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Genome Report

Homoeologous recombination is recurrent in the nascent synthetic allotetraploid *Arachis ipaënsis* × *Arachis correntina*^{4x} and its derivatives

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Abstract

Genome instability in newly synthesized allotetraploids of peanut has breeding implications that have not been fully appreciated. Synthesis of wild species-derived neo-tetraploids offers the opportunity to broaden the gene pool of peanut; however, the dynamics among the newly merged genomes creates predictable and unpredictable variation. Selfed progenies from the neo-tetraploid *Arachis ipaënsis* × *Arachis correntina* (*A. ipaënsis* × *A. correntina*)^{4x} and F_1 hybrids and F_2 progenies from crosses between *A. hypogaea* × [*A. ipaënsis* × *A. correntina*]^{4x} were genotyped by the Axiom *Arachis* 48 K SNP array. Homoeologous recombination between the *A. ipaënsis* and *A. correntina* derived subgenomes was observed in the S_0 generation. Among the S_1 progenies, these recombined segments segregated and new events of homoeologous recombination emerged. The genomic regions undergoing homoeologous recombination segregated mostly disomically in the F_2 progenies from *A. hypogaea* × [*A. ipaënsis* × *A. correntina*]^{4x} crosses. New homoeologous recombination events also occurred in the F_2 population, mostly found on chromosomes 03, 04, 05, and 06. From the breeding perspective, these phenomena offer both possibilities and perils; recombination between genomes increases genetic diversity, but genome instability could lead to instability of traits or even loss of viability within lineages.

Keywords: *Arachis hypogaea* (peanut); homoeologous recombination; synthetic allotetraploid; *A. ipaënsis*; *A. correntina*

Introduction

Peanut (*Arachis hypogaea*) is an important crop valued for its high oil and protein content. Originating from South America, peanut is widely grown in the warmer regions of the world yielding a total of 46 million tons in 2018 (http://www.fao.org/faostat). Cultivated peanut is an allotetraploid with homoeologous subgenomes (AABB; $2n = 4x = 40$) sharing greater than 90% DNA sequence similarity (Bertioli *et al.* 2016). Its origin was via the formation of a hybrid between two diploid wild species, *Arachis ipaënsis* (BB; $2n = 2x = 20$) and *Arachis duranensis* (AA; $2n = 2x = 20$) followed by a single, or very few, natural polyploidization events less than 10,000 years ago (Bertioli *et al.* 2016). This recent polyploid origin created a strong genetic bottleneck and isolated cultivated peanut from its diploid wild relatives (Krapovickas *et al.* 2007). The narrow genetic base of cultivated peanut has resulted in limited resistance to many pathogens and diseases. For instance, only moderate levels of resistance to root-knot nematode (*Meloidogyne arenaria*) and late leaf spot (caused by *Nothopassalora personata*) were identified among over 1,000 peanut plant introductions in the US (Holbrook and Noe 1992; Holbrook and Anderson 1995). Screening over 10,000 plant introductions for rust (caused by *Puccinia arachidis*) yielded only 14 moderately rust resistant lines mostly collected from Peru (Subrahmanyam *et al.* 1985, 1989). In contrast, the wild relatives of peanut harbor strong resistance or immunity to many diseases and pests (Stalker 2017). There are 31 species in the section *Arachis* with only two of them being tetraploid ($2n = 4x = 40$), *i.e.*, *A. hypogaea* and *A. monticola*. The other 29 species are diploids ($2n = 2x = 20$ or $2n = 2x = 18$). High levels of genetic diversity of the diploid species compared to cultivated peanut is well-known (Kochert *et al.* 1996; Moretzsohn *et al.* 2004). An early well-documented introgression event resulted in introduction to the peanut crop of near immunity to root-knot nematode from the diploid species *Arachis cardenasii* (Simpson *et al.* 1993, 2003; Holbrook *et al.* 2008a; Nagy *et al.* 2010). This introgression used a hybridization scheme known as the tetraploid route (albeit in a complex three-way cross; Simpson 1991). First, an A genome hybrid was made by crossing *A. cardenasii* with *A. diogoi*. Then, the B genome (*sensu lato*) species *A. batizocoi* was crossed with the A genome hybrid to create a sterile AB hybrid. The AB hybrid was treated with colchicine to

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double the chromosome number and restore fertility thereby gaining sexual compatibility with cultivated peanut. Subsequently, efforts have focused on the tetraploid route in the simpler form, starting with one A and one B genome species (Favero *et al.* 2006; Stalker 2017; Leal-Bertioli *et al.* 2018). Recent introgressions from the tetraploid route include a new strong resistance to root-knot nematode from *A. stenosperma* (Ballen-Taborda *et al.* 2019) and improved pod and seed characteristics from *A. ipaënsis* and *A. duranensis* (Fonceka *et al.* 2009, 2012). Besides peanut, introgression from wild relatives brought in significant benefits to other crops such as improved seed yield in *Brassica napus* (Qian *et al.* 2005), fiber quality in cotton (Zhang *et al.* 2014), and disease resistance in wheat (Ali *et al.* 2016; Rahmatov *et al.* 2016).

Following interspecific hybridization and chromosome duplication, active homoeologous recombination can occur between the two distinct types of chromosomes as a consequence of bivalent and tetravalent formation during meiosis (Soltis and Soltis 1999). While bivalent pairing of chromosomes maintains the status of two separate subgenomes, the formation of multivalents leads to the breakdown of their separate identities (Stebbins 1947). The pairing of homoeologous chromosomes can result in replacement of a segment by a copy of the paired homoeologous region through both meiotic crossover and noncrossover (Youds and Boulton 2011). Pioneering cytogenetic studies showed that meiotic chromosomes in peanut consisted of 20 chromosome bivalents in 88–98% of cells; the remainder of cells harbored mostly bivalents together with one or a few univalents, trivalents, or quadrivalents (Husted 1936; Smartt *et al.* 1978). This clearly indicated the likelihood of genetic recombination between subgenomes. However, in spite of these findings, almost all genetic studies using DNA markers have assumed only recombination within subgenomes. Only more recently has recombination between subgenomes begun to be quantified, and the effects on genome structure recognized with most of the research focused on neo-tetraploids generated from crosses of cultivated peanut's putative diploid progenitors (Leal-Bertioli *et al.* 2015, 2018; Clevenger *et al.* 2017).

This study used a neo-tetraploid formed from two wild diploid species. *A. ipaënsis* Krapov. & W.C. Greg. K30076 (*Ipa*), and *A. correntina* (Burkart) Krapov. & W.C. Greg. 9530 (*Cor*). The former is the B genome progenitor of cultivated peanut. The latter is an A genome, nonprogenitor diploid species that is resistant to late leaf spot, rust, tomato spotted wilt virus, peanut mottle virus, fall armyworm, corn earworm, and aphids (Stalker 2017). New tetraploids [*A. ipaënsis* K30076 × *A. correntina* 9530]^{4x} (*IpaCor*^{4x}) were created from hybrids between *Ipa* and *Cor* through colchicine treatment. The first objective of this research was to study the occurrence of homoeologous recombination in the nascent synthetic allotetraploid and the derivative lines from crosses with cultivated peanut. The second objective was to determine the genomic regions and chromosomes predominantly impacted by the homoeologous recombination. The impact of homoeologous recombination was found to increase through generation advancement and was propagated among progenies from *A. hypogaea* × *IpaCor*^{4x} crosses, a phenomenon which has been called "the polyploid ratchet" (Gaeta and Pires 2010). The implications of homoeologous recombination events for breeding are discussed.

Materials and methods

Genetic materials

Interspecific hybrids were made between the two diploid species *A. ipaënsis* K30076 (*Ipa*; female) and *A. correntina* 9530 (*Cor*; male) at North Carolina State University. Multiple plants of each diploid species were used for crossing. Cuttings from the sterile interspecific hybrids were established and shipped to the University of Georgia Tifton Campus for colchicine treatment. Sterility is expected in interspecific hybrids, and the hybrid nature of putative F_1s was confirmed by the presence of greater than 80% aborted pollen grains using the Alexander blue staining method (Alexander 1969).

For chromosome doubling, 300 cuttings of the diploid hybrid (~20 cm long) were immersed in 0.2% colchicine solution for 12–14 hours at room temperature. The treated cuttings were rinsed under continuously running tap water for 1 hour to remove excess colchicine. The cuttings were shortened by 2 cm from the end of the existing cut. The 18 cm long piece was further cut in half yielding two approximately 9 cm long pieces. Fresh cut ends were dipped in Clonex rooting gel (Growth Technology, Western Way, TA, UK) before being planted in Jiffy peat pots (5.7 cm^2 sq. × 5.7 cm H) filled with Promix BX growth medium (Premier Tech Horticulture, Quakertown, PA, USA). The cuttings were kept in seed trays enclosed with a clear cover to reach 100% humidity. The colchicine-treated cuttings were grown under 16/8 hours light/dark condition at room temperature for 3–4 weeks to allow root formation before transplanting to a plastic tub (87 × 55 × 20 cm; LxWxH) filled with Promix growth medium in the greenhouse. Cuttings were periodically checked for the formation of pegs and marked with flags. Pods were harvested 40–50 days after peg identification.

