

Comparisons of recombination in elite and wide crosses of durum wheat

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By

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ABSTRACT

Recombination rates along wheat chromosomes can vary significantly. Recombination hotspots are common in the telomeric regions of the wheat chromosomes while largely void in centromeric regions. This has consequences for plant breeders who ideally would like maximum recombination among all genes in order to maximize variability. Disturbances in meiosis can lead to changes in the rate and distribution of chiasmata within paired homologues. In this thesis, the influence of alien chromatin on recombination in two tetraploid wheat backgrounds was examined. The material was developed from Langdon triticale (AABBRR; Langdon X Rye-13) and alien addition line DGE-1 along with two tetraploid (AABB) durum wheats, Langdon and W9262-260D₃. Three crosses were made in which the first cross was the normal durum wheat cross (Pop1; Langdon/W9262-260D₃), the second was between the hexaploid triticale and durum wheat (Pop2; Langdon triticale/W9262-260D₃) so that rye univalents would be present during the F₁ meiosis. The third was between an addition line and durum wheat named as Pop3 (DGE-1/W9262-260D₃). For each F₂ population, the genetic mapping of extracted DNA samples was performed using genotypic data derived from the wheat 90K iSelect array and the recombination rates were estimated using MareyMap. The genetic maps from all of these crosses were compared with the map of the durum DH population (Kofa/W9262-260D₃). Comparative analysis revealed the presence of alien chromatin both increased and suppressed recombination in the chromosomes. In Pop2 and Pop3, the telomeric regions showed maximum recombination in chromosomes 1A, 1B, 2A, 2B, 3A, 3B, 6A, 6B, and 7A. On the other hand, Pop2 showed suppressed recombination at some points in chromosome 2A, 2B, 3A, 5B, and 6A whereas in Pop3, in chromosomes 3A, 4B, 5A, and 7B, recombination was low at some points as compared to Pop1 and DH population. However, the maximum recombination occurred in the pericentromeric and telomeric regions for both the populations with alien chromatin. Hence, the results showed the positive impact of alien chromatin on genetic recombination in the wheat homologous chromosomes and the presence of alien chromatin can be helpful in enhancing recombination rates in wheat which could be a useful breeding strategy.

This thesis is dedicated to my family.

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LIST OF ABBREVIATIONS

AAFC- Agriculture and Agri-Food Canada

Cas9- CRISPR-associated protein 9

CDC- Crop Development Centre

CO- Crossover

CRISPR- Clustered regularly interspaced short palindromic repeat

DH- Double haploid

IWGSC- International Wheat Genome Sequencing Consortium

LSD- Least significant difference

ORDC- Ottawa Research and Development Centre

PAV- Presence-absence variation

QTL- Quantitative Trait Locus

SNP- Single nucleotide polymorphism

1.0 INTRODUCTION

1.1 Background

Genetic diversity is the basis for crop improvement, and germplasm diversity plays a significant role in the improvement of crop plants (Huang *et al.*, 2002). Plant breeders often intercross among elite materials when developing new cultivars, but this results in a narrow genetic base and can slow genetic gains (Lambing *et al.*, 2017). To broaden the genetic variation in wheat breeding, one strategy is to utilize the genetic diversity available in the secondary and tertiary gene pools of wheat (Huang *et al.*, 2002).

Wheat is one of the oldest and most important cereal crops. It is the staple crop in various developing countries and its consumption is increasing globally. Bread wheat (*Triticum aestivum* L. em Thell) and durum wheat (*Triticum turgidum* spp. *durum*) are the two major wheat species grown throughout the world (Shewry and Hey, 2015), and were domesticated approximately 10,000 years ago. The first allopolyploidization event resulted in the extant tetraploid emmer wheat (AABB, $2n=4x=28$) which involved the A subgenome from *Triticum urartu*, and the B subgenome from an unknown relative of *Aegilops speltoides* (Marcussen *et al.*, 2014). This tetraploid wheat was then hybridized with the D subgenome from *Aegilops tauschii* to form modern bread wheat with the hexaploid genome (AABBDD, $2n=6x=42$ chromosomes) (Marcussen *et al.*, 2014). Hence, polyploidization and domestication initially, and more recently modern plant breeding, has resulted in a narrow genetic base (Dubcovsky and Dvorak, 2007; Charmet, 2011). Domestication and farmer selections gave rise to landraces adapted to the local climate. This marked the start of a reduction in genetic variation through genetic drift and selection (Smale *et al.*, 2005). Hence, most grain crops are facing the problem of a narrow genetic base which limits their potential for adaptation to climate change and resistance to biotic and abiotic stresses. The wild relatives of wheat are an abundant source of agronomically important traits as resistance to biotic stress (fungal diseases and insect attack)/abiotic stress (heat, drought, and salinity), known for wider adaptation and plant production as photosynthetic capacity, quality, yield and for the development of new crop species and varieties (Reif *et al.*, 2005). However, utilization of wild relatives in breeding is often associated with linkage drag resulting in deleterious traits that limit the gain of useful alleles (Mondal *et al.*, 2016; Gardiner *et al.*, 2019). Linkage drag is challenging to break especially in the regions of chromosome with

low recombination (Wulff and Moscou, 2014). Hence, strategies to promote recombination can be helpful in breaking up undesirable linkage blocks to introduce desirable genes (Gardiner *et al.*, 2019).

Recombination is a fundamental biological process which includes reshuffling of genetic information which leads to the production of new haplotypes and hence, an evolutionary requirement to incorporate genetic diversity across a species (Jordan *et al.*, 2018).

Recombination, being an important part of meiosis, can help in breaking linkage among the alleles that have either deleterious or beneficial effects in the genetic background and also helps in enhancing the response to selection by increasing genetic variability (Hill and Robertson, 1966; Comeron *et al.*, 2008). Various strategies have been pursued to modulate the recombination frequency along the length of chromosomes especially in the peri-centromeric regions. These strategies include the use of knock-out mutants of anti-crossover genes, crosses among different ploidy levels, clustered regularly interspaced short palindromic repeat (CRISPR)/CRISPR-associated protein 9 (Cas9) mediated gene targeting, and abiotic and biotic treatments to alter recombination (Tourrette *et al.*, 2019, Huang and Puchta, 2019, Lambing *et al.*, 2017). Intercrossing species with varying ploidy levels results in the introduction of univalents in the genome which activate meiotic checkpoints promoting an extended active recombination state with a resulting improvement in the crossover (CO) number and their distribution. This can result in changing recombination along the length of chromosomes especially in the peri-centromeric regions (Suay *et al.*, 2014). Hence, to facilitate sustainable wheat production and quality along with future selection gain, recombination can be used for the modification of genome-wide gene networks by making new crosses in order to control expression of various complex traits (IWGSC, 2018).

1.2 Project hypotheses

1. Distribution of COs and recombination is uneven along durum wheat chromosome pairs.
2. The presence of unpaired univalents at meiosis will affect the distribution of COs among wheat chromosome pairs, and hence recombination between paired chromosomes, and be evident by differences between the F₂ linkage map of two durum parents and the maps produced when univalents are present at the F₁ meiosis.

1.3 Project Objectives

1. To estimate the recombination rates of durum chromosomes for Kofa/W9262-260D3 population to check the difference in recombination rates.
2. To develop genetic maps of three populations (wheat x wheat, wheat x triticales with seven univalents at the F_1 meiosis and wheat x an addition line with one univalent at the F_1 meiosis).
3. To compare the recombination rates, CO distribution and/or frequency among linkage groups of the three populations to determine whether they were affected by the presence of univalents at meiosis.

2.0 LITERATURE REVIEW

2.1 Wheat: production and importance in Canada and worldwide

Wheat (*Triticum* spp.) is a monocotyledonous plant, a member of the Poaceae family and widely cultivated for its grain. The Fertile Crescent region around the Tigris and Euphrates rivers is known to be the center of origin of wheat (Campbell, 2013; Marcussen *et al.*, 2014). Wheat is one of the most important food grain sources for humans and has been the primary food for 10,000 years in Europe, Southwest Asia and North Africa (Curtis and Halford, 2014) and was introduced to North America in the late 15th and 16th century (Campbell, 2013). Wheat evolved from natural crossings of wild species and was domesticated further by humans. Common wheat (*Triticum aestivum* L. em Thell) and durum wheat (*Triticum turgidum* spp. *durum*) are the most important crops grown around the world (Marcussen *et al.*, 2014). In Canada, spring-habit types are preferred by growers, with winter types accounting for only five percent of wheat production. The minimum and maximum temperature, required for wheat growth, are 3° to 4°C and 30° to 32°C, respectively, but the optimum temperature is 25°C (Curtis and Halford, 2014).

In Canada, Port-Royal (near Annapolis Royal, Nova Scotia) was the first place where wheat was grown in 1605 (Campbell, 2013). Canada is the sixth-largest producer of wheat with an average of over 25 million tonnes and exporting around 15 million tonnes. Saskatchewan, followed by Alberta and Manitoba are the largest producers of wheat in Canada (Campbell, 2013). For 2019-20 Canadian durum production decreased by 13% from 2018-19 to 4.98 million tonnes (Mt). Saskatchewan produced 86.5%, followed by Alberta and Manitoba with 13% and 0.5% production, respectively. Excluding durum, wheat production increased by 3.5% from 2018-19 to 27.4 Mt. Saskatchewan produces 39.5% of Canada's wheat. Alberta, Manitoba, Ontario, and Quebec accounted for 35%, 18%, 5.5%, and 1% of the wheat production, respectively. The remaining 1% was from the Maritimes and British Columbia (Anonymous, 2019a).

Wheat has high economic importance as it contributes to the human diet as a staple food for millions of people worldwide and also animal feed (Curtis and Halford, 2014). It provides 327 calories (per 100 grams) and is also a rich source of protein, fiber, manganese, phosphorus, and niacin. The wheat caryopsis consists of 13% water, 13% protein (75-80% gluten), 71% carbohydrates and 1.5% fat. It contributes about one-fifth of the calories consumed by humans, including nutritional factors, bioactive phytochemicals namely, phenolic acids, carotenoids,

tocopherols, alkylresorcinols, benzoxazinoids, phytosterols, and lignans as well as the dietary fiber component (Shewry and Hey, 2015). Wheat is easy to store. It can be easily converted from grain to flour and is a major ingredient in bread, biscuits, pancakes, pies, pastries, cakes, cookies, doughnuts, noodles, pasta as well as instant breakfast cereals (Shewry and Hey, 2015).

2.2 Meiosis and recombination

Meiosis is a significant and specialized process of cell division that gives rise to the formation of gametes with half the chromosome number, thereby allowing the restoration of the ploidy level during fertilization (Lambing *et al.*, 2017). In most of the eukaryotes, this phenomenon is conserved (Mercier *et al.*, 2015). It consists of two types of divisions, a reductional and an equational division respectively. The first division includes the pairing of homologous chromosomes as well as their subsequent segregation and the second division is similar to mitosis in which the segregation of sister chromatids take place. Recombination occurs during prophase-I which is the longest and very important phase of meiosis. During recombination, the homologous chromosome pairs form tetrads. Within the tetrad, chromatid arms of paired chromosomes can overlap and fuse which is called crossing over (CO) (Mercier *et al.*, 2015; Schwarzscher, 2003). Cytologically, the COs between homologues are manifested in the form of chiasmata. A CO is formed as a result of the recombinational repairing process of a section of DNA double-strand breaks (DSB). At the start of meiotic prophase-I, topoisomerase-like SPO11 protein gives rise to DSB. These CO sites are the regions where two homologous non-sister chromatids exchange genetic information (Keeney *et al.*, 1997). CO serves an important function of protecting physical connections between homologous chromosomes which is helpful in their co-orientation and proper disjunction at meiosis-I. However, the number of COs is tightly controlled as too many or too few COs are disadvantageous (Jones and Franklin, 2006). Two aspects are responsible for CO control, namely, obligate CO and CO interference. At least one CO per chromosome pair exists to assure the correct segregation of homologues. This “obligate” CO is important for the balanced distribution of chromosomes among the gametes (Jones, 1984). Typically, one to three COs can occur between homologous chromosomes regardless of chromosome size. It is very rare to find chromosomes that do not undergo CO. Interference also affects the position of CO, the formation of a CO in one region limits the probability that a second CO can occur simultaneously in an adjacent region (Muller, 1916; Sturtevant, 1915). COs

are not evenly distributed along the length of chromosome (Lukaszewski and Curtis, 1992). However, the number of DSBs is found to be at least 10-50 fold greater than the number of COs and the number of COs rarely exceed three for each bivalent chromosome per meiosis (Mercier *et al.*, 2015). Distribution of recombination/COs is significantly different in physically short and long arms of chromosomes. In short arms, the recombination events are more concentrated to the distal segments whereas in long arms, both distal and interstitial recombination was observed (Maccaferri *et al.*, 2019). This recombination pattern was found to be a result of telomeric pairing initiation as well as due to strong positive chiasma interference (Lukaszewski and Curtis, 1992). Hence, recombination includes the points of exchange of genetic material between a pair of homologous chromosomes. The random disjunction and recombination of parental chromosomes (and genes) gives rise to new and different allelic combinations and hence contributes to genetic variability (Schwarzacher, 2003). This gene reshuffling is essential in a breeding program for crop improvement.

2.3 Measuring recombination rates

Genotyping determines the genetic variants possessed by an individual by studying their DNA sequence. Genotyping reveals the alleles of an individual at defined loci in the genome. Depending on the variants of interest and availability of resources, there are various methods to perform genotyping (Anonymous, 2019b). High density single nucleotide polymorphism (SNP) genotyping arrays are widely used for studying genome-wide patterns of genetic variation and can be helpful in identifying putative targets of selection by dissecting complex traits in the wheat genome (Cavanagh *et al.*, 2013; Wang *et al.*, 2014). As SNPs are a ubiquitous kind of genetic variation, they are ideally used for the construction of high-resolution genetic maps and to discover marker-trait association in quantitative trait locus (QTL) mapping experiments (Akhunov *et al.*, 2009). The wheat iSelect array, comprising of 81,687 gene-associated SNPs, was developed for the dense coverage of the wheat genome using eight mapping populations. Out of those, 46,977 SNP markers were mapped genetically and create a resource for studying genome-wide variation and haplotype structure in allohexaploid and allotetraploid wheat populations (Wang *et al.*, 2014) and for establishment of wheat consensus linkage maps (Wang *et al.*, 2014; Maccaferri *et al.*, 2015). In order to achieve high quality genotype calling, density-based spatial clustering algorithms were used because in polyploids the ratio of allelic variants

show deviation from the ratio in diploid organisms, and interference of paralogous loci and secondary SNPs with genotyping oligonucleotide annealing which makes genotype clusters formed as a result difficult to analyse (Akhunov *et al.*, 2009; Wang *et al.*, 2014). In the presence of multiple clusters, these algorithms provide high quality genotype calling and even show low intensity signal in case of presence-absence variations (PAVs) and sequence divergence of SNP assay probe hybridization sites. Hence, SNP based platforms are very useful as these are easy to use with reduced computational data processing, high quality genotype call frequency, and a low error rate (Wang *et al.*, 2014). The classical approach used for the estimation of recombination rates is to build a high-density genetic linkage map and then match these maps to the corresponding physical maps which can help in measuring recombination rate from genetic distance divided by physical distance (Gion *et al.*, 2016). Hence, the wheat 90K iSelect array is helpful in generating high-density genetic maps for analysing genome-wide variations in wheat as these assays provide information related to the structural organization of the wheat genome unfolding old and newly characterized rearrangements between homoeologous chromosomes (Wang *et al.*, 2014).

2.4 Meiosis and crossover distribution in wheat

At meiosis, both hexaploid and tetraploid wheats show regular pairing at metaphase-I and behave as diploids. The homologous chromosomes of wheat strictly form bivalents ignoring their genetic similarity with homoeologues and show a disomic inheritance (Sears, 1976). The *Ph1* locus, present on the long arm of 5B chromosome, has a major dominant effect on the diploid-like meiotic behavior of wheat (Riley and Chapman, 1958). Previous studies in wheat revealed that recombination increases gradually from centromere to telomere and preferably occurs in the telomeric regions of chromosomes (Lukaszewski and Curtis, 1992; Erayman *et al.* 2004). Saintenac *et al.* (2009) also showed that the frequency of CO occurrence (recombination) is higher in sub-telomeric regions and lower in interstitial regions. They studied the pattern of CO along chromosome 3B of bread wheat. Almost 90% of COs occurred in the distal (subtelomeric) region, about 40% of the chromosome. A very low CO frequency was recorded in the proximal regions surrounding the centromere, about 27% of the chromosome (Saintenac *et al.*, 2009). The fully assembled genome of the modern durum wheat cultivar (cv.) Svevo gave genome-wide information of recombination (Maccaferri *et al.*, 2019). Alignment of this genome with high-

density SNP genetic maps revealed highly recombinogenic distal regions showing a linear relationship between genetic and physical distance and these distal regions showed an average recombination rate of 1.8 Mb cM^{-1} which was about 22% of the genome (Maccaferri *et al.*, 2019). Whereas the peri-centromeric regions were found to be devoid of recombination covering about 44% of the genome (Maccaferri *et al.*, 2019). Hence, distal regions of chromosomes are the preferential targets of meiotic recombination and are known to be the fastest evolving (IWGSC, 2018). The International Wheat Genome Sequencing Consortium (IWGSC) released annotated and ordered reference genome sequence of the wheat landrace “Chinese Spring”, which provides insights into the distribution of meiotic recombination frequency and genomic diversity which can be helpful in strategies to bring desirable alleles which lie especially in less-recombinant regions of the wheat genome (IWGSC, 2018).

2.5 Manipulating crossover distribution

It has been demonstrated that the CO frequency can be manipulated experimentally in a chromosome segment (Jones *et al.*, 2002). The genetic mapping in normal, deletion (Del1B45L) and deficiency (Df1B23L) chromosome arms 1BL of hexaploid wheat cv ‘Chinese Spring’ was performed to check the overall pairing and recombination frequencies. The development of genetic linkage maps of chromosome constructs was done using eight markers including the *Glu-B1* locus, the centromere and six microsatellite markers: *Xgwm124*, *Xgwm131*, *Xgwm140*, *Xgwm259*, *Xgwm268*, and *Xpr3100*. The pairing between the normal arms was in the range of 90 to 95% and observed that the total genetic length has an average of about 1.6 CO per arm. Normal chromosome arm 1BL and Del1B45L (deleting the proximal 45% of the arm) were structurally similar in the terminal regions and their Meiosis I-pairing was normal. It was found that pairing of Del1B45L with the normal 1BL arm showed no significant effect but the average number of COs per arm was significantly reduced to 1.2 CO. Also, the maps of the complete and deletion chromosomes showed similar distribution of the distal markers. In the deficiency chromosome, missing the terminal 23% of the normal arm makes direct monitoring of recombination impossible in most of the arm because of the removal of five distal markers. The recombination frequency was estimated by its MI pairing frequency. In the terminal segment of the deficiency chromosome, the recombination rate was found to be much higher than that in the same segment of the pairing of complete arm. This shows that recombination frequency of a

segment depends on its position on the centromere-telomere axis. Hence, they concluded that shortening of the chromosome decreased the frequency of multiple CO significantly in the proximal regions of the chromosome but did not affect the distal CO distribution, presumably the first CO in the arm.

In cereals, COs are predominantly positioned towards the distal regions of the chromosome (Saintenac *et al.*, 2009). In barley, Higgins *et al.* (2012) investigated some factors which contribute to the pattern of recombination in barley. They revealed that the pattern of events, including the initiation and progression of meiosis, chromosome axis formation, and synapsis, is connected to the relative timing of DNA replication for heterochromatin and euchromatin-rich DNA. Early recombination initiation is spatially linked with euchromatic DNA which is early replicating and can be found mostly in distal regions. Higgins *et al.* (2012) found that a change in temperature from 22°C to 30°C resulted in an increase in interstitial and proximal chiasmata. There was no change in the duration of meiosis (~43 h at both 22 and 30°C), but this temperature shift is responsible for disturbing S-phase, which results in a disruption of meiotic control and causes early replication of heterochromatin-rich DNA followed by a change in the frequency and distribution of chiasmata. At the distal regions, the replication was completed in 0-4 hour at both temperatures (22 and 30°C) without any effect and there was no apparent change in euchromatin abundance, but at 30°C, the interstitial and proximal heterochromatic regions showed fast replication and subsequently, enter meiosis early. They observed a significant increase in interstitial/proximal chiasmata as 0.58 to 1.13 chiasmata per cell. Higgins *et al.* (2012) suggested this could be a potential way to change recombination in cereals.

In barley, work done by Phillips *et al.* (2015) tested whether the effect of CO can be shifted to more proximal regions just by elevating growth temperature and can help in increasing overall recombination frequency. Heterochiasmy, that is, difference of recombination rates between male and female and elevated growth temperature are the two important factors in the control of recombination in which male and female meiosis show different CO frequencies and distribution. The significant differences were found between male and female recombination frequencies by performing reciprocal crosses. At 15°C, the CO frequencies showed a slight elevation in male meiosis as compared to the female with a ratio of 1.05, but the difference was not that significant. At 25 and 30°C, CO frequencies in the male showed an incremental rise,

with ratios of 1.20 and 1.58, respectively. However, there was a fall in female CO frequencies with increasing temperature. They suspected that an increase in CO frequency in male meiosis might be associated with an increase in the average single CO length of the bivalents in response to temperature. Also, as suggested by Higgins *et al.* (2012), genes, responsible for controlling the cell cycle and chromatin state as in pre-meiotic and early meiotic stages, are also involved in changing the CO frequencies and distribution under different rising temperatures.

Si *et al.* (2015) performed fine-scale mapping of CO in rice and revealed that genes present in recombination hotspots were involved in responses to environmental stimuli. To confirm this, some F₁ plants were grown in normal growth conditions, whereas others were treated with abiotic or biotic stresses (pathogen attack using rice blast spores), drought, UV-B radiation, high (38°C day/32°C night) and low (20°C day/10°C night) temperature during the period of meiosis, at least 10 days before the booting stage and continued until the maturation of the seeds. Hundreds of F₂ seeds were harvested from these F₁ plants and grown under the same normal growth conditions. The CO events were counted in 41 rice individuals (including normal and stressed F₂ plants along with their normal F₁ parents) mapped using 900,000 markers. They found that COs were distributed unevenly among and along the chromosomes. The average number of CO events (35.8, ranging from 24 to 52) per meiosis in stressed individuals was slightly larger than that of normal individuals (32.8 ranging from 23 to 42). On the basis of the distribution of meiotic CO events along the chromosomes, there were 13 cold spot regions, marked ~13.9% of the rice genome, without even a single CO event. Out of these, 11 regions were found on centromeres and peri-centromeric regions. About 27 regions, defined as hot spots, were detected with extremely high recombination rates and were about 0.72% of the genome with approximately 9.1% CO events clustered within a few hundreds or thousands of base pairs. Hence, frequent recombination has a vital role in the adaptive evolution of the plants surviving in the frequently changing environment (Si *et al.*, 2015).

Genomic structure is also responsible for regulating the frequency and placement of CO. During meiosis, homologous chromosomes undergo recombination. Ziolkowski *et al.* (2015) found that sequence differences between homologs are responsible for inhibiting the nearby CO. In *Arabidopsis*, lines carrying fluorescent CO reporters were crossed with 32 diverse accessions to find the relation between heterozygosity and recombination. By studying the recombinant progenies, they observed that there was an increase in CO in heterozygous regions when there

were homozygous regions in its proximity. Whereas, they found a decrease in the number of CO in the homozygous areas. The increased number of COs in the heterozygous areas was thought to cause an increase in the strength of CO interference which results in preventing COs from occurring in the adjacent homozygous regions. The balance of interfering and non-interfering CO repair was altered in hybrids due to heterozygosity. They found that at homozygosity-heterozygosity junctions, the non-interfering repair was inefficient. Due to this, higher levels of CO interference were reported in heterozygous regions and this interference is responsible for the change in the CO pattern across the homozygosity-heterozygosity junctions. In conclusion, the variation in homolog polymorphism patterns could control the meiotic recombination (Ziolkowski *et al.*, 2015).

In *Caenorhabditis elegans*, Carlton *et al.* (2006) showed that the presence of a single pair of univalents during meiosis is responsible for inducing an increase in COs in the remaining bivalents. The presence of unsynapsed chromosomes resulted in delaying normal progression of meiotic nuclear reorganization from early to late pachytene. Nuclei that linger in early pachytene, containing unsynapsed chromosomes, have more chances for exchange to occur. This exchange can either happen through the beginning of new recombination events or by the conversion of existing recombination intermediates into COs and hence increase the CO recombination on the normally synapsed chromosomes (Carlton *et al.*, 2006).

Andronic (2012) performed some experiments to prove that plant viruses can trigger DNA re-arrangements in host plants and to induce genetic variability in susceptible hosts. Assessment of microsporogenesis was done in tomato infected with tomato aspermy virus and barley infected with barley stripe mosaic virus. Viral infection leads to deviations in the conjugation (pairing) of homologous chromosomes, segregation of genetic material and changes in the position and number of terminal and interstitial chiasmata. Chromosomal aberrations and the mean percentage of abnormal pollen mother cells used in the cytogenetic evaluation of microsporogenesis revealed significant changes in the chiasmata position and number. In some viral treatments, new synaptic cohesions were observed, as there was an increase in bivalents with one or two interstitial chiasmata. The critical observation was that the chromosomal figures in diakinesis showed some synaptic cohesion with chiasma formation or failure/losses of conjugation, giving rise to univalents and considered as an interchromosomal effect in regulating the meiotic recombination. The univalent induction was deemed to be caused by asynapsis or

desynapsis. In asynapsis, the failure of conjugation between homologous chromosomes caused the synaptic arrest whereas in desynapsis, the primary cohesion was there, but disassembly of the synaptonemal complex was seen at diplotene-diakinesis, giving unsynapsed chromosomes. In desynapsis, at diakinesis, chromosomal figures showed synaptic cohesion and chiasma formation or conjugation failures, forming univalents. It was observed that viral infection has an impact on the meiotic conjugation and its abnormality can cause the deviation in the following mitotic stages and can further reduce the number of normal microsporocytes.

Suay *et al.* (2014) studied the CO rate between homologous chromosomes in the presence of univalents and found their effect on the regulation of interference in canola by comparing genetic map lengths. They found that in *Brassica napus* (AACC, $2n=38$), homologous recombination can be increased between A genome chromosomes in the presence of C univalents in AAC hybrids. Various factors are responsible for regulating the frequency of COs on the recombining chromosomes. Firstly, the number of C genome univalents present significantly affects the CO frequency as the map lengths (and recombination rates) were found to be more when the number of univalents was greater. Secondly, the ratio of the number of univalents and bivalents to each other also regulates the CO frequency. The recombination rate was higher for each pair of hybrids with $2n=32$ (13II + 6I) or $2n=35$ (16II + 3I) chromosomes. Concerning the map size of the A7 linkage group, it was significantly larger in the progeny of the 16II + 3I hybrid than the 13II + 6I hybrid. From the number of recombinant intervals per chromatid, it was found that the hybrids carrying more bivalents had more COs than the hybrids carrying fewer bivalents. Furthermore, the identity of univalent affects the triploid hybrid *B. napus* (AAC) by showing a significant increase in the recombination between A genome chromosomes in AA hybrids carrying specific univalents. The presence of one chromosome C-9 showed a reduction in CO interference and hence, significantly affects the recombination rate. The recombination rates were 1.4 times higher in the hybrids having C-6 and 2.7 times higher in C-9 than in the control (0C). The rates showed further increase to 3.1 and 4.1 times in hybrids having only C-6 and C-9, respectively (Suay *et al.*, 2014).

