frontiers in Plant Science

ORIGINAL RESEARCH
published: 01 November 2016
doi: 10.3389/fpls.2016.01635

Evidence of Genomic Exchanges between Homeologous Chromosomes in a Cross of Peanut with Newly Synthetized Allotetraploid Hybrids

*Joel R. Nguepjop[1], Hodo-Abalo Tossim[1], Joseph M. Bell[2], Jean-François Rami[3], Shivali Sharma[4], Brigitte Courtois[1], Nalini Mallikarjuna[4], Djibril Sane[5] and Daniel Fonceka[1,3]**

[1] Centre d'Etudes Régional pour l'Amélioration de l'Adaptation à la Sécheresse, Thies, Senegal, [2] Département de Biologie et Physiologie Végétales, Université de Yaoundé I, Yaoundé, Cameroon, [3] UMR AGAP, Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Montpellier, France, [4] International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India, [5] Département de Biologie Végétale, Université Cheikh Anta Diop, Dakar, Senegal

OPEN ACCESS

Edited by:
Changbin Chen,
University of Minnesota, USA

Reviewed by:
Erik Wijnker,
Wageningen University, Netherlands
Junhua Li,
Henan Normal University, China

***Correspondence:**
Daniel Fonceka
daniel.fonceka@cirad.fr

Specialty section:
This article was submitted to Plant Genetics and Genomics, a section of the journal Frontiers in Plant Science

Received: *07 July 2016*
Accepted: *17 October 2016*
Published: *01 November 2016*

Citation:
Nguepjop JR, Tossim H-A, Bell JM, Rami J-F, Sharma S, Courtois B, Mallikarjuna N, Sane D and Fonceka D (2016) Evidence of Genomic Exchanges between Homeologous Chromosomes in a Cross of Peanut with Newly Synthetized Allotetraploid Hybrids. Front. Plant Sci. 7:1635. doi: 10.3389/fpls.2016.01635

Cultivated peanut and synthetics are allotetraploids ($2n = 4x = 40$) with two homeologous sets of chromosomes. Meiosis in allotetraploid peanut is generally thought to show diploid-like behavior. However, a recent study pointed out the occurrence of recombination between homeologous chromosomes, especially when synthetic allotetraploids are used, challenging the view of disomic inheritance in peanut. In this study, we investigated the meiotic behavior of allotetraploid peanut using 380 SSR markers and 90 F_2 progeny derived from the cross between *Arachis hypogaea* cv Fleur 11 (AABB) and ISATGR278-18 (AAKK), a synthetic allotetraploid that harbors a K-genome that was reported to pair with the cultivated B-genome during meiosis. Segregation analysis of SSR markers showed 42 codominant SSRs with unexpected null bands among some progeny. Chi-square tests for these loci deviate from the expected 1:2:1 Mendelian ratio under disomic inheritance. A linkage map of 357 codominant loci aligned on 20 linkage groups (LGs) with a total length of 1728 cM, averaging 5.1 cM between markers, was developed. Among the 10 homeologous sets of LGs, one set consisted of markers that all segregated in a polysomic-like pattern, six in a likely disomic pattern and the three remaining in a mixed pattern with disomic and polysomic loci clustered on the same LG. Moreover, we reported a substitution of homeologous chromosomes in some progeny. Our results suggest that the homeologous recombination events occurred between the A and K genomes in the newly synthesized allotetraploid and have been highlighted in the progeny. Homeologous exchanges are rarely observed in tetraploid peanut and have not yet been reported for AAKK and AABB genomes. The implications of these results on peanut breeding are discussed.

Keywords: genetic map, disomic, polysomic, breeding, inheritance, peanut, allotetraploid

INTRODUCTION

Allopolyploids and autopolyploids are two different types of polyploids, each resulting from a different genetic origin and showing a distinct meiotic behavior (Xu et al., 2015). In autopolyploids, all chromosome sets are identical or very closely related, while allopolyploids have divergent chromosome sets (Leitch and Leitch, 2008; Soltis et al., 2014). Sets of homologous chromosomes are considered "homeologous" to other sets from the other genomes (Sybenga, 1975, Sybenga, 1996). Thus, in classic autopolyploids, each chromosome may pair randomly with any of its homologs in equal frequencies during meiosis (Muller, 1914), leading to a polysomic inheritance. Autopolyploids can undergo double reduction where the segments of two sister chromatids end up in the same gamete (Haynes and Douches, 1993; Mather, 1936). In contrast to the situation in autopolyploids, the cytological diploidization of allopolyploids requires a nonrandom assortment of chromosomes into pairs, of which crossovers are exclusively formed between homologous chromosomes with disomic inheritance at each locus (Cifuentes et al., 2010; Gaeta and Chris Pires, 2010). However, in addition to these extremes, an intermediate pattern of genetic inheritance has also been described (Stebbins, 1947; Sybenga, 1996; Stift et al., 2008; Jeridi et al., 2012).

Cultivated peanut, *Arachis hypogaea* L., is one of the major oilseeds and cash crops worldwide for which genetic improvement can tremendously benefit from its wild relatives (Rami et al., 2014). This species is autogamous and allotetraploid ($2n = 4x = 40$), harboring homeologous A and B genomes (Husted, 1936; Smartt et al., 1978). It is assumed that it originated from a single hybridization event between two wild diploid taxa (Simpson et al., 2001), most likely *Arachis duranensis* (A genome) and *Arachis ipaensis* (B genome), followed by a spontaneous chromosome duplication (Seijo et al., 2004, 2007; Bertioli et al., 2016). The single origin of the crop, superimposed with domestication, resulted in a severe genetic bottleneck. Therefore, closely related diploid wild species, which have maintained a high genetic diversity, were considered suitable to broaden the genetic basis of the cultivated gene pool (Simpson, 2001; Favero et al., 2006; Foncéka et al., 2009). The wild relatives of cultivated peanut are mostly diploid ($2n = 2x = 20$) and contain species with A, B, D, K, and F genomes (Smartt et al., 1978; Stalker, 1991; Robledo and Seijo, 2010).

Given the ploidy difference between the wild and cultivated peanut, the production of colchicine-induced allotetraploids was used as a pathway to introduce wild alleles into the cultivated gene pool (Simpson, 1991). Several synthetic allotetraploids that have been produced by crossing different diploid species have proven to be cross-fertile with *A. hypogaea* (Mallikarjuna et al., 2011). Moreover, the development of peanut genomics tools has made possible the marker-assisted introgression of wild genes into a cultivated background (Fonceka et al., 2012).

However, this breeding approach has raised new fundamental questions on the meiotic behavior of the synthetic allotetraploid used in breeding programs and the possible genetic changes related to their genomic composition. Meiotic instabilities are common in interspecific and resynthesized lines (Gaeta et al., 2007; Lyrene, 2016). In some allopolyploid plants, recombination between subgenomes during meiosis was suspected to occur in newly formed polyploids (Ramsey and Schemske, 2002; Soltis et al., 2010) but was rarely observed among stabilized allopolyploids (Salmon et al., 2010; Ainouche and Wendel, 2014).

Based on the classic genetic behavior of the allotetraploid genome and cytogenetic observations, several genetic mapping studies in peanut have been conducted considering a diploid-like behavior at meiosis (Burow et al., 2001; Hong et al., 2008, 2010; Varshney et al., 2008; Foncéka et al., 2009; Qin et al., 2011; Shirasawa et al., 2013; Zhou et al., 2014). However, recently, thanks to a thorough analysis of genotyping data, Leal-Bertioli et al. (2015) reported unexpected missing and rare single nucleotide polymorphism (SNP) genotypes in recombinant inbred lines derived from a cross between a cultivated peanut and a synthetic allotetraploid. The authors showed that these missing data could be explained by the occurrence of partial tetrasomic recombination. Recombination among homeologous chromosomes is poorly understood in tetraploid peanut and the exact types of meiotic behavior remain unclear although the determination of these factors is important for our knowledge and for the development of appropriate breeding strategies. In addition, the classical impact of non-disomic inheritance on the genomic structure, such as segregation distortion and double reduction have not yet been reported.

In this study, we investigated the meiotic behavior of tetraploid peanut based on the segregation patterns of 380 microsatellites markers in F_2 progeny derived from the cross between the cultivated peanut *Arachis hypogaea* and a synthetic allotetraploid *(Arachis duranensis* × *Arachis batizocoi)*^{4x}. To obtain more insight into the mode of inheritance at the genome scale, we analyzed recombination events between homologous and homeologous chromosomes in relation to their position on a genetic linkage map. We reported the occurrence of a mixture of disomic and polysomic modes of inheritance of SSR loci, confirming the recent partial tetrasomic assumption made by Leal-Bertioli et al. (2015). We showed that this mixed inheritance was consistently associated with segregation distortion and homeologous chromosome substitution in some progeny. Our results suggest that the homeologous recombination events occurred between the A and K genomes in the newly synthesized allotetraploid and have been highlighted in the progeny.

