

Review Article

Genome Diversity in Maize

Victor Llaca,¹ Matthew A. Campbell,² and Stéphane Deschamps¹

¹ DuPont Agricultural Biotechnology, Experimental Station, P.O. Box 80353, Wilmington, DE 19880-0353, USA

² Pioneer Hi-Bred International Inc., A DuPont Company, 7300 NW 62nd Avenue, P.O. Box 1004, Johnston, IA 50131-1004, USA

Correspondence should be addressed to Victor Llaca, victor.llaca@usa.dupont.com

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Zea mays (maize) has historically been used as a model species for genetics, development, physiology and more recently, genome structure. The maize genome is complex with striking intraspecific variation in gene order, repetitive DNA content, and allelic content exceeding the levels observed between primate species. Maize genome complexity is primarily driven by polyploidization and explosive amplification of LTR retrotransposons, with the counteracting effect of unequal and illegitimate crossover. Transposable elements have been shown to capture genic content, create chimeras, and amplify those sequences via transposition. New sequencing platforms and hybridization-based strategies have appeared over the past decade which are being applied to maize and providing the first genome-wide comprehensive view of structural variation and will provide the basis for investigating the interplay between repeats and genes as well as the amount of species level diversity within maize.

1. Introduction

Maize is among the most extensively studied plant species in the history of genetics. Beyond its considerable agricultural and economic value as a crop for food, feed and fuel, maize presents unparalleled biological attributes as a research model for genetic diversity and genome evolution [1, 2]. The maize genetic pool includes a large natural diversity among both wild and cultivated relatives. Well-established breeding strategies, inbred lines, mutant collections, easy-to-follow phenotypes, and large distinctive chromosomes are just some of the characteristics that allowed the construction of the first plant genetic map [3], proof of meiotic recombination linked with the recombination of genetic traits, and support for the chromosomal theory of inheritance [4, 5]. Subsequent research using maize as a genetic model led to the discovery of epigenetic modifications (in the form of paramutation) as well as transposable elements (TEs) (later found to be common to most, if not all, eukaryotic and prokaryotic organisms) [6–9].

The accumulated cytogenetic and genetic data and more recently, vast sequence information derived from genome project initiatives in grasses, have provided a wealth of information on the structure and evolution of the maize genome. A BAC-by-BAC, mapped draft of the genome of

the maize inbred line B73 is currently available ([10]; latest release, AGPv2 available at <http://www.maizesequence.org/>). Additional structural and sequence data for diverse maize genotypes are accumulating thanks to the use of improved comparative genomics hybridization (CGH) techniques and deep resequencing using next-generation sequencing platforms [11–14]. Furthermore, an increasing number of finished genome sequences within the Poaceae (i.e., grass family) provide an important resource for comparative genomics [15]. Currently, there are relatively complete physical assemblies for four nonmaize grass species: rice (*Oryza sativa* [16]), sorghum (*Sorghum bicolor* [17]), purple false broom (*Brachypodium distachyon*) [18], and foxtail millet (*Setaria italica* [19]; Bennetzen et al., unpublished results; <http://www.phytozome.net/foxtailmillet.php/>).

In this review, we focus on the diversity of the nuclear genome of maize. As we will describe in this paper, this is a dynamic genome, with multiple processes playing a role in its expansion, contraction, and sequence diversification.

2. General Characteristics of the Maize Genome

The maize genome is genetically diploid and consists of 10 chromosomes with an estimate size ranging from 2.3

to 2.7 Gb [9, 10, 20, 21]. As is the case with other large genomes in plant species, the maize genome consists mostly of a nongenic, repetitive fraction punctuated by islands of unique, or low-copy DNA that harbor single genes or small groups of genes. The repetitive elements contribute significantly to the wide range of diversity within the species and include transposable elements (TEs), ribosomal DNA (rDNA), and high-copy short-tandem repeats mostly present at the telomeres, centromeres, and heterochromatin knobs [5, 22–24].

Transposable elements are mobile, “selfish” sequences of DNA that have the capacity of moving from an original location to different parts of the genome. They are classified as Class I (retrotransposons) and Class II (DNA transposons), according to whether the transposition intermediate is RNA or DNA, respectively, [25].

Retrotransposons are duplicated *in situ* via reverse transcription, with the new copy inserting itself in a new location in the genome, producing a net gain of one element. Most Class II transposable elements, on the other hand, follow a transposition process by cutting and pasting. Members of one family of DNA transposons in plants are proposed to have replicative transposition which uses a rolling circle DNA replication mechanism [26]. Class I and Class II transposons are either autonomous, which is defined as containing all the components necessary for transposition, or nonautonomous, indicating that their transposition is dependent upon the presence of the cognate autonomous element [25]. The most abundant class of TEs in plants is long terminal repeats (LTRs) retrotransposons, which are retrovirus-like mobile genetic elements characterized by having long terminal repeats. Most LTR retrotransposons are bounded by target site duplications (TSDs), show extensive CpG and CHG methylation, as well as being generally organized into large clusters and commonly nested inside other LTR retrotransposons [27, 28]. Over 1 million LTR retrotransposon fragments, corresponding to more than 75% of the total nuclear genome sequence, have been identified in the maize genome. The actual number of elements is hard to define due to the nested nature of retrotransposition in maize and the fragmentation of the data [29] although some estimates have ranged from 150,000 to 250,000 elements [27]. To date, 441 families of LTR retrotransposons have been annotated, most of them present at relatively low copy numbers (less than 10 copies) and constituting a small proportion of the genome. However, two families (*Copia* and *Gypsy*) are highly abundant and constitute about 80% of the total retroelements. Retrotransposons do not follow a random distribution, with *Copia*-like elements usually present in genic regions and *Gypsy*-like elements overrepresented in pericentromeric and other heterochromatic regions [10]. Finally, LINES (Long Interspersed Nuclear Elements) and their short derivatives, SINES (Short Interspersed Nuclear Elements), are less-defined, non-LTR retroelements. LINES are commonly identified by the presence of TSDs (typically generated during insertion) and one end terminated with a homopolymer, usually poly(T), while SINEs have an internal RNA polymerase III promoter sequence and one homopolymer end, and their transposition is dependent

upon the presence of the autonomous LINE [29]. LINES and SINES are relatively infrequent in maize and constitute approximately 1% of the genome.