Various attempts have been made and are in progress to introgress important traits from wild relatives into wheat. In interspecific hybrids, COs do not take place between homoeologous chromosomes during meiosis (observations made at metaphase I) due to the presence of *ph1* locus. However, this problem can be solved by the use of mutant lines. Recently, Rey *et al.*

(2017) found that in chemically induced mutant lines, the *ZIP4* homologue within *Ph1* locus (*Tazip4-B2*), can be more useful than mutants with whole *Ph1* locus deletions. As these mutant lines on crossing with wild relatives, showed high levels of homoeologous COs and may be more stable over multiple generations because of lower multivalent formation which will lead to fewer chromosome translocations (Rey *et al.*, 2017). Li *et al* (2019) demonstrated a strategy to modulate recombination by targeting a specific alien chromosome with a specific wheat chromosome. The evidence showed that the introgression of *Su1-Ph1*, a suppressor of the *Ph1* gene of wheat, from *Aegilops speltoides* into durum wheat cv. Langdon enhanced the level of recombination between alien and wheat chromosomes. The Langdon plants targeted for recombination were heterozygous for *Su1-Ph1* containing a single Langdon chromosome 5B and a single *Aegilops searsii* chromosome 5S^{sc}. The wheat 90K Illumina SNP assay was used for the genotyping of 28 BC₁F₁ and 84 F₂ progenies. In homoeologous maps, overall recombination was low with recombination being nearly absent in the short arm. The expected recombination rate estimated from 5B and 5S^{sc} meiotic pairing was doubled but was depressed in the proximal regions of the long arm in comparison to that between 5B chromosomes. In wheat and its diploid relatives, distal regions are the preferential regions of recombination between homologues and recombination declines from distal to proximal direction. In comparison to this, recombination between 5B and 5S^{sc} chromosomes was low but there was a slow increase in recombination in the proximal region of the long arm. Rare recombination events like more COs were seen in the proximal regions and low recombination regions including proximally located *Ph1* region (Li *et al.*, 2019). CRISPR/Cas9-mediated gene targeting is also utilized in introducing desired modifications within a target locus to improve the recombination by inducing double-strand breaks using site specific nucleases (Huang and Puchta, 2019). Recently, in *Drosophila*, it was found that CRISPR-induced double-strand breaks can be helpful in triggering recombination between homologous chromosome arms up to 39% (Brunner *et al.*, 2019). However, it was also revealed that precise editing is helpful in specifically editing the locus as instructed by provided endogenous or exogenous template and on the other hand, imprecise double-strand repair may lead to random mutations (Brunner *et al.*, 2019). IWGSC RefSeq v1.0 could speed up the diagnostic marker development and designing of targets using CRISPR-Cas9-based gene editing as this technique has also been used for controlling the flowering genes by refining the annotations of their sequences which helped in identifying high-confidence genes and designing

of guide RNAs to target the specific genes (IWGSC, 2018). IWGSC RefSeq v1.0 unfolds the wheat genome by providing access to regulatory regions, and QTLs. This knowledge along with genomic diversity and distribution of meiotic recombination can help breeders to potentially overcome the challenges for the crop improvement by accessing genes lying in low-recombination regions of the wheat genome (IWGSC, 2018).

3.0 MATERIAL AND METHODS

3.1 Plant material

1. The DH mapping population derived from the cross Kofa/W9262-260D3, was used for this study. This population was used extensively by Nilsen *et al.* (2017) for the study of the major stem-solidness locus *SSt1* in durum. Kofa is a hollow-stemmed cultivar from the United States whereas W9262-260D3 is derived from the cross Kyle*2/Biodur and is a solid-stemmed cultivar (Houshmand *et al.*, 2007).
2. The plant material used for the second hypothesis included the durum wheat lines Langdon, and W9262-260D3, obtained from the CDC (Saskatoon), the synthetic amphiploid Langdon/Rye-13 (named as Langdon triticales hereafter) obtained from Agriculture and Agri-Food Canada - Ottawa Research and Development Centre (ORDC), and the disomic addition line DGE-1 ($2n= 28+2$), tetraploid wheat Langdon with a wheat grass (*Lophopyron elongatum* L.) chromosome pair, obtained from United States Department of Agriculture (USDA), Fargo, USA.

Crosses are shown in Fig. 3. The first cross was between two durum wheat parents, Langdon and W9262-260D3 (Fig. 3.1(a)). In the second cross, the tetraploid wheat W9262-260D3 was used as female and Langdon triticales was used as a male (Fig. 3.1(b)). The third cross was done in which the addition line DGE-1 was crossed with tetraploid wheat W9262-260D3 (Fig. 3.1(c)). Langdon is the common durum parent in all the crosses and the normal cross between durum parents was used as a reference to compare the recombination rates with other populations.

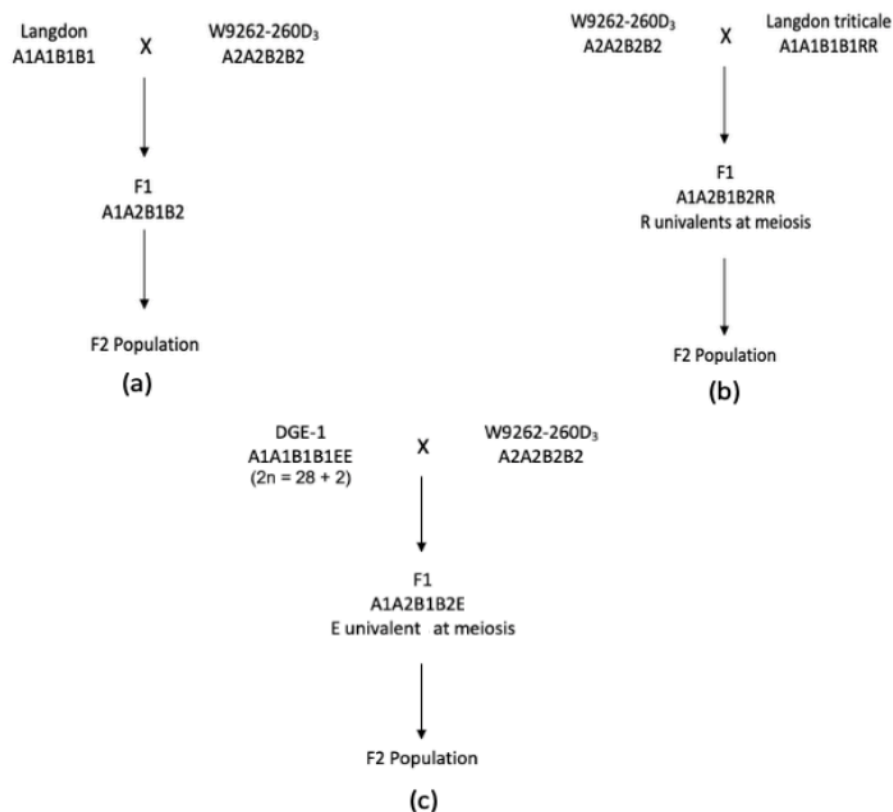


Fig. 3.1 Schematic representation of the production of hybrids. (a) Normal genetic mapping of crossed tetraploid wheat parents. (b) Genetic mapping of the cross between W9262-260D₃ and DH (Langdon/Rye-13). (c) Genetic mapping of the cross between DGE-1 (addition line) and tetraploid wheat carrying E univalent.

3.2 Genotyping

The DNA was extracted from 155 durum DH lines of cross (Kofa/W9262-260D₃) using a modified CTAB approach (CIMMYT, 2005). Agarose gels were used to check the DNA quality. DNA was diluted to 50 ng μL^{-1} and genotyping was done using the wheat 90K array (Nilsen *et al.* 2017). For the three cross populations, F₁ seeds were sown in pots (8" x 7" – 150 x 180 mm) and kept at 4°C for 24 hours in the growth chamber then shifted to the normal growth conditions 16 hours day, and 23/17°C day/night temperature in growth chambers. The DNA was extracted from the F₁s and parents at the seedling stage (2-3 leaf stage; Zadoks growth stage- Z12, Z13) using a modified CTAB method (CIMMYT, 2005) and KASP analysis using a gene specific marker of *Cdu1*, a gene responsible for controlling grain cadmium accumulation in tetraploid wheat (Wiebe *et al.*, 2010). This was performed to confirm and advance only those F₁ plants that

were true hybrids. For KASP analysis, a reaction plate was made by dispensing the genotyping mix, including DNA (1.2 µl), water (2.69 µl), primers (0.11 µl) (listed in Wiebe et al., 2010) and the SNP-specific KASP assay (4 µl), in the plate (Anonymous, 2014). A thermal cycling reaction was then performed with the following PCR conditions: hot start activation at 94 °C for 15 min, followed by 10 touch down cycles as 94 °C for 20 sec; touch down at 61-55 °C for 60 sec initially and dropping by 0.6-1 °C per cycle for 25 sec, and then followed by 26 more cycles of annealing as 94 °C for 20 sec; 55 °C for 60 sec (Anonymous, 2014) . Each DNA sample represented individual data point. The KASP results were analyzed by viewing the fluorescence values of these data points in the form of cluster plots. Same genotype samples produced similar levels of fluorescence and hence clustered together (Anonymous, 2014). The F₁ plants confirmed to be true hybrids were then grown to maturity and F₂ grain from all the plants was harvested for further germination and DNA extraction.

Two hundred F₂ seeds from the crosses were grown, and DNA extraction was made from fresh leaves as described by modified CTAB approach (CIMMYT, 2005). To determine the concentration and quality of DNA, the samples were checked by electrophoresis on 2.0-2.5% agarose gels at 140V for 1.5 hours in 1X TBE buffer and stained with ethidium bromide (0.5 µg/ml) and diluted to 50 ng µl⁻¹, using lambda DNA as a standard. The DNA banding patterns were visualized with UV light and recorded by a Canon Power Shot 7 digital camera and UVP imaging system.

The wheat 90k iSelect assay was used for genotyping all the three populations along with their parents (Wang *et al.*, 2014). The clustering and genotype calling of SNP alleles was performed in Genome Studio (Illumina Inc., San Diego, CA, USA). The clustering includes identifying the assays which were producing three distinct clusters referring to the AA (homozygous with A allele), AB (heterozygous) and BB (homozygous with B allele) genotypes for biallelic SNPs. The sorting of parents was random including all probable cases. The construction of linkage maps was then done by filtering the SNPs on the basis of polymorphism between parents and missing data (>25%).

3.3 Construction of genetic linkage maps

The genotypic data of mapping population was filtered for the polymorphic markers. The distortion of molecular markers was tested using Chi-square (χ^2) test.

1. For Kofa/W9262-260D3, the markers with expected 1:1 ratio for DH populations were kept using a chi-square (χ^2) test. Markers showing significant segregation distortion (deviation from 1:1 ratio) were removed.
2. For the remaining three populations, markers showing significant segregation distortion from the expected chi-square ratio 1:2:1, 3:1, and 1:3 for F₂ populations were removed.

The MSTMap software (Wu *et al.*, 2008) was used for generating draft maps with a *p*-value of $1e^{-10}$. MapDisto v1.7.5 software (Lorieux, 2012) was used further for refining of the maps using a threshold LOD score of 3.0. For grouping SNPs into linkage groups, the maximum distance between the markers was kept at 15cM for Kofa/W9262-260D3 population (Nilsen *et al.*, 2017) whereas for other three populations, the maximum distance was 30.0 cM and was calculated using Kosambi function. The linkage groups (LGs) were refined using “AutoCheckInversions”, “AutoOrder”, and “AutoRipple” to find the best order and also scanned as well as corrected for double recombinants. The marker positions were confirmed, and chromosomes were assigned to LGs using the high density 90K wheat consensus maps (Maccaferri *et al.*, 2014; Wang *et al.*, 2014).

3.4 Estimation of recombination rates

The physical position of each marker was determined by mapping the iSelect probe sequence to the Svevo durum wheat genome assembly (Maccaferri *et al.* 2019). Both physical positions and genetic positions were used for estimating the local recombination rates along each chromosome using MareyMap (Rezvoy *et al.*, 2007). Scatter plots for each LG were generated to compare genetic (cM) versus physical position (Mb) in each cross population. The recombination rate at any given position was estimated by the slope of the curve in relation to genetic and physical maps. Recombination was analysed in non-overlapping 1 Mb windows with the ‘Loess’ method using MareyMap (Rezvoy *et al.*, 2007).

3.5 Statistical analyses

Data were analysed for each chromosome in Statistical Analysis Software (SAS) ver. 9.4. (SAS Institute Inc., Cary, NC). Mean comparisons of recombination rates were performed for each linkage group per chromosome using Fisher’s protected least significant difference (LSD) procedure to protect against Type-II error. For the Kofa/W9262-260D3 population, the mean comparisons among all durum chromosomes were used as a reference for comparative analysis

with the remaining two populations. The comparison between A and B sub-genomes was also performed to estimate the difference in recombination rates across the sub-genomes of wheat. The mean comparisons for the F₂ populations was in all combinations as well as with Kofa/W9262-260D3 population to analyse the effect of univalents on recombination.

4.0 RESULTS

4.1 Recombination rate studies among durum (Kofa/W9262-260D3) chromosomes

4.1.1 Recombination along the length of each durum (Kofa/W9262-260D3) chromosome

For this analysis a linkage map was developed for the (Kofa/W9262-260D3) and was similar to that developed by Nilsen *et al.* (2017) who used the same population. Both ‘Kofa’ and ‘W9262-260D3’ are elite durum wheat lines. A total of 4,227 SNP markers were polymorphic between parents and the map spanned a total of 2,282 cM (Appendix A) (Nilsen *et al.*, 2017). In the present study, we compared the recombination rates along all chromosomes (Fig. 4.1). There was variation in recombination over the length of all chromosomes. As expected, the centromeric regions had suppressed recombination whereas telomeric regions showed higher recombination as compared to peri-centromeric regions (Fig. 4.1). For all the chromosomes, the linkage groups with high marker density had small and long arm junctions which are likely associated with the centromeric region (marked with red lines on x-axis) (Fig. 4.1) whereas the chromosomes 1A, 1B, and 5B, only showed recombination in their long arms and therefore putative centromeric regions could not be identified (Fig. 4.1). The distribution of monomorphic markers (green color) can also be seen in the Fig. 4.1 and showed large regions of the genome that are identical by state. These were large in number which is normal. The large represents the region where there was missing data and no mapped markers. The distribution of markers is according to the presence of genes. According to wheat 90k SNP assay, the number of mapped SNP loci for A genome chromosomes was 16,662 and for B genome was 23411 (Wang *et al.*, 2014). The list of monomorphic markers can be seen in appendix F.

Differences in recombination profiles were observed between the short and long arms of the chromosomes. In comparison to long arms, in short arms the proportion of distal recombination was higher than that of proximal and interstitial recombination (with no or very low recombination). In long arms, recombination was absent in the regions adjacent to

centromere and was mainly concentrated in the distal regions with less recombination in the interstitial regions. For example, in chromosome 1A, 1B, and 5A, the long arm showed maximum recombination in the telomeric and peri-centromeric regions of the chromosomes and in chromosome 2A, 3A, and 4B, the short arms can be seen with maximum recombination in the telomeric regions only with no recombination in peri-centromeric regions (Fig. 4.1). Hence, 25-30 % of total recombination occurred in the distal regions of chromosome. The regions with high recombination rates can be termed as recombination hotspots. On the other hand, the regions devoid of recombination are the coldspots.

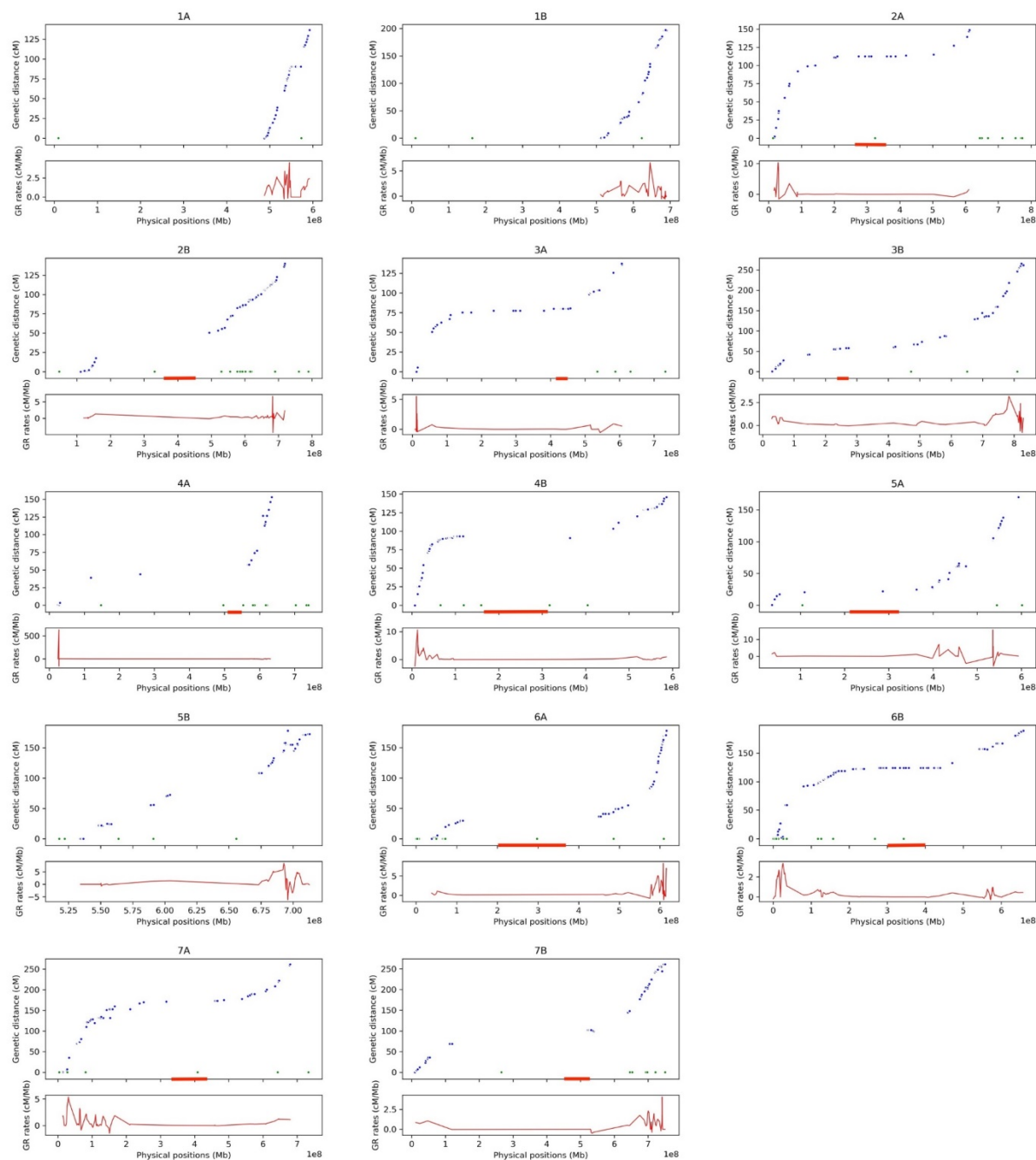


Fig 4.1. Graphic representation of the correlation of genetic and physical maps, the estimated local recombination rates along with their distribution over chromosomal regions. In scatter plots, the blue dots represent the genetic and physical positions of markers. The red curves on x-axes represent the estimated local recombination rates. The red mark on x-axes depicts the estimated centromere position based on consensus maps. The green dots represent the monomorphic markers distributed in each chromosome.

Table 4.1. Least square means' comparisons for recombination rates in 'Kofa/W9262-260D3'. According to Fisher's least significant difference (LSD), means followed by the same letter are not statistically significantly different at $P=0.05$. The rates were recorded in cM/Mb.

Chromosome	Mean	Standard error of mean	Max. recombination rate
6A	1.33 a	0.09	8.18
5B	1.22 ab	0.08	8.45
4A	1.10 a-d	0.17	6.72
1A	1.07 bc	0.08	4.48
5A	0.97 b-e	0.15	15.81
4B	0.88 cde	0.08	10.64
1B	0.86 cde	0.09	6.57
2A	0.85 c-g	0.16	10.31
2B	0.77 def	0.08	6.67
7B	0.66 efg	0.08	4.09
3B	0.56 fgh	0.08	3.20
7A	0.54 gh	0.08	5.40
6B	0.40 hi	0.06	3.35
3A	0.29 i	0.09	5.51

4.1.2 Comparisons of the mean and maximum recombination rates among all chromosomes

In both A and B genomes, high mean recombination rates were observed for 6A (1.33 cM/Mb), 5B (1.22 cM/Mb), 4A (1.10 cM/Mb), and 1A (1.07 cM/Mb) chromosomes (Table 4.1). The mean recombination rates for these chromosomes were not statistically significantly different from each other. There were significant differences between chromosomes 6A, 5B, 4A, and 1A (mean of approximately 1 cM/Mb) and the chromosomes 7A, 6B, and 3A (mean equal to or less than 0.5 cM/Mb). The maximum recombination rate was observed on chromosome 5A (15.81 cM/Mb) followed by 4B (10.64 cM/Mb) and 2A (10.31 cM/Mb) whereas the lowest maximum recombination rate was on chromosome 1A (4.48 cM/Mb) (Table 4.1). For all the chromosomes,

the minimum recombination rate recorded was 0 cM/Mb which indicated no recombination or there was at least one individual RIL in the population for which at least one chromosome was of parental type. On average, the A genome (0.83 cM/Mb) showed higher recombination than the B genome (0.73 cM/Mb) (Table 4.2). The mean recombination rate for chromosomes 1A, and 6A was higher and significantly different from their homoeologous chromosomes 1B, and 6B, respectively. Whereas the mean recombination rate for 2A, 4A, 5A, and 7A was not significantly different from 2B, 4B, 5B, and 7B, respectively. Only chromosome 3B showed more recombination than its homoeologous chromosome 3A (Table 4.1).

Table 4.2 Least square means' comparisons for recombination rates in (Kofa/W9262-260D3) for A and B genome. According to Fisher's least significant difference (LSD), means followed by the same letter are not statistically significantly different at $P=0.05$. The rates were recorded in cM/Mb.

Genome	Mean	Standard error of mean
A	0.83 a	0.04
B	0.73 b	0.03

4.2 Recombination rate studies in the presence of univalents for three populations (Langdon/W9262-260D3, W9262-260D3/Langdon triticales, and DGE-1/W9262-260D3)

4.2.1 F₁ seeds and their KASP analysis

The total number of F₁s harvested from the cross W9262-260D3/Langdon triticales was 25 (Fig. 4.2 (b)). The seeds were very shriveled and only 14 seeds germinated. The F₁ seeds harvested from the cross Langdon/W9262-260D3 were healthy and showed good germination (Fig. 4.2 (a)). The F₁ seeds from DGE-1/W9262-260D3 were a little shriveled (Fig. 4.2 (c)) but germinated well. The total number of seeds harvested from all the crosses are listed in Table 4.3.

Table 4.3. Total number of seeds per cross

Cross	Number of seeds
(Langdon/W9262-260D3)	>100
(W9262-260D3/Langdon triticales)	25
(DGE-1/W9262-260D3)	>100

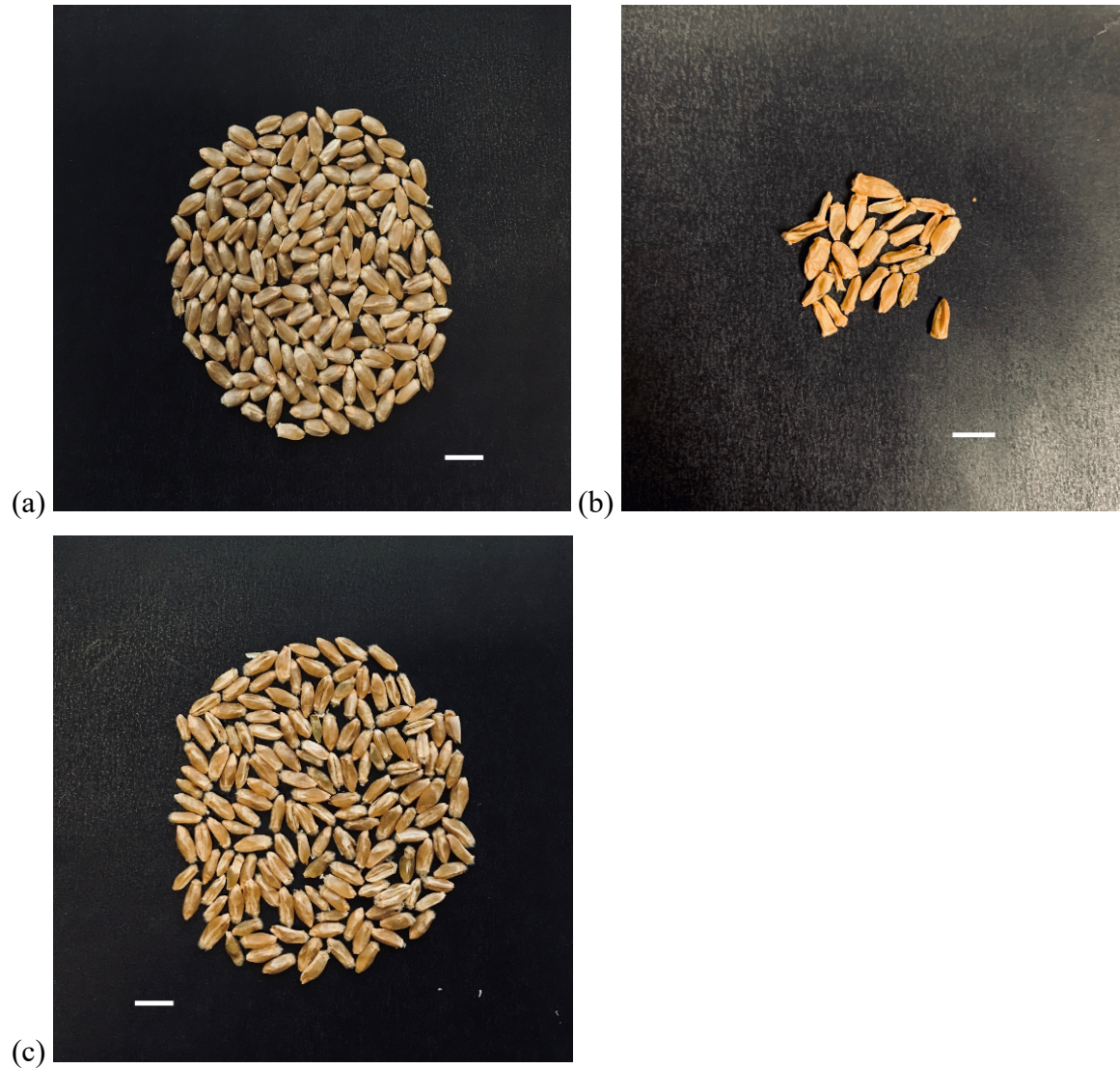


Fig. 4.2. F1 seed of (a) (Langdon/W9262-260D3) (b) (W9262-260D3/Langdon triticales), and (c) (DGE-1/W9262-260D3). The scale bar, representing 1cm, is highlighted with white line.

Seeds from the crosses, (W9262-260D3/Langdon triticales) and (DGE-1/W9262-260D3) were analyzed using KASP markers to check whether they were crosses or not. For the cross W9262-260D3/Langdon triticales, out of 14 seeds, 8 were found to be crosses (Fig. 4.3 (a)) and in the cross of wheat addition line DGE-1 with W9262-260D3, out of 32 seeds, 29 were crossed seeds with only 3 selfed ones (Fig. 4.3 (b)).