MATERIALS AND METHODS

Plant Material and Population Development

The study was conducted using an F_2 population derived from the cross between the cultivated variety Fleur 11 and the synthetic allotetraploid ISATGR 278-18 *(Arachis duranensis* × *Arachis batizocoi)*^{4x}. Fleur 11 is a Spanish type with erect growth habit widely cultivated in West Africa. ISATGR 278-18 was developed and kindly provided by ICRISAT-India (Mallikarjuna et al., 2011). The synthetic allotetraploid combines the AA genome of *A. duranensis* (ICG 8138; $2n = 2x = 20$), a close wild relative and

one of the most probable ancestors of *A. hypogaea*, and the KK genome of *A. batizocoï* (ICG 13160; $2n = 2x = 20$), a wild relative taxa that was reported to pair with the B genome of the cultivated species during meiosis (Burow et al., 2001; Mallikarjuna et al., 2011; Leal-Bertioli et al., 2014).

ISATGR 278-18 was reported to have a normal chromosome configuration with 20 bivalents (Mallikarjuna et al., 2011). However, several cycles of self-pollination were performed at CERAAS prior to hybridization with Fleur 11. Five plants of the synthetic allotetraploid were used as male to cross with five plants of Fleur 11 used as female. The F_1 plants were differentiated from plants derived from self-pollination of Fleur 11 using morphological traits (dark green leaves and procumbent growth habit). The F_2 progeny were produced from the self-pollination of 15 F_1 plants. All crosses were performed in plastic pots under greenhouse conditions at the Centre d'Etudes Régional pour l'Amélioration de l'Adaptation à la Sécheresse (CERAAS) in Senegal during 2011 and 2013.

SSR Marker Analysis

Genomic DNA of both parents and F_2 progeny was extracted from young leaves according to the MATAB protocol as described by Foncéka et al. (2009). Polymorphisms were assessed in the parents using 602 primer pairs, mainly selected from a previous study (Foncéka et al., 2009). The parents and F_2 progeny were genotyped with polymorphic SSR markers. PCR was carried out in 96-wellplates in a total volume of 10 µl consisting of 5 µl of 5 ng/µl of the DNA template and 5 µl of a mixture of 0.1 µM of each SSR primer, 0.2 mM of each dNTP, 1X PCR buffer, 2.5 mM MgCl2, 0.1U/µl of Taq polymerase and 0.1 mM of IR700 or IR800-labeled M13 primer (MWG Germany) for fluorescence detection of SSR amplicons. A forward primer pair was labeled with a fluorescent (LI-COR Biosciences). Reactions were performed in an Eppendorf Mastercycler epgradient thermocycler. The PCR products were separated by electrophoresis run at a constant 95 W for 1−2 h in a DNA Sequencer (LI-COR 4300 DNA Analyzer, Lincoln, NE, USA).

Scoring of the SSR bands was performed visually on electrophoresis profiles using the application Jelly 2.017b (Rami, unpublished). For a codominant marker in an F_2 population, we denoted "A" as the genotype of cultivated parent, "B" as the genotype of wild parent, and "H" as the genotype of their heterozygous hybrids. When one marker was dominant, the two non-separated genotypes "H" and "A" were denoted "D" and the two non-separated genotypes "H" and "B" were denoted "C". For each SSR, the sub-genomic origin (A or K) of the wild alleles was assigned by comparing them to the alleles of the wild diploid progenitors. The sub-genomic origin of the cultivated allele was inferred by analyzing its co-inheritance with the wild alleles in the F_2 progeny. Loci were suffixed by <A> or <B> for differentiating subgenomic origin. In all scenarios, missing data were scored as "x" and the unexpected null bands were scored as "N".

Meiotic Behavior Analysis

Based on the genotyping data for each SSR marker, we analyzed the genotype of the F_2 progeny and deduced the allelic constitution of the gamete produced by the F_1 hybrid. The genome of the cultivated species was noted "A_1A_1BB" and that of the wild species "A_2A_2KK". Chromosomes "A_1" and "A_2" and "B" and "K" are homologous, while chromosomes "A_1" and "B", "A_1" and "K", "A_2" and "B", and "A_2" and "K" are homeologous.

When recombination occurred only between homologous genomes, for SSRs that amplified only one locus on a given sub-genome, two segregating bands were expected and the segregation ratio in the F_2 progeny was $1A_1A_1$: $2A_1A_2$: $1A_2A_2$ or 1BB: 2BK: 1KK. For SSR that amplified the two homeologous genomes up to four segregating bands were expected. The segregation ratio in the F_2 progeny is shown in **Table 1**. In this

TABLE 1 | Phenotypes and genotypes expected under tetrasomic and disomic inheritance if a SSR primer pair marks the homeologous genomes of the allotetraploid parents.

	Expected					
	Polysomic inheritance			Disomic inheritance		
	Phenotypes	Genotypes	Frequency	Phenotypes	Genotypes	Frequency
1	A_1B	A_1A_1BB	1/36 (2.5)[a]	A_1B	A_1A_1BB	1/16 (5.6)
2	A_1BK	A_1A_1BK, A_1BBK, A_1BKK	6/36 (15)	A_1BK	A_1A_1BK	2/16 (11.3)
3	A_1A_2B	A_1A_2BB, $A_1A_1A_2B$, $A_1A_2A_2B$	6/36 (15)	A_1A_2B	A_1A_2BB	2/16 (11.3)
4	A_1A_2BK	A_1A_2BK	6/36 (15)	A_1A_2BK	A_1A_2BK	4/16 (22.5)
5	A_1A_2K	A_1A_2KK, $A_1A_2A_2K$, $A_1A_2A_2K$	6/36 (15)	A_1A_2K	A_1A_2KK	2/16 (11.3)
6	A_2BK	A_2A_2BK, A_2BBK, A_2BKK	6/36 (15)	A_2BK	A_2A_2BK	2/16 (11.3)
7	A_1K	A_1A_1KK	1/36 (2.5)	A_1K	A_1A_1KK	1/16 (5.6)
8	A_2B	A_2A_2BB	1/36 (2.5)	A_2B	A_2A_2BB	1/16 (5.6)
9	A_2K	A_2A_2KK	1/36 (2.5)	A_2K	A_2A_2KK	1/16 (5.6)
10	A_1A_2	$A_1A_1A_2A_2$	1/36 (2.5)	/	/	/
11	BK	BBKK	1/36 (2.5)	/	/	/

[a]*The expected frequency of the 90 F_2 progeny is indicated in brackets.*

case, the cultivated and wild parents produced each one type of gamete (A_1B and A_2K, respectively) and the F_1 hybrid (A_1A_2BK) would produce 4 types of gametes (A_1B, A_1K, A_2B and A_2K).

When recombination occurred between homeologous genomes, for SSRs that amplified only one locus on a given sub-genome, a fourth 'null' genotype is expected to appear in addition to the three expected genotypes in an F_2 population. For SSRs that amplified the two loci, one on each of the homeologous genomes, 11 phenotypic bands are expected in the gel (**Table 1**). The segregation ratio in the F_2 progeny depends on the genomic constitution of the F_1 hybrids. For F_1 with normal genomic constitution (without homeologous recombination during parental meiosis), the expected segregation ratio in the F_2 progeny is shown in **Table 1**. It is not straightforward to estimate the genotypic frequencies in F_2 progeny derived from "aberrant" F_1 (resulting from homeologous recombination events during parental meiosis). In contrast to the homologous pairings, two specific phenotypes, A_1A_2 and BK, are observed in homeologous pairings. In this study, we use the terminology "homeologous-recombinant genotypes" for the progeny that carried these two peculiar phenotypes.

Allele Number in the Homeologous Recombinant Genotypes

In the electrophoresis profiles, the band intensities of the homeologous-recombinant progeny were analyzed to determine the number of copies of each allele. The band intensities were determined using ImageJ version 1.46 (Ferreira and Rasband, 2012), and the dosage ratio between bands was compared to the relationships expected between alleles in the hypothetical configurations. For example, for the homeologous-recombinant progeny with A_1A_2 band-phenotype on the gels, three genotypes are possible with ratios of allelic combinations of 3:1 ($A_1A_1A_1A_2$), 1:1 ($A_1A_1A_2A_2$) or 1:3 ($A_1A_2A_2A_2$). The genotype was then determined based on allelic dosage. The F_2 progeny with four different alleles (i.e., A_1A_2BK) were used as a reference for determination, as these progeny involve single-copy alleles.

Segregation Analysis

The segregation of codominant and dominant loci was compared to the segregation ratios expected under disomic inheritance (1:2:1 for codominant loci and 3:1 for dominant loci), using the chi-square test of the software "Calculation for the chi-square test" (Preacher, 2001). Data scored as "N" (null phenotype) as well as missing data were not considered in the analysis. Loci that deviated significantly ($P < 0.05$) from the theoretically expected ratios were considered distorted and were represented by an asterisk on the genetic map.

Linkage Analysis and Map Construction

Linkage analysis was performed using the MapDisto software (Lorieux, 2012) using only the co-dominant loci. The linkage map was constructed in several steps. In the first step, markers that showed distorted segregation ($P < 0.05$) and those with unexpected null data were excluded. The non-distorted loci were grouped into LGs using a minimum LOD of 3, a maximum recombination frequency r of 0.3 and the Kosambi mapping function (Kosambi, 1943). The order of markers within each linkage group (LG) was determined using the "order" and "ripple" commands. In a second step, the distorted loci and loci with unexpected null data were progressively added into the established LGs if their presence did not significantly affect the marker order. The position of the loci with unexpected null data was adjusted iteratively and the poorly mapped loci were removed. The synteny analysis between the homeologous genome was performed on the basis of the mapped homeologous loci (Foncéka et al., 2009). The graphical linkage maps were drawn using SpiderMap software (Rami, unpublished) and the graphical genotype was drawn using the GGT software (van Berloo, 2008).