Class II elements, DNA transposons, constitute a smaller proportion of the genome in maize than retrotransposons, about 8.6%. The first descriptions of mobile elements were class II maize transposons, discovered by Barbara McClintock during her study of chromosomal duplications, inversions, and translocations produced by the *Ac/Ds* elements [6, 30]. Since then, additional families of DNA transposons have been identified and classified which include: *Tc1-Mariner*, *hAT*, *Mutator*, *PIF_Harbinger*, and their nonautonomous derivatives which are termed MITES (Miniature Inverted Transposable Elements) [25, 31]. These Class II elements are usually bounded by terminal inverted repeats (TIRs) and are flanked by short TSDs. Autonomous elements encode transposase and/or additional genes that are necessary for their transposition, while nonautonomous elements tend to be short, have nonconserved internal sequences, and/or carry captured DNA elements [25, 32]. Like retrotransposons, class II elements do not have a randomized distribution in the genome and most families, with the exception of elements from the *CACTA* family, have insertional preference for genic regions [10]. Methylation seems to have a role in the regulation and silencing of class I and II transposable elements, and activation is correlated with de-methylation of TIRs [33–35].

High-copy tandem repeats are present in different parts of the genome including centromeres, telomeres, knobs, and rDNA. The centromeric regions include a combination of repeats and retrotransposons in or near sequences that participate in the formation of the kinetochore and in the attachment of microtubules on chromosomes during mitosis and meiosis. Maize centromeres consist of thousands of a 156-bp unit called CentC [23] (reviewed in [36]). Centromeres evolve very quickly and centromere repeats have little or no homology between species. However the same repeats are found in all maize chromosomes [37]. Due to difficulties sequencing large regions with tandem repeats, the number of copies in most centromeres has not been determined. The only centromeres that have been fully assembled are those on chromosome 2 and 5 which are thought to be the shortest [38]. The maize ZmB73v1 reference genome assembly contains an estimated 54% of the genome's total CentC content [38]. Analysis of stretched DNA fibers suggests that the total length of CentC arrays varies less than 100 kb to several Megabases [37]. Four types of retrotransposons, CRM1, CRM2, CRM3/CentA, and CRM4 have been described as centromeric and are interspersed among CentC tandem repeat sequences [10]. One additional repeat sequence, Cent4, is at or near the primary constriction of chromosome 4 [39]. Heterochromatic knobs, cytological features that can be observed as dark round structures, consist of megabase-sized tandem repeats of derivations of one of two repeats (180 and 350 bp long) that comprise 0.6% to 6% of the total genome. They can be found in more than 20 specific locations in pachytene chromosomes [40], and their structural differences among maize varieties suggested significant intraspecific diversity of

the maize genome as we will discuss later. Knobs can also have retroelements inserted [22, 41–43]. The rDNA regions consist of thousands of tandem repeats encoding for rRNA. It has been estimated that the maize genome has between 1,600 to 23,000 9-kb tandem copies of genes encoding the 45S RNA precursor for the 18S, 5.8S, and 28S ribosomal RNA on the short arm of chromosome 6. This arrangement constitutes the nucleolus organizer region (NOR), another early observable cytogenetic feature in the maize genome [44]. Each of these ribosomal genes in the repeat is separated by a non-transcribed spacer. Precursors for 5S ribosomal RNA genes are clustered as 342-bp tandem repeats in an additional, smaller cluster in long arm of chromosome 2 [45, 46]. Telomeres, first named by Muller in 1938 but defined by McClintock in maize several years earlier [5], include tandem-repeated telomeric and subtelomeric sequences that protect the frequent rearrangements that naturally occur at the ends of DNA molecules [47]. Finally the maize genome includes thousands of simple sequence satellites and a few megatracts of trinucleotide repeats, namely, AGT and AGC [48].

The total number of nontransposon-related genes, pseudogenes and miRNAs constitute the rest of the maize genome, approximately 5% of the total [49]. While it is difficult to estimate accurately the total number of genes due to the incomplete nature of the current B73 physical assembly, it has been estimated recently to be approximately 32,000, classified in 11,892 families and a total of 150 loci encoding miRNA [10]. However, syntenic arrangements of genes are not necessarily conserved across individuals within the *Zea* genus as we will discuss below.

3. Intraspecific Diversity of Maize

Early cytogenetic studies showed considerable line-specific differences in heterochromatin, or C, banding, and heterochromatic knob distribution. Supernumerary chromosomes, or B chromosomes, were also found in some maize and teosintes [50–54]. These cytogenetic differences have been positively correlated to differences in DNA content [55–57]. Using Southern hybridization, Rivin et al. [41] found that copy numbers of tandem-repeated sequences such as ribosomal DNA and knob repeats varied among North American genotypes for as much as two to three fold. Intraspecific variations of as much as 38.8% from the average of 5.5 pg/2n nucleus have been reported in *Zea mays* [55, 56, 58–60]. More recently, sequencing data has demonstrated that the maize genome exhibits rather variable levels of naturally occurring genetic diversity depending on the lines involved in the comparison [49, 61]. On average, the frequency of single nucleotide polymorphism between two maize inbreds is approximately 1 substitution per 100 bases [62, 63]. Interestingly, this level of intraspecific polymorphism is striking when compared to mammals; this average rate of polymorphism is 10 times higher than that observed between humans and also higher than that observed between human and chimpanzees [64].

Maize seems to be tolerant of increases in large amounts of DNA content per nucleus without noticeable effect on plant phenotype. In maize, the most significant recent contributions to genome size have been by LTR retrotransposons, and their number and distribution have been shown to vary considerably in different haplotypes [65, 66]. Copy number variation has been found in tandem repeats at centromeres, knobs, and rDNA loci [43, 67, 68].

Major focus has been given recently to regions with copy number variation (CNV) and presence-absence variation (PAV). With the improvement of genome-wide hybridization technologies and increasing information on the sequences of multiple maize lines by next-generation technologies, it is becoming clear that CNV and PAVs have a major role in the diversity of the maize genome, and potentially its heterosis. Springer et al. [69] analyzed the structural variation present between the genomes of the inbred lines B73 and Mo17 using comparative genomic hybridization (CGH). This study showed megabase-size B73 regions that were absent in Mo17. By using PCR analysis in 22 additional lines, they were able to identify a 2 Mb region on chromosome 6 that was present or absent from the lines as a single haplotype block. Beló et al. [70] used an expression array to perform CGH analysis on 13 North American maize inbreds with the reference inbred B73 and found a total of 2,109 potential CNVs; the authors screened a subset of 15 CNV loci via PCR and were able to confirm that 12 loci (80%) were true insertion/deletion events. Two of the CNV regions were shown to be at least hundreds of kilobases long with the remaining validated CNVs being fewer than 10 kb in length. Swanson-Wagner et al. [71] used array-based CGH to compare content and copy number variation of 32,500 genes among 19 diverse maize inbred lines and 14 teosinte accessions, relative to the B73 reference genome. They found variation in about 10% of the targets, with 479 genes showing higher and 3,410 genes showing lower copy number or missing in B73. Most down genes were single copy in B73 and therefore considered PAV. A number of genes were higher in some lines and lower/absent in others. Interestingly they discovered that the majority of these polymorphisms predated the origin of maize from teosinte.

