Cheng et al. 1996)
	MRP-1	Zm00001d010889	Myb-related protein-1, regulator of the differentiation of transfer cells	(Gómez et al. 2002)
	Nkd1	Zm00001d002654	INDETERMINATE DOMAIN (IDD) TF, regulator of endosperm development	(Gontarek et al. 2016)
	Nkd2	Zm00001d026113	INDETERMINATE DOMAIN (IDD) TF, regulator of endosperm development	(Gontarek et al. 2016)
	Ppr20	Zm00001d039548	PPR protein, RNA splicing	(Yang et al. 2020b)
	Ppr2263	Zm00001d045089	PPR protein, RNA editing	(Sosso et al. 2012b)
	qKW9	Zm00001d048451	PPR protein, RNA editing	(Huang et al. 2020)
	qVE5/ZmPORB2	Zm00001d013937	Chloroplast protochlorophyllide oxidoreductase, chlorophyll metabolism	(Zhan et al. 2019)
	RBR1	Zm00001d007407	Retinoblastoma-related (RBR) genes, inhibit the cell cycle	(Sabelli et al. 2005; Sabelli et al. 2009)
	RBR3	Zm00001d031678	Retinoblastoma-related (RBR) genes, inhibit the cell cycle	(Sabelli et al. 2005; Sabelli et al. 2009)
	Rgh3	Zm00001d016836	U2AF(35) Related Protein, U2-, and U12-type intron splicing	(Fouquet et al. 2011; Gault et al. 2017)
	Sal1	Zm00001d046599	Human Chmp1 homolog, BETL differentiation	(Shen et al. 2003)
	SWEET4c	Zm00001d015912	Sucrose-transporting homologs, hexose transport	(Sosso et al. 2015)
	thk1	Zm00001d027278	NOT1 subunit of the CCR4-NOT complex, cell division, signaling, differentiation and metabolism	(Wu et al. 2020)

Table 1 (continued)

Mutant phenotype	Gene name	B73 v4 ID	Functional annotation	References
	Ubl1	Zm00001d017432	U6 biogenesis-like 1, pre-mRNA splicing	(Li et al. 2017a)
	Urb2	Zm00001d028096	Urb2 domain-containing protein, pre-ribosomal RNA processing	(Wang et al. 2018b)
	Vks1	Zm00001d018624	ZmKIN11, regulates mitosis and cytokinesis	(Huang et al. 2019b)
	Ysl2	Zm00001d017427	Metal-nicotianamine (NA) transporter, Fe distribution	(Zang et al. 2020)
	ZmAFL1	Zm00001d021790	B3 domain TF, kernel filling	(Grimault et al. 2015)
	ZmAFL2	Zm00001d011712	B3 domain TF, kernel filling	(Grimault et al. 2015)
	Vp1	Zm00001d042396	B3 domain TF, regulator of AL development and embryo-endosperm protein reallocation	(McCarty et al. 1989; Zheng et al. 2019)
	ZmAFL4	Zm00001d001838	B3 domain TF, kernel filling	(Grimault et al. 2015)
	ZmAFL5	Zm00001d034965	B3 domain TF, kernel filling	(Grimault et al. 2015)
	ZmAFL6	Zm00001d052750	B3 domain TF, kernel filling	(Grimault et al. 2015)
	Mdh4	Zm00001d032695	Cytosolic malate dehydrogenase, catalyzes the conversion from OAA to malate	(Chen et al. 2020b)
	ZmDof3	Zm00001d035651	Dof TF, starch accumulation and aleurone development	(Qi et al. 2017c)
	ZmGE2	Zm00001d029526	Cytochrome p450 protein, embryo to endosperm ratio (EER)	(Zhang et al. 2012)
	Zmsmu2	Zm00001d023239	RNA-splicing factor, protein synthesis and RNA processing	(Chung et al. 2007)
	ZmSMR4	Zm00001d047159	CKI, regulates the transition between the mitotic cycle and endoreduplication	(Li et al. 2019a)
	ZmTar1	Zm00001d037498	ZmTA-Related1, IAA biosynthesis	(Chourey et al. 2010)
	ZmPIN1a	Zm00001d044812	PIN-FORMED (PIN) family protein, auxin transport	(Carraro et al. 2006; Forestan et al. 2010)
	ZmPIN1b	Zm00001d018024	PIN-FORMED (PIN) family protein, auxin transport	(Carraro et al. 2006; Forestan et al. 2010)
	ZmPIN1c	Zm00001d052269	PIN-FORMED (PIN) family protein, auxin transport	(Carraro et al. 2006; Forestan et al. 2010)
	ZmVPS29	Zm00001d053371	Retromer complex component, kernel morphology	(Chen et al. 2020a)

the largest mutant categories with cloned genes in maize. These mutants can be classified into several major kernel mutant types according to their mutant phenotypes. For example, the *defective kernel* (*dek*) mutants refer to those with affected development in both embryo and endosperm (Neuffer and Sheridan 1980), the *empty pericarp* (*emp*) mutants refer to those with empty pericarp or papery kernel (Scanlon et al. 1994), and the *embryo specific* (*emb)* mutants refer to those with morphogenic effects specific to the embryo (Clark and Sheridan 1991), etc. The cloning and functional analysis of numerous kernel development related genes greatly expanded our understanding of the molecular mechanisms during maize kernel development.

Together with recent advancements in high informative genetic mapping technology, such as GWAS, natural genetic variations related to maize kernel traits had been analyzed and captured (Xiao et al. 2017; Yan et al. 2011; Mir et al. 2019). The quick development of high-throughput sequencing technologies, such as RNA-seq, provided massive gene expression profiles during maize kernel development. Here, we provide an overview of recent progress in maize kernel development, with an emphasis on genetic mapping of kernel traits, transcriptome analysis during kernel development, functional gene

identification of kernel mutants, and genetic engineering of kernel traits.

Genetic mapping of maize kernel traits

In crops, many quantitative agronomical traits, such as grain yield and plant architecture, are governed by quantitative trait loci (QTL). Genetic mapping and molecular characterization of these functional loci facilitate molecular marker assisted breeding in crop improvement. Linkage mapping is a well-established tool for studying the genetic basis of quantitative traits in plants. During the last three decades, numerous studies were conducted and thousands of QTLs associated with various traits have been identified using molecular markers in maize (reviewed in Xiao et al. 2017; Yan et al. 2011; Mir et al. 2019).

Of particular interests, hundreds of QTLs regulating kernel-related traits, such as kernel weight and kernel size, were identified under multiple kernel developmental stages and environments (Zhang et al. 2014; Zhang et al. 2016; Hao et al. 2019; Li et al. 2013b; Raihan et al. 2016; Yang et al. 2019; Peng et al. 2011; Jiang et al. 2015; Martinez et al. 2016; Chen et al. 2016a, b; Liu et al. 2017; Chen et al. 2017a; Zhang et al. 2017b). For example, Zhang et al. (2014) collected a total of 54 unconditional main QTLs for five kernel-related traits, including kernel weight (KW), volume (KV), length (KL), thickness (KT), and width (KWI) from an immortalized F2 (IF2) maize population. Using conditional mapping analysis, they found that KWI and KV had the strongest influence on KW at the individual QTL level, followed by KT and KL; KV was mostly strongly influenced by KT, followed by KWI and KL. Chen et al. (2016a) identified 56 main-effect QTLs for yield per plant (YPP), seven ear-related traits, and seven kernel-related traits, based on the genetic linkage map constructed using 2091 bins as markers. In particular, *GRMZM2G168229*, which encodes an SBP-box domain protein, was identified as the candidate gene for *qKRN4-3* involving in the patterning of kernel row number (Chen et al. 2016a). Liu et al. (2017) identified a total of 729 QTLs regarding KL, KWI, KT, hundred KW, and kernel test weight in 10 recombinant inbred line populations. They identified 30 candidate genes that are orthologs of 18 rice genes associated with kernel size and weight, and confirmed the effects of five genes on maize kernel size/weight in an independent association mapping panel with 540 lines by candidate gene association analysis (Liu et al. 2017). For example, overexpression of *ZmINCW1*, an ortholog of the rice seed weight gene *GRAIN INCOMPLETE FILLING1* (*GIF1*), can rescue the reduced weight of the Arabidopsis homozygous mutant line in *AtcwINV2* (Arabidopsis ortholog of *ZmINCW1*), suggesting that these genes are conserved in both monocots and dicots.