RESULTS

Polymorphism of the SSR Markers and Segregation of Parental Alleles in the F_2 Progeny

Among the 602 SSR markers screened, 447 (74%) detected a polymorphism between the parental genomes. A total of 431 (71.6%) SSR loci were polymorphic between the A homologous genomes (A_1 and A_2) and 465 (77.2%) between the B/K homologous genomes. From these polymorphic SSR markers, 380 that provided accurate amplification profiles were analyzed in the F_2 progeny and generated 562 loci, out of which 378 (67%) segregated as codominant and 184 (33%) segregated as dominant. Among the 378 codominant loci, 194 (51%) were assigned to the A-genomes and 184 (49%) were assigned to the B/K-genomes. Among the 184 dominant loci, 70 (38%) were from the A-genomes, whereas 114 (62%) were from the B/K-genomes.

The segregation of the SSRs was assessed with regard to their informativity for distinguishing polysomic versus disomic inheritance. This allowed for the classification of the SSR into ten classes (**Table 2**). The SSR markers within class 1 appeared as the most informative ones because they marked the homeologous genomes in both parents, allowing the identification of the expected genotypes for each of the meiotic behaviors in the F_2 progeny. They were chosen to illustrate the type of inheritance.

Inheritance Patterns of SSR Markers in the F_2 Progeny

The segregation analysis of 380 SSR markers revealed that 338 (88.9%) were inherited in an F_2 population, as expected under disomic behavior. Two compelling examples of disomic segregations are shown in **Figure 1** for the SSR markers Seq8D09 and AC3C02. These primer pairs marked the homeologous genomes in both parents and amplified up to four segregating bands. Each band was assigned to a subgenomic allele ("A_1", "B", "A_2" and "K"). The homologous bands of A-genomes ("A_1" and "A_2") and B/K-genomes ("B" and "K") are inherited as two independent codominant loci in the F_2 progeny, Aa at one locus and Bb at the other (**Figure 1**).

TABLE 2 | Segregation of parental alleles and informativeness of polymorphic SSR markers to distinguish polysomic vs. disomic inheritance in the F_2 progeny.

Marker class	Cultivated parent	Wild Parent	Relative frequency (%)	Segregation in the F_2 progeny		Informative polysomic vs. disomic inheritance
				A-genome	B-genome	
1	A_1A_1BB	A_2A_2 KK	25.1	<ABH>	<ABH>	Completely
2	A_1A_1BB	A_2A_2KK	1.4	<ABH>	none[a]	Highly
3	A_1A_1BB	A_2A_2 KK	11.3	None[a]	<ABH>	Highly
4	A_1A_1--	A_2A_2 KK	7.9	<ABH>	<AC>	Moderately
5	A_1A_1BB	-- KK	3.4	<ABH>	<ABH>	Moderately
6	A_1A_1--	A_2A_2--	18.1	<ABH>		Partially
7	--BB	-- KK	10.5		<ABH>	Partially
8[b]	A_1A_1--	----	2.0	<BD>		Lowly
9[b]	----	-- KK	5.1		<AC>	Lowly
10	Duplicated		15.3			Lowly

Genotypes were scored as "A", "B", and "H" for codominant loci and "B" and "D" (or "A" and "C") for dominant loci. [a]*Indicates homologous alleles of identical size on the gel (monomorphism).* [b]*Dominant allele could be provided either by the cultivated or the wild parents.*

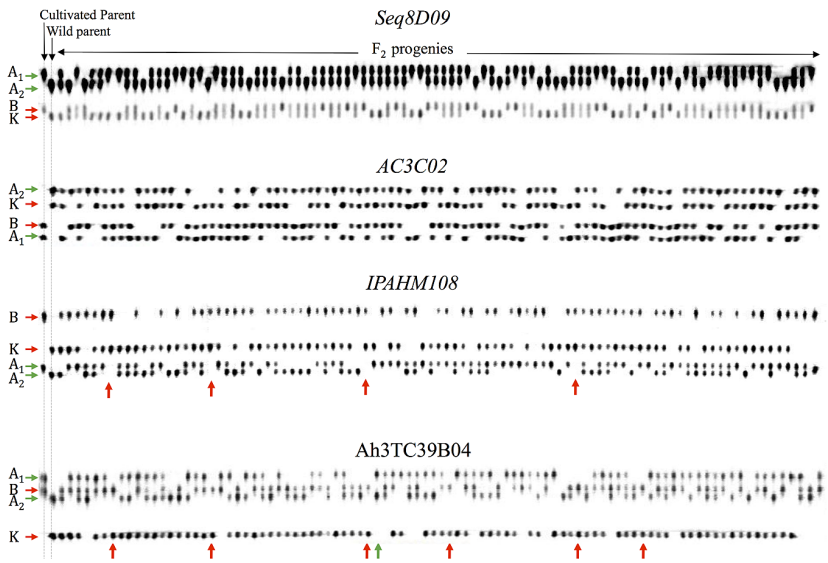

FIGURE 1 | Images of the segregation of four SSR markers. The cultivated and wild parents are in lanes 1 and 2, respectively. The F_2 progeny are distributed from lane 3 to the end. Each primer pair amplified two segregating bands in both parents. Each band (allele) was assigned to a subgenome figured with arrows on the left. For the Seq8D09 and AC3C02 markers, the homologous bands inherited as two independent codominant loci in the F_2 progeny, i.e., A_1A_2 genotype at one locus and BK at the other, as expected under disomic inheritance. At IPAHM108 and Ah3TC39B04 markers, the red and green arrows show the homeologous-recombinant F_2 progeny that own the BK and Aa by A_1A_2 respectively. The homologous bands of the A-genome ("A_1" and "A_2") are lacking whereas the homologous bands of the B/K-genome are systematically observed in 4 and 6 progeny (red arrows). Reciprocally, the "B" and "K" bands are lacking in one F_2 progeny, whereas, the "A_1" and "A_2" bands are observed (green arrow).

Interestingly, 42 (11.1%) SSR markers exhibited several unexpected F_2 band-phenotypes, which are impossible to explain under disomic behavior. Null bands for one of the homologous genomes were observed in some progeny, although the primer pair amplified the two homeologous genomes. Two examples of these unexpected F_2 phenotypes are shown in **Figure 1** for the SSR markers IPAHM108 and Ah3TC39B04. These markers amplified up to 4 segregating bands. However, the homologous bands of the A-genomes ("A1" and "A2") are lacking for some F_2 progeny, whereas the homologous bands of the B/K-genomes ("B" and "K") are observed, excluding the missing data assumption. Those F_2 progeny are indicated with red arrows on **Figure 1**. Reciprocally, for the Ah3TC39B04 marker, the homologous bands of the B/K-genomes are missing, while the homologous bands of the A-genome are observed in one F_2 progeny (marked with a green arrow on **Figure 1**). These A_1A_2- and BK-phenotypes are unexpected under disomic behavior, but are expected under polysomic behavior (**Table 1**). These phenotypes occurred if and only if the homologous alleles ended up in the same gamete during the parental and/or the F_1 meiosis.

Remarkably, the value of the intensity of the "B" and "K" bands varied significantly among the BK-phenotypes for the SSR

markers that segregated in a polysomic-like pattern, suggesting differences in the number of alleles. For example, in some BK-phenotypes, the more intense bands ("K") represent two and three doses, while the less intense bands ("B") represent a single dose (Supplementary Tables S1−S10). The K/B intensity ratio ranged from 1 to 3, indicating that the genotype of the BK F_2 band-phenotypes was either BBKK (1:1) or BKKK (1:3). The BKKK genotype is unexpected in the F_2 progeny derived from the A_1A_2BK F_1 hybrid (**Table 1**). The presence of BKKK genotypes suggests the occurrence of homeologous recombination during the meiosis of the parents, particularly in the synthetic allotetraploid.

Moreover, for three polysomic SSR such as RN13D04, only one allele was observed in one F_2 progeny whereas two alleles were present in both parents with up to four alleles segregating in the population (data not shown).

Segregation Distortion Analysis

Among the 378 codominant loci scored in the F_2 progeny, 336 showed disomic inheritance. Of these, 279 (83%) followed the 1:2:1 Mendelian segregation ratio expected in an F_2 population and the remaining 57 (16%) loci deviated significantly from it ($P < 0.05$). A total of 17 and 40 loci were distorted for the A and B/K-genomes, respectively (**Table 3**). Of the 17 distorted loci for the A-genome, 14 were skewed toward the cultivated genotypes, whereas one and two loci were distorted in favor of the wild and heterozygous genotypes, respectively. Inversely, among the 40 loci distorted for the B/K-genome, 26 and 14 were skewed toward the wild and heterozygous genotypes, respectively. These results indicated differences between genomes and genotypes for SD.

All the 42 codominant SSR markers that showed an unexpected genotype under disomic inheritance were distorted when tested under the 1:2:1 Mendelian segregation ratio. We were not able to test for the segregation ratio expected under polysomic behavior (1:34:1) since the genomic constitution of the F_1 hybrids was unknown and unexpected genotypes could result from "aberrant" F_1 hybrids. Nonetheless, as indicated on the map below, these codominant distorted markers were clustered in particular regions on different LG, suggesting that such distortion likely originated from homeologous pairing.