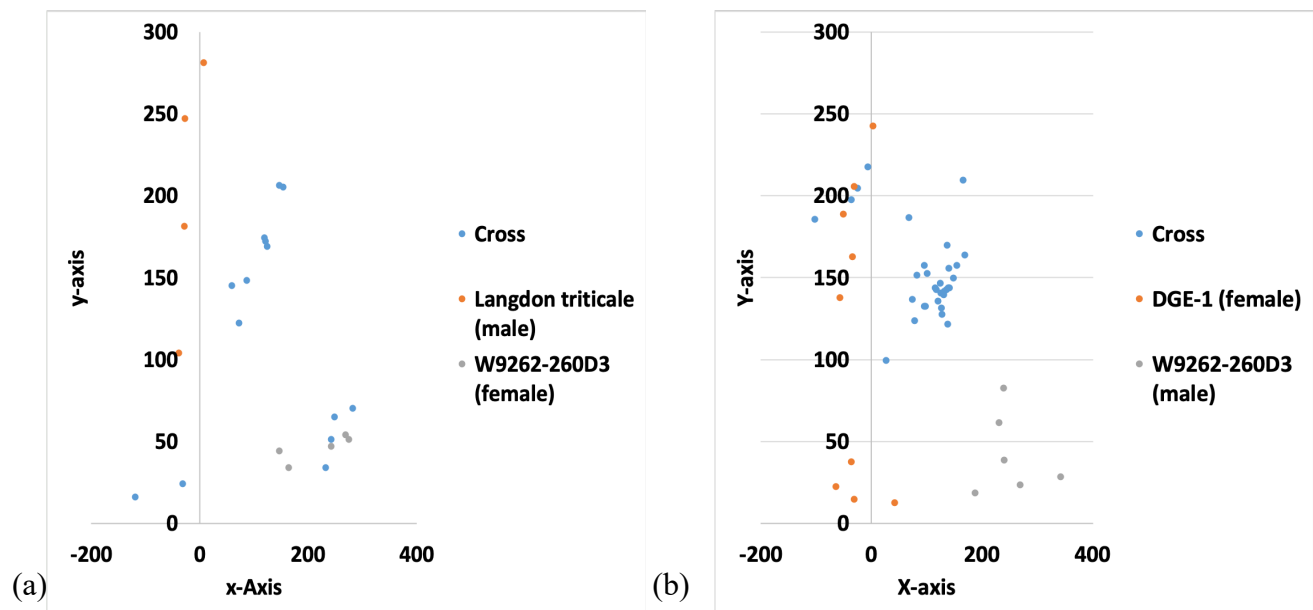


Fig. 4.3. KASP analysis plots using *Cdu1* markers showing a cluster plot with two genotyping parental clusters along with its heterozygous progenies. In these plots, x-axis is assigned as homozygous alleles for W9262-260D3 and y-axis as homozygous alleles for Langdon triticales and DGE-1 parents, respectively. (a) W9262-260D3/Langdon triticales (b) DGE-1/W9262-260D3

4.2.2 F₂ seeds and their data

All the F₁ plants were grown and the number of seeds per spike were counted for each plant in all the three crosses (Langdon/W9262-260D3), (W9262-260D3/Langdon triticales) and (DGE-1/W9262-260D3). The number of seeds varied for each plant and many seeds were found to be shriveled. In first cross (Langdon/W9262-260D3), the plants were very healthy. The number of spikes and seed count per plant can be seen in Table 4.4.

Table 4.4. Data from cross (W9262-260D3/Langdon triticales)

F₁ Plant No.	Number of spikes	Number of seeds
L-1	42	635
L-2	35	487
L-3	40	577
L-4	33	492
L-5	36	609

From the cross (W9262-260D3/Langdon triticales), the plant P-9 had the maximum number of seeds including the shriveled seeds (Fig. 4.4). DNA was extracted from more than 200 seedlings. The seed count for all plants is shown in Table 4.5. The smallest number of seeds were found in P-7 and all of those were very shriveled (Fig. 4.4).

Table 4.5 Data from cross (W9262-260D3/ Langdon triticales)

F₁ Plant No.	Number of spikes	Number of seeds
P-1	17	250
P-4	21	165
P-6	19	420
P-7	12	26
P-9	33	655
P-11	16	375
P-13	15	163
P-14	15	585

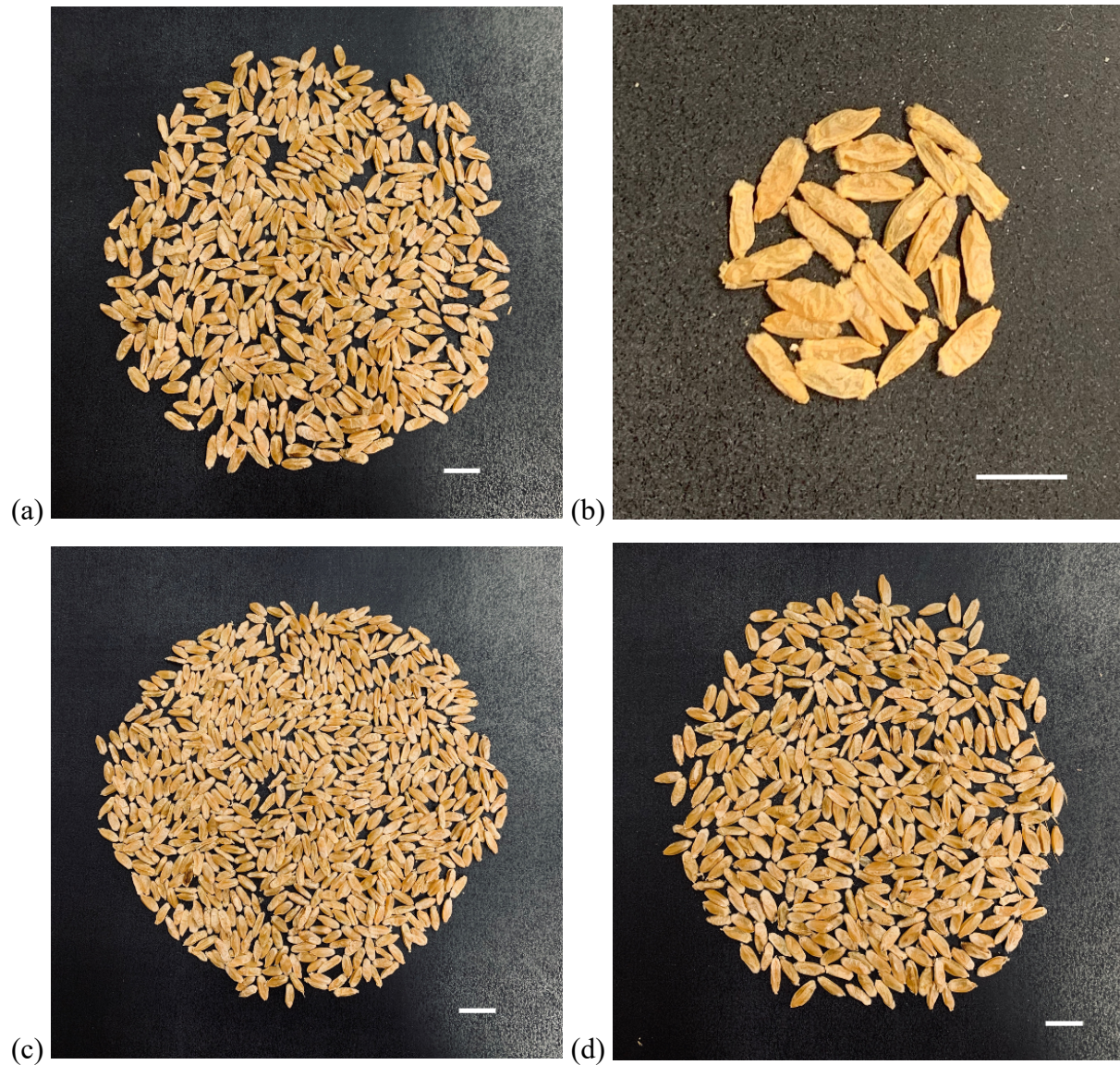
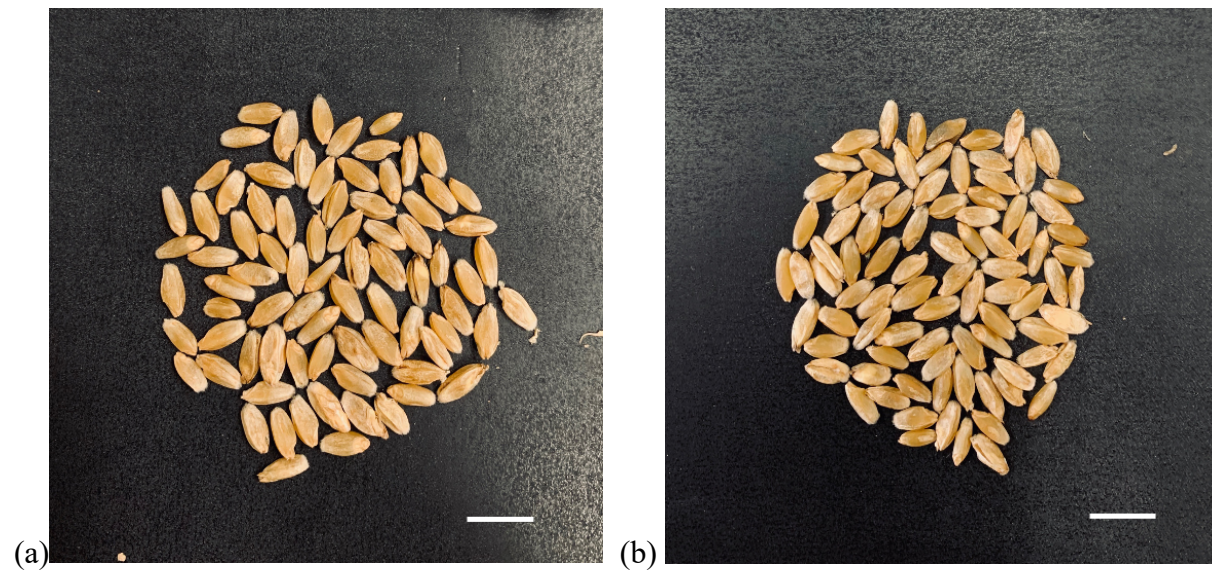


Fig. 4.4. F₂ seeds from cross (W9262-260D3/Langdon triticale): (a) P-6 (b) P-7 (c) P-9 (d) P-11. The scale bar, representing 1cm, is highlighted with a white line.

In the cross with wheat addition line (DGE-1/W9262-260D3), a few plants were kept, and seed count was done. From F₂ population, plant D-19, DNA was extracted from 180 young leaf samples. Some of the seeds were shriveled (Fig. 4.5) and the number of seeds per plant was different (Table 4.6). From the plants D-2, D-6, and D-15, the number of seeds per plant were fewer than 100 because of spike sterility and shriveled seeds (Table 4.5).

Table 4.6. Data from Cross (DGE-1/W9262-260D3)

Plant No.	Number of spikes	Number of seeds
D-2	15	81
D-6	18	87
D-12	19	191
D-15	15	72
D-16	18	274
D-19	12	350
D-20	26	162



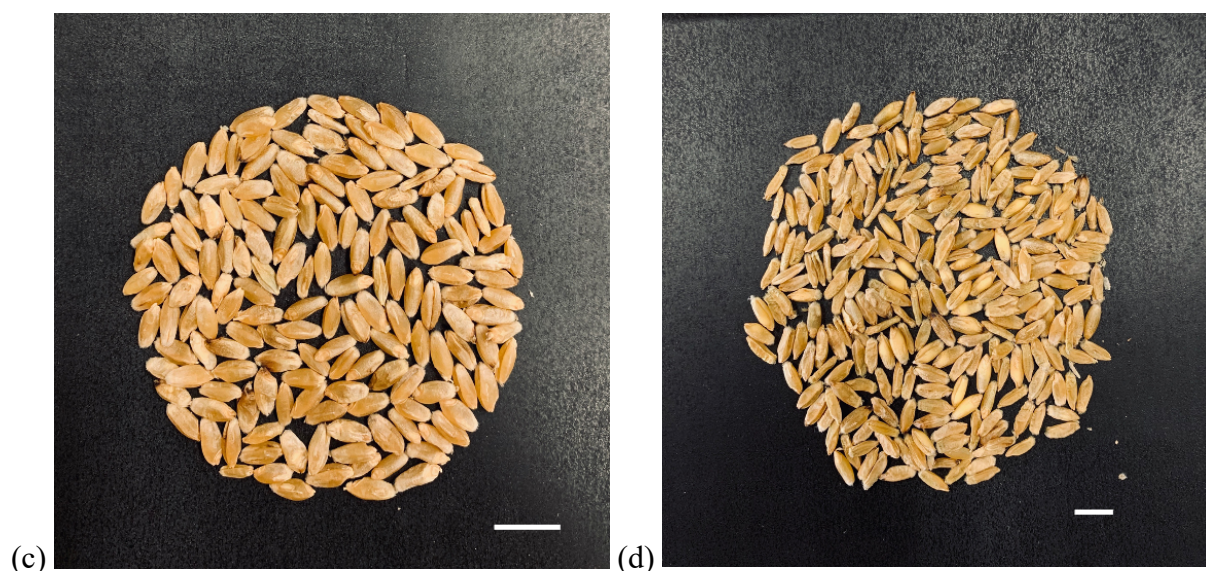


Fig. 4.5. F₂ seeds from cross (DGE-1/W9262-260D3): (a) D-2 (b) D-6 (c) D-15 (d) D-16. The scale bar, representing 1cm, is highlighted with a white line.

4.2.3 Comparative analysis in recombination rates in three populations

A total of three populations i.e. Pop1 (Langdon/W9262-260D3), Pop2 (W9262-260D3/Langdon Triticale), and Pop3 (DGE-1/W9262-260D3) comprising 190, 212, and 172 recombinant lines, respectively, were genotyped using the wheat Illumina 90K iSelect SNP assay (consisting of 81,687 SNPs) (Wang *et al.* 2014). Using the Chi-square statistic, a total of 2825, 1857, and 3110 polymorphic markers, showing expected segregation of either 1:2:1, 1:3, or 3:1 ratio were extracted from Pop1, Pop2, and Pop3, respectively. The difference in the number of polymorphic SNP markers per chromosomes is shown in Fig. 4.6. For each chromosome of all populations, approximately 1-4 linkage groups were found, and for instance, if chromosome 1A has three linkage groups then it can be written as 1A-1, 1A-2 and 1A-3 (Table 4.7). The data regarding genetic mapping as number of linkage groups, number of markers, length and largest interval group is shown in Table 4.7. The genetic maps of all these populations can be seen in Appendix B, C, and D.

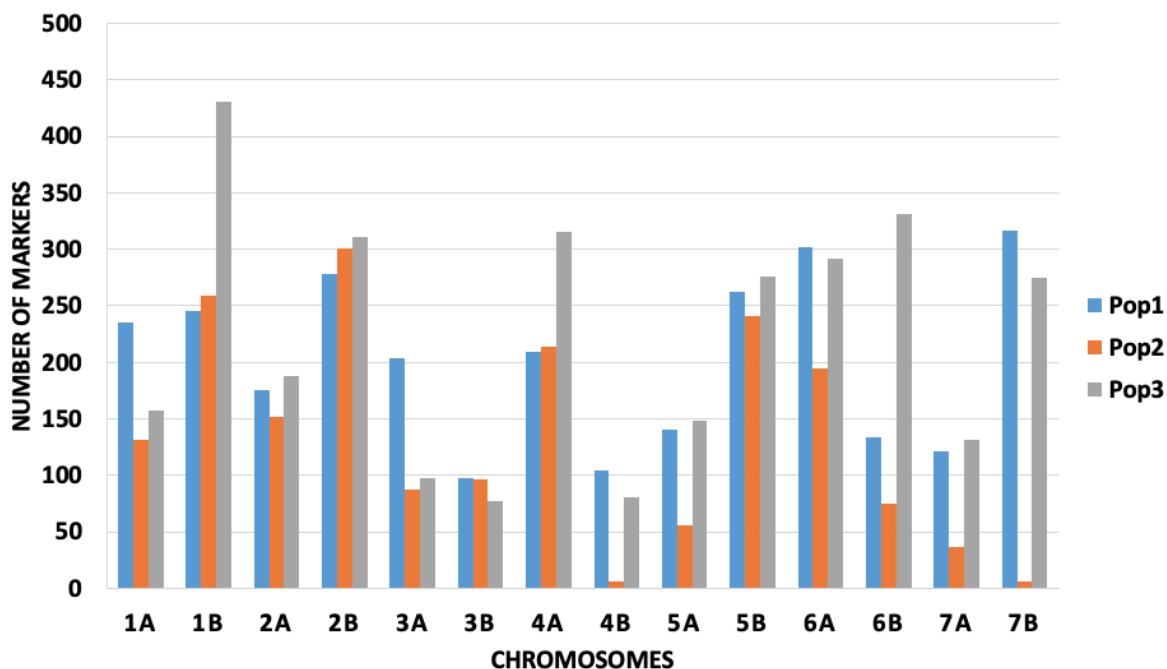


Fig. 4.6. Difference in the number of polymorphic single nucleotide polymorphism (SNP) markers per chromosome for each population.

Table 4.7. Descriptive statistics of genetic maps of three populations.

Pop1 (Langdon/W9262-260D3)				
Chromosome	No. of markers	Length (cM)	Markers per cM	Largest interval (cM)
1A_1	47	18.1	0.39	5.2
1A_2	148	51.8	0.35	14.4
1A_3	40	12.1	0.30	2.4
1B_1	143	49.7	0.35	20.1
1B_2	59	6.8	0.12	1.0
1B_3	44	6.6	0.15	4.7
2A_1	4	19.5	4.88	19.5
2A_2	18	7.9	0.44	3.9
2A_3	121	42.9	0.35	17.2
2A_4	32	27.6	0.86	22.4
2B_1	142	80.1	0.56	22.3
2B_2	93	14.7	0.16	3.0

2B_3	43	5.1	0.12	2.7
3A_1	141	91.5	0.65	29.9
3A_2	19	36.6	1.93	30.1
3A_3	44	9.7	0.22	3.3
3B_1	56	30.4	0.54	7.6
4A_1	201	194.3	0.97	28.8
4A_2	8	0	0	0
4B_1	67	32.9	0.49	14.0
4B_2	27	5.2	0.19	4.2
4B_3	11	7.7	0.70	5.4
5A_1	25	16.2	0.65	8.4
5A_2	116	118.5	1.02	13.2
5B	262	205.6	0.78	29.5
6A_1	128	51.7	0.40	17.6
6A_2	57	7.8	0.14	2.2
6A_3	117	42.3	0.36	25.0
6B_1	16	6.8	0.43	5.2
6B_2	118	32.9	0.28	11.3
7A_1	37	0.3	0.01	0.3
7A_2	71	103.9	1.46	30.2
7A_3	13	7.8	0.60	4.2
7B_1	202	79.4	0.39	19.7
7B_2	114	10.8	0.09	1.9
Pop2 (W9262-260D3/Langdon Triticale)				
1A_1	47	17.7	0.38	3
1A_2	85	24.5	0.29	6.8
1B_1	114	23.6	0.21	12.3
1B_2	145	37.1	0.26	12
2A_1	46	41.5	0.90	23.4
2A_2	85	28.9	0.34	12.4
2A_3	8	0	0	0

2A_4	13	0.2	0.02	0.2
2B_1	15	5.8	0.39	3.6
2B_2	286	139.4	0.49	26.8
3A_1	63	55.4	0.88	28.8
3A_2	24	1.2	0.05	0.3
3B_1	73	47.7	0.65	19.2
3B_2	23	10.1	0.44	5
4A_1	64	60.3	0.94	13
4A_2	150	44.6	0.30	21.1
4B	6	4.2	0.70	3.9
5A	56	3.6	0.06	2.9
5B	241	116.7	0.48	25.7
6A_1	154	25.3	0.16	4
6A_2	41	15.2	0.37	5
6B_1	43	13.7	0.32	10.3
6B_2	32	12.4	0.39	8.1
7A	37	68.8	1.86	24.6
7B	6	2.8	0.47	2.1
Pop3 (DGE-1/W9262-260D3)				
1A_1	47	17.5	0.37	4.2
1A_2	70	54.5	0.78	18
1A_3	40	5.8	0.14	1.8
1B_1	143	52.2	0.37	15.1
1B_2	287	79.5	0.28	9.8
2A_1	35	44.1	1.26	17.8
2A_2	120	37.9	0.32	17.1
2A_3	32	24.2	0.76	19
2B	311	156.9	0.50	29.5
3A_1	65	86.2	1.33	27.7
3A_2	33	3.9	0.12	2.4
3B_1	48	34.5	0.72	22.3

3B_2	6	18.7	3.12	7.4
3B_3	23	5.4	0.23	3.9
4A	315	173.5	0.55	25.8
4B_1	70	46	0.66	15.9
4B_2	11	10.4	0.95	5.9
5A_1	33	30.8	0.93	10.7
5A_2	115	71.4	0.62	13.3
5B_1	191	134.2	0.70	25.8
5B_2	85	23.5	0.28	8
6A	292	147.3	0.50	28.9
6B_1	13	5.6	0.43	4
6B_2	312	40.7	0.13	7.4
6B_3	6	29.7	4.95	29.4
7A_1	36	0.3	0.01	0.3
7A_2	33	4.3	0.13	1.6
7A_3	49	57.6	1.18	25.8
7A_4	13	7	0.54	3.4
7B_1	161	63.2	0.39	17.3
7B_2	114	12.2	0.11	1.6

4.2.4. Comparison of genome-wide recombination rates

The recombination rates were estimated for each chromosome using the genetic and physical positions of the SNP markers (Gion *et al.*, 2016). The genome-wide recombination rates varied significantly along the length of each chromosome in all the populations. The least square means comparisons were calculated for all three populations for each chromosome. Higher recombination rates were observed at distal ends than the proximal chromosomal regions in all the populations. The recombination rate was maximum in Pop2, followed by Pop3, and least in Pop1 at certain regions in each chromosome. The minimum recombination rate recorded was 0 cM/Mb in all the populations whereas the highest varied among all (Table 4.8). For instance, in chromosome 2B, the highest mean recombination rate was found in Pop3 (0.48 cM/Mb), followed by Pop2 (0.34 cM/Mb), and least in Pop1 (0.24 cM/Mb). The maximum recombination

rate for Pop1, Pop2, and Pop3 was recorded as 0.73, 0.96, and 1.08 cM/Mb, respectively (Table 4.8). Also, in chromosome 3A, Pop2 (0.48 cM/Mb) showed high mean of recombination than Pop1 (0.29 cM/Mb) and Pop3 (0.15 cM/Mb). There was no significance difference found in means of Pop1 and Pop3. The maximum recombination rate was recorded in Pop2 as 4.62 cM/Mb (Table 4.8).

Table 4.8. Least square means' comparisons for recombination rates in the three populations. Means followed by the same letter are not statistically significantly different according to Fisher's least significant difference (LSD) at $P = 0.05$.

Chromosome	Population	Mean	Standard error of mean	Max. recombination rate
1A	Pop1	0.67 a	0.08	3.35
	Pop2	0.69 a	0.10	6.92
	Pop3	0.63 a	0.09	7.61
1B	Pop1	0.39 a	0.03	1.50
	Pop2	0.42 a	0.03	1.68
	Pop3	0.62 b	0.02	1.32
2A	Pop1	0.09 a	0.02	1.44
	Pop2	0.14 ab	0.02	1.97
	Pop3	0.16 b	0.02	1.79
2B	Pop1	0.24 a	0.01	0.73
	Pop2	0.34 b	0.01	0.96
	Pop3	0.48 c	0.01	1.08
3A	Pop1	0.29 a	0.04	2.09
	Pop2	0.48 b	0.06	4.62
	Pop3	0.15 a	0.06	0.50
3B	Pop1	0.04 a	0.05	0.82
	Pop2	0.53 b	0.04	1.27
	Pop3	0.16 a	0.04	1.43
4A	Pop1	0.50 a	0.02	1.41

4B	Pop2	0.45 ab	0.02	0.92
	Pop3	0.43 b	0.02	0.70
	Pop1	0.23 a	0.03	2.50
5A	Pop2	-	-	-
	Pop3	0.12 b	0.04	0.31
	Pop1	0.73 a	0.04	1.91
5B	Pop2	-	-	-
	Pop3	0.36 b	0.03	0.85
	Pop1	0.54 a	0.01	0.78
6A	Pop2	0.27 b	0.01	0.66
	Pop3	0.37 c	0.01	0.94
	Pop1	0.54 a	0.03	1.91
6B	Pop2	0.49 a	0.04	2.80
	Pop3	1.31 b	0.08	8.18
	Pop1	0.16 a	0.01	0.30
7A	Pop2	0.11 b	0.01	0.56
	Pop3	0.08 c	0.00	0.16
	Pop1	0.20 a	0.03	0.81
7B	Pop2	0.24 a	0.05	0.75
	Pop3	0.15 a	0.03	2.26
	Pop1	0.24 a	0.01	0.54
	Pop2	-	-	-
	Pop3	0.15 b	0.01	0.43

4.3 Overall comparison of recombination rates of three populations with (Kofa/W9262-260D3) population

The comparison among the populations showed that the presence of alien chromatin was responsible not only for the increased recombination in some chromosomes but also suppressed recombination in others. The differences in recombination were seen in Pop2 and Pop3 in comparison to Pop1 and Kofa/W9262-260D3 population. For instance, in the short arm of chromosome 1A, the maximum recombination rate was recorded in Pop2 (peak value 6.92

cM/Mb), and Pop3 (peak value 4.40 cM/Mb) whereas in the long arm, Pop3 showed more recombination in the telomeric region (peak value 7.61 cM/Mb) than Kofa/W9262-260D3 (peak value 4.48 cM/Mb) (Table 5.1). In chromosomes 1B, 2A, and 2B, the recombination was maximum in Pop2 and Pop3 with increased recombination hotspot regions in the peri-centromeric regions along with telomeric regions. For chromosome 3A, again Pop2 was found to have increased recombination hotspot region in the long arm with a maximum recombination rate of 4.62 cM/Mb and Pop3 also showed recombination hotspots in peri-centromeric regions (Table 5.1). Although, Pop2 and Pop3 were identified to have recombination coldspots in some parts of the chromosomes, recombination was seen to cover the peri-centromeric regions as well as telomeric regions of the chromosomes. Hence, overall recombination was found to be changed across the length of some chromosomes in the presence of alien chromatin.

Table 5.1 Comparison of recombination among all populations: Kofa/W9262-260D3, Pop1 (Langdon/W9262-260D3), Pop2 (W9262-260D3/Langdon triticale, Pop3 (DGE-1/W9262-260D3). The recombination region is described using start and end of physical position on particular arm of each chromosome for each population. The peak recombination value (cM/Mb) is depicted to show the maximum recombination happening in the region.