These QTLs potentially contain major genes associated with the kernel development process and can be used to improve kernel yield and quality through marker-assisted selection. However, only few kernel-related QTLs have been cloned and characterized so far. For example, with the advantage of the reference genome of small-kernel inbred line, *BARELY ANY MERISTEM1d* (*ZmBAM1d*) was identified as the QTL responsible for kernel weight variation in maize (Yang et al. 2019). Other studies reported the cloning and characterization of previously identified major QTLs, *qKM4.08* (Li et al. 2013b), *qVE5* (Wang et al. 2018b), and *qKW9* (Raihan et al. 2016; Yang et al. 2019), implementing the list of characterized kernel-related QTLs in maize (Zhan et al. 2019; Huang et al. 2020; Chen et al. 2020a). *qVE5* encodes a chloroplast protochlorophyllide oxidoreductase (ZmPORB2) that is involved in chlorophyll metabolism enabling the production of phytol (Zhan et al. 2019). Overexpression of ZmPORB2 increased tocopherol content in both leaves and kernels. Interestingly, the tocopherol content was mainly determined by maternal effect (Zhan et al. 2019). The kernel size-related QTL *qKW9* encodes a pentatricopeptide repeat (PPR) protein that affects photosynthesis and grain filling (Huang et al. 2020), highlighting the importance of optimizing photosynthesis for maize grain yield production. *qKM4.08* encodes a retromer complex component ZmVPS29, overexpression of which confers a slender kernel morphology and increases the yield per plant in different maize genetic backgrounds (Chen et al. 2020a).

Association mapping has recently emerged as a tool to resolve complex trait variation by exploiting historical and evolutionary recombination events at the population level (Risch and Merikangas 1996; Nordborg and Tavaré 2002), providing a powerful tool for the dissection of complex agronomic traits in plants and animals (Altshuler et al. 2008; Hunter and Crawford 2008; Zhu et al. 2008; Rafalski 2010). With the development of next-generation sequencing technologies, and the release of the maize B73 reference genome (Schnable

et al. 2009), great progress has been made in QTL mapping using genome-wide association analysis (GWAS) in maize. A great number of traits including molecular and cellular, developmental and agronomic, yield, and stress resistance have been comprehensively investigated using association analysis, along with a number of cloned and candidate genes for corresponding traits (reviewed in Xiao et al. 2017; Yan et al. 2011). Several studies identified more loci associated with kernel-related traits using association analysis, revealing the genetic structure of complex quantitative traits during maize kernel development (Li et al. 2013c; Li et al. 2018a; Liu et al. 2020b; Zhang et al. 2020b; Zhang et al. 2017a). For example, kernel components-related traits, such as oil/fatty acid (Li et al. 2013c) and amylose (Li et al. 2018a), were identified using 9 million single nucleotide polymorphisms (SNPs) from 464 inbred maize lines, and 1.03 million SNPs characterized in 368 maize inbred lines, respectively. Li et al. (2013c) identified 74 loci significantly associated with kernel oil concentration and fatty acid composition, and the 26 loci associated with oil concentration could explain up to 83% of the phenotypic variation using a simple additive model. Li et al. (2018a) identified 27 associated loci involving 39 candidate genes that were linked to amylose content including transcription factors, glycosyltransferases, glycosidases, and hydrolases. A recent study reported the investigation of the genetic basis of three kernel-related traits, KL, KWI, and KT, in an association panel and a biparental population (Liu et al. 2020b). Fifty QTLs controlling these traits were detected with a total of 73 candidate genes in seven environments in the intermated B73 × Mo17 (IBM) Syn10 doubled haploid (DH) population. These studies provide insights into the mechanism of maize kernel development and the improvement of molecular marker-assisted selection for high-yield breeding in maize.

Transcriptome analysis of developing maize kernels

With the emergence of RNA-seq (Marioni et al. 2008), many transcriptome profiling studies have been conducted to uncover kernel development in different plant species, such as *Arabidopsis thaliana* (Le et al. 2010; Belmonte et al. 2013) and *Oryza sativa* (Gao et al. 2013; Xu et al. 2012). A detailed transcriptome during maize kernel development can greatly enhance our understanding of mechanisms of gene functions and cellular processes during maize kernel development.

The first transcriptome profiling investigation of maize kernel development was conducted on 9 DAP embryo and endosperm (Lu et al. 2013). The RNA-seq generated about 11 million paired-end reads from both the endosperm and the embryo. About 50.7% (8556 of 16,878) of multiexonic genes were found to be alternatively spliced, among which some transcript isoforms were specifically expressed either in the endosperm or in the embryo. In addition, many metabolic activities were specifically assigned to the endosperm or the embryo, and a number of TFs and imprinting genes were found to be specifically expressed in the endosperm or the embryo (Lu et al. 2013). A preliminary atlas of temporal and spatial gene expression patterns for early kernel development was established using RNA-seq analysis at five stages of whole kernels (0, 2, 3, 4, and 6 DAP) and three stages of isolated endosperms (8, 10, and 12 DAP) of the B73 inbred line (Li et al. 2014a). In this study, the RNA-seq generated nearly 34,000 mRNAs in the 0–6 DAP kernel and 33,000 mRNAs in endosperm at 8–12 DAP. A total of 7629 temporally regulated genes were identified, and several of the temporal patterns correlate with key developmental transitions associated with kernel and endosperm development (Li et al. 2014a). This atlas revealed a correlation between the major temporal programs and specific spatial expression programs in different compartments or tissue types of the developing endosperm. In another RNA-seq analysis of maize endosperm development at 5, 10, 15, and 20 DAP (Qu et al. 2016), more than 11,000 alternative spliced protein-coding genes and 7633 differentially expressed genes were detected during the four developmental stages. A comprehensive study of gene regulatory networks (GRNs) using 78 maize seed transcriptome profiles identified highly interwoven network communities (Xiong et al. 2017). For example, the kernel phenotype contributing community is composed of mostly unknown genes interacting with *Opaque2*, *Brittle endosperm1*, and *Shrunken2*. This study predicted important candidate genes in interwoven network communities that may be crucial to maize kernel development. These studies provided comprehensive insights into the transcriptome dynamics during maize kernel development.

A comprehensive study of endosperm cell differentiation was conducted in major endosperm cell types (AL, BETL, ESR, SE, central starchy endosperm

(CSE), and conducting zone (CZ)), the embryo, and four maternal compartments (nucellus (NU), placento-chalazal region (PC), pericarp (PE), and pedicel (PED)) using a coupled laser-capture microdissection and RNA-Seq strategy (Zhan et al. 2015). A total of 13,009 compartment-specific genes were identified for all captured compartments at 8 DAP. Coexpression modules associated with single or multiple kernel compartments were also identified using gene coexpression network analysis (Zhan et al. 2015). For example, a detailed analysis of a coexpression module highly correlated with the BETL identified a regulatory module activated by a previously characterized BETL regulator MRP-1 (Gómez et al. 2002). This study revealed the diverged gene expression programs between filial and maternal compartments, as well as an unexpected close correlation between the embryo and the endosperm. During early kernel development, the interface between the endosperm and the embryo is developmentally dynamic (Nowack et al. 2010; Bommert and Werr 2001; Ingram and Gutierrez-Marcos 2015). Indeed, the endosperm adjacent to scutellum (EAS) was recently identified through RNA-seq analysis, representing a developmentally dynamic interface influenced by the neighboring growing embryo (Doll et al. 2020). Further phenotypic analysis of loss-of-function mutants of genes enriched in the EAS will elucidate the biological role of this newly discovered endosperm subdomain.

On the other hand, two high-resolution studies provided highly valuable temporal transcriptome landscapes of maize kernel development (Chen et al. 2014; Yi et al. 2019). Using RNA-seq data generated from 53 samples at an interval of 2 days from 0 to 38 DAP kernels, Chen et al. (2014) detected a total of 26,105 seed-expressed genes, which includes 1614 TFs and 1258 kernel-specific genes. They clearly classified the detected genes into 16, 14, and 10 coexpression modules for the embryo, endosperm, and the whole kernel, respectively. For example, the coexpression modules C5 to C8 are the active storage accumulation phase which exhibits high expression of carbohydrate metabolism genes (Chen et al. 2014). This study provides a valuable resource for the in-depth understanding of the dynamics of gene expression throughout maize kernel development. A recent study from the same group reported a high temporal-resolution investigation of transcriptomes using 31 samples collected at an interval of 4 or 6 h within the first 6 days of maize kernel development (Yi et al. 2019). In this study, they detected a total of 22,790 expressed genes in the early stages of maize kernel development, including 1415 TFs and 1093 kernel-specific genes. In the first 16 h after pollination, coenocyte formation, cellularization, and differentiation stage, 160, 22, 112, and 569 kernel-specific genes were identified to have predominant expression, respectively. Using network analysis, they also predicted 31,256 interactions among 1317 TFs and 14,540 genes, uncovering major signaling such as calcium signaling, nucleosome, auxin response, and mitosis pathways in early developmental stage.