Map Construction and Linkage Analysis

In our study, the genetic map was developed progressively due to the mixture in the dataset of codominant loci that segregated in a disomic or polysomic form, combined in some cases with the distortion of segregation. The map constructed without the distorted and the polysomic loci comprised 270 loci distributed on 16 LGs, while 34 loci remained unlinked. Distorted loci were then included in the map using LOD score values comprised between 4 and 7, $r = 0.3$. This allowed for the addition of two new LGs (LGB2 and LGB9) that were mainly formed by distorted loci (**Figure 2**). At this step, the map comprised 304 loci clustered in 18 LGs. In the third step, when adding the polysomic loci, two new LGs (LGA4 and LGB4) were formed and two initially distinct LGs (LGA3 and LGB3) clustered together. The clustered LGs were dissociated by removing three polysomic loci (Seq16F01, Ah3TC31H02, and Seq2H11). At this step, the resulted genetic map comprised 20 LGs, and 12 loci remained unlinked. The loci were then ordered within each LG. Finally, the estimated linkage map included 357 codominant loci distributed into 20 LGs and covering a total genetic distance of 1,728 cM, with an average interval of 5.1 cM between two adjacent markers.

We analyzed the distribution of the loci in the A and B/K-genomes. For the A-genome, 179 loci were mapped in 10 LGs with an average number of 18 markers per LG, ranging from 10 (LG A5) to 36 (LG A1). The length of the LGs ranged from 28.0 cM (LG A5) to 165.2 cM (LG A1), with an average of 104.3 cM. For the B/K-genome, 178 loci were mapped on 10 LGs with an average number of 18 markers per LGs ranging from 13 (LG B10) to 28 (LG B1). The length of the LGs ranged from 33.3 cM (LG B10) to 111.4 cM (LG B1), with an average of 68.5 cM (**Table 4**). The average interval between adjacent markers was 6.4 and 4.0 cM for the A- and B/K-genomes, respectively.

Ten homeologous LGs were clearly identified based on the common homeologous loci (**Figure 2**). The number of bridge markers within each pair of homeologous LGs ranged from 3 to 16 (**Figure 2**). A good collinearity was observed among seven pairs of homeologous LGs (A2/B2; A3/B3; A4/B4; A5/B5; A7/B7; A8/B8; and A10/B10). Except for one major inversion on LG6, two local rearrangements on LG9 and three on LG1, a good synteny of the markers along the LGs was observed (**Figure 2**).

Except for three loci, all distorted loci ($P < 0.05$) were clustered along the LGs. Only 17 distorted loci were mapped in the A-genome, whereas 40 were mapped for the B genome. The distorted loci mapped in the A-genome were skewed toward the cultivated genotype (A4, A7, and A9 LGs), whereas those distorted in the B-genome were mainly skewed toward the wild genotype (B2 and B9 LGs) or the heterozygous genotype (B3, B4, B6, B7, and B10 LGs) (**Figure 2**). Overall, with few exceptions, we found that SD occurred in the regions that displayed homeologous recombination uncovering that homeologous pairing plays an important role in shaping SD in the tetraploid peanut genome.

TABLE 3 | Segregation of the loci in the F_2 population.

Types of segregation	Types of heredity			Total
	Disomic		Polysomic	
	A-Genome	B/K-Genome		
Codominant	167 (17)[a]	169 (40)	42 (42)	378
Dominant	70 (8)	114 (27)		

[a] *The number of distorted loci is indicated in parenthesis.*

Distribution of Disomic and Polysomic Loci along the LGs

One of the most remarkable features of this map is the distribution of the disomic and polysomic loci along the LGs.

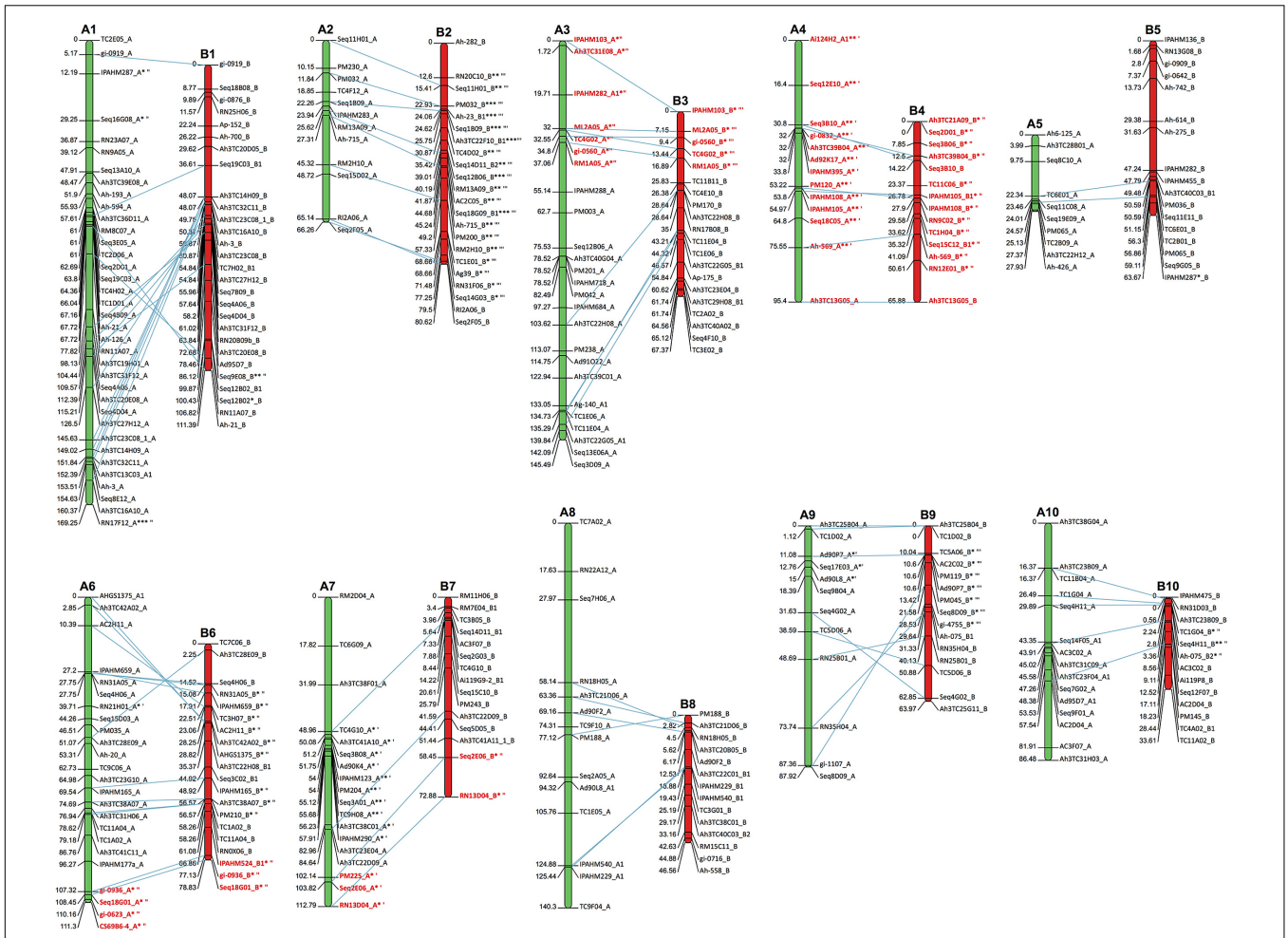

FIGURE 2 | Genetic linkage map based on 90 F_2 progeny and distribution of the disomic and polysomic codominant loci in the linkage groups (LG). The green and red segments indicate the LGs deriving from the A genome, named from A1 to A10 and the B genome named from B1 to B10, respectively. The map distances in Kosambi map units (cM) of each LG are shown on the left, and the loci names are shown on the right. The LGs were grouped into homeologous pairs based on common homeologous loci connected by blue dashed lines. The polysomic and disomic markers are indicated in red and black colors, respectively. Duplicated loci are identified by the number 1 or 2 after the suffix A or B. The distorted loci are identified by asterisks after the locus name. The number of asterisks indicates the intensity of the distortion of segregation ($*P < 0.05$, $**P < 0.01$, and $***P < 0.001$). The symbols after the asterisk specify the direction of the distortion of segregation <′>, <″>, and <‴> indicate the distortion in favor of the cultivated genotype, heterozygous, and wild, respectively.

Among the ten homeologous sets of LGs, six sets consisted of markers that segregated in a likely disomic pattern and three in a mixed pattern with the disomic and polysomic loci clustered on the same LG (**Figure 2**). Surprisingly, one set (LG4) consisted of markers that all segregated in a polysomic way. The percentage of polysomic loci along the LGs ranged from 13.3% (LG6) to 100% (LG4) with an average of 39.9%.

Homeologous Recombination along the LGs and Homeologous Genome Substitution

The co-inheritance of the polysomic loci allowed for the estimation of the portion of the genome that underwent homeologous recombination. These portions ranged from 14.9 cM for LG6 to 95.5 cM for LG4, with an average of 43.7 cM (**Table 3**). Our study clearly showed that for some progeny, the chromosomes were a mosaic of homologous and homeologous regions (**Figure 3**). Taking the physical distance covered by the LGs into account, a completed substitution of the A chromosome by its homeologous counterparts was observed in three F_2 genotypes (**Figure 3**).