S_0 plants of *IpaCor*^{4x} were used as male parents to cross with two advanced peanut breeding lines 13-2113 [(Tifguard × Florida-07) × C725-19-25] and 13-1014 [(Tifguard × Florida-07) × Georgia-06G]. Florida-07 (Gorbet and Tillman 2009), Tifguard (Holbrook *et al.* 2008a), and Georgia-06G (Branch 2007) are elite peanut cultivars adapted to US southeastern peanut growing regions. C725-19-25 is a high-yielding breeding line with resistance to tomato spotted wilt virus (Holbrook *et al.* 2008b). Two F_2 populations from F_1 hybrids (13-1014 × *IpaCor*^{4x}_$S_{0.2}$)_$F_{1.4}$ and (13-1014 × *IpaCor*^{4x}_$S_{0.5}$)_$F_{1.4}$ were grown in the greenhouse for tissue collection and DNA extraction. Each F_2 population consisted of 456 individuals.

Genotyping by SNP array

Genetic materials genotyped by the Axiom *Arachis* 48 K SNP array (Thermofisher Scientific, Waltham, MA, USA) (Clevenger *et al.* 2018; Korani *et al.* 2019) included DNA from two plants of *Ipa* and two plants of *Cor* (Supplementary Table S1). These four plants were sister lines to the original parents used to produce the *IpaCor*^{4x} neo-tetraploid. The diploid hybrids before and after colchicine treatment were included. Six *IpaCor*^{4x}_S_0 and seven *IpaCor*^{4x}_S_1 neo-tetraploid plants were genotyped. All of the S_1 plants were progenies from one mother plant *i.e.*, *IpaCor*^{4x}_$S_{0.2}$. Thirty-seven F_1s of the *A. hypogaea* × *IpaCor*^{4x}_S_0 crosses were genotyped together with their *A. hypogaea* female parents 13-2113 and 13-1014. Two F_2 populations (456 lines in each population) descending from (13-1014 × *IpaCor*^{4x}_$S_{0.2}$)_$F_{1.4}$ and (13-1014 × *IpaCor*^{4x}_$S_{0.5}$)_$F_{1.4}$ were genotyped as well. Genomic DNAs were extracted from unexpanded young leaves by Qiagen Plant DNeasy kit (Qiagen, Germantown, MD, USA) and quantified by Quant-iT Picogreen dsDNA assay kit (Thermofisher Scientific, Waltham, MA, USA). Genotyping data were analyzed with the Axiom Analysis Suite (Thermofisher Scientific, Waltham, MA, USA). Based on SNP QC matrix developed by the software, SNP markers were grouped in six categories, *i.e.*, PolyHighResolution, NoMinorHom, MonoHighResolution, CallRateBelowThreshold,

OfftargetVariant, and Other. All data analysis in this study was performed with the markers in the PolyHighResolution category since this group of markers has the clearest signal separation.

Curation of homoeologous recombination events in *IpaCor*^{4x} neo-tetraploid

To study the recombination between the two subgenomes of *IpaCor*^{4x}, diploid parents, *IpaCor*^{2x} hybrids, and all of the *IpaCor*^{4x} S_0 and S_1 plants were subjected to analysis. To curate the genomic regions hosting homoeologous recombination, we focused on polymorphic markers between *Ipa* and *Cor* which would have opposite genotype calls AA versus BB. Without taking into account recombination between subgenomes, we would naively expect *IpaCor*^{4x} plants would form homoeologous genotyping clusters with AB genotype calls at these loci. In reality, we encountered unexpected genotype calls. All of the genotype calls in four categories AA, BB, AB, and NoCall were output as "call codes" using the Axiom analysis software. The data set was first filtered for polymorphic markers between *Ipa* and *Cor* using the "if" argument of Excel. Subsequently, the "countif" function was applied to curate the genotyping of *IpaCor*^{4x}_S_0 and S_1 plants deviating from expected homoeologous clusters. All of the markers with this type of sample distribution were visually inspected for clustering patterns. Markers with DNA samples clearly forming a separate cluster between homozygous and heterozygous clusters were assembled. The genotype calls of individuals falling in the separate cluster were adjusted to 75% of the closest homozygous calls. A stretch of at least three consecutive markers demonstrating the same recombination pattern was considered an event of homoeologous recombination.

Curation of new homoeologous recombination events in the F_2 populations of *A. hypogaea* × *IpaCor*^{4x}_S_0 crosses

Manually curating homoeologous recombination events among polymorphic markers of the F_2 populations is an arduous task due to the large population size and the abundance of markers. However, monomorphic markers with F_2 individuals grouped outside the majority of the population indicated the presence of new homoeologous recombination in these F_2 outliers. To curate this type of new homoeologous recombination event, monomorphic markers with F_2 individuals demonstrating genotype calls other than the expected AB calls were curated by Excel sorting and countif functions.

Figures of the clustering patterns were exported from the Axiom Analysis Suite software, which carried out clustering in two dimensions (Axiom Analysis Suite User Guide, Affymetrix.com). The X dimension is called "contrast" and the Y dimension is called "size." They are log-linear combinations of the two allele signal intensities. To illustrate the allele exchange among the groups, sampler nucleotides G and C were used. The actual nucleotides at the targeted loci could be any one of the A, T, C, G. Superscripts next to the nucleotides denoted the sources of alleles. For instance, in the allele combinations such as $G^{ac}G^{ac}$, $C^{bi}C^{bi}$, and $G^{ah}C^{ah}$, ^{ac} superscript indicated A genome from *Cor*, ^{bi} superscript denoted B genome from *Ipa* and ^{ah} denoted genome composition from *A. hypogaea*.

To determine the frequency of homoeologous recombination across the genome, the number of lines hosting the recombination was counted for each marker. Genome positions of markers demonstrating homoeologous recombination were referenced to the *Ipa* genome (Bertioli *et al.* 2016).

Results

Homoeologous recombination in the *IpaCor*^{4x} neo-tetraploid

Out of 300 cuttings of *IpaCor*^{2x} hybrids treated by colchicine, 21 S_0 seeds were harvested. The new *IpaCor*^{4x} allotetraploid was highly fertile. DNAs from six of the S_0 seedlings were genotyped by the SNP array. The occurrence and segregation of chromosome regions demonstrating homoeologous recombination were curated in *IpaCor*^{4x}_$S_{0.2}$ and its seven progenies *IpaCor*^{4x} _$S_{0.2}$_$S_{1.1}$ to $S_{1.7}$ (Table 1). During meiosis of *IpaCor*^{4x}, genomic regions undergoing homoeologous pairing may result in homoeologous recombination. As one segment of the chromatid is replaced by the opposite subgenome, a set of contiguous homoeologous markers within the replaced chromosome segment should shift as a block from the expected "heterozygote" cluster (alternate SNPs in the two homoeologs are detected) toward the donor cluster. As illustrated at SNP marker AX-147221175 (Figure 1), diploid parents *Cor* (red triangles, example base call as $G^{ac}G^{ac}$; ^{ac} denotes A subgenome from *Cor*) and *Ipa* (blue triangles, $C^{bi}C^{bi}$; ^{bi} denotes B subgenome from *Ipa*) were grouped in the genotype clusters AA and BB respectively. Most of the *IpaCor*^{4x}_S_0 plants ($S_{0.5}$, $S_{0.6}$, $S_{0.8}$, $S_{0.10}$, $S_{0.11}$, and $S_{0.12}$) ($G^{ac}G^{ac}C^{bi}C^{bi}$, magenta circles) were grouped in the AB cluster as expected indicating their allele composition as $G^{ac}G^{ac}C^{bi}C^{bi}$ due to the merging of the *Ipa* and *Cor* genomes. However, *IpaCor*^{4x}_$S_{0.2}$ (two circled magenta triangles) was an outlier since it had a genotype call of AA. This was caused by the replacement of one chromosome segment from *Ipa* by the homoeologous region from *Cor*. Consequently, the allele composition became $G^{ac}G^{ac}G^{ac}C^{bi}$ and the hybridization signal was shifted toward the AA cluster where *Cor* samples were located. Although the software assigned AA genotype calls for the two DNA samples from *IpaCor*^{4x}_$S_{0.2}$, the clustering pattern clearly indicated that *IpaCor*^{4x}_$S_{0.2}$ and four of her S_1 progenies ($S_{1.2}$, $S_{1.3}$, $S_{1.4}$, and $S_{1.7}$) actually formed a fourth cluster (green oval) between the AB and AA clusters. Their genotype calls were adjusted to 75% of AA (re-coded as 75% of 0 in Table 1) implying one allele from the *Ipa* subgenome was replaced by *Cor*. The remaining three S_1 progenies $S_{1.1}$, $S_{1.5}$, and $S_{1.6}$ were grouped with *Cor*. This implied that the allele composition of these individuals became $G^{ac}G^{ac}G^{ac}G^{ac}$ *i.e.*, quadriplex for *Cor*. A set of 19 adjacent markers at the end of chromosome A04/B04 demonstrated the same pattern of homoeologous recombination and segregation among the S_1 progenies of *IpaCor*^{4x}_ $S_{0.2}$ (Table 1). The size of the chromosome segment was 6.7 Mbp with a marker density of 353 kb/marker. This was the only homoeologous recombination event identified in *IpaCor*^{4x}_$S_{0.2}$.