Gene cloning analysis of maize kernel mutants

PPR genes

A surprising outcome from the gene cloning of maize kernel mutants is that an overwhelming portion of cloned genes encodes PPR proteins (Table 2). The PPR proteins are recognized to be members of the alpha-solenoid superfamily proteins (Kobe and Kajava 2000; Small and Peeters 2000), which are found in all eukaryotes and function universally in organellar gene expression (Barkan and Small 2014). In angiosperms, the PPR family is one of the largest gene families accounting for 1–2% of nearly all genomes sequenced so far (Lurin et al. 2004; Wei and Han 2016; Chen et al. 2018a; Xing et al. 2018; Liu et al. 2016; Chen et al. 2018b; O'Toole et al. 2008). PPR proteins serve as sequence-specific RNA-binding proteins inside organelles (Barkan et al. 2012; Takenaka et al. 2013; Yagi et al. 2013; Yin et al. 2013; Cheng et al. 2016), and function in every step of organellar gene expression, including RNA stabilization, RNA cleavage, RNA translation, RNA splicing, and RNA editing (Schmitz-Linneweber and Small 2008; Fujii and Small 2011; Shikanai and Fujii 2013; Dahan and Mireau 2013). The plant PPR family consists of two major subfamilies, defined as P and PLS (Lurin et al. 2004), which exhibit diverse repertories of molecular functions, mostly in mitochondria and chloroplast (Colcombet et al. 2013).

Early studies of PPR mutants characterized a number of chloroplast-localized PPR genes involved in translation, RNA stability, and RNA splicing, such as *chloroplast RNA processing 1* (*crp1*) (Barkan et al. 1994; Fisk et al. 1999), *ppr2* (Williams and Barkan 2003), *ppr4* (Schmitz-Linneweber et al. 2006), *ppr5* (Williams-Carrier et al. 2008; Beick et al. 2008), and *ppr10*

Table 2 Mitochondrial PPR proteins characterized in maize

PPR type	Gene name	Mutant phenotype	B73 v4 ID	Functional annotation	References
PLS-type	*Dek10*	*dek*	Zm00001d053802	RNA editing, nad3-61, 62, and cox2-550	(Qi et al. 2017a)
	Dek36	*dek*	Zm00001d013136	RNA editing, atp4-59, nad7-383, and ccmFN-302	(Wang et al. 2017)
	Dek39	*dek*	Zm00001d047013	RNA editing, nad3-247 and nad3-275	(Li et al. 2018c)
	Dek45	*dek*	Zm00001d023331	RNA editing, cox3-314, nad2-26, and nad5-1916	(Ren et al. 2019a)
	Dek46	*dek*	Zm00001d043107	RNA editing, D5-C22 of nad7 intron 3 and 4	(Xu et al. 2020)
	Dek53	*dek*	Zm00001d041326	RNA editing, multiple sites	(Dai et al. 2020)
	Dek605	*dek*	Zm00001d016798	RNA editing, nad1-608	(Fan et al. 2020)
	Emp5	*emp*	Zm00001d042039	RNA editing, multiple sites	(Liu et al. 2013)
	Emp7	*emp*	Zm00001d008298	RNA editing, ccmFN-1553	(Sun et al. 2015a)
	Emp9	*emp*	Zm00001d022480	RNA editing, ccmB-43 and rps4-335	(Yang et al. 2017a)
	Emp18	*emp*	Zm00001d034253	RNA editing, atp6-635 and cox2-449	(Li et al. 2019b)
	Emp21	*emp*	Zm00001d033495	RNA editing, multiple sites	(Wang et al. 2019b)
	Ppr27	*emp*	Zm00001d029061	RNA editing, ccmFN-1357, rps3-707, rps12-221, rps13-100, 256, 287, nad2-355, and cox2-482	(Liu et al. 2020d)
	Ppr2263	*smk*	Zm00001d045089	RNA editing, nad5-1550 and cob-908	(Sosso et al. 2012b)
	Smk1	*smk*	Zm00001d007100	RNA editing, nad7-836	(Li et al. 2014b)
	Smk4	*smk*	Zm00001d049196	RNA editing, cox1-1489	(Wang et al. 2019a)
	Smk6	*smk*	Zm00001d025446	RNA editing, nad1-740, nad4L-110, nad7-739, and mttB-138,139	(Ding et al. 2019)
P-type	*Dek2*	*dek*	Zm00001d034882	RNA splicing, nad1 intron 1	(Qi et al. 2017b)
	Dek35	*dek*	Zm00001d033749	RNA splicing, nad4 intron 1	(Chen et al. 2017b)
	Dek37	*dek*	Zm00001d003543	RNA splicing, nad2 intron 1	(Dai et al. 2018)
	Dek41/Dek43	*dek*	Zm00001d021053	RNA splicing, nad4 intron 1 and 3	(Zhu et al. 2019; Ren et al. 2020)
	Emp8	*emp*	Zm00001d049796	RNA splicing, nad1 intron 4, nad2 intron 1, and nad4 intron 1	(Sun et al. 2018)
	Emp10	*emp*	Zm00001d033992	RNA splicing, nad2 intron 1	(Cai et al. 2017)
	Emp11	*emp*	Zm00001d052450	RNA splicing, nad1 intron 1, 2, 3, and 4	(Ren et al. 2017)
	Emp12	*emp*	Zm00001d002098	RNA splicing, nad2 intron 1, 2, and 4	(Sun et al. 2019)
	Emp16	*emp*	Zm00001d011559	RNA splicing, nad2 intron 4	(Xiu et al. 2016)
	Emp32	*emp*	Zm00001d040363	PPR protein, RNA splicing	(Yang et al. 2020c)
	Emp602	*emp*	Zm00001d028046	RNA splicing, nad4 intron 1 and 3	(Ren et al. 2019b)
	MPPR6	*smk*	Zm00001d034111	Translation, rps3 mRNA	(Manavski et al. 2012)
	Ppr14	*emp*	Zm00001d002157	RNA splicing, nad2 intron 3, nad7 intron 1 and 2	(Wang et al. 2020)
	Ppr18	*emp*	Zm00001d007927	RNA splicing, nad4 intron1	(Liu et al. 2020c)
	Ppr20	*dek/smk*	Zm00001d039548	RNA splicing, nad2 intron3	(Yang et al. 2020b)
	Ppr78	*smk*	Zm00001d034428	RNA stabilization, nad5 mature mRNA	(Zhang et al. 2017c)
	Ppr101	*emp*	Zm00001d010942	RNA splicing, nad5 introns 1 and 2	(Yang et al. 2020a)
	Ppr231	*emp*	Zm00001d018219	RNA splicing, nad5 introns 1, 2, 3, and nad2 intron 3	(Yang et al. 2020a)
	Ppr-smr1	*emp*	Zm00001d002345	RNA splicing, multiple introns	(Chen et al. 2019)

(Pfalz et al. 2009). Homozygous kernels of these mutants can still germinate and survive as chlorophyll-deficient seedlings until kernel reserves are exhausted (Stern et al. 2004). A later study of *PPR8522* reported the first case to associate the loss of a chloroplast-localized PPR gene with an embryo-lethal phenotype in maize (Sosso et al. 2012a). *PPR8522* is necessary for the transcription of nearly all plastid-encoded genes, and the *ppr8522* mutation caused an embryo-lethal phenotype, however, depending on the genetic background. A recently characterized PPR protein EMB-7L (Yuan et al. 2019), provided more evidence that chloroplast-localized PPR proteins play major roles in plastid translation, the mutation of which could possibly lead to embryo lethality.