The location of the homeologous recombination breakpoints along the chromosomes was assessed for LG4, which displayed a full homeologous pairing. Of the 17 regions in which the homeologous exchanges occurred, 10 regions of the B-genome were replaced by the A corresponding region and the seven others exhibited the reciprocal situation (**Figure 3**). The number of the homeologous recombination breakpoints along the LGs 4A and 4B ranged from 1 to 3.

DISCUSSION

The segregation patterns of SSR loci in tetraploid peanut ($2n = 4x = 40$) were determined by studying their inheritance and by mapping genetic exchanges between homeologous genomes. Our results strongly support a mixed disomic and polysomic modes of genetic inheritance of SSR loci in the cross between a cultivated peanut variety and a synthetic allotetraploid. Mixed inheritance is rarely observed in tetraploid peanut and has not yet been reported when the AAKK and AABB genomes were involved.

Evidence of Disomic and Polysomic SSR Inheritance

In our study, we showed that a large number of SSR markers were inherited likely in a disomic way, but some others showed genetic inheritance as a polysomic mode leading to a complex meiotic behavior.

Inheritance patterns of molecular markers have been considered a powerful method for determining meiotic behavior in polyploidy species (Lerceteau-Köhler et al., 2003) and have generated interesting conclusions about the genome behavior of several species including bermugrass (Guo et al., 2015), mimulus (Modliszewski and Willis, 2014), chrysanthemum (Klie et al., 2014), kiwifruit (Wu et al., 2013), roses (Koning-Boucoiran et al., 2012), yam (Bousalem et al., 2006; Nemorin et al., 2012), citrus (Kamiri et al., 2011), swithgrass (Okada et al., 2010), Yellow Cress (Stift et al., 2008), tomato (Barone et al., 2002), birdsfoot trefoil (Fjellstrom et al., 2001), sugar cane (Hoarau et al., 2001), and alfalfa (Diwan et al., 2000). The molecular methods used to distinguish disomy and polysomy are usually based on the signal intensity of PCR products and comparison of the number of loci linked in coupling versus the repulsion phase. However, the interpretation of multiple dose markers is often difficult in polyploids and is impossible in some species with polysomic inheritance (Esselink et al., 2004; Landergott et al., 2006).

In our study, to partially overcome the problem of complex electrophoresis profiles, we undertook a direct interpretation of SSR bands, suitably assigned to the subgenome of both parents. Using this approach, we observed that some markers followed the disomic inheritance as usually reported in allotetraploid peanut (Burow et al., 2001; Foncéka et al., 2009; Shirasawa et al., 2013) but some others exhibited an F_2 genotype unexpected under disomic inheritance, but that fitted with a polysomic segregation. The exclusive presence of homologous alleles among some F_2 genotypes for SSRs that mark homeologous genomes indicates that the homologous alleles ended up in the same gamete during the parental and/or the F_1 meiosis. Our findings are consistent with the recent study published by Leal-Bertioli et al. (2015) that explained the missing data observed among genotypes by tetrasomic recombination.

In some cases, the segregation patterns of SSR loci were similar to that observed in case of double reduction. We observed a

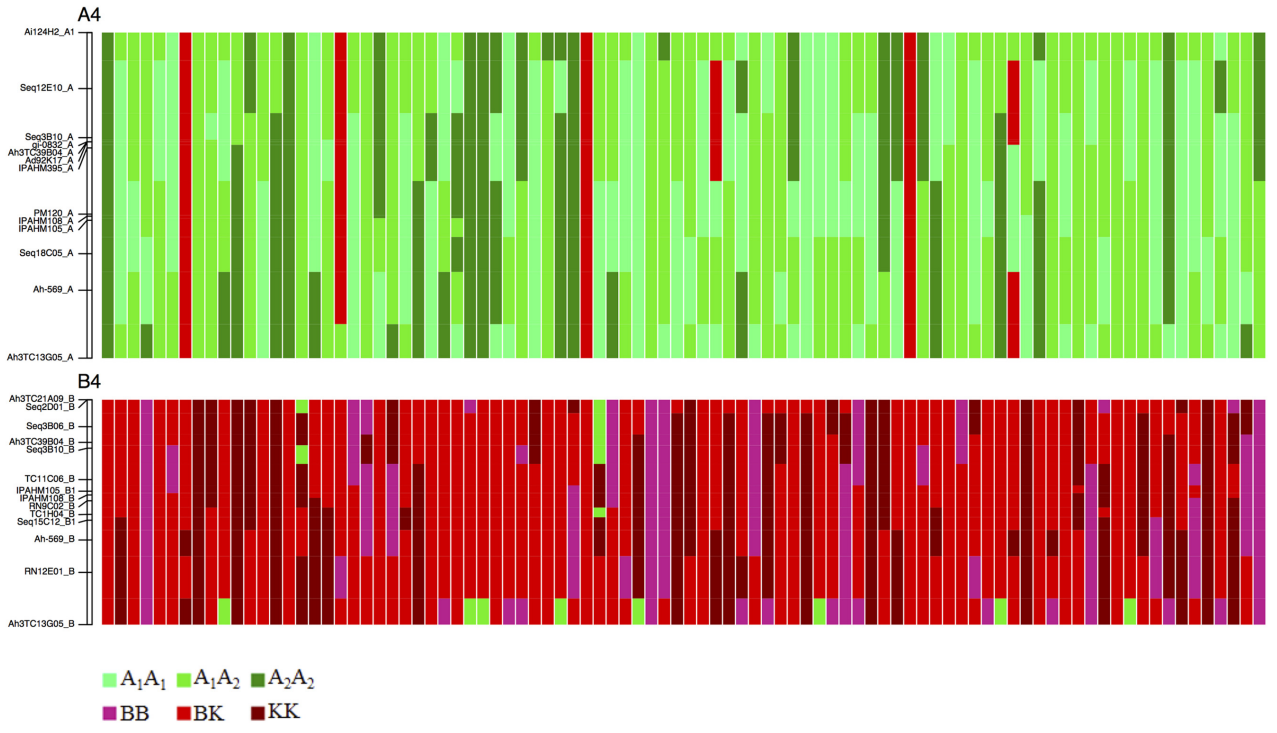

FIGURE 3 | Graphical genotype of the 90 F_2 progeny at LG A4 and B4. Loci name is shown on the left. Each column represents a F_2 progeny. The green and red colors indicate the A and B/K genomes, respectively. The light-green, green, and dark-green colors indicate of the cultivated, heterozygous, and wild genotypes for A genome, respectively. The pink, red, and dark red colors indicate the cultivated, heterozygous and wild genotypes for the B/K genomes, respectively.

TABLE 4 | Description of the genetic linkage map.

Linkage groups (LG)	Mapped loci	Total distance (cM)	Largest Gap (cM)	Mean interval (cM)	Homeologous recombination	
					Distance (cM)	Coverage (%)
A1	36	169.3	17.1	4.8		
B1	28	111.4	10.7	4.1		
A2	12	66.3	16.4	6.0		
B2	22	80.6	12.6	3.8		
A3	25	145.5	18.1	6.1	46.1	31.7
B3	20	67.4	8.9	3.5	21.4	31.7
A4	13	95.4	19.4	8.0	95.4	100.0
B4	14	65.9	15.3	5.1	65.9	100.0
A5	10	27.9	12.6	3.1		
B5	17	63.7	15.7	4.0		
A6	24	111.3	16.8	4.8	9.5	8.5
B6	20	78.8	12.3	4.1	14.9	18.8
A7	18	112.8	17.8	6.6	19.4	17.2
B7	15	72.9	15.8	5.2	17.9	24.6
A8	14	140.3	30.2	10.8		
B8	14	46.6	9.5	3.6		
A9	12	87.9	25.0	8.0		
B9	15	64.0	12.0	4.6		
A10	15	86.5	13.5	6.2		
B10	13	33.6	10.2	2.8		

phenotypic class with only one allele in some F_2 progeny, whereas up to 4 alleles segregate in the population. Double reduction refers to the fact that for a specific locus, the sister alleles come together in the same gamete during meiosis. It has been reported that the rate of double reduction is expected to increase towards the telomeres (Koning-Boucoiran et al., 2012; Bourke et al., 2015). In our study, the loci that showed this peculiar pattern of segregation are located at the extremity of LG3 (IPAHM103 and IPAHM282) and LG7 (RN13D04). However, since the genotype of the F_1 plant that gave rise to the F_2 progeny is unknown one cannot exclude that this pattern of segregation arose from the fusion of male and female gametes with the same haplotype (i.e., KK × KK).

Mapping Genetic Exchanges between Homeologous Genomes

The construction of the linkage map allowed us to locate the regions where the genetic exchanges occurred between the homeologous genomes. The LGs 3, 4, 6, and 7, which underwent homeologous recombination in our study, are consistent with the findings of Leal-Bertioli et al. (2015). However, the percentage of markers involved in homeologous recombination was higher in our study compared to that mentioned in Leal-Bertioli et al. (2015) (11% vs. 3%). Moreover, in LG4, we report a complete substitution of the A-chromosome by its B/K homeologous genome in three progeny. In the study of Leal-Bertioli et al. (2015), the LG4 of the induced tetraploid parent was involved in an almost complete substitution of the B-chromosome by the A-chromosome. The similarity of the results between these two studies using different synthetic allotetraploids raised questions about the factors that drive homeologous recombination.