4. Mechanisms of Maize Genome Evolution and Diversity

Major mechanisms have an effect in the evolution of the maize genome and the generation of intraspecific genome diversity (1) whole genome duplications (polyploidization) and segmental duplications, (2) DNA transposition and retrotransposition, (3) capture and translocation of genes or gene segments by transposons, (4) recombination and gene conversion events, and (5) single base mutations and expansion/contraction of simple sequence repeats (SSRs). These mechanisms are described below and added to the genome diversity generated by the gene flow between maize populations and introgression between maize and related species (teosinte) [49, 72].

4.1. Duplication and Polyploidization. Like in other cereals and plants in general, polyploidization has played an important role in the evolution of the maize genome [73, 74]. Evidence for both segmental duplications and whole genome duplication by wide crosses was initially found in linkage and comparative genetic analysis, which showed extensive chromosome duplications in maize [75]. More recently, comparative sequence information has supported the idea that the maize genome has undergone at least two polyploidization events. In the first event, approximately 70 to 80 Myr ago, a common ancestor to cereals underwent whole genome duplication, followed by gene loss. More than 68% of the duplicated genes from this event, which are currently collinear between rice and sorghum, retain only one copy. However, 99% of these genes are orthologous between the two species, suggesting that early gene loss predated the divergence among the cereals [76]. Genes have been preferentially removed from one of the homologs, a process called biased fractionation [77]. The second polyploidization event in maize occurred from 5 to 12 Myr ago and occurred after the divergence from the last common ancestor to sorghum. Two progenitors of maize hybridized at some point between 4.8 and 11.9 Myr [78–80], giving rise to a tetraploid followed by large-scale loss and movement of duplicated genes (up to 50%) and chromosomal rearrangements that eventually returned the genome to a diploid behavior [81, 82]. The number of maize B73 high-confidence protein-coding genes predicted under high stringency is 32,540, higher than similar estimates for *Brachypodium* (25,532), rice (29,717), or sorghum (27,640) [10, 17, 18, 83]. This number is likely to be an underestimate due to the missing genic content in the current physical assembly. While there are stable tetraploid maize varieties reported [68], the most important effect of polyploidization in modern maize is the redundancy that the early polyploidization generated, with the subsequent relaxation of selective constraints.

4.2. Retrotransposition and the Expansion of the Maize Genome. While maize and sorghum, close relatives within the Andropogoneae tribe, share the same number of chromosomes, the maize genome is approximately 3 times the size of sorghum (800 Mbp). The secondary polyploidization described above accounts for only part of this difference. The overall size of the maize genome and intergenic distances has expanded dramatically due to LTR retrotransposition within the last 10 Myr. In grasses, the proportion of LTR retrotransposons is correlated to its genome size, while the proportion of Class II transposons remains constant (see Table 1). The small genomes of *Brachypodium* and rice have a retrotransposon content of 23.3% and 25.8%, respectively, compared to 54.5% in sorghum, and 75.9% in maize [84].

The high abundance and nonrandom distribution of LTR retroelements in maize was one of the early observations made as sequence information started accumulating [85–88]. As these elements have long terminal repeats that are identical at the time of the transposition, the analysis of mutations allowed dating of the elements [89]. Initial studies

of nested retroelements found within the *adh* region indicated that a massive retrotransposition event had occurred in the last 3 Myr. [65, 66, 89]. Liu et al. [90] investigated the insertion dynamics of LTR retrotransposons in gene-free and gene-containing BACs and identified two peaks of amplification in gene-free areas, the first around 1.5–2 Mya and a more recent one, within the last 500,000 years. They found only one peak of amplification in gene-containing regions, within the last 1 Myr. The conservative nature of LTR retrotransposition via an RNA intermediate and leaving behind the original element belies the reason why this selfish DNA has colonized and expanded the maize genome.

4.3. Mechanisms for Genome Decrease. Both unequal and illegitimate recombinations are important mechanisms that may counteract the expanding effects of LTR retrotransposition [91]. Unequal homologous recombination within a chromosome (i.e., intrastrand), that is associated with larger (>50 bp) direct repeats (in this case between adjacent LTRs), is proposed to generate a “solo” LTR and leads to the net deletion of the internal sequence plus one LTR sequence [92, 93]. The effects of unequal crossover between homologous LTR sequences at distinct chromosomal locations can have more striking results including a reciprocal deletion and duplication event, inversions and reciprocal translocations [94, 95]. By comparison, illegitimate recombination can occur between smaller lengths of homology than unequal homologous recombination and is proposed to be responsible for the creation of numerous internal deletions and truncated LTR retrotransposons [96]. This form of recombination is presumed to occur via non-homologous end joining or slip-strand mispairing which, in turn, leads to DNA loss [96, 97]. All three of these mechanisms are proposed to counteract the genome expansion in plants which is primarily driven by either increases in ploidy or amplification of repetitive DNA [94].

4.4. Transposons and Genetic Colinearity. Intraspecific genome variation has long been attributed to changes in size of heterochromatic DNA outside coding sequences that contracted or expanded the chromosomes [98]. However, violation of gene microcolinearity has been found in multiple locations since it was first reported by Fu and Dooner [99]. These authors sequenced 230-kb and 110-kb BAC contigs flanking the *bz* locus in the North American inbred lines B73 and McC, respectively, and found extensive differences in content and position of intergenic retrotransposons. More remarkably, out of 10 genes clustered in the McC sequence, 4 were absent in B73. Further sequence analysis of the *bz* locus in multiple lines showed considerable variation in other maize lines, with only 25% to 84% of sequences shared [100]. Similar polymorphisms for the presence/absence of genic sequences have been found in different chromosome locations [101, 102].

Helitrons have been associated to intraspecific violation of genetic colinearity in maize. The role of *Helitrons* leading to genome variation in maize was first reported by Lai et al. [103], using comparative bioinformatics analysis of the *bz*

TABLE 1: Distribution and proportion of features in the annotated genomes of 4 grasses. Table shows a comparison of major genomic element types between 4 published references. N/A indicates these data were not available.