Mutations in mitochondrial PPR proteins are commonly associated with severe defects in kernel development in maize, possibly due to the disruption of respiration. The first functionally characterized maize mitochondrial PPR protein was EMP4, which was shown to be necessary for endosperm development (Gutierrez-Marcos et al. 2007). However, neither its mode of action nor its molecular target(s) is known. A study of *ppr2263* kernel mutant provided the first phenotypic and molecular characterization in maize, in which PPR2263 was shown to be required for RNA editing at mitochondrial *nad5-1550* and *cob-908* sites, mitochondrial complex III assembly, and kernel development (Sosso et al. 2012b). In recent years, the number of characterized mitochondrial PPR proteins is expanding, with functions in almost every step of organellar gene expression, such as RNA splicing, RNA editing, RNA stabilization, and translation (Fig. 1). A summary of the detailed molecular functions of cloned mitochondrial PPR genes from maize kernel mutants is provided in Table 2.

As we shall see, most reported mitochondrial PPR proteins typically function as site-specificity RNA splicing factors (P-type) or RNA editing factors (PLS-type), and each of these proteins is required for splicing or editing of only a small number of sites. The mutation of splicing factors of group II introns usually causes impaired assembly and activity of mitochondrial complexes, which results in defective mitochondrial function and morphology, leading to severe kernel phenotypes, such as *dek* and *emp*. For example, the maize *Dek35* encodes a P-type PPR protein that is required for *cis*-spicing of mitochondrial *nad4* intron 1 (Chen et al. 2017b). The *dek35* mutation caused a deficiency in the complex I assembly and NADH dehydrogenase activity, producing lethal-kernel with a developmental deficiency (Chen et al. 2017b). Loss of function of maize P-type PPR protein EMP8 resulted in defects in *cis*-splicing of *nad1* intron 4, *nad4* intron 1, and *nad2* intron 1, leading to severely arrested kernel development (Sun et al. 2018). However, recent studies of SMR-subgroup PPR-SMR1 revealed exceptions that the *ppr-smr1* mutation affected RNA splicing of many mitochondrial group II introns (Chen et al. 2019). PPR-SMR1 is an SMR domain-containing P-type PPR protein, which is required for the splicing of 16 introns, accounting for nearly 75% of mitochondrial group II introns in maize. The failed splicing of these introns causes a deficiency of these proteins, leading to severe kernel phenotype in *ppr-smr1* mutants (Chen et al. 2019). It is still unknown why PPR-SMR1 facilities splicing of a surprisingly large number of group II introns. The protein-protein interactions between the PPR-SMR1 and Zm-mCSF1 (Chen et al. 2019), as well as between the PPR-SMR1 and PPR14 (Wang et al. 2020) provided clues that these PPR proteins might be involved in the formation of large and dynamic splicing complexes.

PLS-type PPR proteins typically function as site-specific factors in RNA editing. In maize mitochondria, similar to P-type splicing factors, defects in PLS-type editing factors normally result in impaired mitochondrial function and severe kernel phenotype. The first characterized maize organellar RNA editing factor *PPR2263* encoding a DYW domain-containing PPR protein that is required for RNA editing at *nad5-1550* and *cob-908* sites (Sosso et al. 2012b). The *ppr2263* mutation caused reduced embryo and endosperm growth, resulting in small but viable kernels. Maize *dek10* is a classic kernel mutant producing small kernels with delayed development (Qi et al. 2017a). *Dek10* encodes an E-subgroup PPR protein required for RNA editing at *nad3-61*, *nad3-62*, and *cox2-550* sites. Loss of *dek10* function caused reduced assembly of complex IV and activity of NADH dehydrogenase, leading to small and shrunken kernels (Qi et al. 2017a). However, a recent study of maize EMP21, a DYW-subgroup PPR protein, showed the exception that loss of *emp21* function affected RNA editing at 81 mitochondrial C targets, results in inhibited embryogenesis and delayed endosperm development (Wang et al. 2019c). Another interesting example is maize *Dek53*, which encodes an E-subgroup short PLS region-containing PPR protein (Dai et al. 2020). The mutation of *dek53* affected RNA editing at over 60

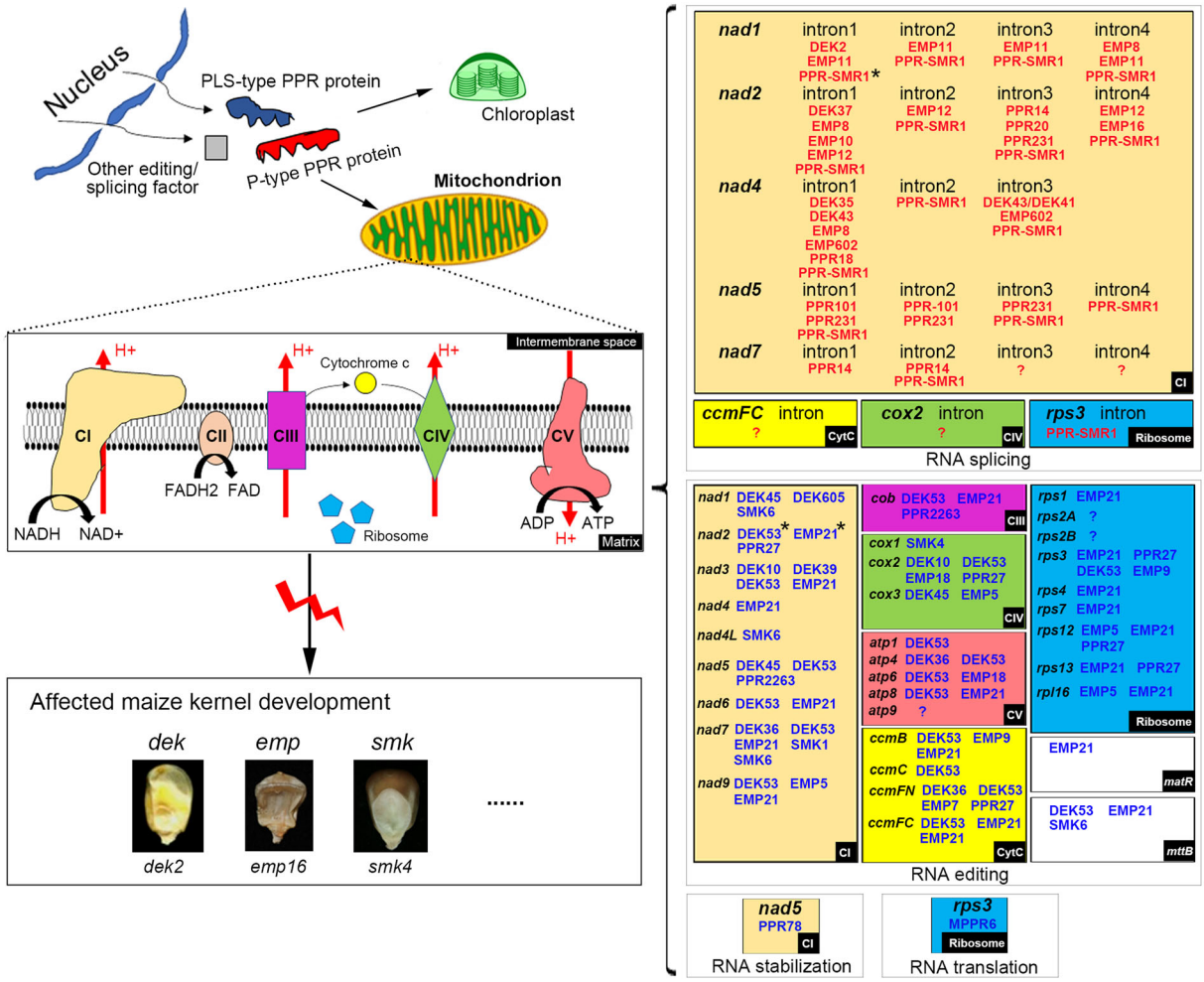

Fig. 1 Maize mitochondrial PPR proteins are important for kernel development. PPR proteins and other organellar editing/splicing factors are encoded in the nucleus, translated in the cytosol, and translocated into each organelle. Loss-of-function of mitochondrial PPR proteins usually causes impaired mitochondrial function and morphology, leading to defective maize kernel development with *dek*, *emp*, or *smk* kernel phenotypes. The *dek* phenotype refers to those with affected development in both embryo and endosperm, the *emp* phenotype refers to those with empty pericarp or papery kernel, and the *smk* phenotype refers to those with smaller kernels and delayed kernel development compared to the wild type. The *dek* and *emp* mutants are generally lethal, while a portion of *smk* mutants can germinate and develop. Shape and color variations indicate different protein families or mitochondrial respiratory components. CI to CV indicate mitochondrial complex I to complex V. PPR genes are listed by initials, targets and functions. The question marks indicate that no corresponding PPR proteins have been reported to be involved in splicing or editing of these specific mitochondrial group II introns or transcripts in maize. The asterisks mark PPR protein with multiple splicing or editing targets in maize mitochondrion

mitochondrial C targets, resulted in the aborted assembly of mitochondrial complex III and lethal kernels (Dai et al. 2020). It was hypothesized that unique binding to specific nucleotides would not be sufficient with only seven repeats units in DEK53 to convey a tight connection within the transcriptome of the 569-kb large maize mitochondrial genome (Clifton et al. 2004). Alternatively, different genetic backgrounds might be responsible for the variation of editing extent at some sites (Kempken et al. 1995; Bentolila et al. 2005; Chu and Wei 2020).