Pairing affinity between different sets of chromosomes was reported to be influenced by structural homology (Mason et al., 2010, 2014; Mandáková, Marhold and Lysak, 2014). Bertioli et al. (2016) reported a close similarity between the A and B wild species genomes based on sequence data comparison of *A. duranensis* and *A. ipaensis*. Moreover, in the present study and in many other genetic mapping studies in peanut (Burow et al., 2001; Foncéka et al., 2009; Shirasawa et al., 2013), a good collinearity was found between the homeologous genomes. These results are in favor of a homology-driven homeologous chromosome pairing.

However, we found some loci rearrangements between homeologous LGs that displayed a mixed inheritance. This was particularly the case for LG6, in which Bertioli et al. (2016) also reported a large inversion. Thus, there are probably others factors that drive the pairing between homeologous genomes in polyploid species. Those factors can be genetic (Cifuentes et al., 2010; Gaeta and Chris Pires, 2010), similar to that exerted by the *Ph-1* locus in wheat (Moore, 2014) in rye (Lukaszewski and Kopecký, 2010) and Brassica (Nicolas et al., 2009). More studies will be needed to decipher the molecular forces that drive homeologous pairing in peanut.

The results of this study suggest that, at least in an interspecific context, the meiotic pairing in tetraploid peanut fits with the intermediate inheritance where pairing of chromosome sets ranged from strict disomic inheritance as in diploids to full polysomic as in autopolyploids (Stebbins, 1947; Sybenga, 1996; Catalán et al., 2006; Xu et al., 2015). Many important plants are polyploids and some of them have been clearly identified as intermediate genetic pattern such as chrysanthemum (Klie et al., 2014), banana (Jeridi et al., 2012), and strawberry (Lerceteau-Köhler et al., 2003). These findings also raised the question of chromosome pairing during meiosis in crosses involving only cultivated peanut varieties. Until now, inter-genomic exchanges have never been reported using genetic mapping approaches in cultivated peanut. Recently, thanks to tetraploid versus diploid sequence comparisons, genomic exchanges between A and B subgenomes have been reported (Bertioli et al., 2016). However, one still has to puzzle out whether these exchanges resulted from ancient recombination events that occured at the infancy of cultivated peanut as a consequence of the genomic shock due to the first hybridization between the A and B subgenomes or were due to something more recent that is still occurring in peanut varieties.

Homeologous Recombination Occurred during the Meiosis of the Parents

The reconstruction of the genotype of the homeologous recombinants suggests that, homeologous pairings have arisen in the synthetic allotetraploid parent. Indeed, the genotype of some homeologous recombinant F_2 progeny was either BKKK or BBKK. If homeologous recombination occurred only during the meiosis of the F_1 plants and not in the meiosis of the parents, the genotype of the homeologous recombinant in the

F_2 progeny would only be $A_1A_1A_2A_2$ or BBKK (**Table 1**). The BKKK genotypic composition was regarded as a consequence of homeologous recombination during the meiosis of the parents particularly in the synthetic allotetraploid. In some species, homeologous pairing during meiosis is suspected to occur in the first generations following polyploid formation (Ramsey and Schemske, 2002; Soltis et al., 2010; Szadkowski et al., 2010).

Implications for Peanut Breeding

The pattern of recombination between chromosomes of related species is a key point to transfer genes between the species. The knowledge about the inheritance mode is essential information not only because it sheds light on homeologous chromosome pairing behavior but can also influence the breeding strategies that are used for cultivar development. In this study, homeologous recombination events have been located in some genomic regions that are common with the ones reported in the study of Leal-Bertioli et al. (2015). One can suppose that these regions are particularly sensitive to homeologous recombination especially when synthetic allotetraploid are used. The SSRs that are located in these specific regions, particularly those that marked the homeologous genome in both parents, have proven to be very efficient in revealing the homeologous recombination events. Thus, they can be used to detect and trace back those events in the synthetic allotetraploid parental lines before crossing, as well as in their related F_1 hybrids.

Mixed inheritance may have unwanted impacts on aberrant meiotic behavior, karyotype destabilization, and fertility reduction. However, it could also speed up the accumulation of rare but favorable alleles through homeologous recombination and marker-assisted introgression. The interspecific breeding population developed in this study would be an ideal genetic material to study the genetic effects of cumulative homologous and homeologous alleles and to transfer valuable alleles from wild species into cultigens. Despite conflicting results around the *A. batizocoi* taxon and its potential usefulness (Leal-Bertioli et al., 2014), its utilization for peanut breeding has been successful reported (Burow et al., 2014; Sukruth et al., 2015). Although erratic fertility was observed in some lines, the advanced backcross population developed from the same cross has a high phenotypic variation for many important agronomic traits, such as plant architecture, yield related traits, drought tolerance and resistance to leaf spot (Nguepjop et al., in preparation). We believe that the genetic variation among AB-QTL lines is increased when homeologous chromosomes pair. The mosaic compositions of the genome and the homeologous chromosome substitutions may speed up novel genetic combinations, opening new horizons for peanut breeding.

CONCLUSION

The inheritance patterns of SSR markers, statistical analysis and genetic mapping provide evidence of a mixed disomic and polysomic mode of genetic inheritance in allotetraploid peanut based on an experimental interspecific cross. The mixed inheritance appears associated with segregation distortion and homeologous chromosome substitutions. These findings contribute to a better understanding of the meiotic behavior of allotetraploid peanut and will provide useful information to breeders that use synthetic tetraploid to move genes in the genetic background of the cultivated peanut species.

AUTHOR CONTRIBUTIONS

JN designed and coordinated the study, performed the experiments, carried out data analyses and map construction, and wrote the manuscript. H-AT was involved in population development. NM and SS have produced the synthetic amphidiploid used in the study. JB, BC, and DS were involved in the design of the study and helped in data analysis. J-FR designed the study involved in map construction and contributed to editing of the manuscript. DF conceived, designed, and coordinated the study, helped in data analysis and editing of the manuscript. All authors read and approved the manuscript.

FUNDING

This work was funded by WAAPP/PPAAO Senegal.

ACKNOWLEDGMENTS

The authors thank the German Academic Exchange Service (DAAD) for providing the Ph.D. scholarship and, Dr. Pamela Soltis and Dr. Annaliese Mason for their valuable comments and suggestions to improve the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpls.2016.01635/full#supplementary-material

REFERENCES

Ainouche, M. L., and Wendel, J. F. (2014). "Polyploid speciation and genome evolution: lessons from recent allopolyploids," in *Evolutionary Biology: Genome Evolution, Speciation, Coevolution and Origin of Life*, ed. P. Pontarotti (Berlin: Springer International Publishing), 87–113.

Barone, A., Li, J., Sebastiano, A., Cardi, T., and Frusciante, L. (2002). Evidence for tetrasomic inheritance in a tetraploid Solanum commersonii (+) *S. tuberosum* somatic hybrid through the use of molecular markers. *Theor. Appl. Genet.* 104, 539–546. doi: 10.1007/s00122-001-0792-1

Bertioli, D. J., Cannon, S. B., Froenicke, L., Huang, G., Farmer, A. D., Cannon, E. K. S., et al. (2016). The genome sequences of *Arachis duranensis* and *Arachis ipaensis*, the diploid ancestors of cultivated peanut. *Nat. Genet.* 48, 438–446. doi: 10.1038/ng.3517

Bourke, P. M., Voorrips, R. E., Visser, R. G. F., and Maliepaard, C. (2015). The double reduction landscape in tetraploid potato as revealed by a

high-density linkage map. *Genetics* 201, 853–863. doi: 10.1534/genetics.115.181008

Bousalem, M., Arnau, G., Hochu, I., Arnolin, R., Viader, V., Santoni, S., et al. (2006). Microsatellite segregation analysis and cytogenetic evidence for tetrasomic inheritance in the American yam *Dioscorea trifida* and a new basic chromosome number in the Dioscoreae. *Theor. Appl. Genet.* 113, 439–451. doi: 10.1007/s00122-006-0309-z

Burow, M. D., Simpson, C. E., Starr, J. L., and Paterson, A. H. (2001). Transmission genetics of chromatin from a synthetic amphidiploid to cultivated peanut (*Arachis hypogaea* L.). broadening the gene pool of a monophyletic polyploid species. *Genetics* 159, 823–837.