Reference sequence completed*	<i>Brachypodium</i> [17]		Rice [15, 115]		Sorghum [16]		Maize [9]	
	Copies	% Genome	Copies	% Genome	Copies	% Genome	Copies*	% Genome
Class I (retroelements)	50,419	23.33	61,900	19.36	216,519	54.47	1,139,990	75.6
LTR Ty1/copia	12,426	4.86	11,600	3.85	19,844	5.18	404,000	23.7
LTR Ty3/gypsy	32,978	16.05	23,500	10.9	38,652	19	477,000	46.4
LTR other	1,870	0.48	N/A	N/A	156,304	30.25	222,000	4.5
Non-LTR (LINE)	3,145	1.94	9,600	1.12	513	0.04	35,000	1
Non-LTR (SINE)	N/A	N/A	1,800	0.06	0	0	1,990	0
Other Class I	N/A	N/A	15,400	3.43	1,206	N/A	N/A	N/A
Class II (DNA Transposon)	29,630	4.78	163,800	12.96	76,883	7.57	142,800	8.6
CACTA	1,523	2.18	10,800	2.69	15,006	4.69	12,400	3.2
hAT	658	0.24	1,100	0.38	296	0.02	31,800	1.1
Mutator	2,854	0.63	8,800	3.64	440	0.06	N/A	N/A
Tc1/mariner	50	0.07	67,000	2.26	22	0	N/A	N/A
PIF/harbinger	862	0.42	N/A	N/A	389	0.13	N/A	N/A
MULE	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
MITE (Stowaway)	N/A	N/A	N/A	N/A	7,191	0.19	12,900	1
MITE (Tourist)	23,563	1.06	57,900	3.26	27,724	0.94	14,000	0.1
Helitron	120	0.18	N/A	N/A	1,017	0.81	49,700	1
Other Class II	N/A	N/A	18,200	0.73	24,798	0.73	22,000	2.2
Protein-encoding genes	25,532	37	29,717	29	27,640	15	32,540	6

region in McC and B73 to reveal the presence/absence of two *Helitrons*, *HelA*, and *HelB*, which account for all of the allelic variation at this locus. Unlike other Class II TEs, *Helitron* elements are not flanked by terminal inverted repeats and do not generate TSDs. They have an 18–25 bp sequence able to form a hairpin near the 3' end and preferentially insert in AT dinucleotides [104, 105]. A more extensive study between inbred lines B73 and Mo17 [106] suggested that a large proportion of differential insertions in the genome between B73 and Mo17 could be attributed to *Helitron* sequences. While most reported *Helitron* genes seem to be truncated versions of their progenitor genes [107], the maize CYP72A27-Zm gene represents a full cytochrome P450 monooxygenase (P450) gene recently captured by a *Helitron* and transposed into an *Opie-2* retrotransposon [108]. Complete *Helitron* elements are widespread in the genome. One study identified 1,930 intact *Helitrons* consisting of 8 families and more than 20,000 *Helitron* fragments [109, 110]. Another study identified 2,791 nonautonomous *Helitron* elements [111]. The majority of the elements identified thus far represent nonautonomous *Helitrons* containing chimeric segments derived from multiple genes although the analysis of the complete sequencing of one single maize inbred line provides only biased information of the extent and diversity of gene capture, transposition, and amplification by *Helitrons* [112].

In addition to *Helitron*, the *Mutator* superfamily possesses non-autonomous elements, called Pack-MULES, that have the ability to capture segments of nuclear gene(s) which can be arranged in chimeras [113, 114]. Further, molecular evidence has revealed that these novel chimeras can be both transcribed and translated, which suggest that this mechanism of gene fragment capture inside of non-autonomous elements can produce, and evolve into, novel protein coding sequences [113, 114]. Much like the *Helitron* elements, Pack-MULE transposition and amplification can lead to deviations in intraspecific synteny, and recent research has shown that Pack-MULES preferentially capture GC-rich genomic segments and displayed biased insertion into the 5' end of coding regions [115]. Pack-MULE elements possess sequences that are associated with small RNAs and can influence the expression profile of the captured genic sequences, and, given the insertional bias towards the beginning of the transcribed region, these elements can have significant effects on the expression of the endogenous genes into which they are inserted [115].

5. Future Prospects

The discovery of the colinearity of the maize and other grass genomes, dating back to 50–80 million years ago, was a major breakthrough in comparative genomics within the Poaceae and helped in the identification of genes, gene families, duplication events, and characterization of the structural variation of the genomes [24, 116, 117]. The accumulation of evidence pointing to high structural polymorphism and the significant sequence diversity among maize inbreds, however, highlights a serious limitation in the use of a single reference genome as a sufficient representative of a species. Thus, in

order to capture the range of sequence diversity (i.e., single nucleotide polymorphisms and small sized indels) as well as larger structural variations (i.e., CNVs, PAVs, and large indels), deep resequencing and assembly of the gene space to create a “pan-genome” is necessary among a range of diverse inbreds [118]. While the B73 reference assembly in its current state has proven invaluable for annotation and basic research into the organization and diversity of gene (and repeat) content, there are estimates of upward of 10% of the genic content missing from the current version [10, 29]. The complexity of the maize genome combined with available resequencing strategies (either Sanger or next-generation sequencing) prevents the creation of a completed physical assembly similar to that in Arabidopsis and rice whose genome sizes are roughly an order of magnitude smaller. With the advent of next-generation sequencing platforms, the ability to rapidly generate the full content of sequences in an inbred with high coverage is now feasible, but *de novo* assembly of these short reads will not create any additional finished assemblies of comparable quality to B73 within maize. Comparative genomic hybridization (CGH) strategies offer a rapid and inexpensive strategy to look at structural variation and alignment of WGS reads to the B73 reference assembly and will produce an equivalent “digital” CGH for a reasonable cost. However, both of these strategies will have a strong B73-centric bias for the foreseeable future. Thus, for a period of time until sequencing technology significantly increases read lengths to promote robust genome assembly from whole genome shotgun (WGS) projects, a large amount of diverse sequences from the *Zea* genus will remain as small, anonymous assemblies which will have to be positioned by laborious or inexact methods including, among others, BAC library screening, syntenic comparisons to sorghum, oat-maize addition line screening, and genetic mapping via GBS on segregating populations. However, these small, genic assemblies from deep resequencing projects can be annotated structurally and functionally in a manner similar to EST and FL-cDNA projects that were initiated prior to significant reference assembly creation in the past two decades. And upon the creation of the large contigs of physical sequence, these small genic assemblies are easily integrated. Therefore, genic diversity in maize can be collected and analyzed in detail for individual inbreds using deep resequencing and assembly, and, upon the advent of upcoming sequencing platforms that will allow rapid *de novo* assembly, these can be easily organized on the physical map.