It is intriguing that many of these reported PPR proteins have interactions with other splicing or editing factors, leading to the speculation that these proteins might function in plant organellar "group II intron spliceosome" (de Longevialle et al. 2010) or "RNA editosome" (Takenaka 2014). Indeed, PPR14 interacts with PPR-SMR1 and Zm-mCSF1 to mediate intron

splicing of several mitochondrial group II introns in maize (Chen et al. 2019; Wang et al. 2020), suggesting that PPR14, PPR-SMR1, and Zm-mCSF1 may form a protein complex. In maize chloroplasts, CAF1 and CAF2 are two closely related proteins that function in concert with CRS2 to facility the splicing of group II introns (Ostheimer et al. 2006; Ostheimer et al. 2003). Several studies provided pieces of evidence that splicing factors could co-regulate the splicing of one or more specific introns by forming potential complexes (de Longevialle et al. 2010). In the case of *cis*-splicing event of mitochondrial *nad2* intron 1, five PPR proteins have been reported to be involved, including EMP10 (Cai et al. 2017), DEK37 (Dai et al. 2018), EMP8 (Sun et al. 2018), EMP12 (Sun et al. 2019), and PPR-SMR1 (Chen et al. 2019). In *Arabidopsis*, several splicing factors, including MTSF1 (Haïli et al. 2013), mCSF1 (Zmudjak et al. 2013), PMH2 (Köhler et al. 2010), nMAT1 (Keren et al. 2012), and ODB1 (Samach et al. 2011), also participate in the splicing of *nad2* intron 1. It is still unclear why the splicing of one specific intron needs several co-factors. It would be interesting to address whether the splicing of this specific intron was mediated by a splicing complex in mitochondria, as a high molecular weight ribonucleoprotein apparatus participating in *psaA* mRNA splicing has been identified in chloroplasts (Reifschneider et al. 2016).

The involvement of coordinated factors in organellar RNA editing has been studied in some detail (Sun et al. 2016), as the composition of a biochemically active editing complex has been determined in the chloroplast (Sandoval et al. 2019; Bentolila et al. 2012; Huang et al. 2019a). For example, RNA editing at *ndhA C437* requires several coordinated factors, including RIPs, OZ1, ORRM1, ISE2, CLB19 and DYW2, which have all been identified in a ~ 670 kDa complex in maize chloroplast extracts (Sandoval et al. 2019), though genetic knockout data of RIPs, OZ1, ORRM1, and ISE2 were still from Arabidopsis mutant plants (Bentolila et al. 2012; Takenaka et al. 2012; Sun et al. 2013; Sun et al. 2015b; Bobik et al. 2017). Mitochondrial protein components of maize RNA editosome have also been reported in several studies, such as DEK53/ZmMORF1/ORRMs (Dai et al. 2020), PPR27/ZmMORF1 (Liu et al. 2020d), and EMP21/ZmMORF8 (Wang et al. 2019c). However, such composition of a biochemically active editing complex has not been identified in maize mitochondrial extracts, and further studies will be needed to determine the exact composition of mitochondrial editing complex.

TFs

TFs play critical roles as key regulators for gene expression during maize kernel development. The first characterized TF in maize is a bZIP family protein OPAQUE2 (O2) (Schmidt et al. 1987), regulating genes in nearly all zein families during endosperm development (Schmidt et al. 1990, 1992; Muth et al. 1996). The *o2* mutation results in the opaque kernel phenotype with reduced levels of 22-kD α-zeins and increased lysine content (Mertz et al. 1964; Schmidt et al. 1987). Genome-wide identification of O2 regulated targets revealed that O2 regulated a diverse array of biological processes apart from zein biosynthesis (Frizzi et al. 2010; Hunter et al. 2002; Jia et al. 2013; Li et al. 2015a; Hartings et al. 2011; Zhan et al. 2018). Some of these diverse roles have been experimentally characterized recently. For example, an SnRK1-ZmRFWD3-O2 signaling axis that transduces source-to-sink signals and coordinates C and N assimilation was recently reported in developing maize kernels (Li et al. 2020). SUS-encoding genes (*Sus1* and *Sus2*) can be specifically recognized and be transactivated by O2, demonstrating that O2 transcriptionally regulates the metabolic source entry for protein and starch synthesis during endosperm filling (Deng et al. 2020). These studies provide extensive evidence that O2 functions as a central player that not only transcriptionally regulates the expression of most zein genes but also, directly and indirectly, regulates starch synthesis.

Several studies subsequently indicate that O2 functions in a complex with other regulatory proteins, such as O2-heterodimerizing proteins (OHPs) (Pysh et al. 1993; Yang et al. 2016; Zhang et al. 2015), Prolamin-box binding factor1 (PBF1) (Vicente-Carbajosa et al. 1997; Zhang et al. 2015), and MADS47 (Qiao et al. 2016). OHP1 and OHP2 are O2-interacting bZIP proteins identified by screening an endosperm cDNA library with an *O2* probe (Pysh et al. 1993). OHP1 and OHP2 can bind to the O2 target site in the promoters of 22-kD zein genes as a homodimer and as a heterodimer with O2 (Pysh et al. 1993) and can cotransactivate the 27-kD γ-zein promoter through protein-protein interaction with PBF1 (Zhang et al. 2015). OHPs recognize and transactivate α-zein promoters with much lower levels than O2 does, and the suppression of OHPs does not cause a significant reduction in the transcription of α-zein genes in the presence of O2 (Yang et al. 2016), indicating that OHPs function as minor TFs in this

process while O2 is the primary TF. Knockdown of *Ohp* expression resulted in dramatically reduced RNA transcript and protein levels of 27-kD γ-zein, leading to a vitreous kernel phenotype (Zhang et al. 2015). PBF1 is a member of the Dof (DNA binding with one finger) class of plant Cys2-Cys2 zinc-finger DNA binding proteins that specifically binds to P-box in the promoters of all zein genes (Vicente-Carbajosa et al. 1997). Knockdown of *Pbf1* expression resulted in opaque kernel phenotype and dramatically reduced synthesis of the 27-kDa γ- and 22-kDa α-zeins (Wu and Messing 2012; Zhang et al. 2015). O2 and PBF1 also affect starch synthesis by directly regulating *Cytoplasmic pyruvate orthophosphate dikinase1* (*cyPpdk1*), *cyPpdk2*, and *Starch synthase III*, which are critical components in the starch biosynthetic enzyme complex (Zhang et al. 2016). A MADS-box protein ZmMADS47 is an O2-interacting protein that binds the CATGT motif in promoters of α-zein and 50-kD γ-zein genes. Transactivation of these promoters by ZmMADS47 requires the interaction with O2, thereby greatly enhances the transactivation activity (Qiao et al. 2016). A recent study identified another endosperm-specific TF, ZmbZIP22, a bZIP-type TF that binds to ACAGCTCA box in the 27-kD γ-zein promoter and activated its expression (Li et al. 2018b). The CRISPR/Cas9-generated *zmbzip22* mutants showed significantly reduced accumulation of 27-kD γ-zein. Interestingly, ZmbZIP22 physically interacts with PBF1, OHP1, and OHP2, but not O2 (Li et al. 2018b), indicating that the expression of the 27-kD γ-zein gene is regulated by a complex mechanism. Two endosperm-specific NAC TFs, ZmNAC128 and ZmNAC130, are also involved in the regulation of zein genes (Zhang et al. 2019d). They specifically activated transcription of the 16-kDa γ-zein gene and *Bt2*, and lack of them caused reduced accumulation of protein and starch, leading to a shrunken kernel phenotype.