Four new homoeologous recombination events were found in three S_1 progenies, *IpaCor*^{4x}_$S_{0.2}$ $S_{1.1}$, $S_{1.5}$, $S_{1.7}$ (Table 2, Supplementary Table S2). At the top of chromosome A03/B03, a 5 Mbp chromatid segment had *Cor* replacing *Ipa* in *IpaCor*^{4x}_ $S_{0.2}$_ $S_{1.1}$. Most of the chromosome B04 (~120 Mbp) had homoeologous recombination in both *IpaCor*^{4x}_ $S_{0.2}$_ $S_{1.1}$ and $S_{1.7}$ yet in opposite directions, *i.e.*, the *Cor* allele replaced the *Ipa* allele in $S_{1.1}$ and *vice versa* in $S_{1.7}$. At the top of chromosome B05, a 14 Mbp segment had one copy of alleles from *Cor* replaced by *Ipa* in *IpaCor*^{4x}_ $S_{0.2}$_ $S_{1.5}$. These new events among the S_1 progenies indicated that active homoeologous recombination continues to occur during generation advancement of the neo-tetraploid.

In addition to the *IpaCor*^{4x}_$S_{0.2}$ family, homoeologous recombination was identified in the four other *IpaCor*^{4x}_S_0 plants on chromosomes A04/B04, A05/B05, and A07/B07 (Table 2). The two events on chromosome A04/B04 were opposite in direction of

Table 1 Homoeologous recombination between A04 and B04 in *IpaCor*^{4x}_$S_{0.2}$ and its segregation among S1 progenies

Probeset_id	Chromosome[a]	SNP Position (bp)	*Ipa*	*Cor*	*IpaCor*^{2x}	*IpaCor*^{4x} _$S_{0.2}$	*IpaCor*^{4x} _$S_{0.2}$_$S_{1.1}$	*IpaCor*^{4x} _$S_{0.2}$_$S_{1.2}$	*IpaCor*^{4x} _$S_{0.2}$_$S_{1.3}$	*IpaCor*^{4x} _$S_{0.2}$_$S_{1.4}$	*IpaCor*^{4x} _$S_{0.2}$_$S_{1.5}$	*IpaCor*^{4x} _$S_{0.2}$ _$S_{1.6}$	*IpaCor*^{4x} _$S_{0.2}$_$S_{1.7}$	Segment size (bp)	bp/marker
AX-147248448	Araip.B04	124,804,923	0	2	1	75% of 2	2	75% of 2	75% of 2	75% of 2	2	2	75% of 2	6,698,921	352,575
AX-147220907	Araip.B04	124,824,690	2	0	1	75% of 0	0	75% of 0	75% of 0	75% of 0	0	0	75% of 0	—	—
AX-147248475	Araip.B04	125,438,618	0	2	1	75% of 2	2	75% of 2	75% of 2	75% of 2	2	2	75% of 2	—	—
AX-147248476	Araip.B04	125,440,304	0	2	1	75% of 2	2	75% of 2	75% of 2	75% of 2	2	2	75% of 2	—	—
AX-147221088	Araip.B04	128,460,377	2	0	1	75% of 0	0	75% of 0	75% of 0	75% of 0	0	0	75% of 0	—	—
AX-147248617	Araip.B04	128,469,894	2	0	1	75% of 0	0	75% of 0	75% of 0	75% of 0	0	0	75% of 0	—	—
AX-147248627	Araip.B04	128,518,680	0	2	1	75% of 2	2	75% of 2	75% of 2	75% of 2	2	2	75% of 2	—	—
AX-147221124	Araip.B04	129,198,098	0	2	1	75% of 2	2	75% of 2	75% of 2	75% of 2	2	2	75% of 2	—	—
AX-147221160	Araip.B04	129,385,417	2	0	1	75% of 0	0	75% of 0	75% of 0	75% of 0	0	0	75% of 0	—	—
AX-147221161	Araip.B04	129,385,840	2	0	1	75% of 0	0	75% of 0	75% of 0	75% of 0	0	0	75% of 0	—	—
AX-147248696	Araip.B04	129,600,869	0	2	1	75% of 2	2	75% of 2	75% of 2	75% of 2	2	2	75% of 2	—	—
AX-147221210	Araip.B04	129,796,029	2	0	1	75% of 0	0	75% of 0	75% of 0	75% of 0	0	0	75% of 0	—	—
AX-147248730	Araip.B04	129,989,016	0	2	1	75% of 2	2	75% of 2	75% of 2	75% of 2	2	2	75% of 2	—	—
AX-147248735	Araip.B04	130,112,475	0	2	1	75% of 2	2	75% of 2	75% of 2	75% of 2	2	2	75% of 2	—	—
AX-147248739	Araip.B04	130,210,807	2	0	1	75% of 0	0	75% of 0	75% of 0	75% of 0	0	0	75% of 0	—	—
AX-176791380	Araip.B04	131,369,085	2	0	1	75% of 0	0	75% of 0	75% of 0	75% of 0	0	0	75% of 0	—	—
AX-147221357	Araip.B04	131,423,712	0	2	1	75% of 2	2	75% of 2	75% of 2	75% of 2	2	2	75% of 2	—	—
AX-147221364	Araip.B04	131,478,950	2	0	1	75% of 0	0	75% of 0	75% of 0	75% of 0	0	0	75% of 0	—	—
AX-147221371	Araip.B04	131,503,844	2	0	1	75% of 0	0	75% of 0	75% of 0	75% of 0	0	0	75% of 0	—	—

Genotype calls from the SNP array were re-coded as follows, genotype call AA = 0; BB = 2; AB = 1 to avoid confusion with the description of subgenomes. Seventy-five percent of a genotype call indicates the dosage of a subgenome allele was increased by 25% as a result of subgenome recombination.

[a]Chromosome and SNP positions were given relative to *Arachis ipaensis* genome (peanutbase.org). The recombination events occurred at these loci were actually between the homoeologous chromosomes.

Figure 1 A SNP marker demonstrating a *Cor allele* replacing an *Ipa* allele in *IpaCor*^{4x}_$S_{0.2}$ and S_1 progenies. *Cor*, red triangles with $G^{ac}G^{ac}$ as an example of base call, and *Ipa* ($C^{bi}C^{bi}$, blue triangles) were grouped in genotype calls of AA and BB respectively. ^{ac} superscript indicates A genome from *Cor*, ^{bi} superscript denotes B genome from *Ipa*. *IpaCor*^{2x} ($G^{ac}C^{bi}$, green circles), and *IpaCor*^{4x}_$S_{0.5, 6, 8, 10,11,12}$($G^{ac}G^{ac}C^{bi}C^{i}$, magenta circles) were clustered in the expected AB group. *IpaCor*^{4x}_$S_{0.2}$ ($G^{ac}G^{ac}G^{ac}C^{bi}$, two circled magenta triangles) and some other samples formed a separate group between cluster AB and AA which was enclosed by a green oval. Four of the S_1 progenies from *IpaCor*^{4x}_$S_{0.2}$ ($G^{ac}G^{ac}G^{ac}C^{bi}$, dark purple triangles) fell in this new group. The remaining three S_1 progenies ($G^{ac}G^{ac}G^{ac}G^{ac}$, dark purple triangles) grouped with *Cor* forming a quadriplex locus.

homoeologous recombination and occurred in two separate S_0 plants. The event in *IpaCor*^{4x}_$S_{0.11}$ spanned a small segment of 0.5 Mbp whereas the event in *IpaCor*^{4x}_$S_{0.12}$ almost covered the whole of chromosome A04/B04 (124 Mbp). The event captured on chromosome A05/B05 also encompassed nearly the whole chromosome (148 Mbp) in *IpaCor*^{4x}_$S_{0.6}$. The event identified on the top of chromosome A07/B07 was 1.4 Mbp in *IpaCor*^{4x}_$S_{0.5}$. Among the nine events found in *IpaCor*^{4x}_S_0 and S_1 plants, five of them had *Ipa* replacing the *Cor* subgenome and four of them had *Cor* replacing the *Ipa* subgenome.

Segregation of genomic regions subjected to recombination among F_1 hybrids

Three of the *IpaCor*^{4x}_S_0 plants $S_{0.2}$, $S_{0.5}$, and $S_{0.6}$ were used as males to cross with two elite *A. hypogaea* breeding lines 13-2113 and 13-1014 and produced 37 F_1 progenies. Hybridity of all 37 F_1 progenies was confirmed by the expected heterozygous calls from 1024 polymorphic markers between the *A. hypogaea* and *IpaCor*^{4x}_S_0 parents (Supplementary Table S3). Each of these three *IpaCor*^{4x}_S_0 male parents had a genomic region with chromosomal recombination on chromosomes A04/B04, A07/B07, and A05/B05, respectively (Tables 1 and 2). Segregation of these genomic regions harboring homoeologous recombination among F_1 hybrids was observed (Supplementary Table S4; red font

Table 2 Homoeologous recombination events in *IpaCor*^{4x}_S_0 and S_1 plants other than those listed in Table 1

Genotype	Direction of subgenome recombination	Chromosome[a]	Left border (bp)	Right border (bp)	Segment size (bp)	No. of markers	bp/marker
IpaCor^{4x}_$S_{0.2}$_$S_{1.1}$	*Cor* replaced 50% of *Ipa*	Araip.B03	2,065,843	7,115,308	5,049,465	19	265,761
IpaCor^{4x}_$S_{0.2}$_$S_{1.1}$	*Cor* replaced 50% of *Ipa*	Araip.B04	4,420,103	124,301,830	119,881,727	96	1,248,768
IpaCor^{4x}_$S_{0.2}$_$S_{1.7}$	*Ipa* replaced 50% of *Cor*	Araip.B04	613,773	124,301,830	123,688,057	109	1,134,753
IpaCor^{4x}_$S_{0.2}$_$S_{1.5}$	*Ipa* replaced 50% of *Cor*	Araip.B05	1,426,280	15,568,257	14,141,977	23	614,869
IpaCor^{4x}_$S_{0.11}$	*Ipa* replaced 50% of *Cor*	Araip.B04	123,807,791	124,301,830	494,039	7	70,577
IpaCor^{4x}_$S_{0.12}$	*Cor* replaced 50% of *Ipa*	Araip.B04	613,773	124,298,527	123,684,754	108	1,145,229
IpaCor^{4x}_$S_{0.6}$	*Cor* replaced 50% of *Ipa*	Araip.B05	1,426,280	148,997,085	147,570,805	91	1,621,657
IpaCor^{4x}_$S_{0.5}$	*Ipa* replaced 50% of *Cor*	Araip.B07	686,538	2,077,018	1,390,480	13	106,960

[a] Chromosome and SNP positions were given relative to *A. ipaensis* genome (peanutbase.org). The recombination events occurred at these loci were actually between the homoeologous chromosomes.

genotype calls). Two examples demonstrating segregation of the inherited homoeologous recombination from the *IpaCor*^{4x}_S_0 parents among F_1 hybrids are illustrated in Supplementary Figures S1 and S2. In both cases, the *IpaCor*^{4x}_S_0 parent had a genomic region with pre-existing homoeologous recombination and the *A. hypogaea* female parent presented in either the heterozygote (Supplementary Figure S2) or homozygote (Supplementary Figure S3) cluster.