Burow, M. D., Starr, J. L., Park, C.-H., Simpson, C. E., and Paterson, A. H. (2014). Introgression of homeologous quantitative trait loci (QTLs) for resistance to the root-knot nematode [*Meloidogyne arenaria* (Neal) Chitwood] in an advanced backcross-QTL population of peanut (*Arachis hypogaea* L.). *Mol. Breed.* 34, 393–406. doi: 10.1007/s11032-014-0042-2

Catalán, P., Segarra-Moragues, J. G., Palop-Esteban, M., Moreno, C., and González-Candelas, F. (2006). A bayesian approach for discriminating among alternative inheritance hypotheses in plant polyploids: the allotetraploid origin of genus borderea (Dioscoreaceae). *Genetics* 172, 1939–1953. doi: 10.1534/genetics.105.042788

Cifuentes, M., Grandont, L., Moore, G., Chèvre, A. M., and Jenczewski, E. (2010). Genetic regulation of meiosis in polyploid species: new insights into an old question. *New Phytol.* 186, 29–36. doi: 10.1111/j.1469-8137.2009.03084.x

Diwan, N., Bouton, J. H., Kochert, G., and Cregan, P. B. (2000). Mapping of simple sequence repeat (SSR) DNA markers in diploid and tetraploid alfalfa. *Theor. Appl. Genet.* 101, 165–172. doi: 10.1007/s001220051465

Esselink, G. D., Nybom, H., and Vosman, B. (2004). Assignment of allelic configuration in polyploids using the MAC-PR (microsatellite DNA allele counting—peak ratios) method. *Theor. Appl. Genet.* 109, 402–408. doi: 10.1007/s00122-004-1645-5

Favero, A. P., Simpson, C. E., Valls, J. F. M., and Vello, N. A. (2006). Study of the evolution of cultivated peanut through crossability studies among *Arachis ipaensis*, A. duranensis, and A. hypogaea. *Crop Sci.* 46, 1546–1552. doi: 10.2135/cropsci2005.09-0331

Ferreira, T., and Rasband, W. (2012). *ImageJ User Guide: IJ 1.42r*. Available at: https://imagej.nih.gov/ij/docs/guide/.

Fjellstrom, R. G., Beuselinck, P. R., and Steiner, J. J. (2001). RFLP marker analysis supports tetrasonic inheritance in *Lotus corniculatus* L. *Theor. Appl. Genet.* 102, 718–725. doi: 10.1007/s001220051702

Foncéka, D., Hodo-Abalo, T., Rivallan, R., Faye, I., Sall, M. N., Ndoye, O., et al. (2009). Genetic mapping of wild introgressions into cultivated peanut: a way toward enlarging the genetic basis of a recent allotetraploid. *BMC Plant Biol.* 9:103. doi: 10.1186/1471-2229-9-103

Fonceka, D., Tossim, H.-A., Rivallan, R., Vignes, H., Lacut, E., de Bellis, F., et al. (2012). Construction of chromosome segment substitution lines in Peanut (*Arachis hypogaea* L.) Using a wild synthetic and QTL mapping for plant morphology. *PLoS ONE* 7:e48642. doi: 10.1371/journal.pone.0048642

Gaeta, R. T., and Chris Pires, J. (2010). Homoeologous recombination in allopolyploids: the polyploid ratchet. *New Phytol.* 186, 18–28. doi: 10.1111/j.1469-8137.2009.03089.x

Gaeta, R. T., Pires, J. C., Iniguez-Luy, F., Leon, E., and Osborn, T. C. (2007). Genomic Changes in Resynthesized *Brassica napus* and their effect on gene expression and phenotype. *Plant Cell* 19, 3403–3417. doi: 10.1105/tpc.107.054346

Guo, Y., Wu, Y., Anderson, J. A., Moss, J. Q., and Zhu, L. (2015). Disomic inheritance and segregation distortion of SSR markers in two populations of *Cynodon dactylon* (L.) Pers. var. dactylon. *PLoS One* 10:e0136332. doi: 10.1371/journal.pone.0136332

Haynes, K. G., and Douches, D. S. (1993). Estimation of the coefficient of double reduction in the cultivated tetraploid potato. *Theor. Appl. Genet.* 85, 857–862. doi: 10.1007/BF00225029

Hoarau, J.-Y., Offmann, B., D'Hont, A., Risterucci, A.-M., Roques, D., Glaszmann, J.-C., et al. (2001). Genetic dissection of a modern sugarcane cultivar (*Saccharum* spp.). I. Genome mapping with AFLP markers. *Theor. Appl. Genet.* 103, 84–97. doi: 10.1007/s001220000390

Hong, Y., Chen, X., Liang, X., Liu, H., Zhou, G., Li, S., et al. (2010). A SSR-based composite genetic linkage map for the cultivated peanut (*Arachis hypogaea* L.) genome. *BMC Plant Biol.* 10:17. doi: 10.1186/1471-2229-10-17

Hong, Y., Liang, X., Chen, X., Liu, H., Zhou, G., Li, S., et al. (2008). Construction of genetic linkage map based on SSR markers in Peanut (*Arachis hypogaea* L.). *Agric. Sci. China* 7, 915–921. doi: 10.1016/S1671-2927(08)60130-3

Husted, L. (1936). Cytological studies of the peanut *Arachis*. II. Chromosome number, morphology, and behavior and their application to the origin of cultivated forms. *Cytologia* 7, 396–423. doi: 10.1508/cytologia.7.396

Jeridi, M., Perrier, X., Rodier-Goud, M., Ferchichi, A., D'Hont, A., and Bakry, F. (2012). Cytogenetic evidence of mixed disomic and polysomic inheritance in an allotetraploid (AABB) musa genotype. *Ann. Bot.* 110, 1593–1606. doi: 10.1093/aob/mcs220

Kamiri, M., Stift, M., Srairi, I., Costantino, G., Moussadik, A. E., Hmyene, A., et al. (2011). Evidence for non-disomic inheritance in a citrus interspecific tetraploid somatic hybrid between C. reticulata and C. limon using SSR markers and cytogenetic analysis. *Plant Cell Rep.* 30, 1415–1425. doi: 10.1007/s00299-011-1050-x

Klie, M., Schie, S., Linde, M., and Debener, T. (2014). The type of ploidy of chrysanthemum is not black or white: a comparison of a molecular approach to published cytological methods. *Front. Plant Sci.* 5:479. doi: 10.3389/fpls.2014.00479

Koning-Boucoiran, C. F. S., Gitonga, V. W., Yan, Z., Dolstra, O., van der Linden, C. G., van der Schoot, J., et al. (2012). The mode of inheritance in tetraploid cut roses. *Theor. Appl. Genet.* 125, 591–607. doi: 10.1007/s00122-012-1855-1

Kosambi, D. D. (1943). The estimation of map distances from recombination values. *Ann. Eugen.* 12, 172–175. doi: 10.1111/j.1469-1809.1943.tb02321.x

Landergott, U., Naciri, Y., Schneller, J. J., and Holderegger, R. (2006). Allelic configuration and polysomic inheritance of highly variable microsatellites in tetraploid gynodioecious *Thymus praecox* agg. *Theor. Appl. Genet.* 113, 453–465. doi: 10.1007/s00122-006-0310-6

Leal-Bertioli, S., Shirasawa, K., Abernathy, B., Moretzsohn, M., Chavarro, C., Clevenger, J., et al. (2015). Tetrasomic recombination is surprisingly frequent in allotetraploid *Arachis*. *Genetics* 199, 1093–1105. doi: 10.1534/genetics.115.174607

Leal-Bertioli, S. C. M., Santos, S. P., Dantas, K. M., Inglis, P. W., Nielen, S., Araujo, A. C. G., et al. (2014). Arachis batizocoi: a study of its relationship to cultivated peanut (*A. hypogaea)* and its potential for introgression of wild genes into the peanut crop using induced allotetraploids. *Ann. Bot.* 115, 237–249. doi: 10.1093/aob/mcu237

Leitch, A. R., and Leitch, I. J. (2008). Genomic plasticity and the diversity of polyploid plants. *Science* 320, 481–483. doi: 10.1126/science.1153585

Lerceteau-Köhler, E., Guérin, G., Laigret, F., and Denoyes-Rothan, B. (2003). Characterization of mixed disomic and polysomic inheritance in the octoploid strawberry (*Fragaria* × ananassa) using AFLP mapping. *Theor. Appl. Genet.* 107, 619–628. doi: 10.1007/s00122-003-1300-6

Lorieux, M. (2012). MapDisto: fast and efficient computation of genetic linkage maps. *Mol. Breed.* 30, 1231–1235. doi: 10.1007/s11032-012-9706-y

Lukaszewski, A. J., and Kopecký, D. (2010). The Ph1 locus from wheat controls meiotic chromosome pairing in autotetraploid rye (*Secale cereale* L.). *Cytogenet. Genome Res.* 129, 117–123. doi: 10.1159/000314279

Lyrene, P. M. (2016). Phenotype and fertility of intersectional hybrids between tetraploid highbush blueberry and colchicine-treated *Vaccinium stamineum*. *HortScience* 51, 15–22.