FLOURY3 (FL3) is an endosperm-specific TF regulated by genomic imprinting (Li et al. 2017). The *fl3* mutation resulted in a semidominant negative mutant that exhibits severe defects in the endosperm. FL3 interacts with two critical factors of the RNA polymerase III, RNA polymerase III subunit 53, and transcription factor class C 1, to regulate maize endosperm development and storage reserve filling (Li et al. 2017). *ZmDof3* encodes a plant-specific Dof TF that is essential for maize endosperm development (Qi et al. 2017c). Suppression of *ZmDof3* resulted in a *dek* phenotype with reduced starch content and a partially patchy aleurone layer. ZmDOF3 directly regulates starch biosynthesis genes *Du1* and *Su2*, and AL-associated TF *Nkd1*, to regulate the signaling system controlling starch accumulation and aleurone development (Qi et al. 2017c).

OPAQUE11 (O11) is an endosperm-specific bHLH TF that plays central roles in endosperm development and nutrient metabolism (Feng et al. 2018). The *o11* mutation resulted in small and opaque endosperm with reduced starch and protein accumulation. O11 directly regulates key TFs in endosperm development and nutrient accumulation, such as NKD2, ZmDOF3, PBF1, and O2. O11 interacts with ZmICE1, an ortholog of Arabidopsis ICE1 functioning in cold tolerance (Chinnusamy et al. 2003) and endosperm development (Denay et al. 2014), to co-regulate genes involved in stress response during endosperm development. In addition, O11 also regulates genes specifically expressed in the ESR, such as *ZmYoda*, indicating that O11 might be a regulator for ESR development. Characterization of O11 highlighted an endosperm regulatory network centered around O11 in endosperm development, nutrient metabolism and stress responses (Feng et al. 2018).

VIVIPAROUS1 (VP1) is a well-documented TF that is specifically expressed in the AL and the embryo (McCarty et al. 1989; McCarty et al. 1991). VP1 is an ortholog of Arabidopsis ABA-INSENSITIVE3 (ABI3) that plays essential roles in kernel development (McCarty et al. 1989) and ABA signaling (Suzuki et al. 2003). Null alleles of *vp1* and *abi3* resulted in the loss of ABA sensitivity, leading to vivipary or non-dormancy in maize (McCarty et al. 1989) and Arabidopsis (Nambara et al. 1992; Nambara et al. 1994). VP1 mediates *trans*-repression of α-amylase expression in the AL, and the *vp1* mutation repressed the germination response in developing mutant kernels (Hoecker et al. 1995). VP1 can also activate the expression of C1 (Hattori et al. 1992), a MYB family TF involved in anthocyanin biosynthesis (Cone et al. 1986; Paz-Ares et al. 1987). As the consequence, the *vp1* mutation resulted in suppressed anthocyanin production in mutant kernels (McCarty et al. 1989). Interestingly, a recent study provided evidence that VP1 is also essential for scutellum development and protein reallocation from the endosperm to embryo (Zheng et al. 2019). This study used maize *zein-RNAi* knockdown mutants as a novel system to study nutrient allocation from the endosperm to embryo. VP1 transactivated many sulfur assimilation- and nutrient metabolism-associated genes that are differentially

expressed between wild-type and *zein-RNAi* knockdown kernels (Zheng et al. 2019), suggesting a role for VP1 as a regulator for endosperm-embryo communication.

The maize *naked endosperm1* (*nkd1*) *nkd2* mutation produced multiple ALs with partially differentiated cells (Yi et al. 2015; Becraft and Asuncion-Crabb 2000). *Nkd1* and *Nkd2* encode the INDETERMINATE1 domain (IDD) containing TFs that are required for endosperm cell patterning and differentiation, possibly by regulating genes associated with cell cycle, cell growth, and division, such as *Retinoblastoma-related1* and *Mitotic cyclin 3B-like* (Gontarek et al. 2016). *nkd* kernels also displayed a propensity for vivipary and anthocyanin-deficient phenotype, providing additional clues to how the NKD genes regulate endosperm development. Indeed, NKD1 and NKD2 directly activate the expression of *Vp1* (Gontarek et al. 2016) and are predicted to directly activate *R1*. In addition, NKD1 and NKD2 can regulate O2 and PBF, indicating that NKD1 and NKD2 promote strorage protein accumulation during endosperm development. These evidences strengthened the concept that the aleurone and the starchy endosperm are not separate lineages (Becraft and Asuncion-Crabb 2000).

A prime example of BETL differentiation is ZmMRP-1, the so far only BETL-specific TF to be identified (Gómez et al. 2002). ZmMRP-1 preceded the formation of transfer cells (Gómez et al. 2002) and regulated the expression of many BETL genes, including *Maternally expressed gene1* (*MEG1*) (Gutiérrez-Marcos et al. 2004), *Transfer cell response regulator ZmTCRR-1* (Muñiz et al. 2006, 2010), and CRP-encoding genes *ZmBETL1*, *ZmBETL2*, *ZmBETL9*, and *ZmBETL10* (Gómez et al. 2002, 2009), suggesting that ZmMRP-1 might be a key player involved in BETL differentiation. Indeed, the ectopic expression of *ZmMRP-1* is sufficient to temporarily transform epidermal cells into transfer cells, and the expression of *ZmMRP-1* is needed to maintain the BETL cell phenotype (Gómez et al. 2009). It is proposed that low base levels of *ZmMn1* and *ZmSWEET4c* allow small amounts of glucose to enter the cell, which in turn induces *ZmMRP-1*, which then induces genes necessary for establishing the transfer cell machinery including *ZmMn1* and *ZmSWEET4c* (Sosso et al. 2015). These properties of ZmMRP-1 had made it a determinant of BETL development.

Embryo-specific (*Emb*) genes

Embryo is the other important portion of fertilized maize kernel. Plant embryogenesis is a complex developmental process characterized by several major events (Kaplan and Cooke 1997). In maize, a number of embryo-specific (*emb*) mutants have been isolated from different genetic resources, making embryo lethality one of the most common mutant traits (Neuffer and Sheridan 1980; Clark and Sheridan 1991; Sheridan and Clark 1993c). In *emb* mutants, the endosperm develops normally, while the embryo shows severe developmental aberrations.

The first cloned *emb* mutant was *lethal embryo1* (*lem1*), which possessed a normally developed endosperm and an aborted embryo at an early developmental stage (Ma and Dooner 2004). *Lem1* encodes a plastid ribosomal protein S9 (RPS9), providing evidence that functional plastids are required for normal maize embryo development (Ma and Dooner 2004). A subsequent study of *emb8516* showed a very similar kernel phenotype to *lem1*, in which the development of mutant embryos deviates as soon as the transition stage from that of wild-type sibling (Magnard et al. 2004). *Emb8516* encodes a plastid ribosomal protein L35 (ZmPRPL35-1), which is part of 50S ribosome in plastids. The mutation caused a deficiency of protein synthesis in plastids, thereby the metabolic deficiency of embryo cells ultimately led to the abortion of the embryo. It is intriguing that several characterized *emb* genes, such as *Ppr8522* (Sosso et al. 2012a), *Emb14* (Li et al. 2015b), *Emb12* (Shen et al. 2013), and *Emb16* (Zhang et al. 2013), all encode plastid proteins as PPR protein, cGTPase, translation initiation factor 3, and DNA/RNA-binding protein WHIRLY1 (WHY1), respectively. Mutations in either gene caused arrested embryo development at the transition stage, suggesting that disrupts in plastid function might be linked to embryo lethality. It is generally not surprising that defects in plastid translation could produce a lethal embryo, as plastids play a fundamental role in the basic metabolism of plant cells, such as photosynthesis, fatty acid synthesis, and plant hormone biosynthesis (Bowsher and Tobin 2001). However, the characterization of some plastid PPR proteins such as PPR2 revealed exceptions, as these *ppr* mutant kernels displayed germinated embryo (Williams and Barkan 2003; Schmitz-Linneweber et al. 2006; Beick et al. 2008; Khrouchtchova et al. 2012). How do plastids affect

embryogenesis has not been defined in maize, though genetic suppression might offer an explanation to the relationship between plastid translation and embryogenesis (Zhang et al. 2013).