At the first locus (Supplementary Figure S2A), *Cor* ($G^{ac}G^{ac}$) and *Ipa* ($C^{bi}C^{bi}$) had genotype calls of AA and BB, respectively. The two DNA samples from *IpaCor*^{4x}_$S_{0.6}$ that showed homoeologous exchange ($G^{ac}G^{ac}G^{ac}C^{bi}$) grouped in a separate cluster between the AB and AA clusters indicating that one *Ipa* allele was replaced by *Cor*. The two *A. hypogaea* female parents had the genotype call of AB indicating the presence of polymorphism between its own subgenomes ($G^{ah}G^{ah}C^{bh}C^{bh}$). Upon hybridization, two F_1 genotypes were expected, *i.e.*, $G^{ah}G^{ac}C^{bh}C^{bi}$ and $G^{ah}G^{ac}G^{ac}C^{bh}$ (Supplementary Figure S2B) and realized; three F_1 hybrids had genotype calls of AB ($G^{ah}G^{ac}C^{bh}C^{bi}$) and seven F_1 hybrids had genotype calls of 75% AA ($G^{ah}G^{ac}G^{ac}C^{bh}$).

At the second locus (Supplementary Figure S3A), *Cor* ($G^{ac}G^{ac}$) and *Ipa* ($C^{bi}C^{bi}$) had genotype calls of AA and BB, respectively. The *IpaCor*^{4x}_$S_{0.6}$ formed a separate group between AB and AA indicating that the *Ipa* allele was replaced by *Cor* ($G^{ac}G^{ac}G^{ac}C^{bi}$). The *A. hypogaea* female parent ($C^{ah}C^{ah}C^{bh}C^{bh}$) was monomorphic between its subgenomes and fell in the BB genotype cluster with *Ipa* and a few other samples. The expected allele compositions of F_1 hybrids were $C^{ah}G^{ac}C^{bh}G^{ac}$ and $C^{ah}G^{ac}C^{bh}C^{bi}$ (Supplementary Figure S3B). Indeed, three of the F_1 hybrids had genotype calls of 75% BB indicating their allele composition of $C^{ah}G^{ac}C^{bh}C^{bi}$; the remaining seven F_1 hybrids had genotype calls of AB indicating their allele composition of $C^{ah}G^{ac}C^{bh}G^{ac}$.

Segregation of pre-existing homoeologous recombination events was found in most of the F_1 hybrids. All of the 10 F_1 hybrids from *A. hypogaea* × *IpaCor*^{4x}_$S_{0.6}$ segregated for most of the 91 markers detecting homoeologous recombination on chromosome A05/B05 (Supplementary Table S4). One F_1 hybrid 13-1014 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.6}$ inherited a truncated 7.9 Mbp recombined segment at the top of chromosome A05/B05 suggesting an additional round of recombination occurred in this F_1 hybrid. Among the 16 F_1 hybrids from *A. hypogaea* × *IpaCor*^{4x}_$S_{0.5}$ crosses, five of them inherited the ~1.4 Mbp segment that showed homoeologous recombination from the male parent and the remaining 11 F_1 hybrids had the same genotype call as the *A. hypogaea* parents at the top of chromosome B07. Expected segregation was found in most of the F_1 hybrids from the *A. hypogaea* × *IpaCor*^{4x}_$S_{0.2}$ crosses. All of the 18 markers within the 6.7 Mbp segment at the bottom of A04/B04 showed segregation, in which six F_1 hybrids shared the genotype call of the male parent and the remaining four shared the genotype call of the female parent (Supplementary Table S4, Table 1). Only one F_1 hybrid from this cross, 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ was an exception. This individual experienced a new round of homoeologous recombination during hybridization. Consequently, it had a homoeologous recombination opposite to the other 10 F_1 siblings, that is, it had one chromosome segment of *Ipa* replacing that of *Cor* in this region. The expected segregation patterns among the F_1 hybrids of the homoeologous recombination events from neo-tetraploid parents confirmed the presence and inheritance of these events.

New homoeologous recombination events captured in F_1 hybrids

In addition to the inherited recombination events, 27 new recombination events on chromosomes A02/B02, A03/B03, A04/B04, A05/B05, A06/B06, and A07/B07 were captured among the F_1 hybrids (Table 3, Supplementary Table S4). There were four events on chromosome 2, where the segment sizes ranged from 2 to 106 Mbp. One event was identified on chromosome 3 with a segment size of 5 Mbp. There were seven events on chromosome 4, where the segment sizes ranged from 0.5 to 130 Mbp. The 0.5 Mbp recombination event was identified in two F_1 hybrids, *i.e.*, 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ and 13-2113 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.6}$. The inheritance of this 0.5 Mbp region in the F_2 population descending from 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ was demonstrated (Table 3). Three events were found on A05/B05 with the segment sizes ranging from 3 to 17 Mbp. Seven events were identified on A06/B06 with segment sizes ranging from 2 to 111 Mbp. Four events were found on A07/B07 with segment sizes ranging from 0.3 to 124 Mbp. As for the direction of genome recombination, there were 16 events where *Cor* alleles replaced the *Ipa* alleles and 11 events that demonstrated the opposite direction of recombination. Most of the recombination break points occurred closer to the ends of the chromosome arms. Most of the events were in different regions except for two consecutive recombination events in opposite directions on A06/B06 in 13-2113 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.6}$ (Supplementary Table S4).

Segregation of the F_2 population descending from 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ at the bottom of chromosome 4

Of the two F_2 populations descending from 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ and 13-1014 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.4}$ that were genotyped by the SNP array, there was only one pre-existing homoeologous genomic region at the bottom of A04/B04 of 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ identified in this study (Supplementary Table S4). In the genotyping profile of the parental lines and F_1 hybrids

Table 3 New homoeologous recombination detected among F_1 progenies of *A. hypogaea* × *IpaCor*^{4x}_S_0 crosses

Genotype	Direction of subgenome recombination	Chromosome[a]	Left border (bp)	Right border (bp)	Segment size (bp)	No. of markers	bp/marker
13-2113 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.1}$	*Cor* replace 50% of *Ipa*	Araip.B02	102,655,016	104,599,332	1,944,316	9	216,03
13-2113 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.1}$	*Cor* replace 50% of *Ipa*	Araip.B02	61,718,684	106,235,603	44,516,919	25	1,780,677
13-1014 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.7}$	*Cor* replace 50% of *Ipa*	Araip.B02	295,929	95,321,834	95,025,905	73	1,301,725
13-1014 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.7}$	*Cor* replace 50% of *Ipa*	Araip.B02	295,929	106,273,695	105,977,766	103	1,028,910
13-2113 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.1}$	*Cor* replace 50% of *Ipa*	Araip.B03	2,029,212	6,739,039	4,709,827	25	188,39
13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$	*Ipa* replace 50% of *Cor*	Araip.B04	123,807,791	124,298,527	490,736	4	122,684
13-2113 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.6}$	*Ipa* replace 50% of *Cor*	Araip.B04	123,807,791	124,298,527	490,736	4	122,684
13-2113 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.3}$	*Ipa* replace 50% of *Cor*	Araip.B04	129,385,417	130,961,045	1,575,628	8	196,954
13-2113 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.7}$	*Cor* replace 50% of *Ipa*	Araip.B04	3,490,627	6,128,842	2,638,215	15	175,881
13-1014 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.1}$	*Cor* replace 50% of *Ipa*	Araip.B04	204,623	6,097,596	5,892,973	44	133,931
13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.1}$	*Ipa* replace 50% of *Cor*	Araip.B04	140,971	23,049,636	22,908,665	70	327,267
13-2113 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.2}$	*Ipa* replace 50% of *Cor*	Araip.B04	647,417	46,100,243	45,452,826	63	721,473
13-1014 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.4}$	*Ipa* replace 50% of *Cor*	Araip.B04	605,143	130,961,045	130,355,902	132	987,545
13-2113 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.2}$	*Cor* replace 50% of *Ipa*	Araip.B05	145,358,753	148,997,085	3,638,332	9	404,259
13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.3}$	*Cor* replace 50% of *Ipa*	Araip.B05	6,425,776	16,814,071	10,388,295	23	451,665
13-2113 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.2}$	*Cor* replace 50% of *Ipa*	Araip.B05	7,141,413	24,364,583	17,223,170	23	748,833
13-1014 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.4}$	*Cor* replace 50% of *Ipa*	Araip.B06	133,505,937	135,831,090	2,325,153	33	70,459
13-2113 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.6}$	*Cor* replace 50% of *Ipa*	Araip.B06	129,731,047	135,639,285	5,908,238	90	65,647
13-2113 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.6}$	*Ipa* replace 50% of *Cor*	Araip.B06	123,590,343	129,526,826	5,936,483	19	312,446
13-2113 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.1}$	*Ipa* replace 50% of *Cor*	Araip.B06	129,740,694	135,831,090	6,090,396	85	71,652
13-2113 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.2}$	*Cor* replace 50% of *Ipa*	Araip.B06	127,136,710	135,831,090	8,694,380	91	95,543
13-2113 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.3}$	*Cor* replace 50% of *Ipa*	Araip.B06	121,832,857	134,519,804	12,686,947	92	137,90
13-1014 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.1}$	*Ipa* replace 50% of *Cor*	Araip.B06	249,894	110,859,588	110,609,694	74	1,494,726
13-2113 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.2}$	*Ipa* replace 50% of *Cor*	Araip.B07	763,999	1,029,451	265,452	3	88,484
13-1014 × *IpaCor*^{4x}_$S_{0.6}$_$F_{1.2}$	*Cor* replace 50% of *Ipa*	Araip.B07	686,538	1,394,692	708,154	8	88,519
13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.2}$	*Ipa* replace 50% of *Cor*	Araip.B07	686,538	5,579,063	4,892,525	41	119,330
13-2113 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.7}$	*Cor* replace 50% of *Ipa*	Araip.B07	2,276,988	125,807,926	123,530,938	96	1,286,781