Chromosome	Population	Physical position (Mb)					
		Short arm			Long arm		
		Start	End	Peak recombination value (cM/Mb)	Start	End	Peak recombination value (cM/Mb)
1A	Kofa/W9262-260D3	-	-	-	487558809	592310495	4.48
	Pop1	1232964	13347506	3.35	434426000	591953158	1.36
	Pop2	1232964	13347506	6.92	426888911	517481253	1.02
	Pop3	1232964	12506822	4.40	356474568	591950271	7.61
1B	Kofa/W9262-260D3	-	-	-	518873282	676271684	6.57
	Pop1	2332679	139070496	1.06	564909286	680867473	1.50
	Pop2	2220599	139070496	0.25	297728896	689555210	1.68
	Pop3	2332679	139070496	1.10	297728896	689000865	1.32
2A	Kofa/W9262-260D3	17040605	87453851	10.31	372230611	610235724	1.54
	Pop1	42390250	141502791	0.65	486204659	747611742	1.44
	Pop2	2647502	141502791	1.97	543625494	771125807	0.12
	Pop3	4790098	49222428	1.79	430951157	771073178	1.21

2B	Kofa/W9262-260D3	111455661	156593851	1.30	520206114	718968246	6.67
	Pop1	50412365	210842786	0.40	520206114	786232089	0.73
	Pop2	53464964	210842786	0.26	527874512	793151178	0.96
	Pop3	53464964	210842786	0.36	527874512	795066076	1.08
3A	Kofa/W9262-260D3	11457479	170382193	5.51	447276014	606429926	0.90
	Pop1	1326004	56676091	2.09	682977691	746352457	1.14
	Pop2	38391603	56676091	0.17	430791114	739397110	4.62
	Pop3	38391603	56676091	0.23	430790353	740350301	0.50
3B	Kofa/W9262-260D3	31697480	242168670	0.99	417373120	823426839	3.20
	Pop1	23599364	53471337	0.82	-	-	-
	Pop2	8808100	49750801	1.27	809611338	828420840	1.07
	Pop3	16442309	63409867	1.43	750863381	754971799	0.49
4A	Kofa/W9262-260D3	27681994	30398573	6.72	576702213	629476633	5.77
	Pop1	3381284	159507011	1.41	567668421	713523112	0.79
	Pop2	16967638	59321657	0.92	567668421	742549898	0.92
	Pop3	3381284	192625740	0.43	525467225	744272100	0.70
4B	Kofa/W9262-260D3	12888651	95708069	10.64	475806832	586069530	1.01
	Pop1	14112477	183521410	0.46	621513784	672937131	2.50
	Pop2	-	-	-	-	-	-
	Pop3	14112477	183521410	0.31	389467685	427276556	0.06
5A	Kofa/W9262-260D3	35656265	45990143	2.21	413418647	593331622	15.81
	Pop1	-	-	-	437219450	685537749	1.91

	Pop2	-	-	-	-	-	-
	Pop3	35656265	46234121	0.77	437219450	685537749	0.85
5B	Kofa/W9262-260D3	-	-	-	589120307	711702429	8.45
	Pop1	10431903	50469708	0.19	475586747	703096727	0.78
	Pop2	-	-	-	275033309	658454554	0.66
	Pop3	5072511	144815814	0.22	275033309	703173188	0.94
6A	Kofa/W9262-260D3	38452876	52397150	1.10	453912489	615791899	8.18
	Pop1	1497357	38452876	1.89	455047390	614669488	1.91
	Pop2	20507521	54178844	1.16	591732549	601473116	2.8
	Pop3	38452876	115023636	1.10	449692860	615791899	8.18
6B	Kofa/W9262-260D3	66291160	169316948	3.35	471167728	657090859	0.98
	Pop1	-	-	-	473069381	632966314	0.30
	Pop2	3385163	17534370	0.56	471167653	471168563	0.07
	Pop3	117850986	238944297	0.10	411100134	662257241	0.16
7A	Kofa/W9262-260D3	14812491	166332270	5.40	485611421	679958624	1.25
	Pop1	61816291	160195633	0.66	726684579	733367384	0.81
	Pop2	88986969	250813906	0.21	451749979	677822559	0.75
	Pop3	65006450	155599959	1.08	668528612	733367384	2.26
7B	Kofa/W9262-260D3	11962600	53646171	1.05	638068647	742465248	4.09
	Pop1	3338766	237490017	0.48	361983506	744405110	0.54
	Pop2	-	-	-	-	-	-
	Pop3	6393757	199767978	0.43	361983506	744405110	0.33

5.0 DISCUSSION

5.1 Intercrossing of species differing in ploidy levels.

The crossing between triticale and wheat is a common practice for improving essential traits and diversity in wheat breeding. Major concerns in crossings include the reduced fertility of hybrids and shriveled kernels. For this thesis, three populations were developed from three crosses. The first cross between the durum wheat parents, Langdon and W9262-260D3 produced good seeds. The F₁s harvested from this cross were healthy and showed good germination. The cross between Langdon triticale and W9262-260D3 (when Langdon triticale was used a female) produced a very low seed set (~10 seeds). The seeds were very shriveled and found to be the result of selfing. In the reciprocal cross, when triticale was used as a male, there was good seed set but again the seeds were shriveled. Out of a total of 25 seeds harvested from this cross, only 14 seeds were able to germinate. This is possibly due to chromosomal imbalance as in previous studies it was found that poor pollen germination, retardation and inhibition of the growth of the pollen tubes in the pistils at the base of the style were found to be the main reasons for poor crossability in triticale and wheat crosses. The seed developed from these crosses is always shriveled (Singh and Khanna, 1983). Scott et al. (1998) also found that seeds developed from crosses between individuals with different ploidy levels were abnormal and usually abort. The factor, responsible for this, was the contribution of more chromosome sets by the mother or father which might be because of their functional inequivalence. In *Arabidopsis thaliana*, a cross between diploid and tetraploid plant, inhibition of endosperm development causing a smaller embryo development was seen when the double dose of maternal genome was there as compared to paternal genome. On the other hand, the double dose of paternal genome promoted the growth of endosperm and embryo. Hence, different doses of maternal or paternal genomes could be another factor responsible for the imbalance in the endosperm development and ultimately the abortion of seeds (Scott et al., 1998). A study was performed by Lukaszewski and coworkers (1982) to check the transmission of chromosomes through egg and pollen of crossed F₁ hybrids (Triticale and Hexaploid wheat). It was found that the seed set from (triticale X wheat) crosses was about 50% and all the seed from the reciprocal cross was inviable due to endosperm imbalance (Lukaszewski *et al.*, 1982). In the addition line x wheat cross, DGE-1 was used as the female and it gave very good seed set. The F₁ seeds were very thin but showed good

germination. This addition line, DGE-1, was meiotically and reproductively stable, generally forms 15 bivalents and was the source of single univalents (Jauhar *et al.*, 2009). The F₁s, from all the crosses, were sown in the petri-plates and were kept at 4°C for three days and then transferred to pots to keep under normal growth conditions. The F₁s from Langdon/W9262-260D3, yielded a good number of F₂ seeds. On the other hand, F₂ seed from the other two crosses varied in number for every plant and were very shriveled, again due to meiotic irregularity and partial sterility. Also, in *Arabidopsis thaliana*, Duszynka *et al.* (2019) found that cross between diploid and tetraploid plants can be able to produce viable F₁ triploid plants. On selfing, these F₁ triploids produce aneuploids with potential to cause F₂ seed abortion. This is probably due to the strong interaction between the two factors as the presence of natural variation and cross direction (Duszynka *et al.*, 2019).

5.2 Genetic mapping and recombination

Genetic maps show the position of the markers on the chromosome along with the genetic distances between them. In the construction of genetic maps, map lengths and marker orders are affected by the type and size of populations, type of markers (dominant or codominant), genotyping errors, segregation distortion, frequency of double recombinants, and statistical procedures used (Hackett and Broadfoot, 2003; Ferreira *et al.*, 2006; Zuo *et al.*, 2019). The precision of the genetic maps increases with the increase in the number of individuals and 200 individuals in total can be sufficient for the construction of accurate genetic maps (Ferreira *et al.*, 2006). In segregation distortion, the distorted markers can have positive impacts on the construction of genetic maps as they can significantly change the grouping markers on their corresponding chromosomes and also increase the linkage map consistency with genome coverage (Zuo *et al.*, 2019). In this thesis, as per the hypothesis, there was no linkage study and hence, these were not included. It is not affecting the expected results. Also, In a study of segregation distortion in soybean by Zuo *et al.* (2019), it was found that the exclusion of the significantly distorted markers will result in decrease of the total genetic distance and marker density but increase the average marker-distance on the chromosomes. In this thesis, the comparisons between DH population and F₂ populations were made. DH population are completely homozygous because of the presence of only one allele for each gene. Whereas the F₂ populations are the ones with maximum genetic variation. Also, before becoming fixed, DH

populations go through only one round of recombination whereas other population types generally go through many rounds of recombination. Hence, on the basis of DH population, the recombination was compared with all populations. The DH haploid map used in this study was a high-density genetic map and was more helpful in correct idea about the recombination.

5.2.1 Recombination rates within durum chromosomes

Recombination is an important characteristic to study in order to exploit the genetic diversity for plant breeding. Durum is an allotetraploid wheat (*Triticum turgidum* L., $2n=4x=28$) with 2 sets of chromosomes, its chromosomal complement has the A genome, derived from *T. urartu* Thum. ($2n=2x=14$, AA genome), and the B genome from an undiscovered or extinct species related to *Aegilops speltoides* Tausch ($2n=2x=14$, SS/BB genome) (Dvorak and Zhang, 1990; Dvorak *et al.*, 1993). In wheat, previous studies also revealed that the telomeric regions were found to be the highly recombinogenic whereas the peri-centromeric regions had less or no recombination (Erayman *et al.*, 2004; Saintenac *et al.*, 2009). COs are not uniformly located along the length of chromosomes as the presence of euchromatin and heterochromatin along the chromosome is linked with CO formation and euchromatin regions, being enriched in genes and under active transcription, are more prone to CO formation in telomeric regions (Naranjo, 2015; Higgins *et al.*, 2014).

The recombination rates were estimated and compared to determine the effects of alien chromatin on recombination rates of native wheat chromosomes. The maximum recombination was recorded in chromosomes 5A, 6B, 6A, 4A, and 1B. The maximum recombination rate measured for these chromosomes was more than 5 cM/Mb. The recombination varied along the length of each chromosome. In physically short arms, the recombination was seen in the telomeric regions only. Whereas in physically long arms, the recombination was found to be high in telomeric regions and less or no in peri-centromeric regions. In chromosomes 2A, 3A, 4B, 6B, and 7A, there was high recombination in the telomeric regions of the short arms as compared to chromosomes 2B, 3B, 5A, 6A, and 7B, where the long arms showed maximum recombination in the telomeric regions. In chromosome 1AL and 1BL, the variation in recombination was found along the whole length. Recombination was higher in sub-telomeric regions than extreme telomeric regions. The peak recombination rates were found in chromosome 1A (4.48 cM/Mb) and chromosome 1B (6.57 cM/Mb) (Fig. 4.1). In chromosomes like 2A, 3A, 4B, 6B and 7A, the recombination was high in telomeric region of the small arm. The recombination was uniformly

low towards centromere and showed a little recombination in the telomeric region of long arm. Whereas in chromosomes 2B, 3B, 5A, 6A, and 7B, the recombination was less in telomeric region of small arm and there was no recombination in centromeric regions. The increase in recombination was found from peri-centromeric position to telomeric position in long arm. Typically, in chromosome 4A, the high recombination was found in telomeric regions of both small and long arm. The maximum recombination rate in small arm was 6.72 cM/Mb whereas in the long arm, it was 5.77 cM/Mb (Fig. 4.1).

Many genes are responsible for controlling the recombination in wheat. *Phl* locus on chromosome 5B is responsible for controlling the homoeologous pairing between the chromosomes A and B genome chromosomes while chromosomes of these diploid species do show pairing in hybrids (Riley and Chapman, 1958; Sears, 1976; Al-Kaff *et al.*, 2008; Griffiths *et al.*, 2006). Recently, the *Su1-Phl* locus, found on the distal (high recombination region) of the long arm of the *Aelilops speltoides* chromosome 3S, was introgressed into wheat to suppress activity of *Phl* locus in order to induce homoeologous recombination (Li *et al.*, 2019). In chromosome 4A and all other chromosomes in the B genome, the peri-centromeric regions are highly rich in heterochromatin and hence there is inhibition in CO formation (Gaut *et al.*, 2007). In chromosome 3BS, the high heterochromatin content found in telomeric region which results in reduced recombination (Saintenac *et al.*, 2009). Particularly in the B genome, the proximal halves appear to be fully capable of meiotic pairing as well as chiasma formation and still do not show recombination. It depends on the time span of chromosome pairing as at or near telomeric regions as the primary initiation of synaptonemal complex take longer time period over there (Holm, 1986). Akhunov and coworkers found that the recombination rate and wheat genome organization with evolution are related to each other as duplication derived loci concentrated preferentially in high recombinogenic distal regions whereas the ancestral copies accumulated in low recombinogenic proximal regions (Akhunov *et al.*, 2003).

5.2.2 Variation in recombination rates among populations that had univalents during F₁ meiosis

In this study, the recombination rates were estimated which depends on the genetic distance and physical position of the markers and outliers were removed, as they were falling out of the graphs and the software gave no reading for those, from the graphs to calculate the

recombination rates. In genetic mapping, Pop3 had the highest number of polymorphic markers and hence, the maps were dense with fewer gaps, followed by Pop1 and then Pop2. In Pop2, there were only 1857 polymorphic markers. The parental source of Langdon and W9262-260D3 was different. There may be heterogeneity among the parents and also the population size was different in all the crosses. However, all the chromosomes had enough markers to calculate and compare recombination rates except chromosome 4B and 7B. The linkage groups were fragmented due to a smaller number of markers, and wherever the genetic distance between the markers exceeded 30 cM, a different linkage group was formed. However, this did not affect the measurement of recombination. In this study, results showed that the presence of alien chromatin gave rise to increased recombination rates in Pop2 and Pop3 in some chromosomes at some points as expected. In chromosome 1B, 2A, 2B, and 3B, the recombination rates were found to be higher in Pop3 and Pop2 than Pop1. In Pop2, rye univalents at meiosis were responsible for increasing the overall recombination in chromosome 3A, 3B, 6B, and 7A. Also, in comparing the recombination rates on the basis of position on chromosome, there were high recombination in the telomeric regions as compared to the peri-centromeric and centromeric regions. On chromosomes 1B, 2B, 3A, 4A, and 6B, the recombination rates were high for both telomeric and peri-centromeric regions in both Pop2 and Pop3 as compared to Pop1, while on chromosome 1A, 1B, 2A, 2B, 3A, 3B, 6A, 6B, and 7A, Pop3 and Pop2 showed very high recombination at some points in the telomeric regions. Suppression of recombination was also seen at some points on the chromosomes, for instance, on chromosome 3A, 4B, 5A, and 7B, Pop3 showed less recombination as compared to Pop1. Similarly, Pop2 also showed suppressed recombination at some points (including telomeric regions) on chromosome 2A, 2B, 3A, 5B, and 6A.

It was found that the suppression of recombination and CO formation in proximal regions of wheat chromosomes is a common feature (Erayman *et al.*, 2004; Saintenac *et al.*, 2009). Heterochromatin and euchromatin distribution along telomere-centromere axis has a link with CO formation and recombination as the presence of heterochromatin is responsible for the inhibition of CO formation and hence takes part in suppressing the recombination in proximal regions of the chromosome (Higgins *et al.*, 2014; Guat *et al.*, 2007). Univalents are known to trigger meiotic recombination as they cause the nucleus to linger in active recombination state and hence influence the remaining chromosomes which synapsed correctly changing their CO number and distribution (Suay *et al.*, 2014; Martinez-Perez & Moore, 2008). Hence, we can say

that recombination highly varied across the length of chromosomes for all the populations. It is possible that univalents can cause change in meiosis leading to alter the CO distribution and frequency.

6.0 CONCLUSIONS AND FUTURE WORK

Durum wheat is a species of great importance just like common wheat, well adapted to more extreme environmental conditions and from a very long time, researchers are working to incorporate desirable traits into elite germplasm (Bozzini, 1988). The allopolyploid genome of wheat is able to tolerate various modifications in structure, chromosomal addition, and elimination without influencing general characteristics and fertility (Silkova *et al.*, 2013). The current scenario to improve wheat is based on the combination of innovative approaches and breeding strategies like mixing of germplasm through crossing, biotechnological techniques, interspecific and intergeneric hybridization, and physiological studies (Reif *et al.*, 2005). However, recombination plays an important role in domestication, genomic evolution and crop improvement. The recombination studies revealed that ploidy level crosses can help in achieving recombination along the entire length of chromosomes. Presence of alien chromatin affects the overall recombination of chromosomes and hence giving more chances to peri-centromeric regions to recombine. In this study, Pop2 and Pop3 were found to cover the peri-centromeric regions as well as telomeric regions more than normal wheat chromosome recombination. In both populations, the recombination rates were also high and suppressed at some points of chromosomal recombination. In future, directed modulation of recombination frequency can be helpful in improving the efficiency of plant breeding programs by expediting attainment of desired combinations of alleles. The disruption of genetic barriers is an important key to enable genetic accessibility of natural variation as well as introgression of desired traits from related or wild species into crops. The work done in this research will utilize existing genetic stocks which are available to the CDC in achieving the genetic gain which can be used in long-term genomic selection programs where its effects can be seen more clearly after four to five generations and can retain genetic diversity for a longer period of time.

7.0 REFERENCES

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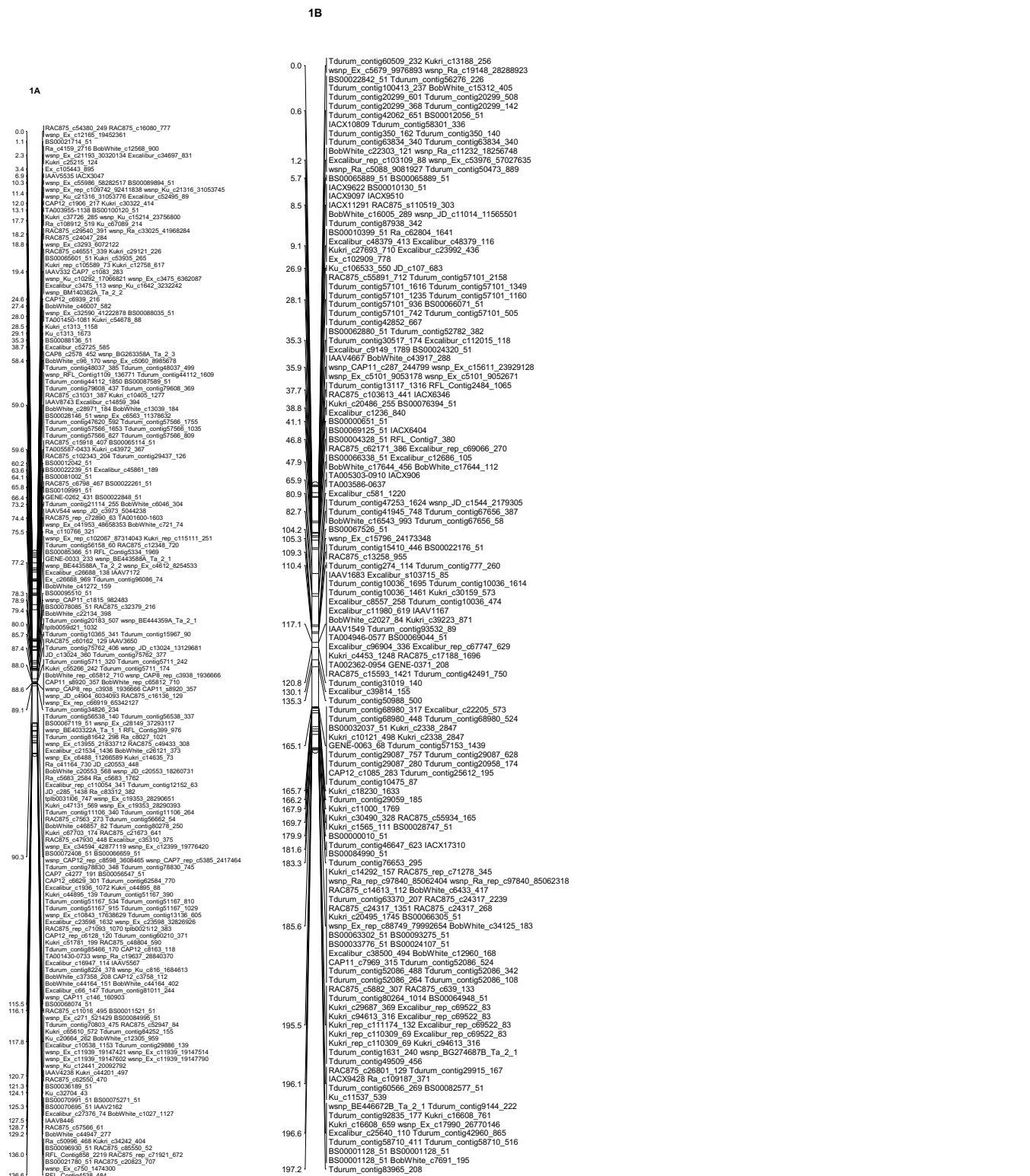
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8.0 APPENDICES

Appendix A. Genetic linkage maps for population (Kofa/W9262-260D3)



2B

0.0 RAC875_rep_c70402_527
1.1 Tdurum_contig77602_931 BobWhite_c26775_217
wsnp_Ex_c12671_20140295 BS00083078_51
BS00063577_51 RAC875_c9562_313
Ex_c12004_1006 Ku_c23446_2209
Kukri_c106282_114 Tdurum_contig79134_450
JD_c39990_130 Kukri_rep_c104676_265
2.3 Tdurum_contig83066_276 BS00065993_51
BS00065994_51 IACX6411
BobWhite_c25503_605 Ra_c6728_590
Tdurum_contig94806_361 GENE-0644_42
GENE-0644_370 GENE-0644_421
Excalibur_c1305_662 BS00088575_51
Ra_c106376_879 GENE-0652_360
6.3 RAC875_rep_c118376_304 BS00065418_51
IAAV6994_JD_c2280_91
6.8 Kukri_rep_c109981_150
8.0 wsnp_CAP12_rep_c4678_2134259 RAC875_c2110_117
RAC875_c11207_1028
12.5 Tdurum_contig62595_466 BS00073447_51
Tdurum_contig18197_86
17.6 BS00040251_51 Kukri_c36783_91
Kukri_c15359_254 Tdurum_contig76426_961
50.4 Excalibur_c22285_762 Excalibur_rep_c86787_98
53.3 Tdurum_contig48833_736
55.6 Tdurum_contig27880_75 Tdurum_contig27880_199
56.7 Kukri_c8177_718 wsnp_Ex_c29445_38480890
Tdurum_contig2998_380
67.1 Excalibur_c8474_199 Tdurum_contig92604_368
67.7 D_contig09015_259
Tdurum_contig26542_457 Tdurum_contig26542_281
71.1 RAC875_rep_c69892_151 RAC875_rep_c70705_84
Tdurum_contig44075_1141 RFL_Contig1967_3440
Tdurum_contig25602_212
72.2 Tdurum_contig25490_434 RAC875_c28185_91
Tdurum_contig11730_153
72.8 Tdurum_contig1778_195 Tdurum_contig2945_155
Tdurum_contig2945_83 Tdurum_contig2945_75
82.6 BobWhite_rep_c53204_309
Excalibur_c37804_518
GENE-1351_273 GENE-1351_291
83.8 RAC875_c56111_61 RFL_Contig4856_71
BS00035335_51 IAAV5350
Kukri_c55688_361
84.4 wsnp_Ex_c7203_12370983
85.0 BobWhite_rep_c48906_121
86.1 TA00195-0588 BS00055427_51
86.7 Ku_c12037_482 wsnp_Ku_c12037_19549078
91.2 CAP12_c2472_60
92.9 Ex_c30517_1207 RAC875_c25035_958
Ra_c14316_850 GENE-1352_214
93.5 Excalibur_c16532_499 RAC875_c7540_118
RAC875_c26278_459 JG_c2092_196
Tdurum_contig66317_77 Tdurum_contig65349_140
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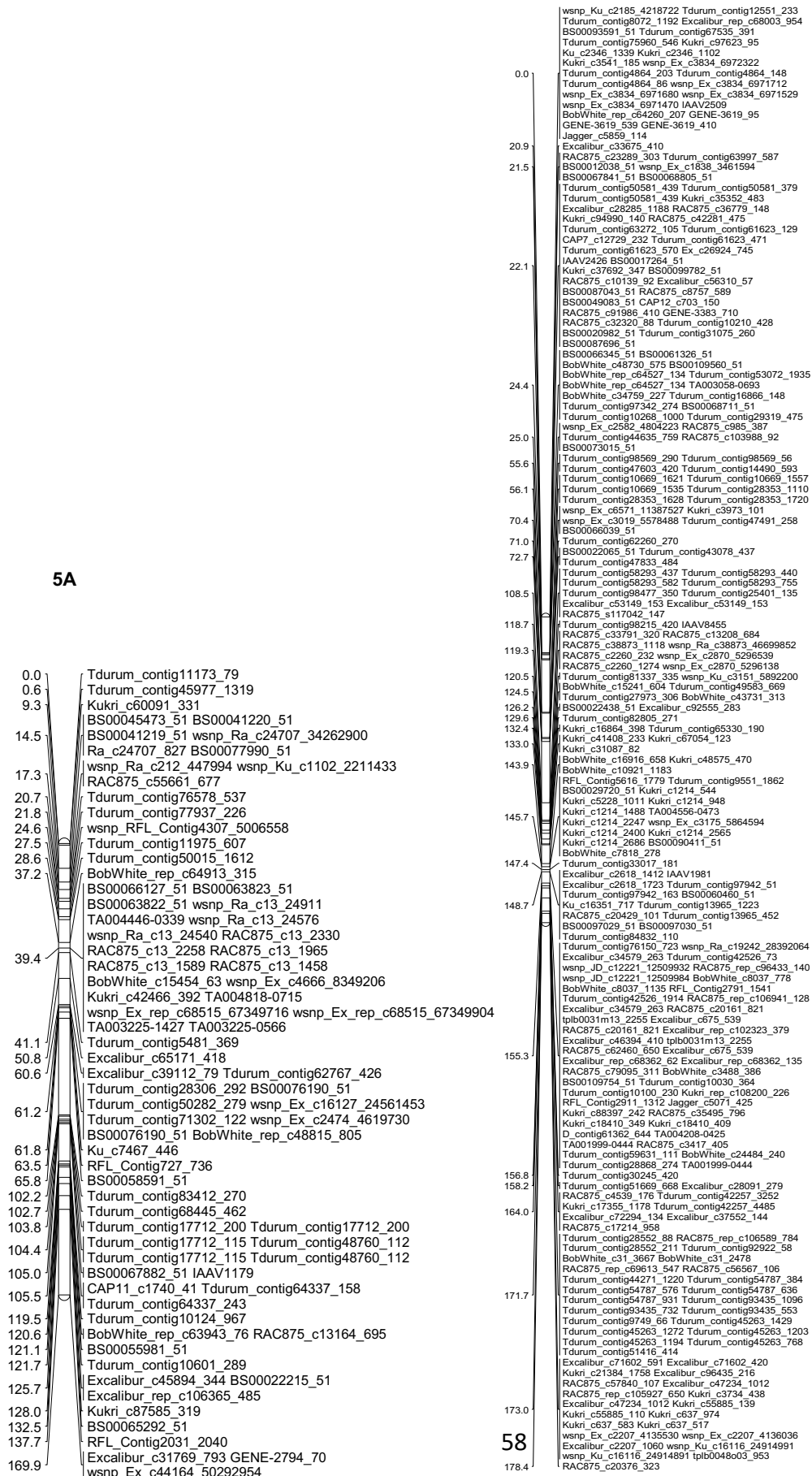
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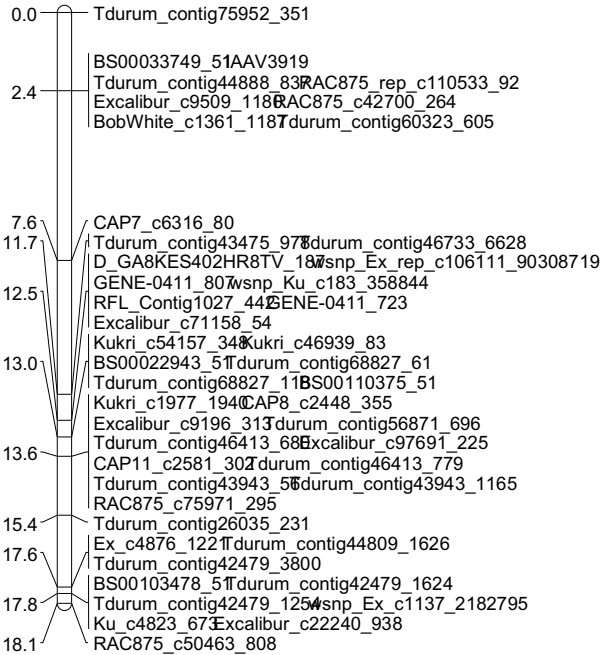
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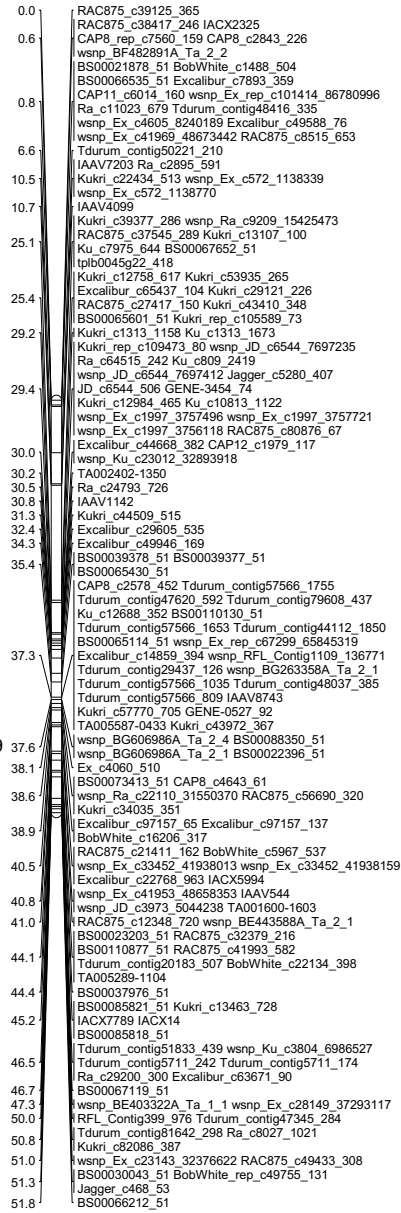
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BobWhite_c25527_980 Tdurum_contig75127_589
Kuku_c11467_993 BS00065265_51
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BobWhite_c2892_211 Tdurum_contig49656_570
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Excaltbur_c23777_74 Excaltbur_c31405_159
BS00066342_51 GENE-1728_107
Tdurum_contig16271_444 Excaltbur_c4484_985
Tdurum_contig44206_1503
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Excaltbur_c3870_288
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RAC875_rep_c114781_165
Tdurum_contig29880_329 Tdurum_contig29880_329
Tdurum_contig29880_329 Tdurum_contig29880_329
Tdurum_contig29880_329 Tdurum_contig8448_363
Tdurum_contig8448_700 Kuku_c10172_396
Kuku_c51004_434 BS00010747_51
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Excaltbur_c19531_169 RAC875_c525_740
RAC875_c525_941 wsnp_JD_c15955_15260646
RAC875_c525_1372 RAC875_c525_1425
RAC875_c525_1885 Excaltbur_c100654_100
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CAP12_c580_105 CAP12_c580_309
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Appendix B. Genetic linkage maps for Pop1(Langdon/W9262-260D3)