References

- [1] E. H. Coe, “The origins of maize genetics,” *Nature Reviews Genetics*, vol. 2, no. 11, pp. 898–905, 2001.
- [2] J. L. Bennetzen, “The future of Maize,” in *Handbook of Maize: Genetics and Genomics*, J. L. Bennetzen and S. Hake, Eds., pp. 771–779, Springer, Berlin, Germany, 2009.
- [3] R. A. Emerson, G. W. Beadle, and A. C. Fraser, “A summary of linkage studies in maize,” *Cornell University Agricultural Experimental Station Memoir*, vol. 180, pp. 1–83, 1935.
- [4] H. B. Creighton and B. McClintock, “A correlation of cytological and genetical crossing-over in *Zea mays*,” *Proceedings*

- of the National Academy of Sciences of the United States of America, vol. 17, no. 8, pp. 492–497, 1931.
- [5] B. McClintock, “The order of genes C, Sh, and Wx in Zea mays with reference to a cytological known point on the chromosome,” *Proceedings of the National Academy of Sciences of the United States of America*, vol. 17, no. 8, pp. 485–491, 1931.
- [6] B. McClintock, “The origin and behavior of mutable loci in maize,” *Proceedings of the National Academy of Sciences of the United States of America*, vol. 36, no. 6, pp. 344–355, 1950.
- [7] R. A. Brink, “A genetic change associated with the R locus in maize which is directed and potentially reversible,” *Genetics*, vol. 41, no. 6, pp. 872–889, 1956.
- [8] V. L. Chandler, W. B. Eggleston, and J. E. Dorweiler, “Par-
amutation in maize,” *Plant Molecular Biology*, vol. 43, no. 2-3, pp. 121–145, 2000.
- [9] J. L. Bennetzen, “Maize genome structure and evolution,” in *Handbook of Maize: Genetics and Genomics*, J. L. Bennetzen and S. Hake, Eds., pp. 179–199, Springer, Berlin, Germany, 2009.
- [10] P. S. Schnable, D. Ware, R. S. Fulton et al., “The B73 maize genome: complexity, diversity, and dynamics,” *Science*, vol. 326, no. 5956, pp. 1112–1115, 2009.
- [11] S. J. Emrich, W. B. Barbazuk, L. Li, and P. S. Schnable, “Gene discovery and annotation using LCM-454 transcriptome sequencing,” *Genome Research*, vol. 17, no. 1, pp. 69–73, 2007.
- [12] M. A. Gore, J. M. Chia, R. J. Elshire et al., “A first-generation haplotype map of maize,” *Science*, vol. 326, no. 5956, pp. 1115–1117, 2009.
- [13] J. P. Vielle-Calzada, O. M. De La Vega, G. Hernández-Guzmán et al., “The palomero genome suggests metal effects on domestication,” *Science*, vol. 326, no. 5956, p. 1078, 2009.
- [14] J. Lai, R. Li, X. Xu et al., “Genome-wide patterns of genetic variation among elite maize inbred lines,” *Nature Genetics*, vol. 42, no. 11, pp. 1027–1030, 2010.
- [15] X. Wang, H. Tang, and A. H. Paterson, “Seventy million years of concerted evolution of a homoeologous chromosome pair, in parallel, in major poaceae lineages,” *Plant Cell*, vol. 23, no. 1, pp. 27–37, 2011.
- [16] T. Sasaki, “The map-based sequence of the rice genome,” *Nature*, vol. 436, no. 7052, pp. 793–800, 2005.
- [17] A. H. Paterson, J. E. Bowers, R. Bruggmann et al., “The Sorghum bicolor genome and the diversification of grasses,” *Nature*, vol. 457, no. 7229, pp. 551–556, 2009.
- [18] J. P. Vogel, D. F. Garvin, T. C. Mockler et al., “Genome sequencing and analysis of the model grass *Brachypodium distachyon*,” *Nature*, vol. 463, no. 7282, pp. 763–768, 2010.
- [19] A. N. Doust, E. A. Kellogg, K. M. Devos, and J. L. Bennetzen, “Foxtail millet: a sequence-driven grass model system,” *Plant Physiology*, vol. 149, no. 1, pp. 137–141, 2009.
- [20] A. L. Rayburn, D. B. Biradar, D. G. Bullock, and L. M. McMurphy, “Nuclear DNA content in F1 hybrids of maize,” *Heredity*, vol. 70, pp. 294–300, 1993.
- [21] S. Zhou, F. Wei, J. Nguyen et al., “A single molecule scaffold for the maize genome,” *PLoS Genetics*, vol. 5, no. 11, Article ID e1000711, 2009.
- [22] W. J. Peacock, E. S. Dennis, M. M. Rhoades, and A. J. Pryor, “Highly repeated DNA sequence limited to knob heterochromatin in maize,” *Proceedings of the National Academy of Sciences of the United States of America*, vol. 78, no. 7, pp. 4490–4494, 1981.
- [23] E. V. Ananiev, R. L. Phillips, and H. W. Rines, “Chromosome-specific molecular organization of maize (*Zea mays* L.) centromeric regions,” *Proceedings of the National Academy of Sciences of the United States of America*, vol. 95, no. 22, pp. 13073–13078, 1998.
- [24] M. Morgante, “Plant genome organisation and diversity: the year of the junk!,” *Current Opinion in Biotechnology*, vol. 17, no. 2, pp. 168–173, 2006.
- [25] C. Feschotte, N. Jiang, and S. R. Wessler, “Plant transposable elements: where genetics meets genomics,” *Nature Reviews Genetics*, vol. 3, no. 5, pp. 329–341, 2002.
- [26] V. V. Kapitonov and J. Jurka, “Rolling-circle transposons in eukaryotes,” *Proceedings of the National Academy of Sciences of the United States of America*, vol. 98, no. 15, pp. 8714–8719, 2001.
- [27] P. J. SanMiguel and C. Vitte, “The LTR-retrotransposons of maize,” in *Handbook of Maize: Genetics and Genomics*, J. L. Bennetzen and S. Hake, Eds., pp. 307–328, Springer, Berlin, Germany, 2009.
- [28] J. B. Hollick and N. Springer, “Epigenetic phenomena and epigenomics in maize,” in *Epigenomics*, A. C. Ferguson-Smith, J. M. Grealley, and R. A. Martienssen, Eds., pp. 119–147, Springer, Berlin, Germany, 2009.
- [29] R. S. Baucom, J. C. Estill, C. Chaparro et al., “Exceptional diversity, non-random distribution, and rapid evolution of retroelements in the B73 maize genome,” *PLoS Genetics*, vol. 5, no. 11, Article ID e1000732, 2009.
- [30] B. McClintock, “Mutation in maize,” *Carnegie Institution of Washington Yearbook*, vol. 52, pp. 227–237, 1953.
- [31] T. Wicker, F. Sabot, A. Hua-Van et al., “A unified classification system for eukaryotic transposable elements,” *Nature Reviews Genetics*, vol. 8, no. 12, pp. 973–982, 2007.
- [32] D. Lisch and N. Jiang, “Mutator and MULE transposons,” in *Handbook of Maize: Genetics and Genomics*, J. L. Bennetzen and S. Hake, Eds., pp. 277–306, Springer, Berlin, Germany, 2009.
- [33] V. L. Chandler and V. Walbot, “DNA modification of a maize transposable element correlates with loss of activity,” *Proceedings of the National Academy of Sciences of the United States of America*, vol. 83, no. 6, pp. 1767–1771, 1986.
- [34] R. A. Martienssen and V. Colot, “DNA methylation and epigenetic inheritance in plants and filamentous fungi,” *Science*, vol. 293, no. 5532, pp. 1070–1074, 2001.
- [35] Y. Jia, D. R. Lisch, K. Ohtsu, M. J. Scanlon, D. Nettleton, and P. S. Schnable, “Loss of RNA-dependent RNA polymerase 2 (RDR2) function causes widespread and unexpected changes in the expression of transposons, genes, and 24-nt small RNAs,” *PLoS Genetics*, vol. 5, no. 11, Article ID e1000737, 2009.
- [36] J. A. Birchler and F. Han, “Maize centromeres: structure, function, epigenetics,” *Annual Review of Genetics*, vol. 43, pp. 287–303, 2009.
- [37] R. K. Dawe, “Maize centromeres and knobs (neocentromeres),” in *Handbook of Maize: Genetics and Genomics*, J. L. Bennetzen and S. Hake, Eds., pp. 239–250, Springer, Berlin, Germany, 2009.
- [38] T. K. Wolfgruber, A. Sharma, K. L. Schneider et al., “Maize centromere structure and evolution: sequence analysis of centromeres 2 and 5 reveals dynamic loci shaped primarily by retrotransposons,” *PLoS Genetics*, vol. 5, no. 11, Article ID e1000743, 2009.
- [39] B. T. Page, M. K. Wanous, and J. A. Birchler, “Characterization of a maize chromosome 4 centromeric sequence: evidence for an evolutionary relationship with the B chromosome centromere,” *Genetics*, vol. 159, no. 1, pp. 291–302, 2001.