[a] Chromosome and SNP positions were given relative to *A. ipaensis* genome (peanutbase.org). The recombination events occurred at these loci were actually between the homoeologous chromosomes.

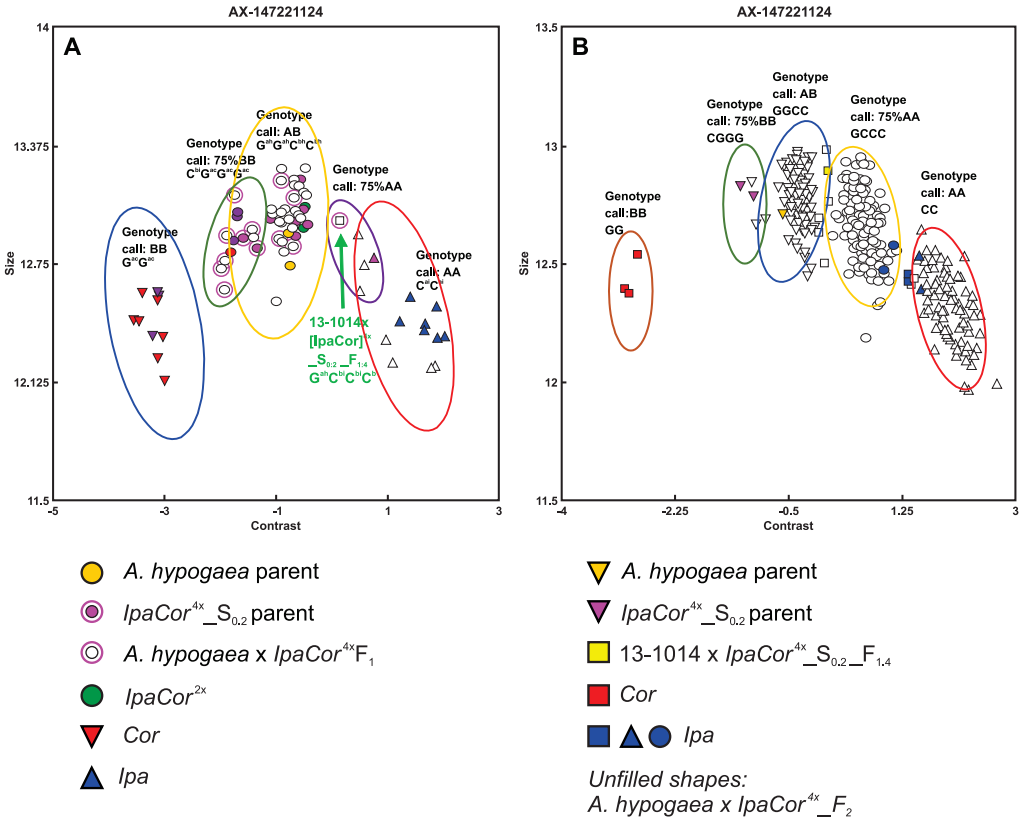
(Figure 2A), *Cor* and *Ipa* had genotype calls of BB ($G^{ac}G^{ac}$) and AA ($C^{bi}C^{bi}$), respectively, at marker AX-147221124 (one of the markers at the end of B04). The *A. hypogaea* female parent was polymorphic between its subgenomes ($G^{ah}G^{ah}C^{bh}C^{bh}$). *IpaCor*^{4x}_$S_{0.2}$ and six F_1 hybrids from *A. hypogaea* × *IpaCor*^{4x}_$S_{0.2}$ had one allele from *Cor* replacing that of *Ipa* ($C^{bi}G^{ac}G^{ac}G^{ac}$) forming a cluster in between genotypes AB and BB. Four other F_1 hybrids fell in the AB cluster as expected. However, *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ and a few other samples formed a cluster between AA and AB ($G^{ah}C^{bi}C^{b}C^{bi}$) indicating that a new round of homoeologous recombination during hybridization led to the opposite direction of exchange in this individual, *i.e.*, *Ipa* replaced *Cor*.

Segregation of the F_2 population descended from 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ confirmed the genome composition of this hybrid. The F_2 population consisted of 456 individuals (Figure 2B). The majority of the population segregated into three clusters following a ratio of 109:219:121 among three genotypes GGCC: GCCC: CCCC as expected from the genotype composition of $G^{ah}C^{bi}C^{b}C^{bi}$ of the F_1 hybrid (Figure 2C). This ratio was close to 1:2:1 (Chi-square = 0.91; $P = 0.63$) indicating that disomic segregation was predominant. In addition, there were three F_2 individuals that clustered with *IpaCor*^{4x}_$S_{0.2}$ (CGGG) indicating a new homoeologous recombination event in these three individuals resulting in 75% allele composition from *Cor* and 25% from *Ipa*. A stretch of 19 adjacent markers including 15 markers within the region inherited from *IpaCor*^{4x}_$S_{0.2}$ and four neighboring markers came from a new homoeologous recombination event in the F_1 hybrid (Table 4).

The last four markers at the end of chromosome A04/B04 (Table 4) shared a different segregation pattern due to the homozygous genotype call of the female parent (Figure 3). At marker AX-147221375, *Cor* and *Ipa* had genotype calls of BB ($G^{ac}G^{ac}$) and AA ($C^{bi}C^{bi}$), respectively. The female parent was monomorphic between its two subgenomes (Figure 3A) and positioned in the genotype BB cluster along with *Cor*. The male parent *IpaCor*^{4x}_$S_{0.2}$ had *Cor* alleles replacing *Ipa* ($G^{ac}G^{ac}G^{ac}C^{bi}$) due to homoeologous recombination. Two types of F_1 hybrids were expected to be produced with genotype compositions of $G^{ah}G^{ac}G^{ah}G^{ac}$ and $G^{ah}G^{ac}G^{bh}C^{bi}$ (Figure 3C). Indeed, six of the F_1 hybrids fell in the 75% BB ($G^{ah}G^{ac}G^{bh}C^{bi}$) genotype group; four of the F_1 hybrids fell in the BB ($G^{ah}G^{ac}G^{ah}G^{ac}$) genotype group. 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ ($G^{ah}C^{bi}G^{b}C^{bi}$) shifted right from the other F_1 hybrids and grouped in the AB genotype due to a new round of homoeologous recombination. As expected, the F_2 population from this hybrid segregated into five clusters, *i.e.*, GGGG, GGGC, GGCC, CCCG, CCCC (Figure 3C) at this locus in a ratio of 30:107:191:102:38 or close to the expectation for a disomic segregation ratio of 1:4:6:4:1 (Chi-square = 6.78; $P = 0.14$) (Table 3). The remaining three markers at the bottom of B04 shared similar segregation ratios. Therefore, disomic segregation of the F_2 population was observed for all of the markers at the bottom of A04/B04 where the subgenome exchange from the male parent was inherited.