Numerous efforts have been made on characterizing *emb* mutants in *Arabidopsis*, providing insights into potential mechanisms of plastid-mediated embryogenesis (Meinke 2020). A comprehensive screen for *emb* mutants altered in plastid proteins summarized three major types of plastid-localized proteins appearing to be most frequently associated with embryo lethality in *Arabidopsis*: (1) enzymes required for the biosynthesis of amino acids, vitamins, nucleotides, and fatty acids; (2) proteins required for the import, modification, and localization of essential proteins within the chloroplast; and (3) proteins required for chloroplast translation (Bryant et al. 2011). It is likely that disruption of a plastid protein should result in the lethal embryo if the function of that protein extends beyond photosynthesis. However, there is a difference in embryogenesis between maize and *Arabidopsis* with respect to the requirement for certain gene functions. Elucidation of this difference occurred in plastid proteins involved in post-transcriptional regulation. For example, AtPPR2 (Lu et al. 2011) and ZmPPR2 (Williams and Barkan 2003) share over 60% sequence identity at the amino acid level and are considered to be orthologous. However, the null mutation of *Atppr2* and *Zmppr2* result in totally different embryo fate. The mutant alleles of *Atppr2* caused lethal embryo (Lu et al. 2011), while *Zmppr2* null mutation did not lead to any defects in embryogenesis (Williams and Barkan 2003). Another example was from the studies of AtCAF2 (Asakura and Barkan 2006), ZmCAF2 (Ostheimer et al. 2003), and OsCAF2 (Shen et al. 2020). Loss of *caf2* function results in plastid ribosome deficiency in all three species; however, embryo lethality only occurs in *Arabidopsis*. It will be interesting to have further evidences underline these striking differences in the developmental significance of plastid function in different plant species.

Genes related to cell cycle regulation

From about 4 to 20 DAP, the endosperm undergoes a phase of mitotic cell proliferation, followed by endoreduplication, during which a dramatic growth of the endosperm and the accumulation of storage compound emerges (Sabelli and Larkins 2009; Larkins et al. 2001). Factors affecting the cell cycle during endosperm development have been studied in maize, especially for cyclin-dependent kinases (CDKs) and CDK inhibitors. In eukaryotes, control of cell cycle progression is dependent on conserved molecular machinery consisting of protein kinases known as CDKs and their regulatory cyclin subunits (CYCs) (Vandepoele et al. 2002). In maize, reduced activity of type A CDK (CDKA), *cdc2ZmA*, inhibited the progression of endoreduplication cell cycles (Colasanti et al. 1991; Leiva-Neto et al. 2004). However, the lower level of endoreduplication did not affect cell size and only slightly reduced starch and storage protein accumulation (Leiva-Neto et al. 2004). CYCB2;2 is a type B2 cyclin that is sustained accumulated during maize endosperm development (Sabelli et al. 2014). The kinase activity of CYCB2;2 was observed in mitotic endosperm but was not or little observed in the immature ear and endoreduplicating endosperm, indicating that CYCB2;2 functions primarily during the mitotic cell cycle (Sabelli et al. 2014). Two CDK inhibitors, KIP-RELATED PROTEIN1 (KRP1) and KRP2, specifically inhibited cyclin A1;3- and cyclin D5;1-associated CDK activities (Coelho et al. 2005). Overexpression of KRP;1 in maize embryonic calli led to an additional round of DNA replication without nuclear division. Other CDK inhibitors, such as KRP1;1 and KRP4;2, are responsible for inhibiting kinase activity in CycD2;2-CDK, CycD4;2-CDK, and CycD5;3-CDK complexes (Godínez-Palma et al. 2017). A recent study of ZmSMR4, a member of SIAMESE-RELATED gene family, provided more evidence that CDK inhibitors play a role in plant growth and responses to abiotic stress (Li et al. 2019a).

Recent studies identified other factors regulating the cell cycle during maize kernel development (He et al. 2019; Huang et al. 2019b; Zhang et al. 2020a). During mitosis and meiosis, cohesin complexes maintain sister chromatid cohesion to ensure proper chromosome segregation (Haering et al. 2002; Nasmyth and Haering 2009). Maize *Dek15* encodes a homolog of SISTER CHROMATID COHESION PROTEIN 4 (SCC4), a loader subunit of the cohesin ring. The *dek15* mutation disrupted the mitotic cell cycle and endoreduplication, resulting in collapsed endosperm and embryo lethality (He et al. 2019). Another cohesin complex subunit structural maintenance of chromosome3 (SMC3) interacts with centromeric histone H3 (CENH3) during meiotic prophase I (Zhang et al. 2020a). Loss of *Zmsmc3* function caused the premature loss of sister chromatid cohesion and mis-segregation of chromosomes in

mitotic spreads (Zhang et al. 2020a). Maize VKS1 is a member of kinesin-14 subfamily that is essential for the migration of free nuclei in the coenocyte, as well as in mitosis and cytokinesis in early mitotic divisions (Huang et al. 2019b). The absence of *vks1* caused reduced cell proliferation, resulting in varied kernel sizes (Huang et al. 2019b). With the advantage of kernel mutant libraries and transcriptome studies, more genes involved in cell cycle regulation might be identified in future studies, thereby further extending our understanding of the cell cycle regulation during maize kernel development.

Genes related with ribosome biogenesis and RNA processing

As a "house-building" function producing all cellular proteins, ribosome biogenesis is a highly regulated and coordinated multistep process (Lempiäinen and Shore 2009). It requires synthesis, processing, and modification of pre-rRNAs, assembly with ribosomal proteins, and transient interaction of numerous non-ribosomal factors with the evolving pre-ribosomal particles (Tschochner and Hurt 2003). A recent study demonstrated that "ITS1-first" and "5' ETS-first" pathways coexist to promote the 35S pre-rRNA processing, highlighting a new 27SA pre-rRNA processing mechanism that is unique to maize and other higher plants (Liu et al. 2020a). In maize, three protein-coding genes related to rRNA and ribosome biosynthesis have been characterized (Gendra et al. 2004; Qi et al. 2016; Wang et al. 2018b). ZmDRH1 is a DEAE box RNA helicase that localizes to the nucleolus and interacts with the RNA binding protein MA6 and FIBRILLARIN (Gendra et al. 2004). MA16, ZmDRH1, and FIBRILLARIN may be forming part of a nucleolar RNP complex, and/or MA16 is an essential RNP-multifunctional protein component serving different functions in the cell. Reas1 is an AAA-ATPase that controls 60S ribosome export from the nucleus to the cytoplasm after ribosome maturation. The *reas1* mutation partly repressed the maturation and export of the 60S ribosomal subunit, resulting in small kernels with delayed development (Qi et al. 2016). Maize Unhealthy Ribosome Biogenesis2 (URB2) is an ortholog of yeast URB2 that is involved in ribosome biogenesis. The *urb2* kernels showed decreased ratios of 60S/40S and 80S/40S and increased ratios of polyribosomes, leading to thin kernels with delayed development (Wang et al. 2018a).

Two splicing factors, ROUGH ENDOSPERM3 (RGH3) (Fouquet et al. 2011; Gault et al. 2017) and RNA-binding motif protein 48 (RBM48)/DEK42 (Bai et al. 2019; Zuo et al. 2019), showed comprehensive evidence that the splicing of U2- and U12-type introns is critical for maize kernel development. *Rgh3* encodes the maize U2AF^{35}-related protein (URP) that is involved in both U2 and U12 splicing (Fouquet et al. 2011). The *rgh3* mutation resulted in retained or miss-spliced U12-type introns, leading to a rough, etched, or pitted endosperm surface as well as a reduced kernel size (Gault et al. 2017). RBM48, also reported as DEK42 (Zuo et al. 2019), is a U12 splicing factor that functions to promote cell differentiation and repress cell proliferation. Mature *rbm48* kernels had reduced endosperm size and lethal embryos (Bai et al. 2019). RBM48 can interact with RGH3, U2 auxiliary factor (U2AF), and armadillo repeat containing 7 (ARMC7), suggesting major and minor spliceosome factors required for intron recognition form complexes with RBM48. These studies greatly extended our understanding of the roles of U2- and U12-type intron splicing during maize kernel development.