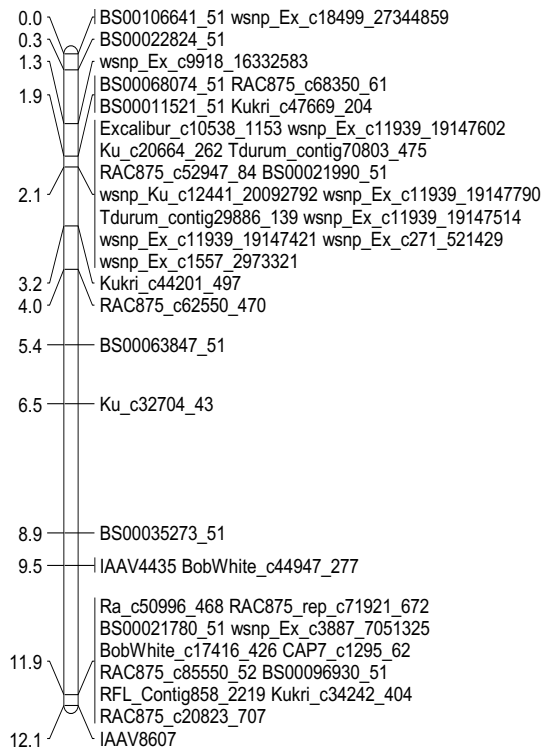
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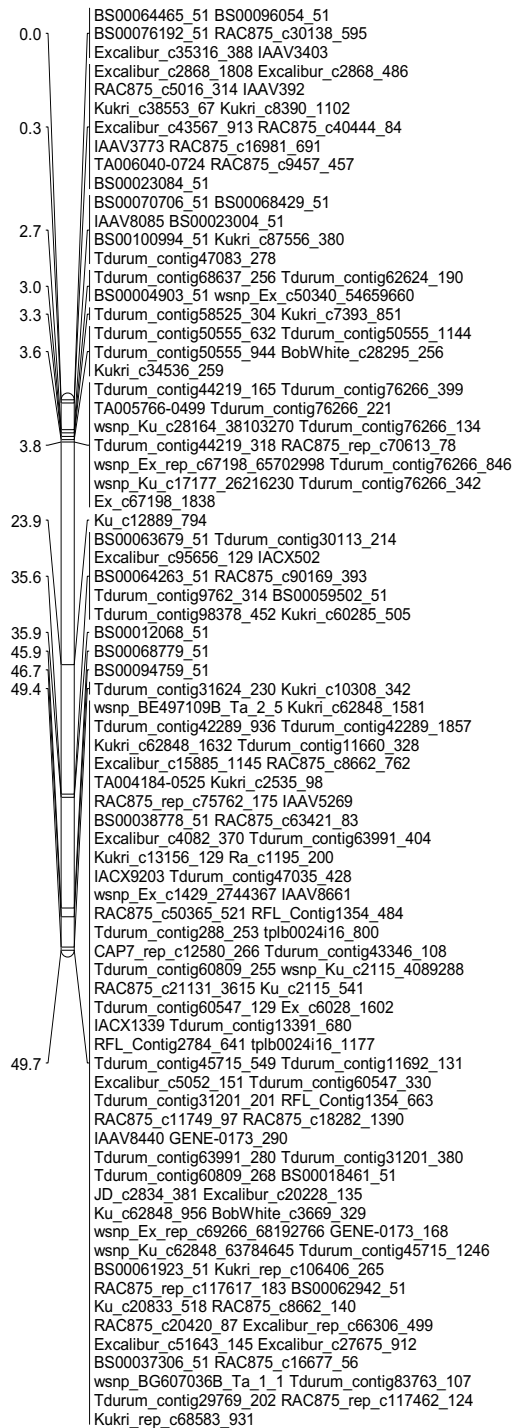
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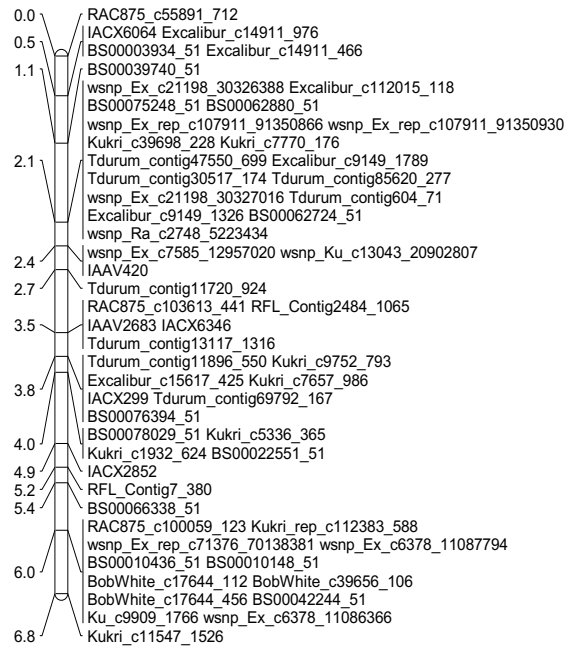
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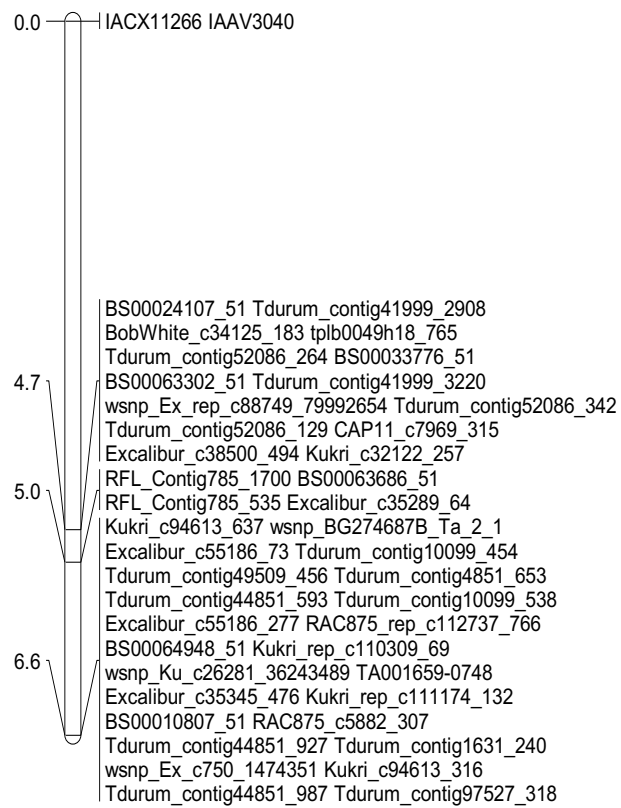
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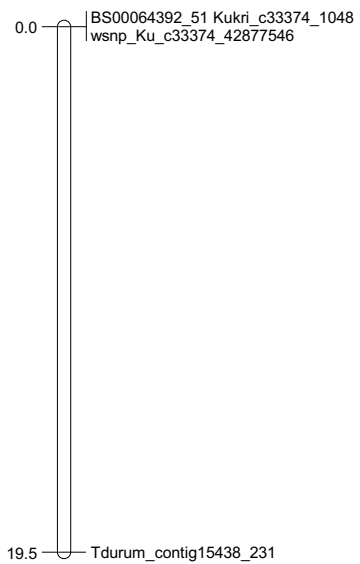
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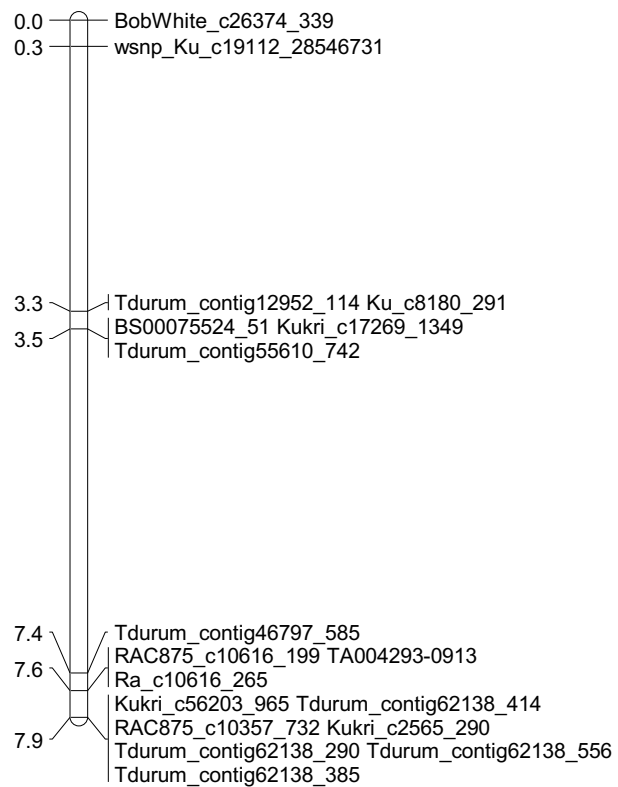
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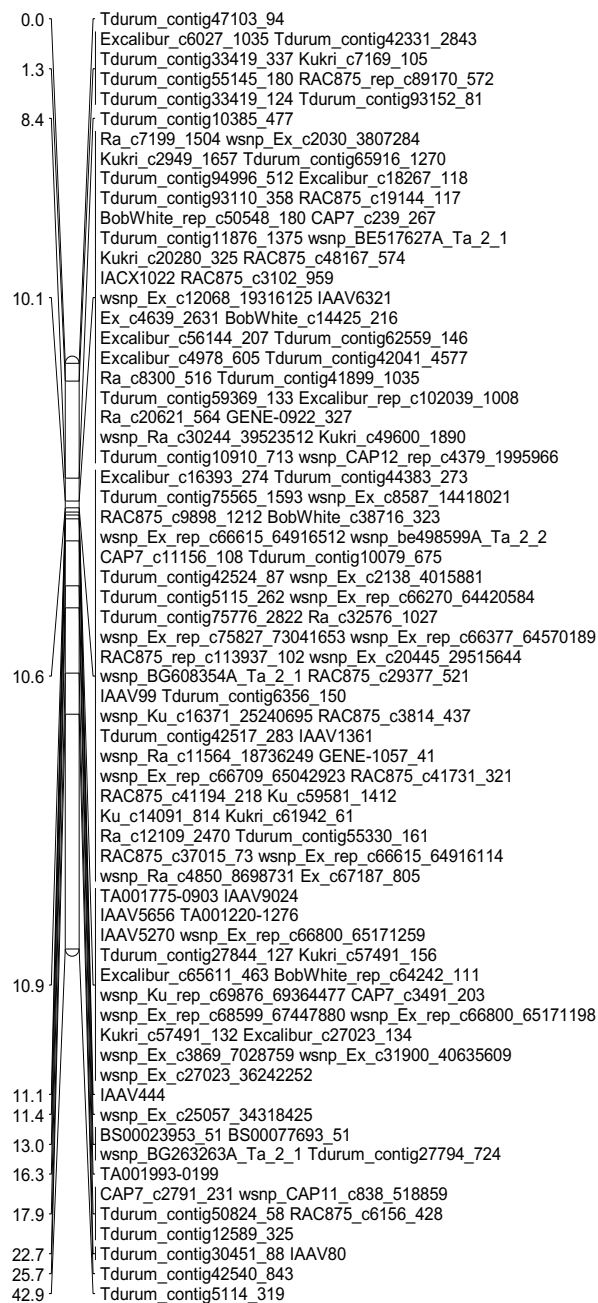
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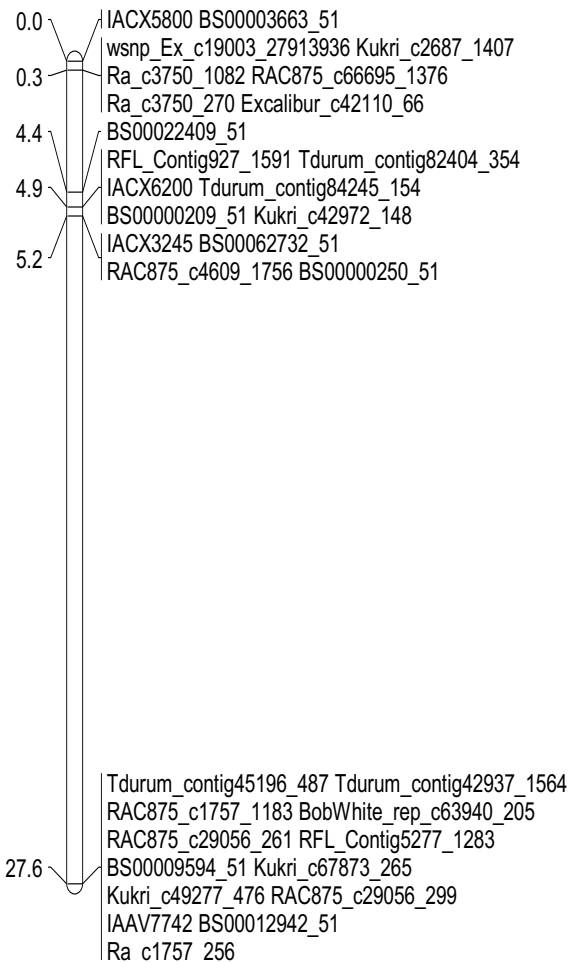
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2A-3



2A-4

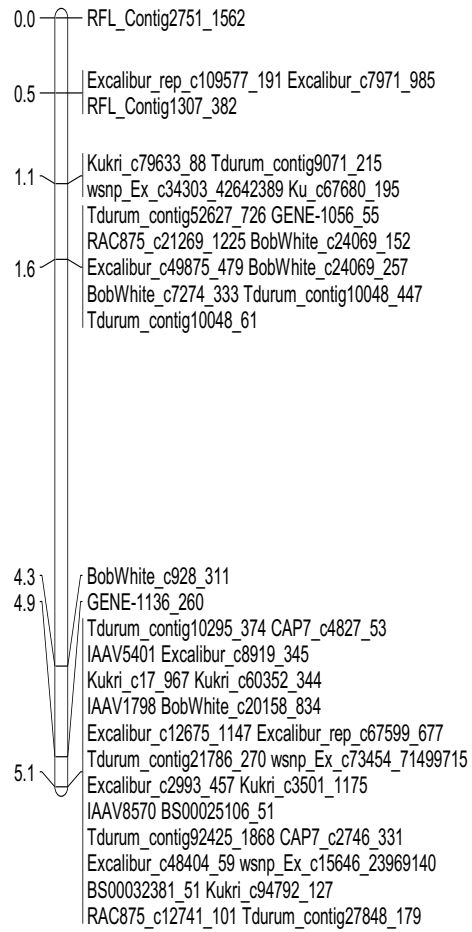


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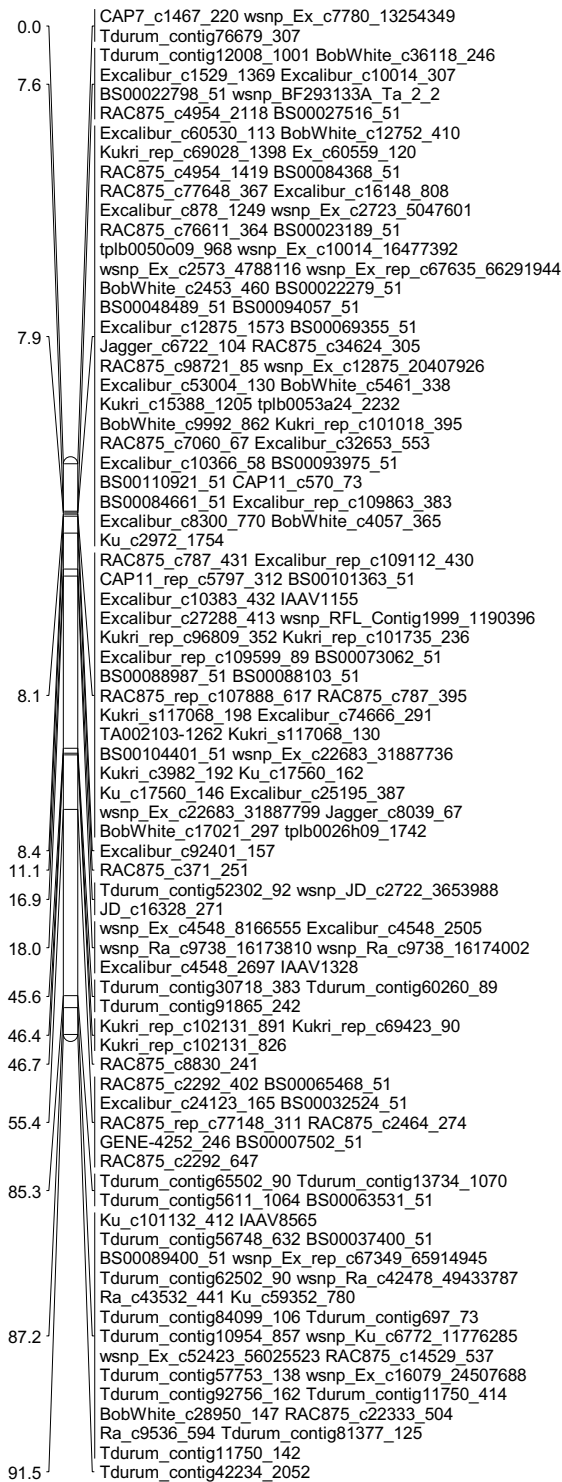
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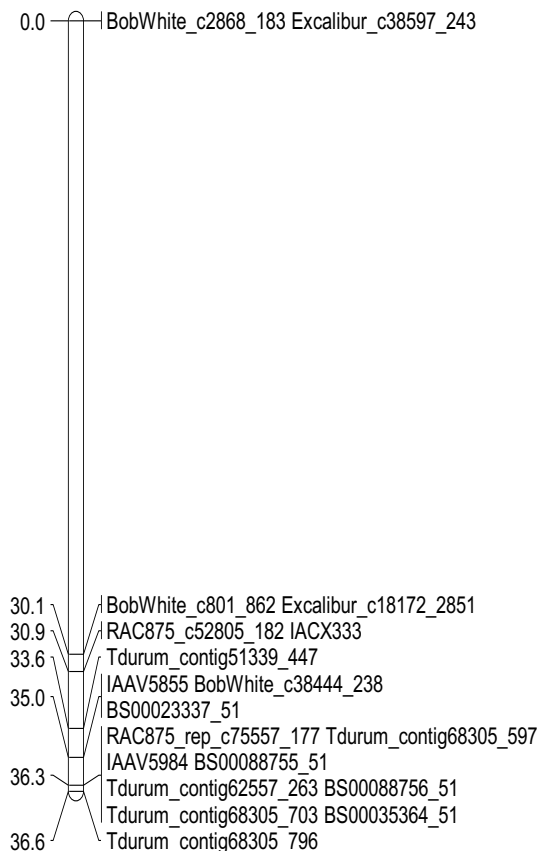
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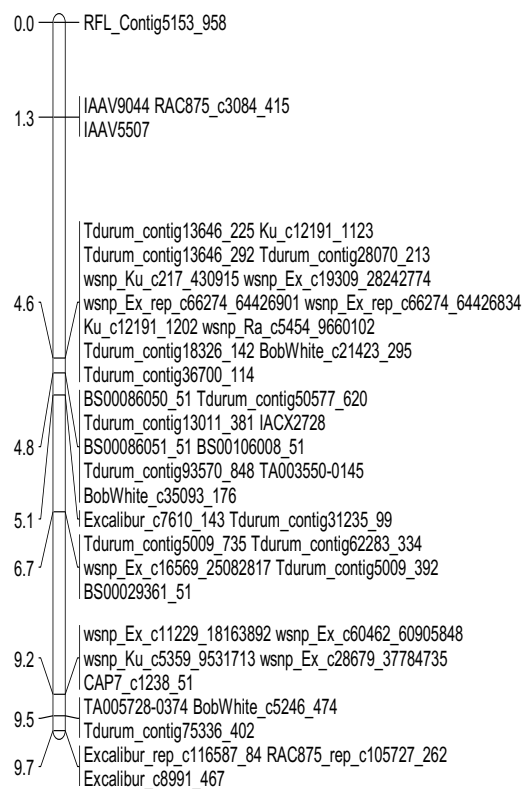
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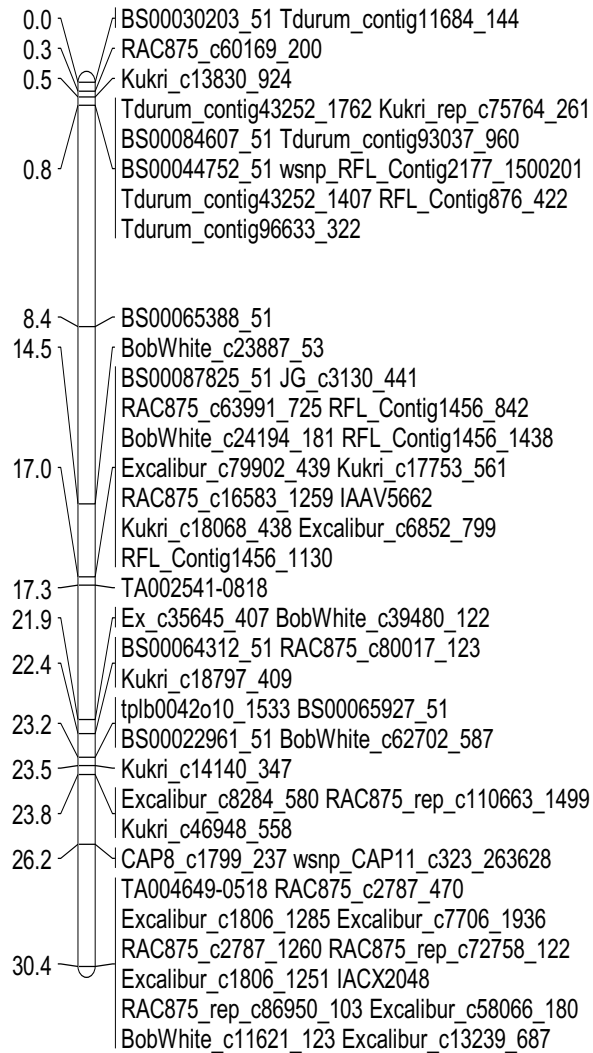
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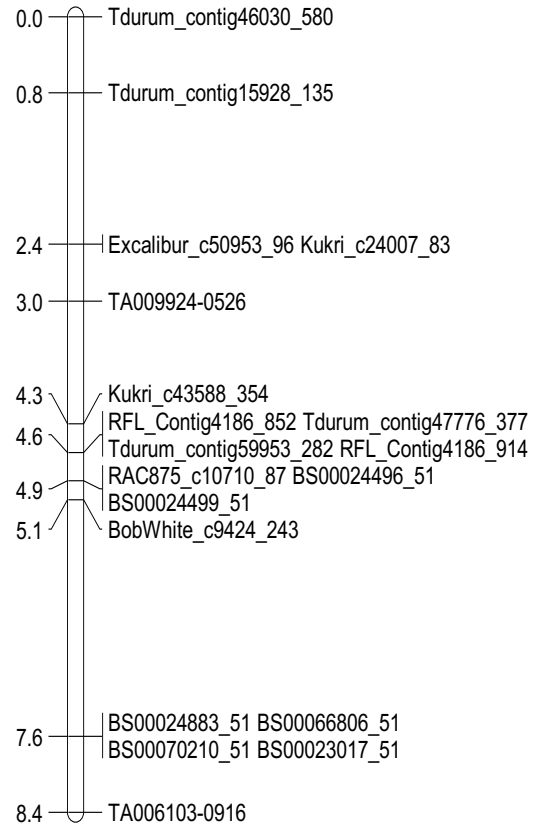
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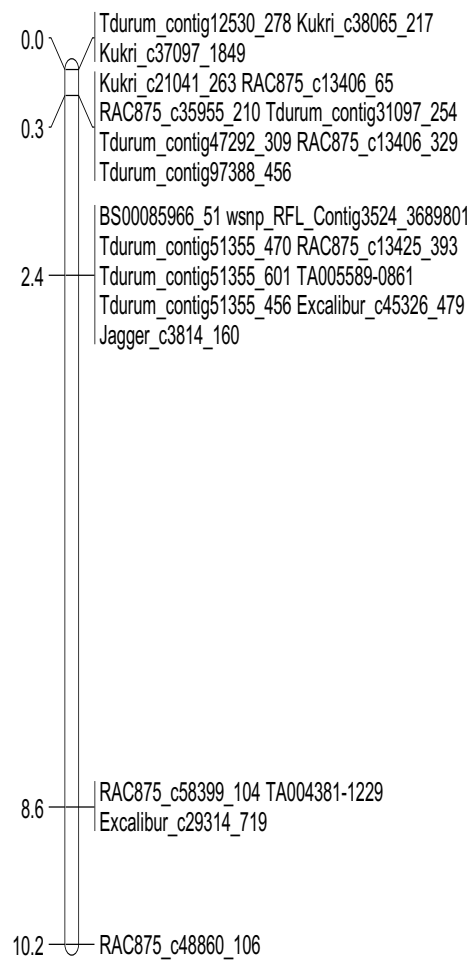
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3B-2