New recombination events captured in the two F_2 populations descending from *A. hypogaea* × *IpaCor*^{4x} crosses

New homoeologous recombination events were captured from the F_2 populations by curating monomorphic markers harbored by F_2 individuals and deviating from the parental calls. At marker AX-176801822 (Figure 4), there were five genotype clusters formed among the parents and the F_2 population. *Cor* ($G^{ac}G^{ac}$) and two F_2 individuals (GGGG) had a genotype call of BB whereas



C

	A. hypogaea $G^{ah}G^{ah}C^{bh}C^{bh}$ ♀	x	*IpaCor*^{4x}_$S_{0:2}$ $C^{bi}G^{ac}G^{ac}G^{ac}$ ♂
meiosis	↓		↓
parental gametes	$G^{ah}C^{bh}$		$C^{bi}G^{ac}$ and $G^{ac}G^{ac}$
crossing	↓		
F_1 hybrids	($G^{ah}G^{ac}C^{ah}G^{ah}$ and $G^{ah}C^{bi}C^{bh}G^{ac}$)		
	$G^{ah}C^{bi}C^{b}C^{bi}$(13-1014 x *IpaCor*^{4x}_$S_{0:2}$_$F_{1:4}$)		
disomic meiosis	↓		
F_1 gametes	$G^{ah}C^{bi}$ $G^{ah}C^{b}$ $C^{bi}C^{bi}$ $C^{bi}C^{b}$		
selfing	↓		
F_2 genotype	GGCC	GCCC	CCCC
disomic segregation ratio	1	2	1
actual distribution of F_2 lines	109	219	121

Figure 2 Segregation of the F_2 population derived from 13-1014 × *IpaCor*^{4x}_$S_{0:2}$_$F_{1:4}$ when the female parent was genotyped as AB at this locus. (A) Genotyping profile from the SNP array of the parental lines and F_1 hybrids. Homoeologs at this locus were detected in the *A. hypogaea* parent ($G^{ah}G^{ah}C^{bh}C^{bh}$; golden circles), and the *IpaCor*^{4x}_$S_{0.2}$ parent ($C^{bi}G^{ac}G^{ac}G^{ac}$; two circled magenta circles) had one allele from *Ipa* replaced by *Cor*. It was expected to produce two types of F_1 hybrids (panel C, black font), *i.e.*, $G^{ah}G^{ac}C^{ah}G^{ac}$ (genotype call 75% BB) and $G^{ah}C^{bi}C^{bh}G^{ac}$ (genotype call AB). Indeed, six of the F_1 hybrids (circled white circles in the green oval) were in the 75% BB group and four F_1 hybrids (circled white triangles in the yellow oval) were in the AB group. The 11th F_1 hybrid, 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ (green font), experienced a new round of homoeologous recombination with the *Ipa* allele replacing *Cor* resulting in $G^{ah}C^{bi}C^{bi}C^{b}$ (genotype call 75% AA). (B) The F_2 population derived from this hybrid segregated disomically in three clusters following a ratio close to the expected 1:2:1. Although most F_2 individuals fall in the expected clusters, there were three F_2s that clustered in the 75% BB group indicating that new homoeologous recombination occurred in these three individuals during selfing. The ^{ac} superscript indicates A subgenome from *A. correntina* (red filled samples), ^{bi} superscript denotes B subgenome from *A. ipaensis* (blue filled samples). The ancestral origin of the *A. hypogaea* parents is unclear at this locus, therefore, ah is used to denote their genome composition.

Table 4 Segregation of the F_2 population from 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ at the end of chromosome B04[a]

Event history	probeset_id	Start position (bp)[a]	*Ipa*	*Cor*	*IpaCor*^{4x} _$S_{0.2}$	13-1014	13-1014 × *IpaCor*^{4x} _$S_{0.2}$_$F_{1.4}$	Genotype distribution of the F_2 population					
								Genotype call 0	Genotype call 75% of 0	Genotype call 1	Genotype call 75% of 2	Genotype call 2	No Call
New event in F_1 hybrid	AX-147248422	123,807,791	0	2	75% of 2	1	75% of 0	103	228	120	2	0	3
	AX-147248424	124,023,584	0	2	75% of 2	1	75% of 0	103	226	123	2	0	2
	AX-147220849	124,269,424	2	0	75% of 0	1	75% of 2	0	2	124	224	103	5
	AX-147248402	124,298,527	2	0	75% of 0	1	75% of 2	0	2	123	225	103	5
Inherited from *IpaCor*^{4x}_$S_{0.2}$	AX-147248448	124,804,923	0	2	75% of 2	1	75% of 0	105	224	121	2	0	4
	AX-147220907	124,824,690	2	0	75% of 0	1	75% of 2	0	2	127	226	103	0
	AX-147248475	125,438,618	0	2	75% of 2	1	75% of 0	102	226	120	2	0	6
	AX-147248476	125,440,304	0	2	75% of 2	1	75% of 0	104	225	125	2	0	0
	AX-147221088	128,460,377	2	0	75% of 0	1	75% of 2	0	3	123	222	107	4
	AX-147248617	128,469,894	2	0	75% of 0	1	75% of 2	0	2	116	220	108	10
	AX-147248627	128,518,680	0	2	75% of 2	1	75% of 0	105	219	121	2	0	9
	AX-147221124	129,198,098	0	2	75% of 2	1	75% of 0	109	219	119	3	0	7
	AX-147221160	129,385,417	2	0	75% of 0	1	75% of 2	0	2	121	215	110	7
	AX-147221161	129,385,840	2	0	75% of 0	1	75% of 2	0	2	119	217	111	7
	AX-147248696	129,600,869	0	2	75% of 2	1	75% of 0	110	219	119	2	0	6
	AX-147221210	129,796,029	2	0	75% of 0	1	75% of 2	0	3	113	218	106	16
	AX-147248730	129,989,016	0	2	75% of 2	1	75% of 0	110	218	117	2	0	9
	AX-147248735	130,112,475	0	2	75% of 2	1	75% of 0	110	218	120	2	0	6
	AX-147248739	130,210,807	2	0	75% of 0	1	75% of 2	0	2	123	216	115	0
	AX-176791380	131,369,085	2	0	75% of 0	0	1	31	101	191	101	32	0
	AX-147221357	131,423,712	0	2	75% of 2	2	1	32	103	191	100	30	0
	AX-147221364	131,478,950	2	0	75% of 0	0	1	30	104	183	107	32	0
	AX-147221371	131,503,844	2	0	75% of 0	0	1	30	103	188	104	31	0

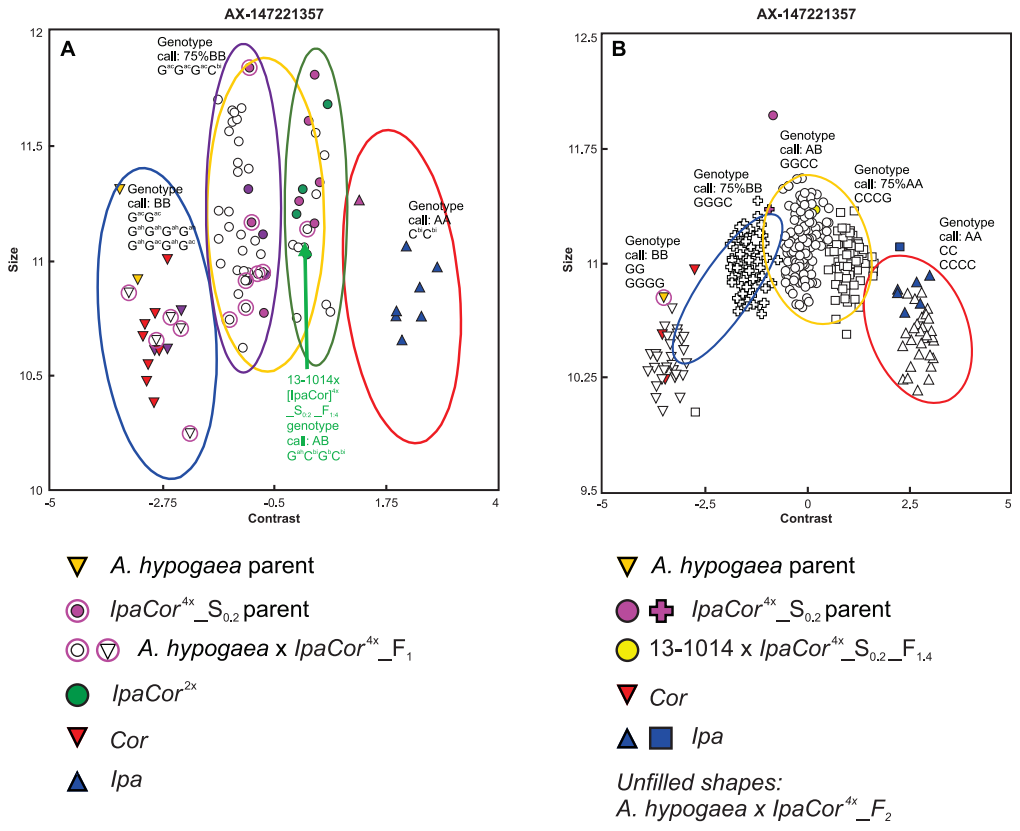
Genotype calls from the SNP array were re-coded as follows: genotype call AA = 0; BB = 2; AB = 1 to avoid confusion with the description of subgenomes. Seventy-five percent of a genotype call indicates the dosage of a subgenome allele was increased by 25% as a result of subgenome recombination.

[a] Chromosome and SNP positions were given relative to *A. ipaensis* genome (peanutbase.org). The recombination events occurred at these loci were actually between the homoeologous chromosomes.