Genes related with metabolism and other functions

Gene cloning of different maize kernel mutants also revealed functional genes involved in other biological processes, such as metabolic processes, ion/sugar transporting, and hormone biosynthesis. Metabolic enzymes, such as DEK33 (Dai et al. 2019) and SMK2 (Yang et al. 2017b), are involved in vitamin biosynthesis. *Dek33* encodes a pyrimidine reductase in vitamin B2 biosynthesis, null mutation of *dek33* caused aborted kernel development at the early developmental stage (Dai et al. 2019). SMK2 is a glutaminase in vitamin B6 biosynthesis, and the *smk2* mutation resulted in arrested embryo development, but had a reduced role in endosperm development (Yang et al. 2017b). Mutation in *pdg3*, the third isozyme of oxPPP enzyme 6-phosphogluconate dehydrogenase (6PGDH), caused a *rough endosperm* kernel phenotype with reduced embryo oil (Spielbauer et al. 2013). *ZmOcd1* encodes the oxalyl-CoA decarboxylase1 which catalyzes oxalyl-CoA, the product of O7 (Wang et al. 2011), into formyl-CoA and CO_2 for degradation. Mutations in *ocd1* caused dramatic alterations in the metabolome in the endosperm, leading to opaque endosperm phenotype (Yang et al. 2018). *SEED CAROTENOID DEFICIENT* (*SCD*) encodes an enzyme that converts 2C-methyl-d-

erytrithol 2,4-cyclodiphosphate to 1-hydroxy-2-methyl-2-(E)-butenyl 4-diphosphate in the penultimate step of the methylerythritol phosphate (MEP) pathway in maize (Zhang et al. 2019b). The *scd* mutant kernels displayed pale-yellow phenotype with a reduced level of MEP-derived isoprenoids (Zhang et al. 2019b). Characterization of IAA biosynthesis genes, such as *De18* (Bernardi et al. 2012; LeClere et al. 2010) and *ZmTAR1* (Chourey et al. 2010), demonstrated the significance of the large abundance of IAA in developing maize kernel (Jensen and Bandurski 1994; LeClere et al. 2008). For example, the *de18* mutation caused a large reduction of free IAA levels compared with *De18*, leading to an approximately 40% reduction of endosperm dry mass (Bernardi et al. 2012).

ZmSWEET4c mediates transepithelial hexose transport across the BETL (Sosso et al. 2015). Mutants of *Zmsweet4c* are defective in seed filling, indicating that a lack of hexose transport at the BETL impairs the further transfer of sugars imported from the maternal phloem (Sosso et al. 2015). A plasma membrane localized metal-nicotianamine (NA) transporter, ZmYSL2, plays an important role in Fe transport during kernel development. The *Zmysl2* mutation produced smaller and collapsed kernels (Zang et al. 2020). Maize *trans*-Golgi associated gene *Big embryo 1* (*Bige1*) encodes a MATE transporter BIGE1 that is required for transport of an intermediate or product associated with the CYP78A pathway. Loss of BIGE1 function caused accelerated leaf and root initiation as well as enlargement of the embryo scutellum (Suzuki et al. 2015). These studies greatly improved our understanding of the essential roles of genes involved in different biological processes during maize kernel development.

Genetic engineering

With the development of plant transformation technologies, genetic engineering became a powerful tool for crop improvement in addition to conventional breeding methods. Knowledge acquired from the identification of gene function and biochemical characterization of target proteins has been successfully applied to enhance the important agronomic traits in maize kernel (Smidansky et al. 2002; Smidansky et al. 2003; Hannah et al. 2012).

Modification of starch synthetic pathway in maize kernel is of particular interest, as the starch is the major component of yield. The synthesis of starch precursor (ADP-Glc) by the ADP-glucose pyrophosphorylase (AGPase) is a rate-limiting step in starch synthesis. AGPase is composed of two identical small and two identical large subunits. The small and large subunits of AGPase in maize endosperm are encoded by the *brittle-2*(*bt2*) and *shrunken-2* (*sh2*) genes, respectively (Hannah 2007). The loss function of *bt2* and *sh2* would greatly reduce starch levels in the endosperm. Because of its allosteric properties and heat-labile characteristics, AGPase represents a suitable target for genetic manipulation. In early studies, site-specific mutagenesis by means of *dissociation* (*Ds*) transposon was used to generate a series of *Sh2* revertants. Interestingly, a phosphate-insensitive mutation form of SH2 would increase seed weight 11–18% without impact the percentage of starch (Giroux et al. 1996). Heat-stable variants of AGP were also isolated by a bacterial expression system, and a single point mutation of *Sh2* (*Sh2hs33*) was found to have increased heat stability through enhanced subunit interactions (Greene and Hannah 1998).Yield increase with enhanced AGPase transgenes was reported in different species with the use of either an engineered maize *Sh2* (*HS33/Rev6 Sh2*) with enhanced heat stability and reduced orthophosphate inhibition or an enhanced *Escherichia coli* glgC-16 AGPase gene (Giroux et al. 1996; Smidansky et al. 2002; Wang et al. 2007; Smidansky et al. 2003; Lee et al. 2008; Obana et al. 2006; Sakulsingharoj et al. 2004). Surprisingly, the yield increase was due to an increased seed number rather than an increase in seed weight by expression *Sh2* (*Sh2hs33*) driven by a native promoter in maize (Hannah et al. 2012). The extent of yield increase is also temperature-dependent. It was proposed that *Sh2* not only played an important role in the endosperm but also functioned in maternal tissue to increase the frequency of seed development from the ovaries (Hannah et al. 2012). Similar to that of *Sh2*, the small subunit of AGPase, *bt2*, was found to function in maternal tissue to enhance the kernel set (Hannah et al. 2017). Nonetheless, it is showed that overexpression of wide type form of *Sh2* and *bt2* could increase individual maize seed weight and starch content compare to the control (Li et al. 2011).

Cell wall invertase is another example of genes which can be genetically engineered to increase maize kernel size and weight (Li et al. 2013a). It has been shown that the cell wall invertase gene plays an important role during the early grain filling (Wang et al. 2008). *Mn1* encodes a cell wall invertase expressed in maize endosperm, loss function of Mn1 results in a significant reduction of seed mass (Cheng et al. 1996). When

constitutively overexpression cell wall invertase gene from *Arabidopsis*, rice or maize, all of them can enforce the enzyme activities and promote biomass production up to ~ 145% in the transgenic maize (Li et al. 2013a). The substantially improved grain yield is due to increased starch content, enlarged kernel size, and enhanced kernel number (Li et al. 2013a).

Recently, overexpression of engineered *Zmda1* and *Zmdar1* in transgenic maize was also reported to enhance the sugar import into the kernels and show an improved kernel weight and kernel number (Xie et al. 2018). The ubiquitin receptor *DA1*/*DA1R* are negative regulators in seed size control, and a single base mutant $DA1R^{358K}$ leads to larger leaves, flowers, and seeds phenotype in *Arabidopsis* (Li et al. 2008). *ZmDA1* and *ZmDAR1* are homologous of *AtDA1* and *AtDAR1* in maize. The mutation forms of *ZmDA1* and *ZmDAR1* with the same single base change at the conserved sites (*Zmda1* and *Zmdar1*) were transformed into maize separately. Three years of field trials confirmed that the overexpression with the mutated *Zmda1* and *Zmdar1* could promote basal endosperm transfer cell layer (BETL) development and the expression of starch synthase genes. On the contrary, overexpression of wild-type *ZmDA1* and *ZmDAR1* transgenic plants showed slowed growth and decreased yield (Xie et al. 2018).

Conclusion

In recent years, thanks to the rapid development of omics technologies, significant progress had been made in the studies of maize kernel development. Particularly, the impressive high-resolution transcriptome profiles for developing maize kernels laid a solid foundation for further studies in functional genes and gene regulatory networks. However, there is still room for improvement in gene expression analysis in the spatial dimensions. Although several studies provided valuable data based on microdissections, transcriptome at higher resolution would depend on single-cell sequencing technologies in the future. A large number of cloned maize kernel mutants greatly expanded our knowledge about functional genes and their regulation during maize kernel development. Nevertheless, compared to the model species such as Arabidopsis and rice, there is still a big gap in the number of functionally characterized genes in maize kernel development. Related to this, the available genes that can be effectively used to improving agronomic trait is very limited. In the following years, the cloning and functional analysis of more genes associated with maize kernel development is the major task. With the progress in functional genome studies and recent breakthroughs in maize stable transformation and CRISPR-Cas9 technology, modern breeding technology could further boost the yield and quality of maize kernels based on synthetic and system biology strategies.

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Compliance with ethical standards

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