- [40] B. McClintock, "Genetic and cytological studies of maize," *Carnegie Institution of Washington Yearbook*, vol. 58, pp. 452–456, 1959.
- [41] C. J. Rivin, C. A. Cullis, and V. Walbot, "Evaluating quantitative variation in the genome of *Zea mays*," *Genetics*, vol. 113, no. 4, pp. 1009–1019, 1986.
- [42] E. V. Ananiev, R. L. Phillips, and H. W. Rines, "Complex structure of knob DNA on maize chromosome 9: retrotransposon invasion into heterochromatin," *Genetics*, vol. 149, no. 4, pp. 2025–2037, 1998.
- [43] E. V. Ananiev, R. L. Phillips, and H. W. Rines, "A knob-associated tandem repeat in maize capable of forming fold-back DNA segments: are chromosome knobs megatransposons?" *Proceedings of the National Academy of Sciences of the United States of America*, vol. 95, no. 18, pp. 10785–10790, 1998.
- [44] M. D. McMullen, B. Hunter, R. L. Phillips, and I. Rubenstein, "The structure of the maize ribosomal DNA spacer region," *Nucleic Acids Research*, vol. 14, no. 12, pp. 4953–4968, 1986.
- [45] P. J. Buescher, R. L. Phillips, and R. Brambi, "Ribosomal RNA contents of maize genotypes with different ribosomal RNA gene numbers," *Biochemical Genetics*, vol. 22, no. 9–10, pp. 923–930, 1984.
- [46] L. Li and K. Arumuganathan, "Physical mapping of 45S and 5S rDNA on maize metaphase and sorted chromosomes by FISH," *Hereditas*, vol. 134, no. 2, pp. 141–145, 2001.
- [47] J. Li, F. Yang, J. Zhu, S. He, and L. Li, "Characterization of a tandemly repeated subtelomeric sequence with inverted telomere repeats in maize," *Genome*, vol. 52, no. 3, pp. 286–293, 2009.
- [48] E. V. Ananiev, M. A. Chamberlin, J. Klaiber, and S. Svitashv, "Microsatellite megatracts in the maize (*Zea mays* L.) genome," *Genome*, vol. 48, no. 6, pp. 1061–1069, 2005.
- [49] A. Rafalski and E. Ananiev, "Genetic diversity, linkage disequilibrium and association mapping," in *Handbook of Maize: Genetics and Genomics*, J. L. Bennetzen and S. Hake, Eds., pp. 201–219, Springer, Berlin, Germany, 2009.
- [50] W. L. Brown, "Numbers and distribution of chromosome knobs in United States maize," *Genetics*, vol. 34, no. 5, pp. 524–536, 1949.
- [51] B. McClintock, A. Kato, and A. Blumenschein, *Chromosome Constitution of Races of Maize. Its Significance in the Interpretation of Relationships between Races and Varieties in the Americas*, Colegio de Postgraduados, Chapingo, Mexico, 1981.
- [52] B. McClintock, "Mechanisms that rapidly reorganize the genome," *Stadler Genetics Symposium*, vol. 10, pp. 25–47, 1978.
- [53] B. McClintock, "Significance of chromosome constitutions in tracing the origin and migration of races of maize in the Americas," in *Maize Breeding and Genetics*, D. B. Walden, Ed., pp. 159–184, John Wiley & Sons, New York, NY, USA, 1978.
- [54] W. R. Carlson, "The B chromosome in maize," in *Handbook of Maize: Genetics and Genomics*, J. L. Bennetzen and S. Hake, Eds., pp. 459–480, Springer, Berlin, Germany, 2009.
- [55] A. L. Rayburn, H. J. Price, J. D. Smith, and J. R. Gold, "C-band heterochromatin and DNA content in *Zea mays*," *American Journal of Botany*, vol. 72, no. 10, pp. 1610–1617, 1985.
- [56] A. L. Rayburn, "Flow cytometric assessment of nucleotide variability and its evolutionary implications," in *Classical and Molecular Cytogenetic Analysis*, W.J. Raup and B.S. Gill, Eds., pp. 110–115, Kansas Agricultural Experimental Station, Manhattan, Kan, USA, 1994.
- [57] C. M. Tito, L. Poggio, and C. A. Naranjo, "Cytogenetic studies in the genus *Zea*. 3. DNA content and heterochromatin in species and hybrids," *Theoretical and Applied Genetics*, vol. 83, no. 1, pp. 58–64, 1991.
- [58] J. H. Lee, K. Arumuganathan, S. M. Kaeppler et al., "Variability of chromosomal DNA contents in maize (*Zea mays* L.) inbred and hybrid lines," *Planta*, vol. 215, no. 4, pp. 666–671, 2002.
- [59] D. A. Laurie and M. D. Bennet, "Nuclear DNA content in the genera *Zea* and *Sorghum*. Intergeneric, interspecific and intraspecific variation," *Heredity*, vol. 55, no. 3, pp. 307–313, 1985.
- [60] D. P. Biradar and A. L. Rayburn, "Heterosis and nuclear DNA content in maize," *Heredity*, vol. 71, no. 3, pp. 300–304, 1993.
- [61] A. Rafalski and M. Morgante, "Corn and humans: recombination and linkage disequilibrium in two genomes of similar size," *Trends in Genetics*, vol. 20, no. 2, pp. 103–111, 2004.
- [62] M. I. Tenailon, M. C. Sawkins, A. D. Long, R. L. Gaut, J. F. Doebley, and B. S. Gaut, "Patterns of DNA sequence polymorphism along chromosome 1 of maize (*Zea mays* ssp. *mays* L.)," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 98, no. 16, pp. 9161–9166, 2001.
- [63] A. Ching, K. S. Caldwell, M. Jung et al., "SNP frequency, haplotype structure and linkage disequilibrium in elite maize inbred lines," *BMC Genetics*, vol. 3, article no. 19, 2002.
- [64] E. S. Buckler, B. S. Gaut, and M. D. McMullen, "Molecular and functional diversity of maize," *Current Opinion in Plant Biology*, vol. 9, no. 2, pp. 172–176, 2006.
- [65] P. SanMiguel, A. Tikhonov, Y. K. Jin et al., "Nested retrotransposons in the intergenic regions of the maize genome," *Science*, vol. 274, no. 5288, pp. 765–768, 1996.
- [66] P. SanMiguel and J. L. Bennetzen, "Evidence that a recent increase in maize genome size was caused by the massive amplification of intergene retrotransposons," *Annals of Botany*, vol. 82, pp. 37–44, 1998.
- [67] A. Kato, J. C. Lamb, and J. A. Birchler, "Chromosome painting using repetitive DNA sequences as probes for somatic chromosome identification in maize," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 101, no. 37, pp. 13554–13559, 2004.
- [68] J. A. Birchler and H. W. Bass, "Cytogenetics and chromosomal structural diversity," in *Handbook of Maize: Genetics and Genomics*, J. L. Bennetzen and S. Hake, Eds., pp. 163–177, Springer, Berlin, Germany, 2009.
- [69] N. M. Springer, K. Ying, Y. Fu et al., "Maize inbreds exhibit high levels of copy number variation (CNV) and presence/absence variation (PAV) in genome content," *PLoS Genetics*, vol. 5, no. 11, Article ID e1000734, 2009.
- [70] A. Beló, M. K. Beatty, D. Hondred, K. A. Fengler, B. Li, and A. Rafalski, "Allelic genome structural variations in maize detected by array comparative genome hybridization," *Theoretical and Applied Genetics*, vol. 120, no. 2, pp. 355–367, 2010.
- [71] R. A. Swanson-Wagner, S. R. Eichten, S. Kumari et al., "Pervasive gene content variation and copy number variation in maize and its undomesticated progenitor," *Genome Research*, vol. 20, no. 12, pp. 1689–1699, 2010.
- [72] J. Doebley, "Molecular evidence for gene flow among *Zea* species," *Bioscience*, vol. 40, no. 6, pp. 443–448, 1990.
- [73] J. F. Wendel, "Genome evolution in polyploids," *Plant Molecular Biology*, vol. 42, no. 1, pp. 225–249, 2000.
- [74] J. Messing, "The polyploid origin of maize," in *Handbook of Maize: Genetics and Genomics*, J. L. Bennetzen and S. Hake, Eds., pp. 221–223, Springer, Berlin, Germany, 2009.