Ipa ($C^{bi}C^{bi}$) had a genotype call of AA. The male parent *IpaCor* ^{4x}_$S_{0.2}$ ($G^{ac}G^{ac}C^{bi}C^{bi}$) had an AB genotype call indicating there was no pre-existing homoeologous recombination in the male parent at this locus. The female parent 13-1014 ($G^{ah}G^{ah}C^{bh}C^{bh}$), 13-1014x*IpaCor* ^{4x}_$S_{0.2}$_ $F_{1.4}$ ($G^{ac}G^{ah}C^{bi}C^{bh}$), and most of the F_2 individuals were grouped in the AB cluster as well. However, there were 18 F_2 individuals that shifted right from the AB cluster and formed a separate cluster (GCCC) between the AB and AA genotype calls. This suggested that an *Ipa* allele replaced a *Cor* allele in these individuals as a result of homoeologous recombination. There were another 29 F_2 individuals that shifted left from the AB cluster and formed a separate cluster (GGGC) between AB and BB genotype calls. These F_2 individuals were evidence of homoeologous recombination with a *Cor* allele replacing an *Ipa* allele at this locus. Two F_2 individuals (GGGG) had become quadriplex at this locus with all alleles from *Cor*. Therefore, there were 49 F_2 progenies that deviated from the expected monomorphic AB calls and demonstrated homoeologous recombination in both directions at this locus. New homoeologous recombination events captured in the two populations were listed (Supplementary Table S5) and presented as a zoomed-out image for global view (Supplementary Figure S4). The two populations shared a similar distribution of recombination events across the chromosomes (Supplementary Figure S4). A03/B03, A04/B04, A05/B05, and A06/B06 were densely populated with homoeologous recombination events and accounted for 95% of the total number of events. The ratio of markers showing *Ipa* replacing the *Cor* subgenome versus those with *Cor* replacing the *Ipa* subgenome was 0.995 across both populations. However, there was a preference for one direction of homoeologous recombination over the other on individual chromosomes (Figure 5). The frequency of *Cor* replacing *Ipa* was higher than the frequency of *Ipa* replacing *Cor* on chromosome A03/B03 and lower on chromosomes A04/B04, A05/B05, and A06/B06. The incidence of homoeologous recombination events was higher at distal regions of chromosomes and lower near the centromeres. Among the 907 F_2 lines, 416 (46%) hosted at least one event of homoeologous recombination. Tetrasomic recombination was identified in four F_2 individuals on chromosome A03/B03 (Supplementary Table S5 dark blue and dark pink highlighted events).

Discussion

In an effort to increase the genetic diversity of cultivated peanut, crosses were made between two peanut diploid relatives *Ipa* and *Cor*. The resulting *IpaCor*^{2x} hybrids were highly sterile, consistent with the well-documented sterility of diploid hybrids from A and B genome species (Krapovickas *et al.* 2007). Formation of seeds from the colchicine-treated hybrids indicated the success of chromosome doubling. In newly formed allotetraploids, the two distinct genomes are expected to function in one cytoplasm and to be inherited through regular meiotic divisions (Lukens *et al.* 2006). However, it is known that while the majority of the genome of many allotetraploids does pair bivalently within each subgenome during meiosis, meiotic recombination between the subgenomes can occur when multivalent associations form. In addition, homoeologous chromosomes may be used as templates to repair double-stranded breaks. Both of these mechanisms, homoeologous meiotic recombination and homoeologous repair, can result in the duplication or elimination of corresponding homoeologous



C

	A. hypogaea $G^{ah}G^{ah}G^{bh}G^{bh}$ ♀	x	***IpaCor*^{4x}_$S_{0:2}$** $G^{ac}G^{ac}G^{ac}C^{bi}$ ♂		
meiosis	↓		↓		
parental gametes	$G^{ah}G^{bh}$		$G^{ac}G^{ac}$ and $G^{ac}C^{bi}$		
crossing	⌄				
F_1 hybrids	($G^{ah}G^{ac}C^{ah}G^{ac}$ and $G^{ah}G^{ac}G^{bh}C^{bi}$)				
	$G^{ah}C^{bi}G^{b}C^{bi}$(13-1014 x *IpaCor*^{4x}_$S_{0:2}$_$F_{1:4}$)				
disomic meiosis	↓				
F_1 gametes	$G^{ah}G^{b}$	$G^{ah}C^{bi}$	$C^{bi}C^{bi}$	$C^{bi}G^{b}$	
selfing	↓				
F_2 genotype	GGGG	GGGC	GGCC	CCCG	CCCC
disomic segregation ratio	1	4	6	4	1
actual distribution of F_2 lines	30	107	191	102	38

Figure 3 Segregation of the F_2 population derived from 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ when the female parent was genotyped as BB at this locus. (A) Genotyping profile from the SNP array for the parents and F_1 hybrids. The *A. hypogaea* parents ($G^{ah}G^{ah}G^{bh}G^{bh}$; golden triangles) were monomorphic at this locus and *IpaCor*^{4x}_$S_{0.2}$ parent ($G^{ac}G^{ac}G^{ac}C^{bi}$; two circled magenta circles) had one allele from *Ipa* replaced by *Cor*. It was expected to produce two types of F_1 hybrids (panel C black font), *i.e.*, $G^{ah}G^{ac}G^{ah}G^{ac}$ (genotype call BB) and $G^{ah}G^{ac}G^{bh}C^{bi}$(genotype call 75% BB). Indeed, six of the F_1 hybrids (circled white circles) were in the 75% BB group and four (circled white triangles) were in the BB group. The 11th F_1 hybrid, 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ (green font), experienced a new round of homoeologous recombination in which the *Ipa* allele replaced *Cor* resulting in the genome composition of $G^{ah}C^{bi}G^{b}C^{bi}$ (genotype call AB). (B) The F_2 population from this hybrid was expected to segregate into five clusters. (C) The distribution of the F_2 population followed a ratio close to the disomic segregation, *i.e.*, 1:4:6:4:1.

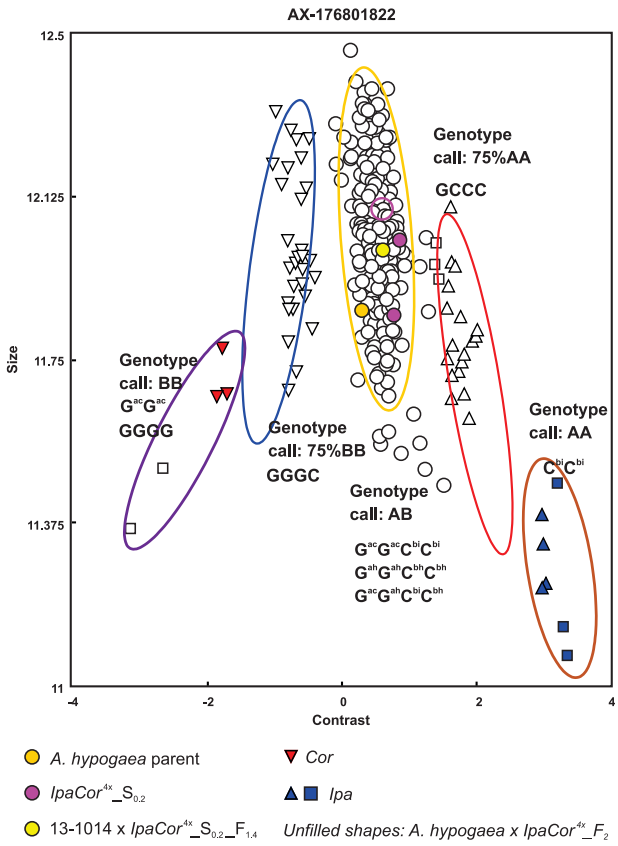


Figure 4 A monomorphic marker between *IpaCor*^{4x}_$S_{0.2}$ and 13-1014 parents demonstrated new homoeologous recombination among the F_2 population. There were five genotype clusters formed among the parents and the population. *Cor* (red triangles, $G^{ac}G^{ac}$) and two F_2 individuals (nonfilled squares, GGGG) grouped in the purple oval with genotype calls of BB. *Ipa* (blue triangles and squares, $C^{bi}C^{bi}$) formed a group in the brown oval with genotype call of AA. The female parent 13-1014 (orange circle; $G^{ah}G^{ah}C^{bh}C^{bh}$), male parent *IpaCor* ^{4x}_$S_{0.2}$ (magenta circles, $G^{ac}G^{ac}C^{bi}C^{bi}$) and 13-1014x*IpaCor* ^{4x}_$S_{0.2}$_ $F_{1.4}$ (yellow circle; $G^{ac}G^{ah}C^{bi}C^{bh}$) were grouped in the yellow oval with AB genotype call indicating there was no pre-existing homoelogous exchange in the male parent and the F_1 hybrid. Most of the F_2 individuals (nonfilled circles) were grouped in the AB cluster as expected from this type of monomorphic marker. However, there were 18 F_2 individuals (upward clear triangles; GCCC) shifted right from the AB genotype cluster and formed a separate cluster (red oval) between the AB and AA genotype calls. This suggests that an *Ipa* replaced a *Cor* allele in these individuals as a result of homeologous recombination. There were another 29 F_2 individuals (downward triangles; GGGC) shifted left from the AB genotype cluster that formed a separate cluster (blue oval) between AB and BB clusters. These F_2 individuals were subjected to homeologous recombination with a *Cor* allele replacing an *Ipa* allele at this locus. Two F_2 individuals (nonfilled squares in the purple circle; GGGG) derived from fusion of recombinant gametes resulted in quadriplex alleles from *Cor* at this locus.

regions and alter gene dosage (Szadkowski *et al.* 2010; Youds and Boulton 2011; Leal-Bertioli *et al.* 2015). Our genotyping data from *IpaCor*^{4x} S_0 plants revealed five independent homoeologous recombination events in each of the five S_0 plants. All had one block of alleles on a chromosome segment replaced by its homoeologous alleles. This observation suggests that during meiosis of the tetraploid cells, multivalent association of homoeologous chromosomes and homoeologous recombination occurred as early as the formation of S_0 neo-tetraploids. Our finding is consistent with previous cytological studies with *Arachis* interspecific F_1 hybrids (Stalker 1991) and F_1 hybrids derived from *A. hypogaea* × allotetraploids (Gardner and Stalker 1983). Both studies presented evidence of multivalent formation in meiotic cells of the hybrids although at low frequencies.