3B-3



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4A-2

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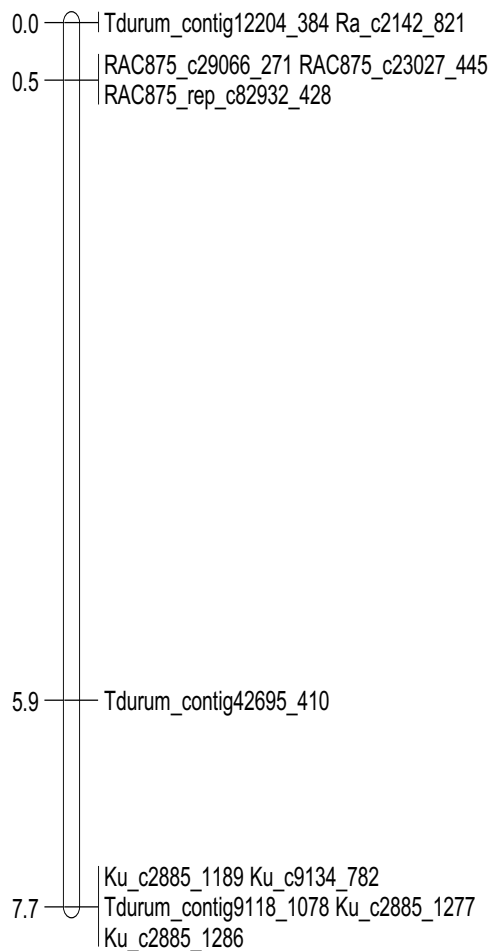
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 Tdurum_contig92977_295 Tdurum_contig10257_608
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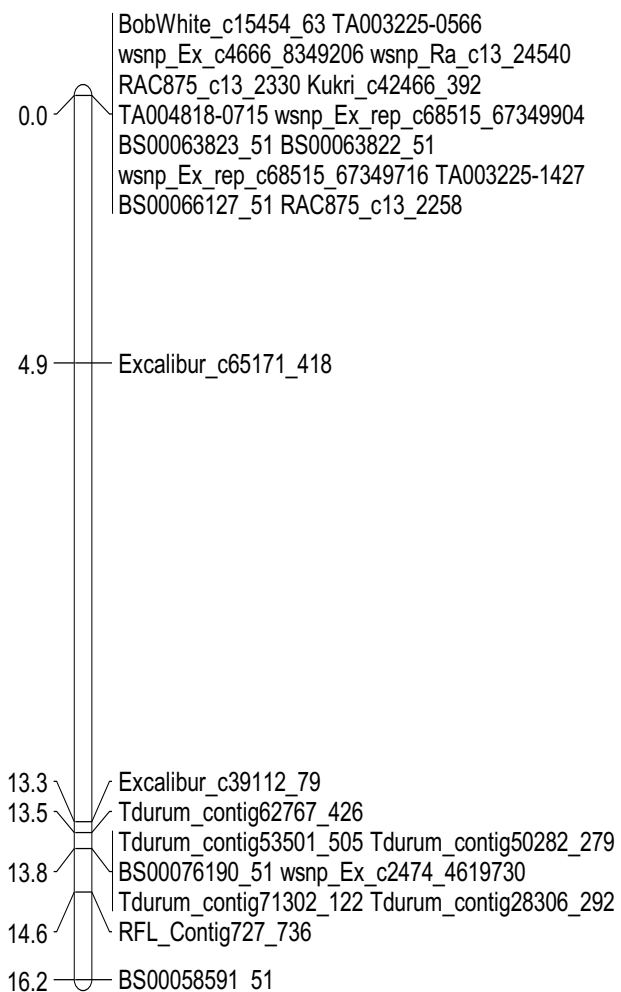
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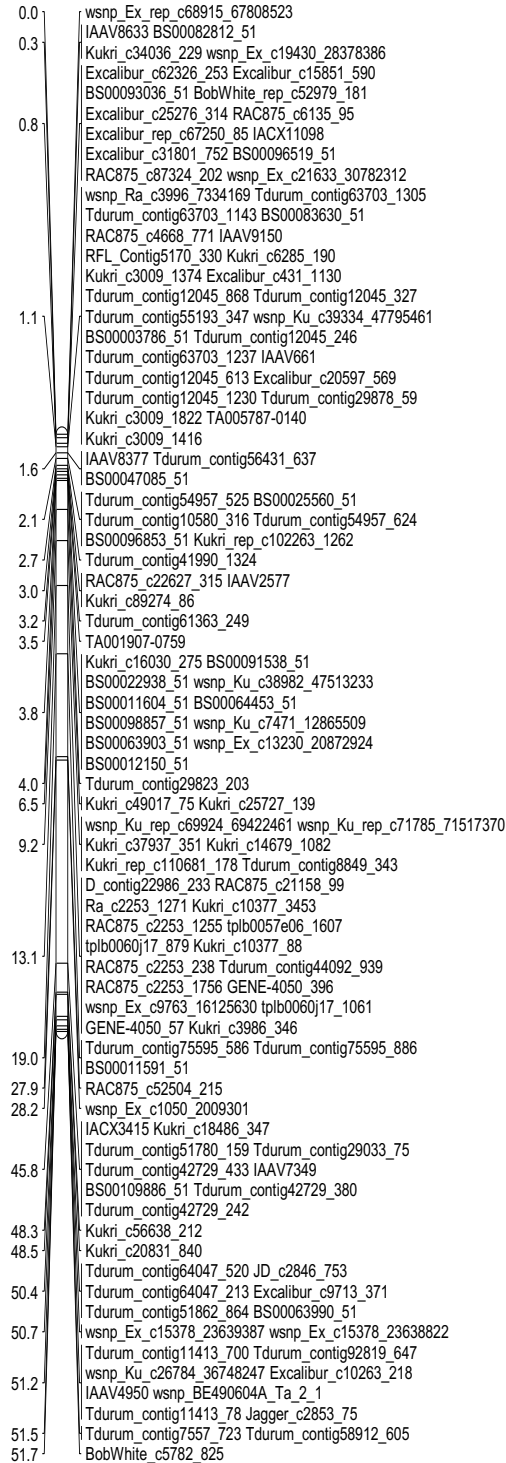


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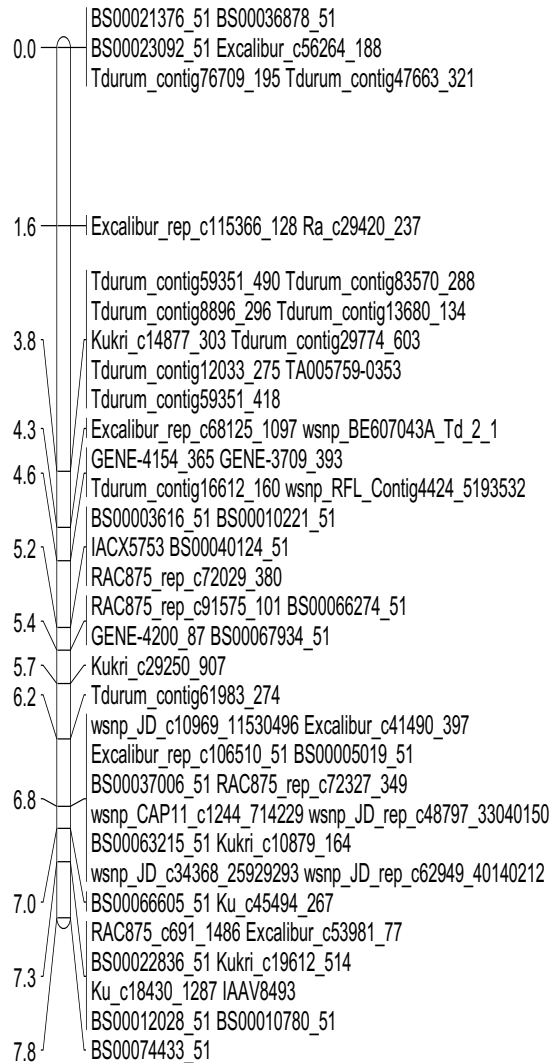


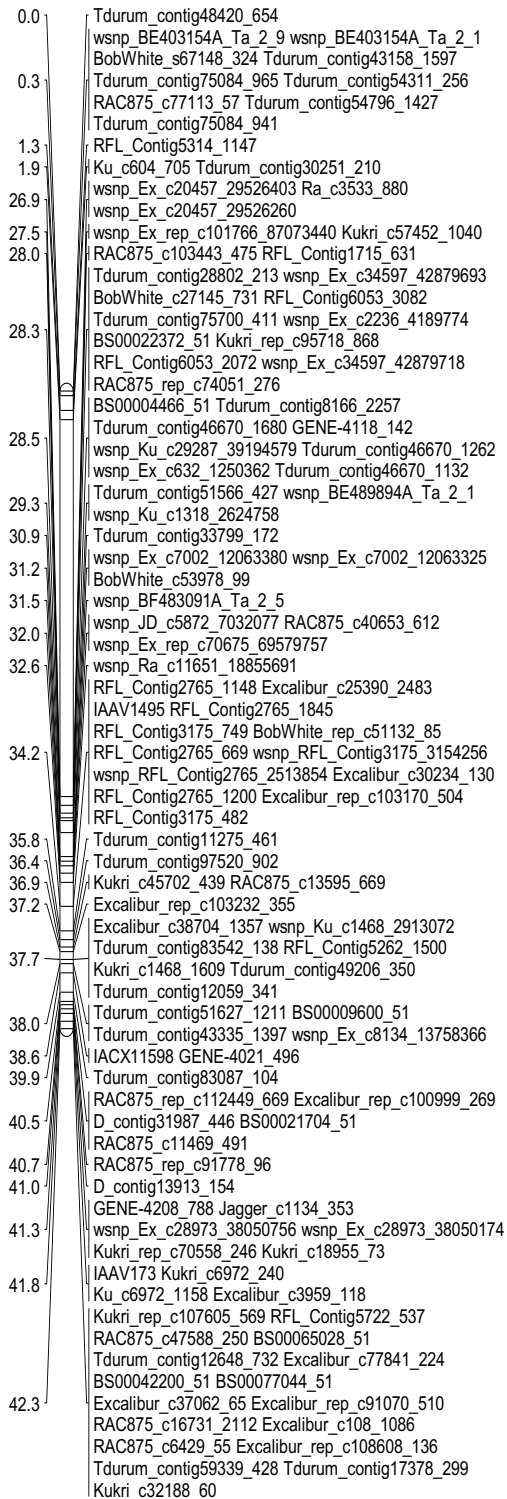
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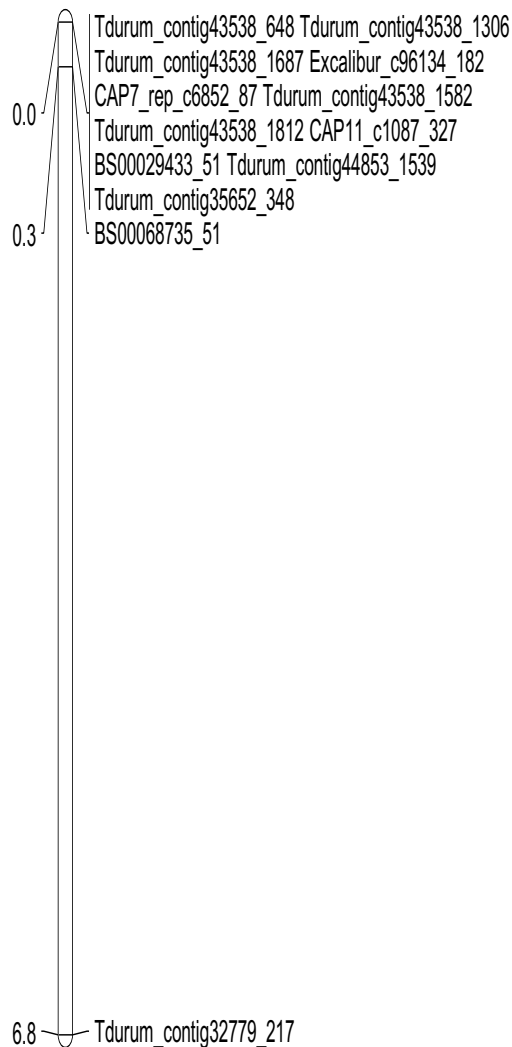


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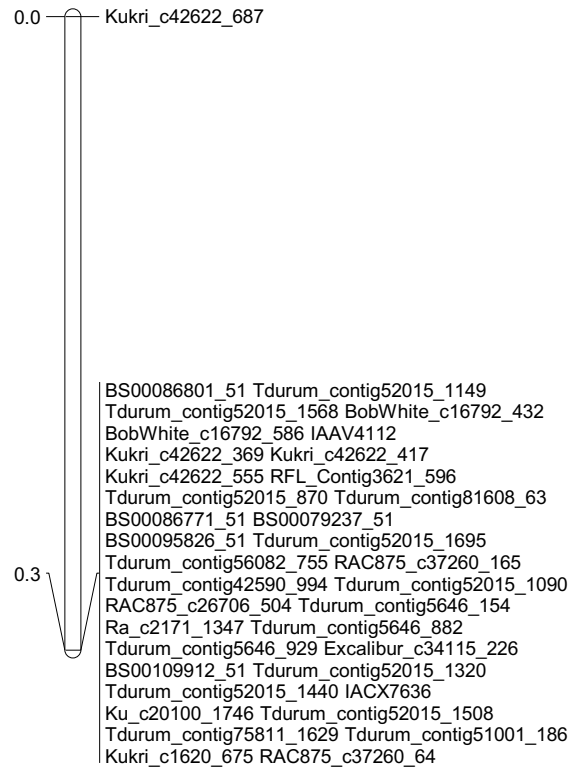


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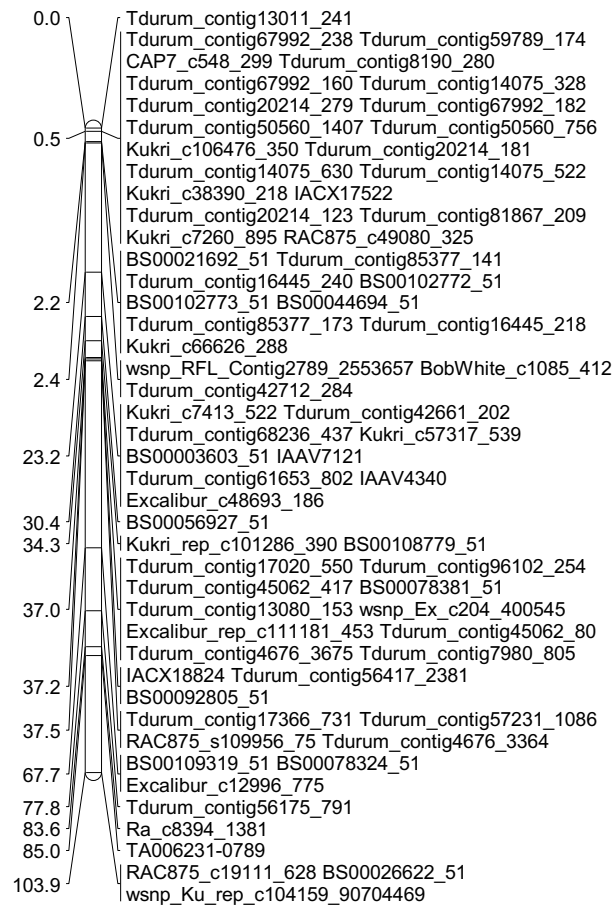


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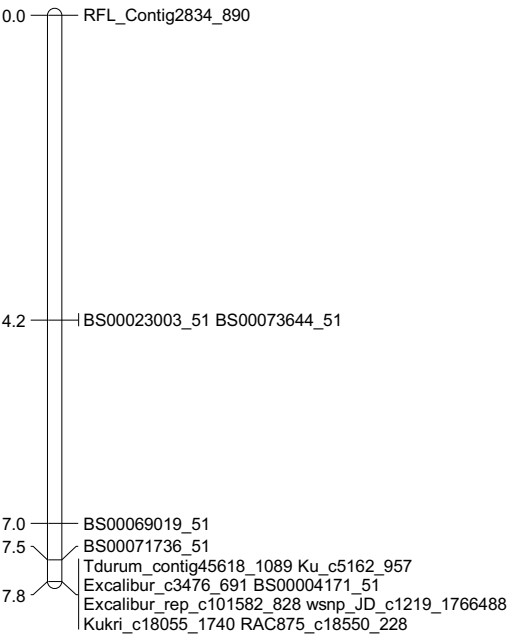
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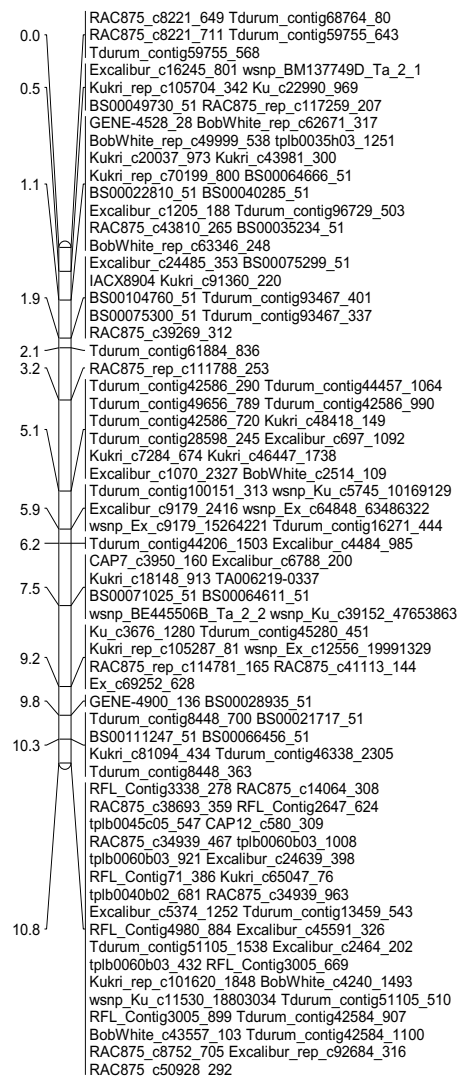
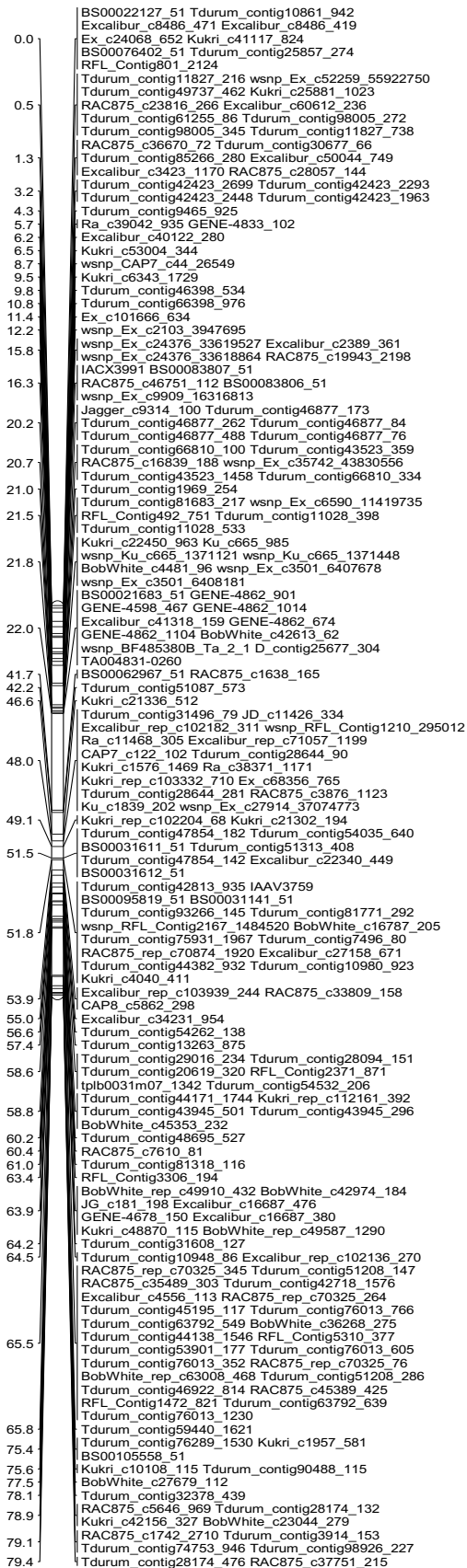


7A-2



7A-3

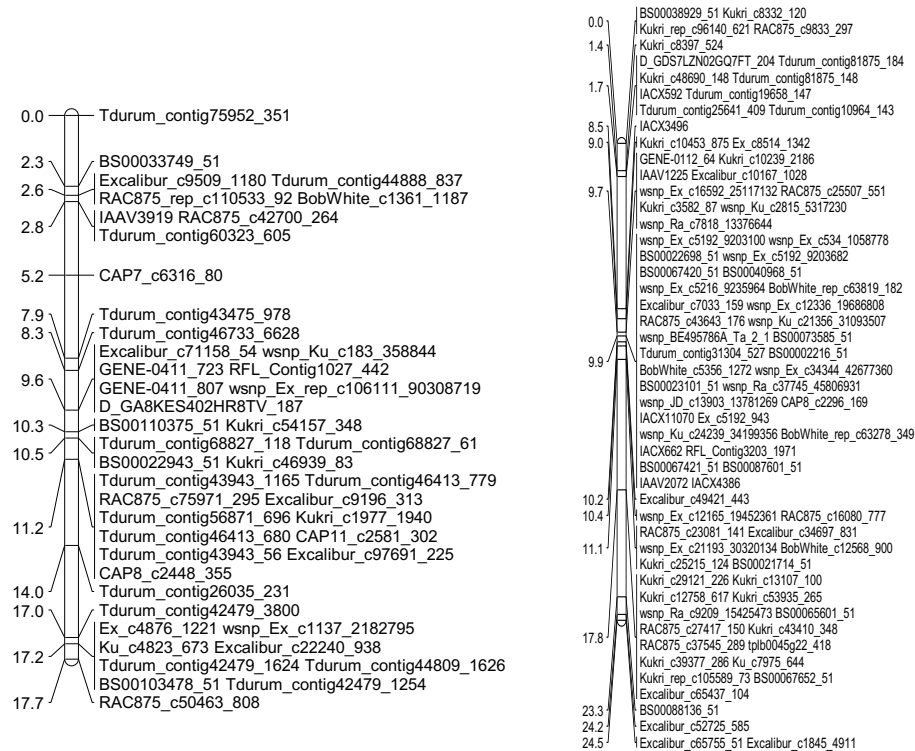




Appendix C. Genetic linkage maps for Pop2 (W9262-260D3/Langdon triticale)

1A-2

1A-1



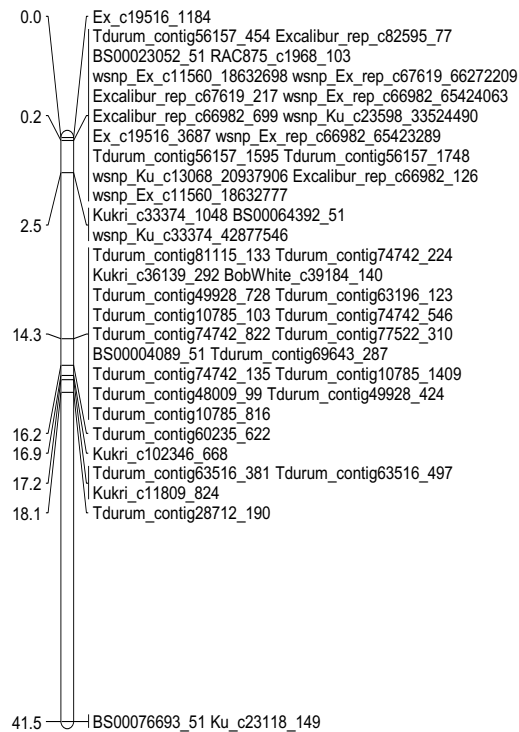
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 3.2 Ku_c12889_794
 15.5 Tdurum_contig98378_452
 15.7 Kukri_c60285_505
 16.0 IACX502 Tdurum_contig30113_214
 BS00064263_51 BS00063679_51
 BS00059502_51 Tdurum_contig9762_314
 Excalibur_c95656_129 BS00012068_51
 RAC875_c90169_393
 BS00068779_51
 BS00094759_51
 18.1 Kukri_c10308_342 Tdurum_contig31624_230
 18.3 Ku_c12031_980 BS00022104_51
 19.8 IAAV3232 CAP7_c1241_128
 Ex_c6473_575 Ku_c2115_541
 TA004324-0491 Tdurum_contig29769_202
 RAC875_c8662_140 RAC875_c8662_762
 Kukri_c2115_622 RAC875_c3457_303
 Excalibur_c51643_145 Excalibur_c32608_500
 RAC875_c21274_235 Kukri_c5398_1061
 Ex_c24969_223 wsnp_Ku_c7377_12718787
 Kukri_rep_c106406_265 Ku_c12031_692
 BS00070623_51 BobWhite_c1456_615
 Tdurum_contig45715_549 Tdurum_contig45715_1246
 wsnp_Ku_c2115_4089288 tpb0024i20_953
 Excalibur_c27675_912
 Ku_c5398_934
 BS00063885_51 wsnp_RFL_Contig4726_5654774
 Kukri_rep_c101550_113
 Kukri_c49091_415
 20.0 Kukri_rep_c71291_155 wsnp_Ku_c1772_3465811
 RAC875_c22244_61 wsnp_Ku_c30982_40765254
 BS00022085_51 Kukri_rep_c91496_1320
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 BS00034018_51
 21.2 Kukri_c2297_181
 21.5 Tdurum_contig11877_785 Tdurum_contig65023_587
 21.7 Kukri_rep_c88171_730 wsnp_Ex_c10233_16784994
 RAC875_rep_c108085_570 wsnp_Ku_c66585_65967792
 Kukri_rep_c95031_104 RAC875_c24109_600
 21.9 GENE-0116_102 JD_c10376_670
 Tdurum_contig11877_414 GENE-1214_159
 Excalibur_c3140_697 Ra_c33845_794
 CAP7_rep_c7114_55 Tdurum_contig11877_429
 Ex_c4382_1187
 Tdurum_contig84184_124 BS00029345_51
 wsnp_Ex_c30805_39678077 BS00009731_51
 Tdurum_contig53888_107 Kukri_rep_c70738_896
 Tdurum_contig47456_182 wsnp_Ex_rep_c68573_67416138
 22.2 Ku_c8767_1245 Kukri_c8308_245
 Tdurum_contig53888_350 RAC875_c5227_1385
 Tdurum_contig76507_422 Kukri_c10593_1064
 wsnp_Ex_c6022_10552811 wsnp_Ex_c15934_24341135
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 RAC875_c2331_2570 Tdurum_contig46780_203
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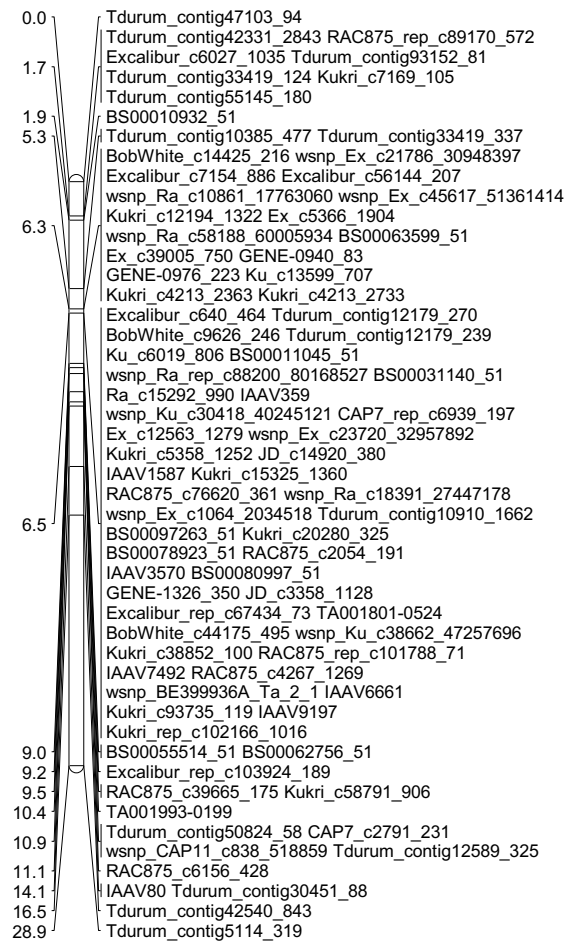
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 BS00070285_51 Tdurum_contig28675_275
 BS00109244_51 CAP7_c199_62
 wsnp_CAP11_c1902_1022590 RFL_Contig1823_1044
 0.7 Excalibur_c8585_701 Tdurum_contig28853_142
 wsnp_RFL_Contig3951_4390396 Tdurum_contig8580_1119
 BS00021934_51 Tdurum_contig8580_1285
 BS00002484_51 BobWhite_c23617_167
 Tdurum_contig11216_942 Kukri_c57725_146
 Excalibur_c50785_525 Kukri_c25512_53
 Tdurum_contig61829_706
 0.9 IAAV565 Tdurum_contig13516_251
 1.2 wsnp_Ex_c13878_21738866
 1.4 wsnp_RFL_Contig395_4387107 Tdurum_contig8840_237
 Tdurum_contig8840_575 Tdurum_contig12518_200
 1.6 BS00061472_51 BS00028476_51
 BS00023173_51
 Tdurum_contig9706_121 Tdurum_contig13136_1017
 Tdurum_contig13136_1383 Tdurum_contig13136_1089
 Tdurum_contig13136_546 RAC875_c36980_248
 Tdurum_contig13136_537 CAP11_c2892_176
 Tdurum_contig13136_1527
 BobWhite_c44460_821 RAC875_c35927_554
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 3.0 Tdurum_contig19203_152
 Tdurum_contig68980_524 TA003411-0583
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 Tdurum_contig68980_317
 4.7 Tdurum_contig13250_137
 4.9 Tdurum_contig57153_1439 GENE-0063_68
 5.4 Tdurum_contig10475_87 Tdurum_contig29087_280
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 5.9 Tdurum_contig25612_195 Tdurum_contig29087_757
 7.5 Kukri_rep_c102001_59
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 7.8 Kukri_c18230_1633
 8.3 Excalibur_rep_c71107_517
 Kukri_c30490_328 Excalibur_c17822_688
 9.0 GENE-0115_375
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 11.6 CAP8_c3752_330
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 TA002645-0060 Kukri_c44604_203
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 24.5 BS00107837_51
 Tdurum_contig8669_131 Tdurum_contig8669_296
 24.7 RAC875_rep_c118984_119
 25.2 RAC875_c14613_112
 RAC875_c24317_1351 Kukri_rep_c111710_80
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 RAC875_c24317_1201 RAC875_rep_c71278_345
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 BobWhite_c6433_417
 Excalibur_c5888_169 Excalibur_c39284_949
 32.5 Kukri_c59535_186
 Kukri_c59535_393
 32.8 Tdurum_contig13879_352
 33.0 Excalibur_c5888_641
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 34.7 RAC875_c5882_307
 35.0 BS00064948_51
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 BS00082577_51 Tdurum_contig49509_456
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 RAC875_c1073_239 Tdurum_contig58710_411
 BS00001128_51 Kukri_c16608_761
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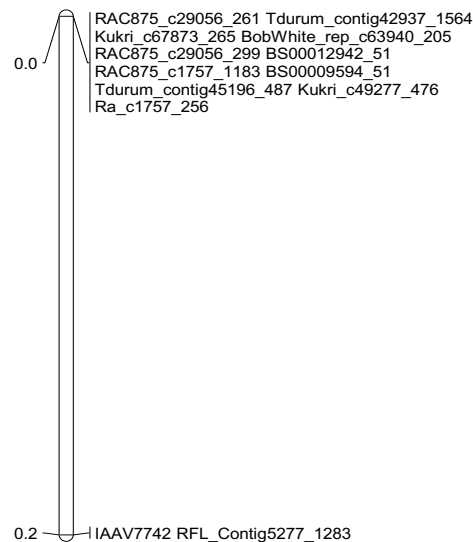
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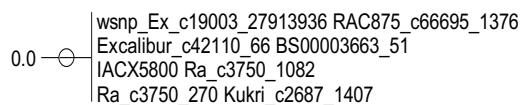
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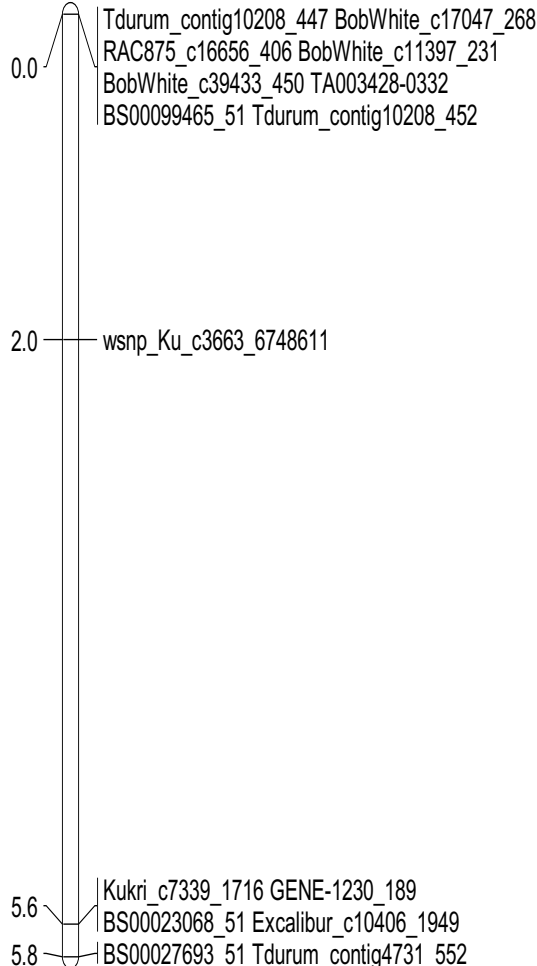
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2A-3