- [75] S. Ahn and S. D. Tanksley, "Comparative linkage maps of the rice and maize genomes," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 90, no. 17, pp. 7980–7984, 1993.
- [76] A. H. Paterson, J. E. Bowers, and B. A. Chapman, "Ancient polyploidization predating divergence of the cereals, and its consequences for comparative genomics," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 101, no. 26, pp. 9903–9908, 2004.
- [77] M. R. Woodhouse, J. C. Schnable, B. S. Pedersen et al., "Following tetraploidy in maize, a short deletion mechanism removed genes preferentially from one of the two homologs," *PLoS Biology*, vol. 8, no. 6, Article ID e1000409, 2010.
- [78] J. Messing, A. K. Bharti, W. M. Karlowski et al., "Sequence composition and genome organization of maize," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 101, no. 40, pp. 14349–14354, 2004.
- [79] Z. Swigonova, J. Lai, J. Ma et al., "On the tetraploid origin of the maize genome," *Comparative and Functional Genomics*, vol. 5, no. 3, pp. 281–284, 2004.
- [80] Z. Swigoňová, J. Lai, J. Ma et al., "Close split of sorghum and maize genome progenitors," *Genome Research*, vol. 14, no. 10A, pp. 1916–1923, 2004.
- [81] R. Song, V. Llaca, and J. Messing, "Mosaic organization of orthologous sequences in grass genomes," *Genome Research*, vol. 12, no. 10, pp. 1549–1555, 2002.
- [82] R. Bruggmann, A. K. Bharti, H. Gundlach et al., "Uneven chromosome contraction and expansion in the maize genome," *Genome Research*, vol. 16, no. 10, pp. 1241–1251, 2006.
- [83] T. Tanaka, B. A. Antonio, S. Kikuchi et al., "The Rice Annotation Project Database (RAP-DB): 2008 update," *Nucleic Acids Research*, vol. 36, supplement 1, pp. D1028–D1033, 2008.
- [84] K. M. Devos, "Grass genome organization and evolution," *Current Opinion in Plant Biology*, vol. 13, no. 2, pp. 139–145, 2010.
- [85] B. C. Meyers, S. V. Tingey, and M. Morgante, "Abundance, distribution, and transcriptional activity of repetitive elements in the maize genome," *Genome Research*, vol. 11, no. 10, pp. 1660–1676, 2001.
- [86] G. Haberer, S. Young, A. K. Bharti et al., "Structure and architecture of the maize genome," *Plant Physiology*, vol. 139, no. 4, pp. 1612–1624, 2005.
- [87] F. Wei, E. Coe, W. Nelson et al., "Physical and genetic structure of the maize genome reflects its complex evolutionary history," *PLoS Genetics*, vol. 3, no. 7, article e123, 2007.
- [88] F. Wei, J. Zhang, S. Zhou et al., "The physical and genetic framework of the maize B73 genome," *PLoS Genetics*, vol. 5, no. 11, Article ID e1000715, 2009.
- [89] P. SanMiguel, B. S. Gaut, A. Tikhonov, Y. Nakajima, and J. L. Bennetzen, "The paleontology of intergene retrotransposons of maize," *Nature Genetics*, vol. 20, no. 1, pp. 43–45, 1998.
- [90] R. Liu, C. Vitte, J. Ma et al., "A GeneTrek analysis of the maize genome," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 104, no. 28, pp. 11844–11849, 2007.
- [91] J. L. Bennetzen, J. Ma, and K. M. Devos, "Mechanisms of recent genome size variation in flowering plants," *Annals of Botany*, vol. 95, no. 1, pp. 127–132, 2005.
- [92] Z. Tian, C. Rizzon, J. Du et al., "Do genetic recombination and gene density shape the pattern of DNA elimination in rice long terminal repeat retrotransposons?" *Genome Research*, vol. 19, no. 12, pp. 2221–2230, 2009.
- [93] J. Ma and J. L. Bennetzen, "Recombination, rearrangement, reshuffling, and divergence in a centromeric region of rice," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 103, no. 2, pp. 383–388, 2006.
- [94] C. Vitte and J. L. Bennetzen, "Analysis of retrotransposon structural diversity uncovers properties and propensities in angiosperm genome evolution," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 103, no. 47, pp. 17638–17643, 2006.
- [95] D. J. Garfinkel, "Genome evolution mediated by Ty elements in *Saccharomyces*," *Cytogenetic and Genome Research*, vol. 110, no. 1–4, pp. 63–69, 2005.
- [96] J. Ma, K. M. Devos, and J. L. Bennetzen, "Analyses of LTR-retrotransposon structures reveal recent and rapid genomic DNA loss in rice," *Genome Research*, vol. 14, no. 5, pp. 860–869, 2004.
- [97] K. M. Devos, J. K. M. Brown, and J. L. Bennetzen, "Genome size reduction through illegitimate recombination counteracts genome expansion in *Arabidopsis*," *Genome Research*, vol. 12, no. 7, pp. 1075–1079, 2002.
- [98] N. Jiang, A. A. Ferguson, R. K. Slotkin, and D. Lisch, "Pack-Mutator-like transposable elements (Pack-MULEs) induce directional modification of genes through biased insertion and DNA acquisition," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 108, no. 4, pp. 1537–1542, 2011.
- [99] V. Llaca and J. Messing, "Amplicons of maize zein genes are conserved within genic but expanded and constricted in intergenic regions," *Plant Journal*, vol. 15, no. 2, pp. 211–220, 1998.
- [100] H. Fu and H. K. Dooner, "Intraspecific violation of genetic colinearity and its implications in maize," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 99, no. 14, pp. 9573–9578, 2002.
- [101] Q. Wang and H. K. Dooner, "Remarkable variation in maize genome structure inferred from haplotype diversity at the *bz* locus," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 103, no. 47, pp. 17644–17649, 2006.
- [102] R. Song and J. Messing, "Contiguous genomic DNA sequence comprising the 19-kD zein gene family from maize," *Plant Physiology*, vol. 130, no. 4, pp. 1626–1635, 2002.
- [103] S. Brunner, K. Fengler, M. Morgante, S. Tingey, and A. Rafalski, "Evolution of DNA sequence nonhomologies among maize inbreds," *Plant Cell*, vol. 17, no. 2, pp. 343–360, 2005.
- [104] J. Lai, Y. Li, J. Messing, and H. K. Dooner, "Gene movement by Helitron transposons contributes to the haplotype variability of maize," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 102, no. 25, pp. 9068–9073, 2005.
- [105] V. V. Kapitonov and J. Jurka, "Rolling-circle transposons in eukaryotes," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 98, no. 15, pp. 8714–8719, 2001.
- [106] S. Brunner, G. Pea, and A. Rafalski, "Origins, genetic organization and transcription of a family of non-autonomous helitron elements in maize," *Plant Journal*, vol. 43, no. 6, pp. 799–810, 2005.
- [107] M. Morgante, S. Brunner, G. Pea, K. Fengler, A. Zuccolo, and A. Rafalski, "Gene duplication and exon shuffling by helitron-like transposons generate intraspecies diversity in maize," *Nature Genetics*, vol. 37, no. 9, pp. 997–1002, 2005.
- [108] S. Gupta, A. Gallavotti, G. A. Stryker, R. J. Schmidt, and S. K. Lal, "A novel class of Helitron-related transposable elements