The homoeologous event in the neoallotetraploid was heritable, as evidenced by the segregation of the recombined region among the S_1 progenies. In our study, three S_1 from *IpaCor*^{4x} $S_{0.2}$ became quadriplex and the other four shared the genotype of the mother plant. This suggests normal segregation of the established homoeologous recombination event during generation advancement. In addition to the inherited recombinant subgenome, four new homoeologous recombination events were found in three of the S_1 progenies indicating that recombination between subgenomes continued throughout generation advancement. Therefore, it is apparent that homoeologous recombination occurred at the nascent and early generations of the neo-tetraploids similar to reports on synthetic polyploids of *Brassica* (Song *et al.* 1995; Lukens *et al.* 2006; Szadkowski *et al.* 2010).

Crossing the neo-tetraploids with cultivated breeding lines initiates introgression of chromosomal segments from wild genomes. The inheritance of the established subgenome exchange from *IpaCor*^{4x} S_0 parents was observed in the F_1 hybrids from crosses between *A. hypogaea* and *IpaCor*^{4x}. In the meantime, new events of homoeologous exchange were identified in the F_1 hybrids suggesting active homoeologous recombinants were captured in the first zygotes of crossing. The established homoeologous recombination event on chromosome 04 captured in the *IpaCor*^{4x} male parent was found to segregate disomically in most of the F_2 population. The impact of homoeologous recombination events on allele dosage is potentially large given their accumulation within the F_2 population with nearly half of the population possessing at least one event. Interestingly, the new events were preferentially distributed on chromosomes A03/B03, A04/B04, A05/B05, and A06/B06. These chromosomes hosted over 95% of the homoeologous recombination events. The *A. hypogaea* genome contains historical quadriplex loci on these chromosomes derived from the homoeologous recombination between the ancestral *A. duranensis* and *Ipa* (*A. ipaënsis*) subgenomes (Leal-Bertioli *et al.* 2015; Bertioli *et al.* 2016, 2019). It is possible that the existing tetrasomic regions in cultivated peanut increase the frequency of homoeologous recombination among progeny derived from crosses between *A. hypogaea* and interspecific materials. Most recently, hot spots of homoeologous recombination were found pre-dominantly located within genic regions in wheat and other polyploids including peanut (Zhang *et al.* 2020). Consequently, novel gene transcripts and proteins produced would contribute to neo- and sub-functionalization of genes and phenotypic changes. For instance, spontaneous flower color change from yellow to orange was reported in the new synthetic allotetraploid *A. ipaënsis* × *A. duranensis*^{4x}, which was ascribed to homoeologous recombination (Bertioli *et al.* 2019). Yield increase due to intersubgeomic heterosis was reported in *B. napus* upon introgression from *Brassica rapa* (Qian *et al.* 2005).

The frequent homoeologous recombination in these genetic materials derived from the neo-tetraploid poses a challenge in genetic mapping. Most often, genetic markers linked to the homoeologous recombination were excluded from genetic map construction since they appear to be present/absent or cause severe segregation distortion from the disomic inheritance model. However, QTL analysis with genetic markers associated with presence and absence (PAV) variations was able to identify major effect QTL for seed quality and flowering pattern in *B. napus* (Stein *et al.* 2017). Disease resistance QTL against *Sclerotinia* stem rot and blackleg disease for oilseed rape were identified in the PAV regions (Gabur *et al.* 2018). Homoeologous recombination

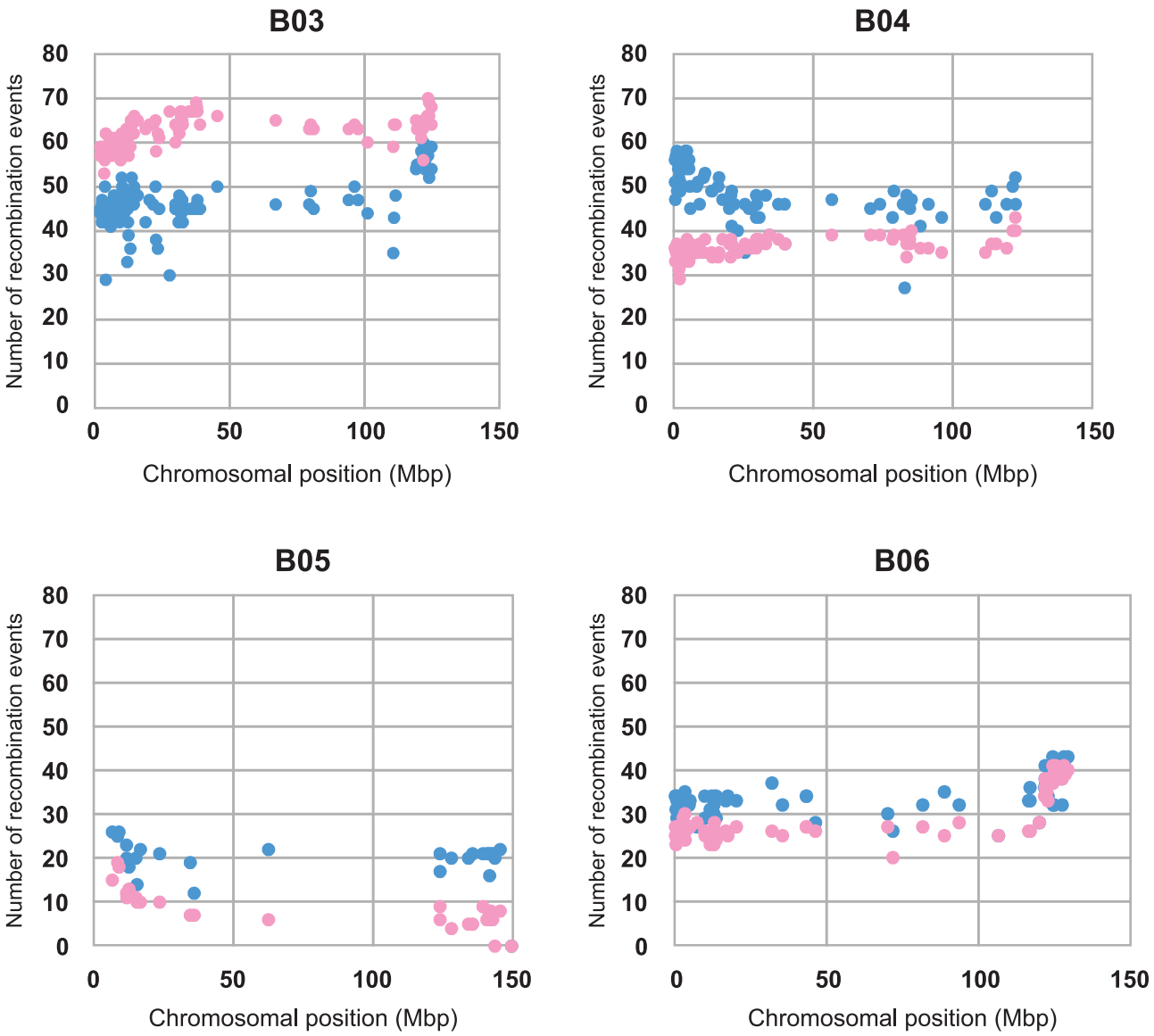


Figure 5 Frequency of new recombination events captured in the F_2 populations descended from 13-1014 × *IpaCor*^{4x}_$S_{0.2}$_$F_{1.4}$ and 13-1014 × *IpaCor*^{4x}_$S_{0.5}$_$F_{1.4}$. Pink dots stand for *Cor* subgenome replacing that of *Ipa*. Blue dots stand for *Ipa* subgenome replacing that of *Cor*. The four chromosomes plotted accounted for 95% of the total number of recombination events.

was found to be the underlying cause of these trait variations. More recently, mixed inheritance following both disomic and tetrasomic patterns of inheritance among the population from a cross between *A. hypogaea* and (*A. duranensis* × *A. batizocoi*)^{4x} supported the occurrence of homoeologous recombination in these progenies (Nguepjop *et al.* 2016). Therefore, genetic analysis of peanut populations with wild introgression needs to consider the markers associated with homoeologous recombination.

The high frequency of genome instability of the neo-tetraploid and its derivative lines may offer both possibilities and perils from the breeding perspective. On the one hand, the instability offers an unprecedented opportunity to introduce new phenotypes and variations. Conversely, the desired traits may be unstable and can be lost as generations advance. Backcross and generation advancement may stabilize the genome and trait expression. To this end, we are advancing a BC_1F_1 population by single seed descent with *A. hypogaea* as the recurrent parent. The population, being on average 75% of the domesticated genome should predominantly express cultivated phenotypes. The other 25% of wild genome composition may be stabilized through generations of selfing. This type of genetic material will provide the peanut breeding community with valuable genetic diversity to improve disease resistance and other agronomic traits in cultivated peanuts.

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Data availability

Five supplemental Tables were included in file Supplemental_Table.xlsx. Four supplemental figures were included in the Supplemental_Figures.pdf file. Supplemental Material available at figshare: https://doi.org/10.25387/g3.14043620.

Author contributions

P.O.-A, H.T.S., and Y.C. conceived the experiments; H.T.S., Y.C., and C.C.H. and C.M.L. executed the experiments; Y.C. and D.B. drafted the manuscript; P.O.-A. secured funding for this research; all authors approved the manuscript.

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