2B-1



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4.1 | Tdurum_contig5413_1011 Tdurum_contig4899_1075

5.0 | BobWhite_c3448_80

5.2 | Tdurum_contig54704_176 Tdurum_contig7495_1029

5.5 | Excalibur_c5958_1398

6.0 | Tdurum_contig51443_336 BobWhite_c41535_52

6.5 | RAC875_c15229_108

6.7 | Tdurum_contig6194_412

7.2 | Excalibur_c10376_375

7.6 | RAC875_c61801_299 RAC875_c26469_363

7.9 | Excalibur_c6502_397 RAC875_c34516_70

8.1 | BobWhite_c11739_325 Tdurum_contig27976_414

8.3 | BobWhite_c10579_272 Excalibur_c25234_143

8.6 | Kukri_rep_c107572_121 Tdurum_contig9716_2337

8.8 | Tdurum_contig9716_1460 Tdurum_contig9716_535

9.1 | Tdurum_contig9716_229

9.3 | Tdurum_contig30680_120

9.5 | Tdurum_contig45255_3473

9.7 | Tdurum_contig5056_173 RAC875_c62278_69

9.9 | Tdurum_contig94176_65 RAC875_c22429_249

10.1 | Kukri_rep_c69803_82 Kukri_c12368_82

10.3 | Kukri_c69885_560 Tdurum_contig61283_131

10.5 | Kukri_c2565_1405 Kukri_rep_c101093_572

10.7 | RAC875_c22619_364

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11.5 | IAAV1903

11.7 | BobWhite_c8113_532 wsnp_Ex_c7003_12065828

11.9 | wsnp_Ex_c7003_12065642

12.1 | BS00076506_51

12.3 | Tdurum_contig12836_418

12.5 | Tdurum_contig25602_212 Tdurum_contig26542_457

12.7 | Tdurum_contig26542_281

12.9 | Tdurum_contig25490_434 RAC875_c28185_91

13.1 | Tdurum_contig11730_153

13.3 | Tdurum_contig2345_75

13.5 | Tdurum_contig2945_83 Tdurum_contig2945_155

13.7 | Kukri_c26968_56 CAP8_rep_c6671_353

13.9 | wsnp_Ex_c13908_21774935

14.1 | Kukri_c19751_873

14.3 | wsnp_Ex_rep_c67543_66165372

14.5 | wsnp_Ex_c10838_17631243 IAAV5226

14.7 | Ex_c55735_1012 Excalibur_c43037_831

14.9 | Ku_c11652_1720 Ra_c5367_387

15.1 | GENE-0872_133 wsnp_Ex_c55735_58127324

15.3 | RAC875_c31162_706 wsnp_Ex_c10251_16815792

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15.7 | RAC875_c93461_87 wsnp_Ex_c17127_25756019

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16.5 | RAC875_c66657_91 IACX2626

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16.9 | Kukri_c56872_402 RAC875_c25035_958

17.1 | RAC875_c14316_584 RAC875_c12803_916

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18.3 | Kukri_rep_c68360_1476 Ex_c68194_1994

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19.1 | Kukri_c920_310 RAC875_c7540_366

19.3 | wsnp_Ex_c54998_57670603 RAC875_rep_c70342_1644

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21.5 | wsnp_Ra_c54256_57628288 JD_c3211_962

21.7 | Tdurum_contig12879_1200

21.9 | Tdurum_contig12879_320 Tdurum_contig12879_201

22.1 | Tdurum_contig12879_1273

22.3 | wsnp_Ex_c3506_6415495 BobWhite_c32038_264

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22.9 | Excalibur_c14988_872 BobWhite_c1472_59

23.1 | wsnp_Ku_c15496_24122936 Kukri_c15498_1679

23.3 | wsnp_Ex_c3506_6414757 Tdurum_contig72054_94

23.5 | BobWhite_c32938_366 BS00047073_51

23.7 | wsnp_Ex_c24135_33382700 Ku_c51309_212

23.9 | BS00009511_51 BS00064740_51

24.1 | Kukri_c15498_657 JD_c9115_354

24.3 | Tdurum_contig12761_125 Tdurum_contig78534_314

24.5 | Excalibur_c5801_177

24.7 | wsnp_Ex_c13353_21046550 Tdurum_contig67613_465

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25.1 | wsnp_Ex_c19772_2871627 RAC875_c81984_707

25.3 | Tdurum_contig42046_1390 Kukri_c16601_822

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26.3 | RAC875_c13240_96

26.5 | Tdurum_contig42680_249 wsnp_Ku_c19251_28705893

26.7 | wsnp_Ex_c20029_29064315 BS00102614_51

26.9 | wsnp_Ra_c3955_7262354

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27.3 | Kukri_rep_c68903_708 D_GCE8AKX01DS17J_273

27.5 | Excalibur_c32980_169 Tdurum_contig14007_916

27.7 | Tdurum_contig62693_581 Excalibur_c14201_111

27.9 | BS00004224_51 Tdurum_contig28113_390

28.1 | Tdurum_contig62393_484

28.3 | Jagger_c6644_121

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29.3 | Excalibur_c33221_381 Tdurum_contig77036_338

29.5 | BobWhite_c10539_201 BS00080760_51

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30.9 | RAC875_c40992_113 wsnp_RFL_Contig3273_3319580

31.1 | Excalibur_c2157_173 BobWhite_c9690_94

31.3 | wsnp_RFL_Contig3917_4326857 Tdurum_contig28795_381

31.5 | RAC875_c26967_589 Excalibur_c37753_655

31.7 | RAC875_c51420_237 Excalibur_c37753_764

31.9 | Tdurum_contig28795_322

32.1 | wsnp_JD_c12346_12606967 BobWhite_c7050_792

32.3 | Excalibur_c91034_141

32.5 | BobWhite_c30140_119

32.7 | RFL_Contig2751_1562

32.9 | Excalibur_c7971_368 Excalibur_rep_c109577_191

33.1 | RFL_Contig1307_382

33.3 | BobWhite_c24069_152 Kukri_c79633_88

33.5 | BobWhite_c24069_257 wsnp_Ex_c34303_42642389

33.7 | Excalibur_c49875_479 Ku_c67680_195

33.9 | Tdurum_contig9071_215

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34.3 | GENE-1056_55 Tdurum_contig52627_726

34.5 | Tdurum_contig10049_61 BobWhite_c7274_333

34.7 | RAC875_c21269_1225

34.9 | BobWhite_c928_311

35.1 | GENE-1136_260

35.3 | Tdurum_contig92425_1868 Excalibur_rep_c67599_677

35.5 | Kukri_c84792_127 RAC875_c12741_101

35.7 | BS00025106_51 CAP7_c4827_53

35.9 | Tdurum_contig10295_374 IAAV5401

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36.3 | Kukri_c17_967 Excalibur_c2993_457

36.5 | Tdurum_contig27848_179 BobWhite_c20158_834

36.7 | Excalibur_c12675_1147 Excalibur_c8919_345

36.9 | Kukri_c3501_1175 wsnp_Ex_c73454_71499715

37.1 | IAAV8570 IAAV1798

37.3 | Tdurum_contig21786_270

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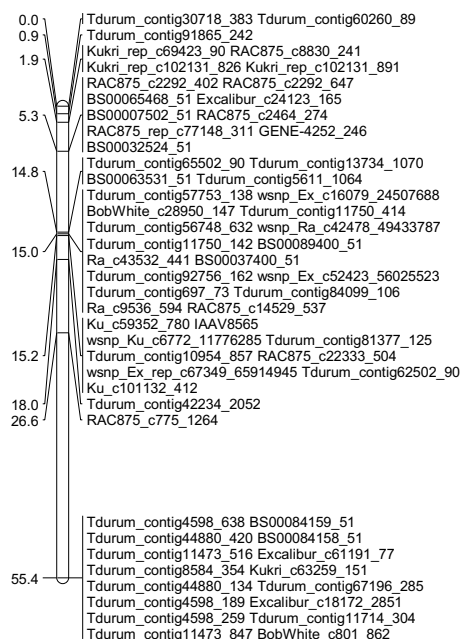
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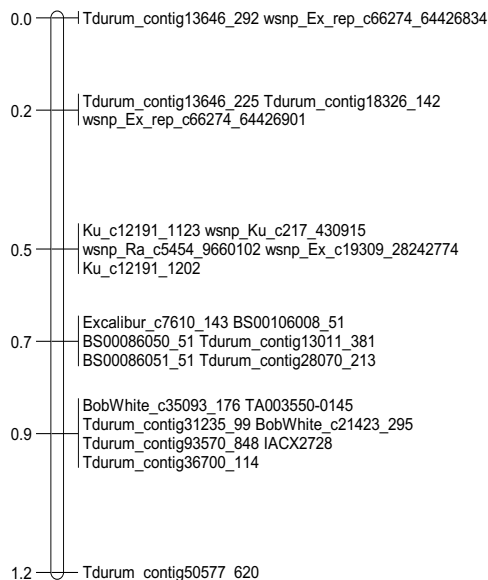
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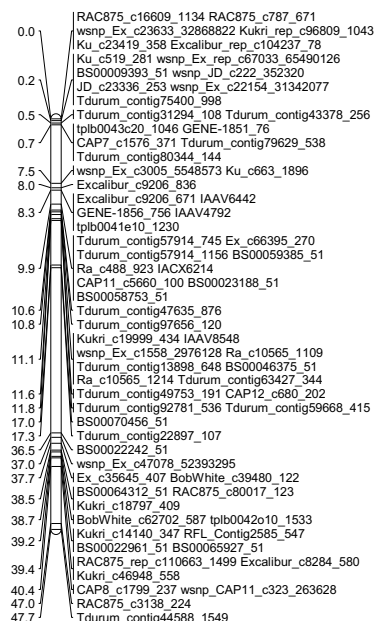
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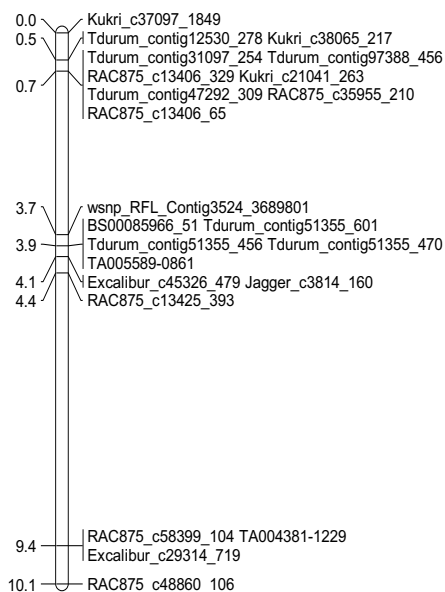
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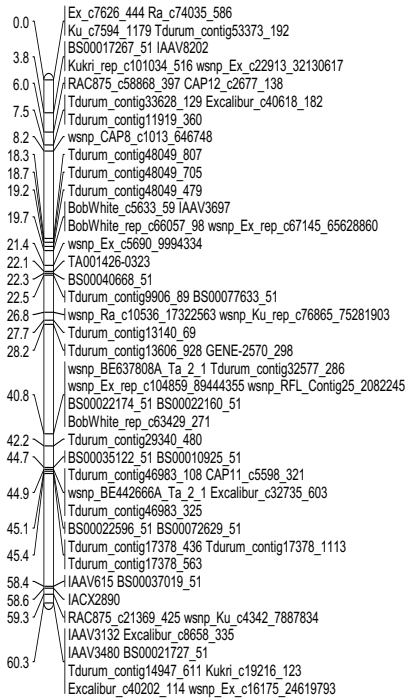
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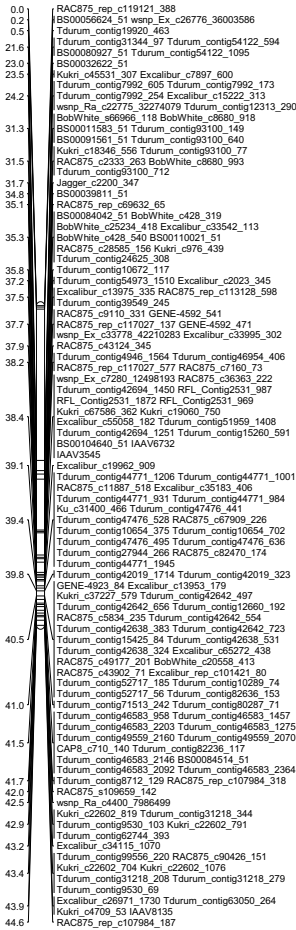
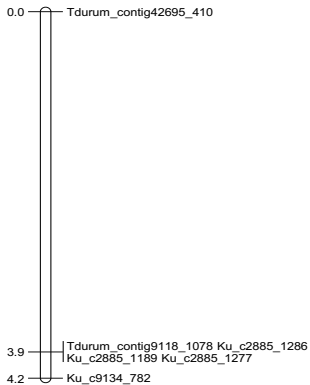
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4A-1

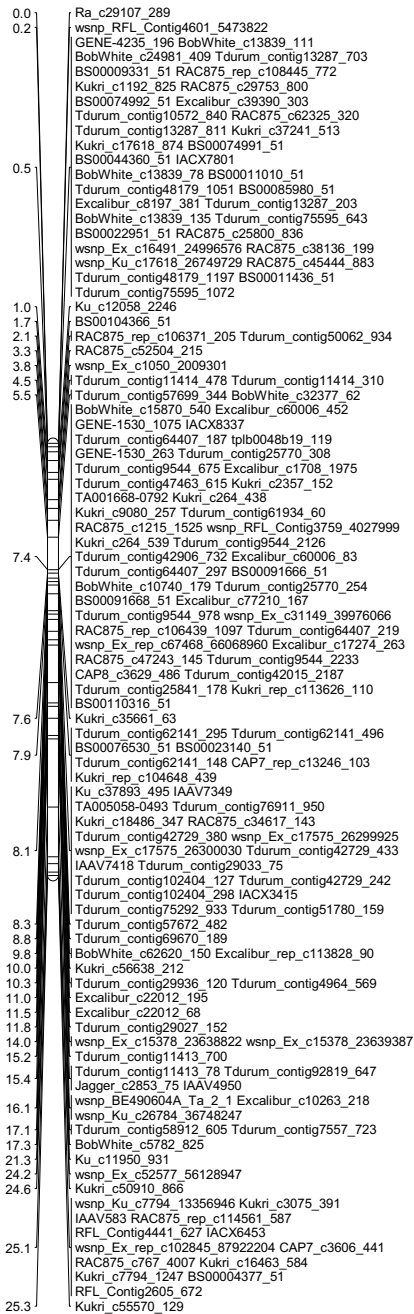


4B

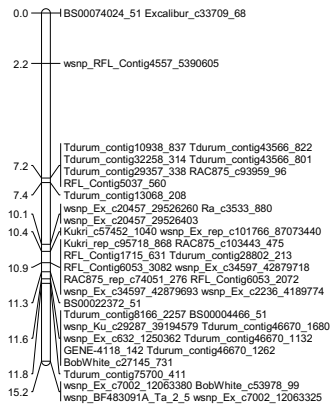


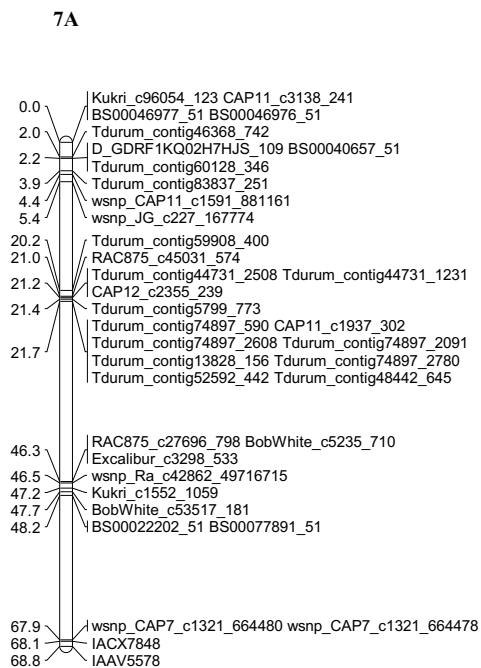
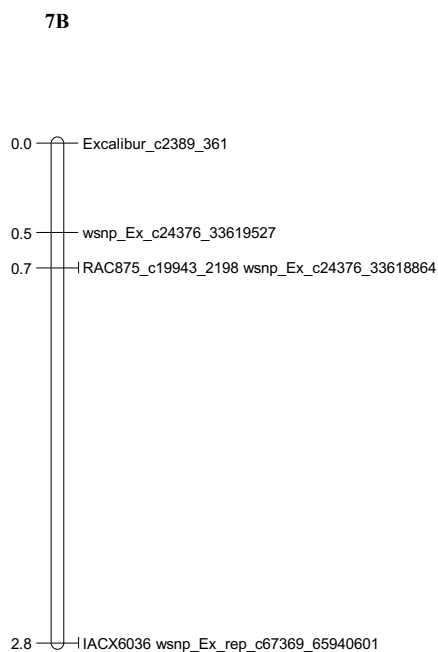
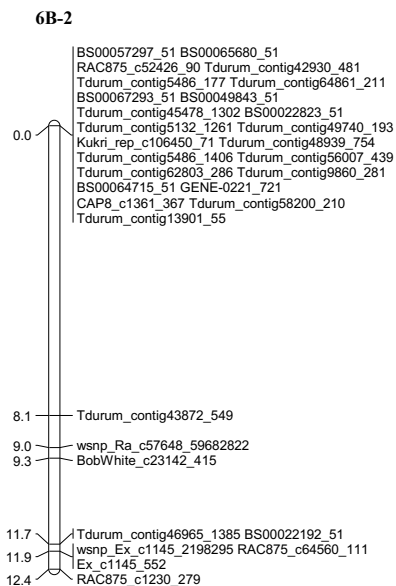
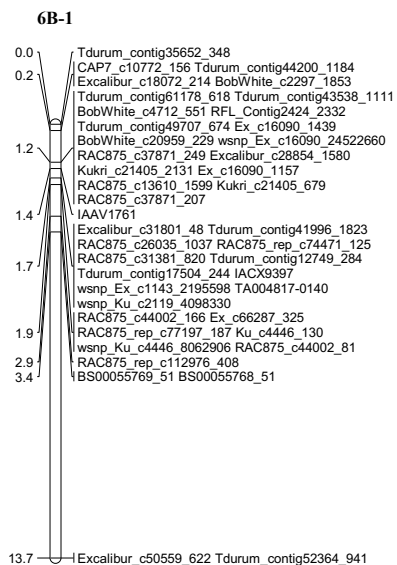


6A-1



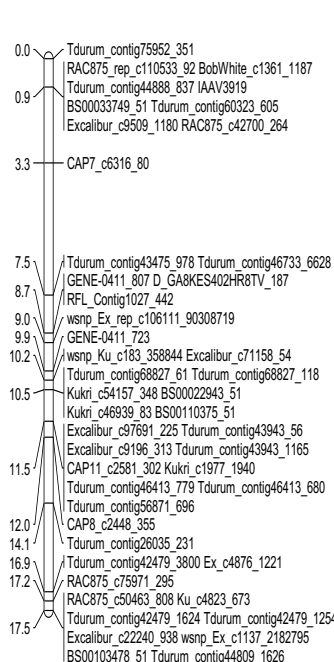
6A-2



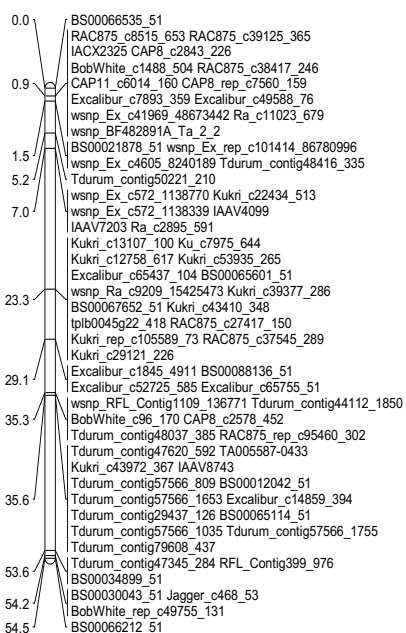


Appendix D. Genetic linkage maps for Pop3 (DGE-1/W9262-260D3)