Mallikarjuna, N., Senthilvel, S., and Hoisington, D. (2011). Development of new sources of tetraploid *Arachis* to broaden the genetic base of cultivated groundnut (*Arachis hypogaea* L.). *Genet. Resour. Crop Evol.* 58, 889–907. doi: 10.1007/s10722-010-9627-8

Mandáková, T., Marhold, K., and Lysak, M. A. (2014). The widespread crucifer species *Cardamine flexuosa* is an allotetraploid with a conserved subgenomic structure. *New Phytol.* 201, 982–992. doi: 10.1111/nph.12567

Mason, A. S., Batley, J., Bayer, P. E., Hayward, A., Cowling, W. A., and Nelson, M. N. (2014). High-resolution molecular karyotyping uncovers pairing between ancestrally related *Brassica* chromosomes. *New Phytol.* 202, 964–974. doi: 10.1111/nph.12706

Mason, A. S., Huteau, V., Eber, F., Coriton, O., Yan, G., Nelson, M. N., et al. (2010). Genome structure affects the rate of autosyndesis and allosyndesis in AABC,

BBAC and CCAB *Brassica* interspecific hybrids. *Chromosome Res.* 18, 655–666. doi: 10.1007/s10577-010-9140-0

Mather, K. (1936). Segregation and linkage in autotetraploids. *J. Genet.* 32, 287–314. doi: 10.1007/BF02982683

Modliszewski, J. L., and Willis, J. H. (2014). Near-absent levels of segregational variation suggest limited opportunities for the introduction of genetic variation via homeologous chromosome pairing in synthetic neoallotetraploid *Mimulus*. *G3* 20, 509–522. doi: 10.1534/g3.113.008441

Moore, G. (2014). The control of recombination in wheat by Ph1 and its use in breeding. *Methods Mol. Biol.* 1145, 143–153. doi: 10.1007/978-1-4939-0446-4_12

Muller, H. J. (1914). A new mode of segregation in Gregory's tetraploid primulas. *Am. Nat.* 48, 508–512. doi: 10.1086/279426

Nemorin, A., Abraham, K., David, J., and Arnau, G. (2012). Inheritance pattern of tetraploid *Dioscorea alata* and evidence of double reduction using microsatellite marker segregation analysis. *Mol. Breed.* 30, 1657–1667. doi: 10.1007/s11032-012-9749-0

Nicolas, S. D., Leflon, M., Monod, H., Eber, F., Coriton, O., Huteau, V., et al. (2009). Genetic regulation of meiotic cross-overs between related genomes in *Brassica napus* haploids and hybrids. *Plant Cell* 21, 373–385. doi: 10.1105/tpc.108.062273

Okada, M., Lanzatella, C., Saha, M. C., Bouton, J., Wu, R., and Tobias, C. M. (2010). Complete switchgrass genetic maps reveal subgenome collinearity, preferential pairing and multilocus interactions. *Genetics* 185, 745–760. doi: 10.1534/genetics.110.113910

Preacher, K. J. (2001). *Interactive Chi-Square Tests*. Available at: http://www.quantpsy.org/chisq/chisq.htm [accessed April 21, 2016]

Qin, H., Feng, S., Chen, C., Guo, Y., Knapp, S., Culbreath, A., et al. (2011). An integrated genetic linkage map of cultivated peanut (*Arachis hypogaea* L.) constructed from two RIL populations. *Theor. Appl. Genet.* 124, 653–664. doi: 10.1007/s00122-011-1737-y

Rami, J.-F., Leal-Bertioli, S. C. M., Foncéka, D., Moretzsohn, M. C., and Bertioli, D. J. (2014). "Groundnut," in *Alien Gene Transfer in Crop Plants*, Vol. 2, eds A. Pratap and J. Kumar (New York, NY: Springer), 253–279.

Ramsey, J., and Schemske, D. W. (2002). Neopolyploidy in flowering plants. *Ann. Review Ecol. Syst.* 33, 589–639. doi: 10.1146/annurev.ecolsys.33.010802.150437

Robledo, G., and Seijo, G. (2010). Species relationships among the wild B genome of *Arachis* species (section *Arachis*) based on FISH mapping of rDNA loci and heterochromatin detection: a new proposal for genome arrangement. *Theor. Appl. Genet.* 121, 1033–1046. doi: 10.1007/s00122-010-1369-7

Salmon, A., Flagel, L., Ying, B., Udall, J. A., and Wendel, J. F. (2010). Homoeologous nonreciprocal recombination in polyploid cotton. *New Phytol.* 186, 123–134. doi: 10.1111/j.1469-8137.2009.03093.x

Seijo, G., Lavia, G. I., Fernandez, A., Krapovickas, A., Ducasse, D. A., Bertioli, D. J., et al. (2007). Genomic relationships between the cultivated peanut (*Arachis hypogaea*, Leguminosae) and its close relatives revealed by double GISH. *Am. J. Bot.* 94, 1963–1971. doi: 10.3732/ajb.94.12.1963

Seijo, J. G., Lavia, G. I., Fernandez, A., Krapovickas, A., Ducasse, D., and Moscone, E. A. (2004). Physical mapping of the 5S and 18S-25S rRNA genes by FISH as evidence that *Arachis duranensis* and A. ipaensis are the wild diploid progenitors of *A. hypogaea* (Leguminosae). *Am. J. Bot.* 91, 1294–1303. doi: 10.3732/ajb.91.9.1294

Shirasawa, K., Bertioli, D. J., Varshney, R. K., Moretzsohn, M. C., Leal-Bertioli, S. C. M., Thudi, M., et al. (2013). Integrated consensus map of cultivated peanut and wild relatives reveals structures of the A and B genomes of *Arachis* and divergence of the legume genomes. *DNA Res.* 20, 173–184. doi: 10.1093/dnares/dss042

Simpson, C. E. (1991). Pathways for introgression of pest resistance into *Arachis hypogaea* L. 1. *Peanut Sci.* 18, 22–26. doi: 10.3146/i0095-3679-18-1-8

Simpson, C. E. (2001). Use of wild *Arachis* Species/introgression of genes into *A. hypogaea* L. *Peanut Sci.* 28, 114–116. doi: 10.3146/i0095-3679-28-2-12

Simpson, C. E., Krapovickas, A., and Valls, J. F. M. (2001). History of *Arachis* including evidence of *A. hypogaea* L. Progenitors. *Peanut Sci.* 28, 78–80. doi: 10.3146/i0095-3679-28-2-7

Smartt, J., Gregory, W. C., and Gregory, M. P. (1978). The genomes of *Arachis hypogaea*. 1. cytogenetic studies of putative genome donors. *Euphytica* 27, 665–675. doi: 10.1007/BF00023701

Soltis, D. E., Buggs, R. J. A., Doyle, J. J., and Soltis, P. S. (2010). What we still don't know about polyploidy. *Taxon* 59, 1387–1403.

Soltis, D. E., Visger, C. J., and Soltis, P. S. (2014). The polyploidy revolution then and now: stebbins revisited. *Am. J. Bot.* 101, 1057–1078. doi: 10.3732/ajb.1400178

Stalker, H. T. (1991). A new species in section *Arachis* of peanuts with a D genome. *Am. J. Bot.* 78, 630–637. doi: 10.2307/2445084

Stebbins, G. L. (1947). Types of polyploids; their classification and significance. *Adv. Genet.* 1, 403–429.

Stift, M., Berenos, C., Kuperus, P., and van Tienderen, P. H. (2008). Segregation models for disomic, tetrasomic and intermediate inheritance in tetraploids: a general procedure applied to rorippa (Yellow Cress) microsatellite data. *Genetics* 179, 2113–2123. doi: 10.1534/genetics.107.085027

Sukruth, M., Paratwagh, S. A., Sujay, V., Kumari, V., Gowda, M. V. C., Nadaf, H. L., et al. (2015). Validation of markers linked to late leaf spot and rust resistance, and selection of superior genotypes among diverse recombinant inbred lines and backcross lines in peanut (*Arachis hypogaea* L.). *Euphytica* 204, 343–351. doi: 10.1007/s10681-014-1339-2

Sybenga, D. J. (1975). "The analysis of chromosome pairing," in *Meiotic Configurations Monographs on Theoretical and Applied Genetics*, ed. R. Frankel (Berlin: Springer), 134–199.

Sybenga, J. (1996). Chromosome pairing affinity and quadrivalent formation in polyploids: do segmental allopolyploids exist? *Genome* 39, 1176–1184. doi: 10.1139/g96-148

Szadkowski, E., Eber, F., Huteau, V., Lodé, M., Huneau, C., Belcram, H., et al. (2010). The first meiosis of resynthesized *Brassica napus*, a genome blender. *New Phytol.* 186, 102–112. doi: 10.1111/j.1469-8137.2010.03182.x

van Berloo, R. (2008). GGT 2.0: versatile software for visualization and analysis of genetic data. *J. Hered* 99, 232–236. doi: 10.1093/jhered/esm109

Varshney, R., Bertioli, D., Moretzsohn, M., Vadez, V., Krishnamurthy, L., Aruna, R., et al. (2008). The first SSR-based genetic linkage map for cultivated groundnut (*Arachis hypogaea* L.). *Theor. Appl. Genet.* 118, 729–739. doi: 10.1007/s00122-008-0933-x

Wu, J.-H., Datson, P. M., Manako, K. I., and Murray, B. G. (2013). Meiotic chromosome pairing behaviour of natural tetraploids and induced autotetraploids of *Actinidia chinensis*. *Theor. Appl. Genet.* 127, 549–557. doi: 10.1007/s00122-013-2238-y

Xu, F., Tong, C., Lyu, Y., Bo, W., Pang, X., and Wu, R. (2015). Allotetraploid and autotetraploid models of linkage analysis. *Brief. Bioinform.* 16, 32–38. doi: 10.1093/bib/bbt075

Zhou, X., Xia, Y., Ren, X., Chen, Y., Huang, L., Huang, S., et al. (2014). Construction of a SNP-based genetic linkage map in cultivated peanut based on large scale marker development using next-generation double-digest restriction-site-associated DNA sequencing (ddRADseq). *BMC Genomics* 15:351. doi: 10.1186/1471-2164-15-351

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.