- in maize contain portions of multiple pseudogenes," *Plant Molecular Biology*, vol. 57, no. 1, pp. 115–127, 2005.
- [109] N. Jameson, N. Georgelis, E. Fouladbash, S. Martens, L. C. Hannah, and S. Lal, "Helitron mediated amplification of cytochrome P450 monooxygenase gene in maize," *Plant Molecular Biology*, vol. 67, no. 3, pp. 295–304, 2008.
- [110] L. Yang and J. L. Bennetzen, "Distribution, diversity, evolution, and survival of Helitrons in the maize genome," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 106, no. 47, pp. 19922–19927, 2009.
- [111] L. Yang and J. L. Bennetzen, "Structure-based discovery and description of plant and animal Helitrons," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 106, no. 31, pp. 12832–12837, 2009.
- [112] C. Du, N. Fefelova, J. Caronna, L. He, and H. K. Dooner, "The polychromatic Helitron landscape of the maize genome," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 106, no. 47, pp. 19916–19921, 2009.
- [113] S. K. Lal, N. Georgelis, and L. C. Hannah, "Helitrons: their impact on maize genome evolution and diversity," in *Handbook of Maize: Genetics and Genomics*, J. L. Bennetzen and S. Hake, Eds., pp. 329–339, Springer, Berlin, Germany, 2009.
- [114] N. Jiang, Z. Bao, X. Zhang, S. R. Eddy, and S. R. Wessler, "Pack-MULE transposable elements mediate gene evolution in plants," *Nature*, vol. 431, no. 7008, pp. 569–573, 2004.
- [115] K. Hanada, V. Vallejo, K. Nobuta et al., "The functional role of pack-MULEs in rice inferred from purifying selection and expression profile," *Plant Cell*, vol. 21, no. 1, pp. 25–38, 2009.
- [116] J. Messing and V. Llaca, "Importance of anchor genomes for any plant genome project," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 95, no. 5, pp. 2017–2020, 1998.
- [117] G. Moore, K. M. Devos, Z. Wang, and M. D. Gale, "Grasses, line up and form a circle," *Current Biology*, vol. 5, no. 7, pp. 737–739, 1995.
- [118] M. Morgante, E. De Paoli, and S. Radovic, "Transposable elements and the plant pan-genomes," *Current Opinion in Plant Biology*, vol. 10, no. 2, pp. 149–155, 2007.



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