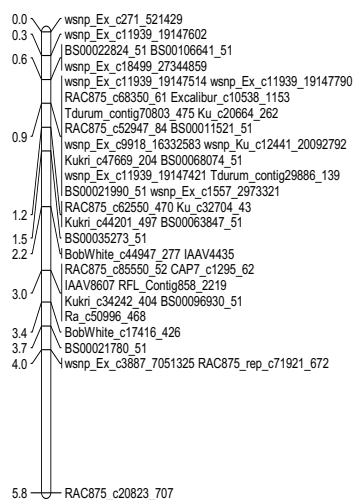
1A-1



1A-2



1A-3

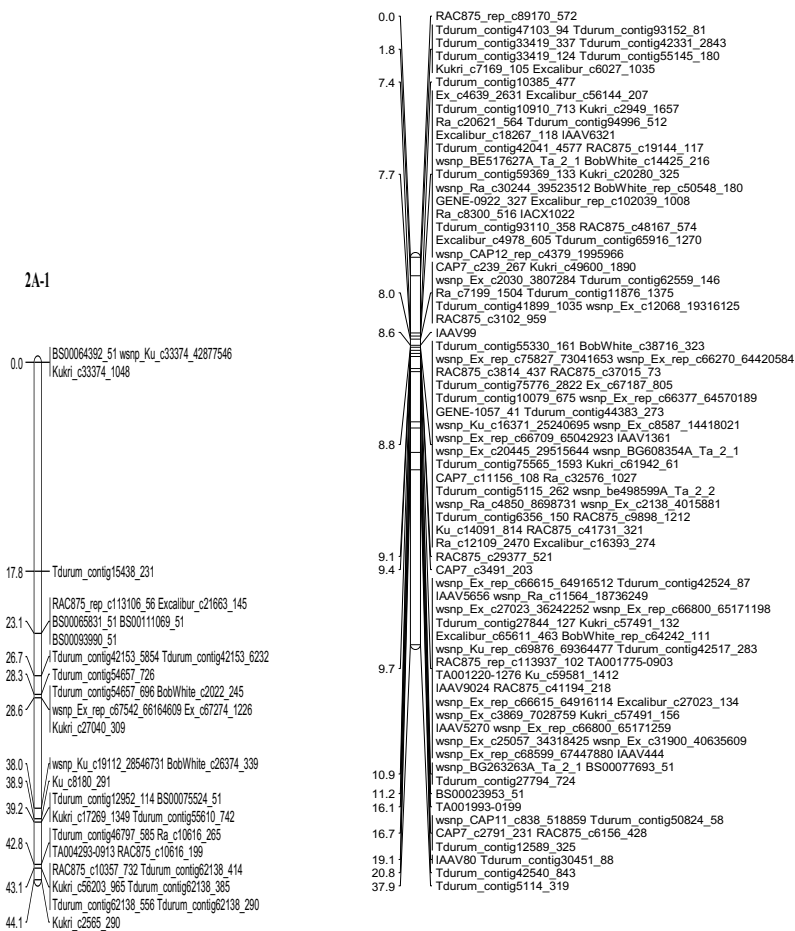


1B-1

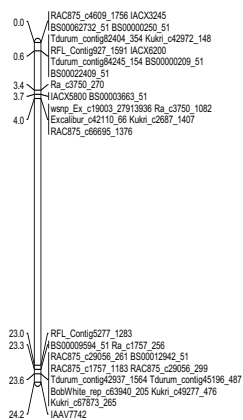
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	wasp_Ex_c21198_30326388 wasp_Ex_rep_c107911_91350930
	Tdurum_contig30517_174
3.3	Tdurum_contig47550_699 Kukri_c7770_176
3.9	BS00039740_51
4.5	Excalibur_c14911_466 Excalibur_c14911_976
4.6	BS00003934_51 IACX6064
5.4	RAC875_c55891_712
7.5	BS00062880_51 Tdurum_contig604_71
	Tdurum_contig65620_277
7.8	BS00062724_51
8.2	IAAV420
8.5	BS00075248_51
	Excalibur_c12015_118 wasp_Ex_rep_c107911_91350866
8.7	Kukri_c39698_228 Tdurum_contig11720_924
	Excalibur_c5149_1789 wasp_Ex_c7585_12957020
9.3	Tdurum_contig13117_1316
9.6	IAAV2883 IACX6346
11.1	Tdurum_contig69792_167 Tdurum_contig11896_550
	Kukri_c9752_793
11.4	BS00076394_51
	Kukri_c5336_365 BS00078029_51
12.4	Kukri_c7687_986 BS00022551_51
	Excalibur_c15617_425 IACX259
	Kukri_c1832_624
12.7	BS00063336_51 Kukri_c11547_1526
	IACX2852 RFL Contig7_380
	BS00001048_51 BS00042244_51
	wasp_Ex_c5378_11087794 Ku_c6909_1766
13.2	BS00010436_51 RAC875_c100059_123
	Kukri_rep_c112383_588 wasp_Ex_rep_c71376_70138381
	BobWhite_c17644_456 BobWhite_c17544_112
	wasp_Ex_c5378_11086366 BobWhite_c39656_106
	Tdurum_contig30536_132 CAP7_c1137_53
15.1	Tdurum_contig27880_478
15.7	BS00062607_51
16.6	Excalibur_rep_c107047_679
	Tdurum_contig96049_200 IACX886
	BS00064162_51 Tdurum_contig27843_281
	BS00022775_51 RAC875_c25957_154
	Kukri_c13978_132 Excalibur_c44818_109
16.9	RAC875_c39401_229 RFL Contig176_1111
	Tdurum_contig85180_99 RFL Contig2176_1163
	RFL Contig2176_932 Excalibur_rep_c107047_469
	Excalibur_rep_c107047_93 BS00023071_51
	Excalibur_rep_c107047_605
18.1	Excalibur_rep_c107047_742 RAC875_c16753_1063
20.3	BS00023940_51 RAC875_c61512_173
20.6	BS00023941_51
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	IACX1891 wasp_Ex_c3147_5816957
	RFL Contig736_827 IACX6280
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	Kukri_c19247_53 Kukri_c19247_711
	wasp_BE590634B_Ta_2_5 Excalibur_c93510_360
21.8	RAC875_c47427_235 Excalibur_rep_c96924_116
	Excalibur_c4808_441 BS00063060_51
	Excalibur_rep_c72368_68 BobWhite_c42716_71
	wasp_Ex_rep_c66255_54400455
22.1	RAC875_c47427_75 RFL Contig5937_1677
22.4	BobWhite_c8016_301 BS00110231_51
24.8	Excalibur_c581_547
25.4	BobWhite_c11309_738
25.7	Tdurum_contig7358_157 RAC875_c66649_186
26.4	wasp_Ku_c18227_2749539
27.0	Tdurum_contig49651_227 wasp_Ex_c5296_9365847
27.3	Tdurum_contig5486_99 Tdurum_contig53772_362
	Tdurum_contig1863_130
27.7	Tdurum_contig58553_534
27.8	BS00022411_51 Tdurum_contig57827_460
	BS00022448_51 Tdurum_contig78627_171
	RAC875_c15190_1089 BobWhite_c20621_541
	wasp_Ex_rep_c76209_74462664 BobWhite_c20621_683
28.7	Jagger_c7236_96
29.0	Tdurum_contig43232_811
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	Kukri_c42354_263 Excalibur_c43076_405
29.3	BS00010767_51 wasp_Ex_c15796_2473348
	RAC875_c22587_1053 RAC875_c30786_411
	BS00039135_51 BobWhite_c2844_569
	Tdurum_contig274_114
	CAP12_c544_164 Excalibur_c56999_109
29.6	RAC875_c50684_155 JD_c3082_514
	Tdurum_contig16506_648 Tdurum_contig15410_446
	TA001769-0538 Kukri_c51735_79
29.9	RAC875_c42275_224 BobWhite_c36862_84
30.0	Excalibur_c57496_271
30.3	IAAV2819
30.9	BS00089700_51 tpb0053e09_1284
	RAC875_c38646_985 Tdurum_contig42491_666
	RAC875_c17188_1696 TA00262-0954
36.0	GENE-0371_208 Excalibur_rep_c67747_629
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41.7	RAC875_c15593_1421 Excalibur_c96904_336
	wasp_CAP11_c1902_1022590
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	Jagger_c3757_131 Excalibur_c5885_701
	wasp_RFL Contig39511_4390396 Tdurum_contig28853_142
42.0	BS00010244_51 Tdurum_contig28675_275
	BS00021934_51 RFL Contig1823_1044
	Tdurum_contig28675_228 BS00070285_51
	BobWhite_c2817_167 Tdurum_contig1216_942
	CAP7_c199_62
42.2	Tdurum_contig8580_1119 Tdurum_contig8580_1285
42.5	BS00035267_51 Tdurum_contig61829_706
	BS00068077_51
	Kukri_c25612_53 wasp_Ex_c13878_21738866
42.9	Tdurum_contig13516_251 IAAV565
	Excalibur_c56748_525
	Tdurum_contig13136_1017 RAC875_c36980_248
	Tdurum_contig8840_575 Tdurum_contig13136_1383
43.4	BS00061472_51 Tdurum_contig12518_200
	BS00023173_51 BS00028476_51
	Tdurum_contig8840_237 wasp_RFL Contig395_4387107
43.8	Tdurum_contig13136_546
	CAP11_c2882_176 Tdurum_contig13136_537
44.1	Tdurum_contig13136_1089 Tdurum_contig13136_1527
	Tdurum_contig9708_121
44.9	BobWhite_c44460_821 BS00071893_51
45.3	RAC875_c35927_554
45.6	TA004059-0492 BobWhite_c39901_338
45.9	Tdurum_contig47566_256
46.8	BS00079088_51
47.4	Tdurum_contig19203_152
48.0	Tdurum_contig68980_317 Tdurum_contig68980_524
48.3	RAC875_c1073_239
49.0	TA003411-0983
50.2	Tdurum_contig13250_137
51.4	Tdurum_contig57153_1356
51.7	CAP12_c590_300
52.0	Tdurum_contig57153_1439 GENE-0063_68
53.5	Tdurum_contig29087_528 Tdurum_contig29087_757
53.8	Kukri_c18230_1633
55.7	Tdurum_contig29059_185
	IAAV5949
57.6	wasp_CAP11_rep_c4138_1957291 Kukri_rep_c103550_213
	CAP6_c7552_330 wasp_CAP11_rep_c4138_1957470
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57.8	Tdurum_contig4904_2923 Ex_c4436_1947
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63.6	IACX11266
63.9	IAAV3040
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73.7	BS00024107_51 RFL Contig785_535
	BobWhite_c54125_183 BS00033776_51
	Tdurum_contig11959_3220 Tdurum_contig41999_2908
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	Tdurum_contig52086_129 Excalibur_c35289_64
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74.6	BS00063302_51 CAP11_c7969_315
77.1	Tdurum_contig10099_538
77.4	Tdurum_contig44851_593 Excalibur_c55186_73
77.7	wasp_Ku_c26281_3624389
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	Kukri_c94813_316 Kukri_rep_c111174_132
	RAC875_c5862_307 Tdurum_contig1651_240
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	Tdurum_contig490509_456 Kukri_c94613_637
	Kukri_rep_c110309_69
	Tdurum_contig97527_318 Excalibur_c55186_277
	BS00010807_51 wasp_Ex_c750_1474351
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2A-2

2A-1

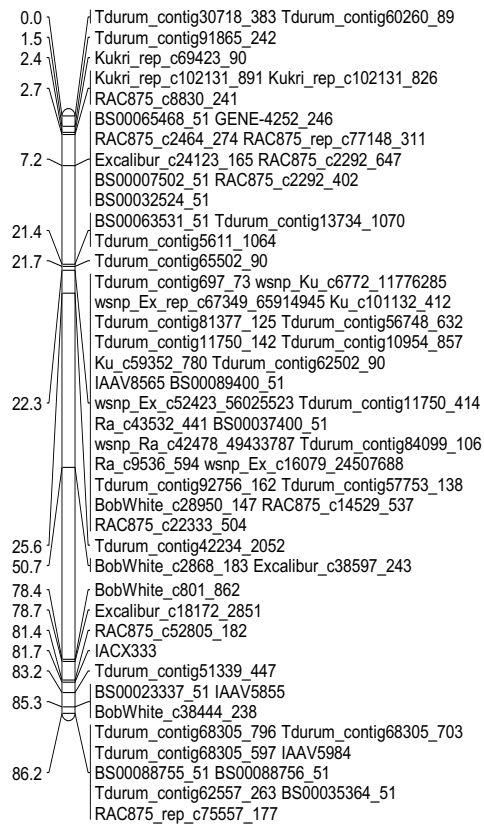


2A-3

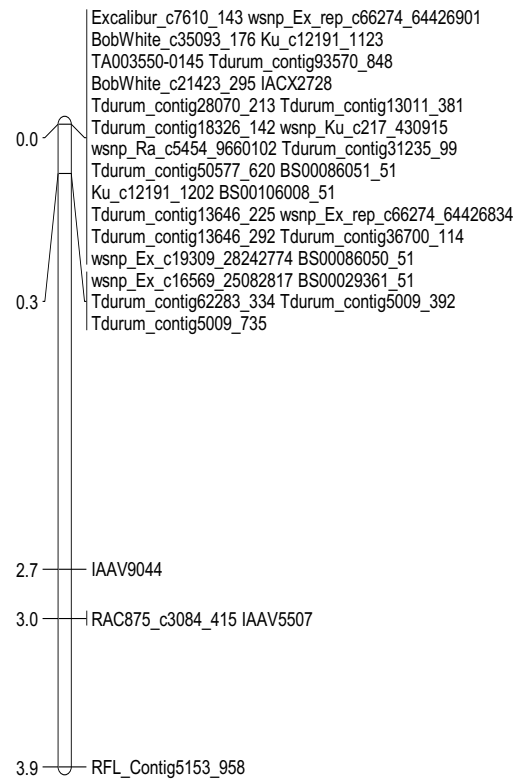


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Tdurum_contig51443_364 BobWhite_c3448_80
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Tdurum_contig7495_799
2.1 RAC875_c15228_108 RAC875_c61801_299
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RAC875_c34516_70 Tdurum_contig6194_412
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Tdurum_contig27876_414 Excalibur_c8502_387
BobWhite_c10578_272
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Tdurum_contig9716_2337 Tdurum_contig9716_1460
Tdurum_contig9716_229
4.2 Tdurum_contig30680_120 RAC875_c62278_69
RAC875_c22429_249 Kukri_c12368_82
Tdurum_contig45255_3473 Kukri_rep_c59803_82
4.8 Tdurum_contig5056_173
5.1 Kukri_rep_c101093_572
wsnp_Ex_c6099_10674508 Kukri_c59585_560
Tdurum_contig91293_131 Kukri_c2565_1405
5.4 Tdurum_contig94176_65 wsnp_Ex_c6099_10674406
wsnp_Ra_c8489_14382125
Kukri_c25843_689 RAC875_c6751_609
Kukri_c44_1476 RAC875_rep_c99492_65
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Ku_c68578_524 JD_c11869_1297
12.8 RFL_Contig996_350
13.1 Tdurum_contig2458_179
13.4 BobWhite_c5511_323 BobWhite_c1611_1365
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16.9 Kukri_rep_c104810_341 Ku_c2387_1855
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19.0 RAC875_c2566_447
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36.6 BS00041921_51 RAC875_c7827_218
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39.9 wsnp_JD_c4699_5834958 Kukri_c42244_809
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57.3 Tdurum_contig12836_418
62.7 Tdurum_contig26542_457
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63.3 Tdurum_contig26490_434 Tdurum_contig11730_153
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63.6 Tdurum_contig2945_83 Tdurum_contig2945_155
Tdurum_contig2945_75
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98.4 Tdurum_contig12879_1273
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101.5 JD_c9115_954
104.5 Tdurum_contig64795_432
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106.6 Tdurum_contig14007_918 Kukri_rep_c68903_708
Jagger_c6844_121
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Tdurum_contig28113_390 Kukri_rep_c68903_301
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108.1 BS00065471_51 BS00009537_51
109.0 Excalibur_c32980_169 D_GCEBAKX01DS17J_273
110.9 BobWhite_c13525_262 Kukri_c57014_168
111.5 Excalibur_c33221_681
111.8 Tdurum_contig77036_338
113.3 Excalibur_c18165_395 BobWhite_c10539_201
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113.9 Ku_c3478_1035
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114.2 wsnp_Ex_c12223_19533158 IAAV1776
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BS00030361_51 wsnp_Ku_c48694_54811376
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121.1 RAC875_rep_c114621_200 Excalibur_c37727_66
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Kukri_c50391_219 Excalibur_c9752_289
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GENE-1355_266 GENE-0995_82
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Kukri_c78358_129 Jagger_c7688_98
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BS00011047_51 BobWhite_c32310_268
134.6 RFL_Contig2751_1562
136.8 Kukri_c79633_88 Excalibur_rep_c109577_191
136.1 Excalibur_c7571_985
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Excalibur_c12675_1147 Excalibur_c48404_59
Excalibur_c2993_457 wsnp_Ex_c15646_23969140
Kukri_c3501_1175 Kukri_c84752_127
Kukri_c60352_344 CAP7_c2746_331
Tdurum_contig10295_973 IAAV5401
Tdurum_contig21786_270 wsnp_Ex_c73454_71499715
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Excalibur_c25761_232 Excalibur_c28710_490

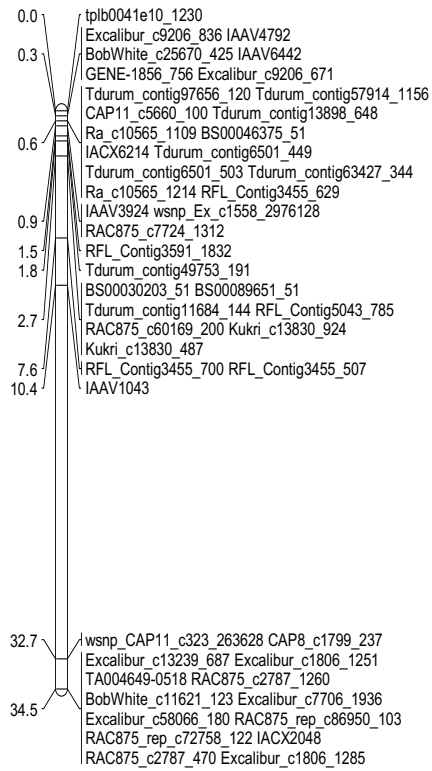
3A-1



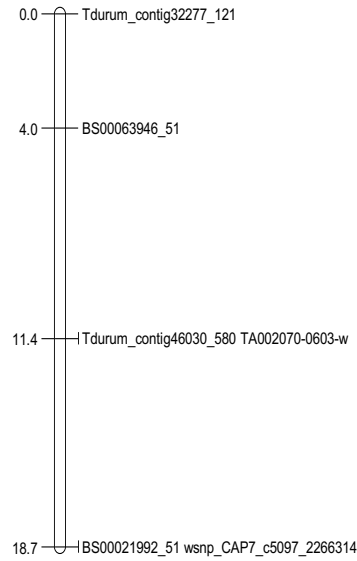
3A-2



3B-1



3B-2

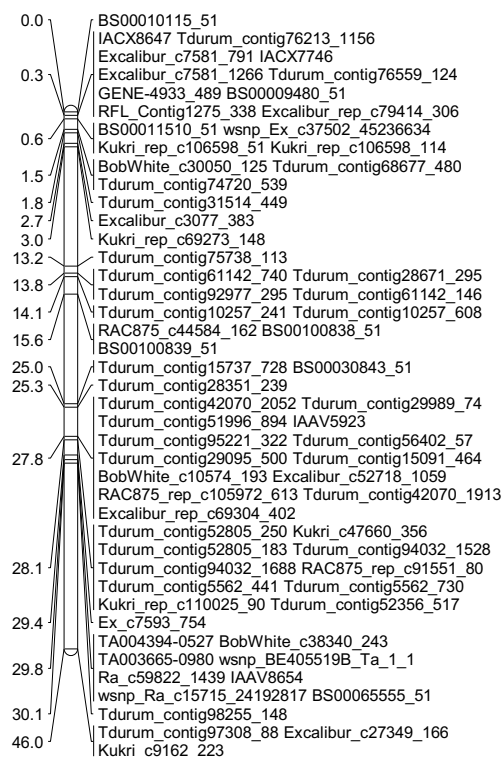


Phylogenetic tree showing relationships between various plant accessions. The tree is rooted at the top and branches downwards. The y-axis represents genetic distance with markers at 0.0, 0.3, 1.2, 5.1, and 5.4. Accessions are labeled at the tips of the branches.

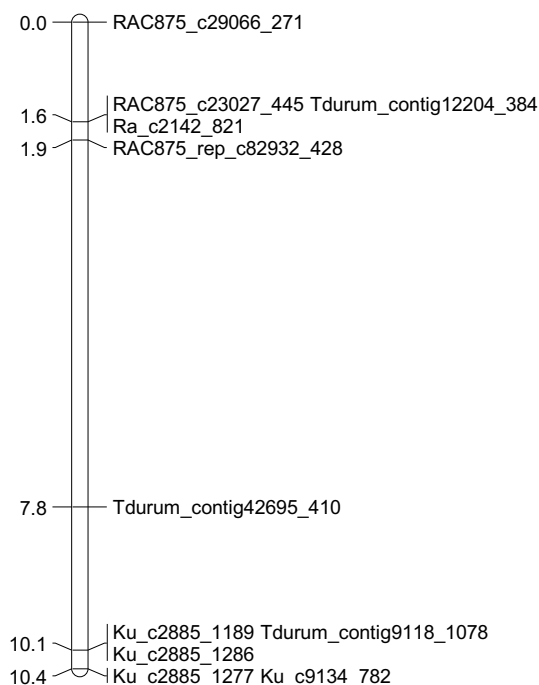
Accessions and their corresponding genetic distance markers:

- 0.0: Tdurum_contig47292_309
- 0.3: RAC875_c13406_65 RAC875_c35955_210
Tdurum_contig31097_254 Kukri_c37097_1849
Kukri_c38065_217 RAC875_c13406_329
Tdurum_contig97388_456 Kukri_c21041_263
Tdurum_contig12530_278
BS00085966_51 Tdurum_contig51355_470
RAC875_c13425_393 Excalibur_c45326_479
- 1.2: Tdurum_contig51355_601 Jagger_c3814_160
wsnp_RFL_Contig3524_3689801 TA005589-0861
Tdurum_contig51355_456
- 5.1: TA004381-1229 Excalibur_c29314_719
RAC875_c58399_104
- 5.4: RAC875_c48860_106

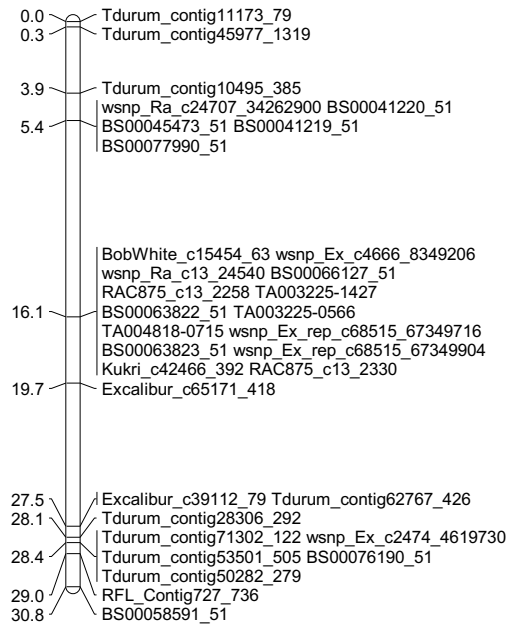
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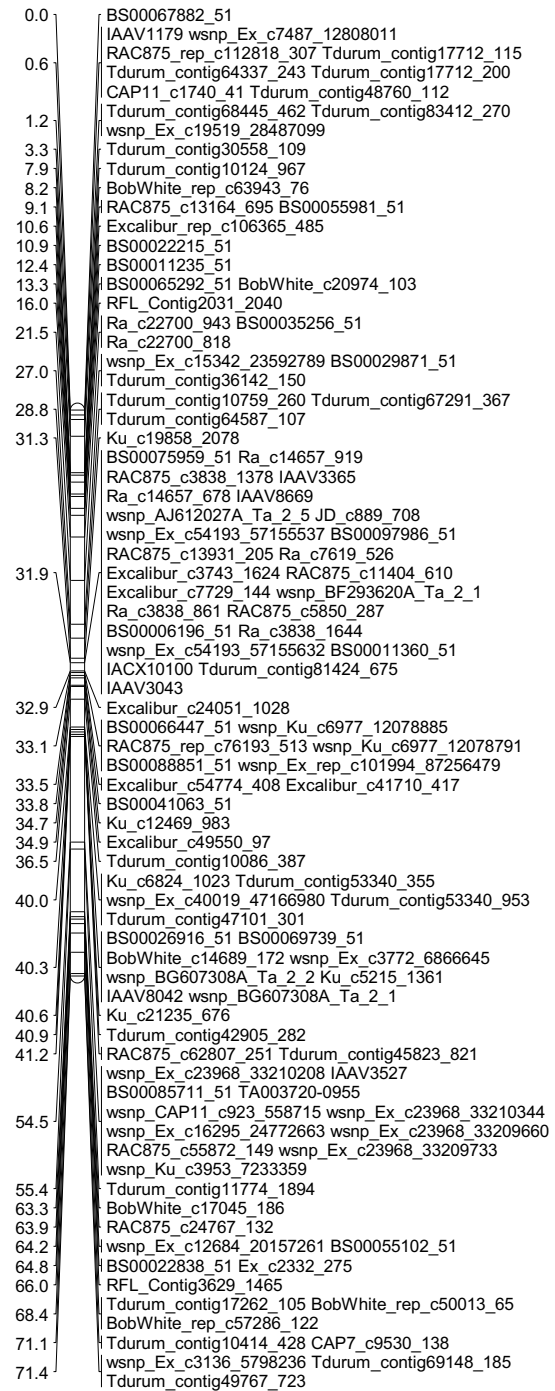
4B-2



5A-1



5A-2



0.0 | Excalibur_c47452_183
 0.6 | Excalibur_c22465_625 BobWhite_c16775_503
 0.9 | Kukri_rep_c95804_93
 RAC875_c39204_91
 Excalibur_c25026_175 BS00102828_51
 wsnp_CAP11_rep_c4382_2067038 BS00067985_51
 1.2 | tpb0060p09_735 BS00079166_51
 IACX5872 Kukri_c60115_164
 BobWhite_rep_c63710_181
 6.4 | BS00062280_51
 BS00067550_51 RFL_Contig1899_2863
 7.0 | BS00083715_51 wsnp_Ex_c2459_4591587
 Excalibur_rep_c102143_58 wsnp_Ex_c56629_58677561
 wsnp_Ku_rep_c103274_90057407 BS00022525_51
 wsnp_Ex_rep_c68504_67334656 Tdurum_contig14130_315
 7.3 | Tdurum_contig14130_245 BS00063476_51
 wsnp_Ex_c33932_42333941 RAC875_c28831_558
 wsnp_Ex_c831_1625061 RAC875_rep_c106241_304
 8.5 | Tdurum_contig44048_276 wsnp_JD_c1845_2564931
 BobWhite_c137_203 wsnp_Ex_c37410_45162932
 BS00080746_51 wsnp_Ex_c37410_45162707
 10.0 | JD_c51907_59 Ex_c37410_1026
 BS00064042_51
 25.7 | wsnp_Ex_c26252_35497729
 31.6 | RAC875_rep_c74170_236
 32.5 | BS00068592_51
 34.7 | RAC875_c16827_292 Tdurum_contig44985_304
 37.1 | Kukri_c51_98
 38.3 | Tdurum_contig11649_320
 Kukri_rep_c101981_260 RAC875_c53903_318
 Ku_c33217_323 wsnp_RFL_Contig4574_5416228
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 Kukri_c11815_706 wsnp_Ex_rep_c66667_64981526
 Tdurum_contig68343_339 RAC875_c38511_91
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 wsnp_Ex_c47152_52446529 Tdurum_contig41907_1014
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 66.0 | Ku_c1083_1261
 66.3 | wsnp_Ex_c19724_28721580
 wsnp_Ra_c26091_35652620 Jagger_c3110_214
 68.4 | Kukri_rep_c103253_565
 wsnp_Ex_c7244_12439355 Ra_c22877_813
 73.8 | Excalibur_c8675_1550 IAAV547
 Excalibur_c9846_678 IAAV613
 85.6 | wsnp_Ex_rep_c66358_64543089 RAC875_c19099_434
 RAC875_c19099_308
 86.1 | BS00042014_51 Ex_c5594_2630
 86.5 | CAP7_c1155_57
 103.9 | Tdurum_contig49576_898
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 Kukri_c17396_2448 Kukri_c90424_72
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 Ra_c38583_333
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 BobWhite_c27244_211 Excalibur_rep_c105399_213
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 RAC875_c10139_336 BS00044388_51
 RAC875_c42281_475 Tdurum_contig61623_570
 Tdurum_contig63272_105 Tdurum_contig61623_129
 BS00067696_51 RAC875_c91986_410
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 RAC875_c8757_589 CAP12_c703_150
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 CAP7_c12729_232
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 BS00012038_51 BS00067841_51
 111.2 | Excalibur_c33675_410 Tdurum_contig63997_587
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 wsnp_Ex_c8322_14030310 Ku_c11429_519
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 BS00109560_51 Tdurum_contig16866_148
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 Tdurum_contig10268_1000 Tdurum_contig11228_274
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 Tdurum_contig58669_273 Tdurum_contig29319_256
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 BS00062762_51
 118.6 | BS00022673_51
 123.1 | Kukri_c6176_1400
 124.3 | Tdurum_contig28353_1628 Tdurum_contig28353_1720
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 Tdurum_contig47512_972 Tdurum_contig70651_234
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 16.6 | Kukri_c46676_324 Kukri_c13870_154
 16.9 | BobWhite_c26082_239
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 CAP11_c2765_78 RAC875_c20429_421
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 Tdurum_contig10100_659 Tdurum_contig10030_364
 21.4 | Tdurum_contig10100_523
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 23.5 | Tdurum_contig76150_816

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 RAC875_c6135_95 RAC875_c87324_202
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 Tdurum_contig12045_327 Excalibur_c431_1130
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 BS00006619_51 BS00083630_51
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 Tdurum_contig10580_316 BS00025660_51
 Tdurum_contig1990_1324 BS00099853_51
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 Tdurum_contig29823_203 BS00098857_51
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6B-1

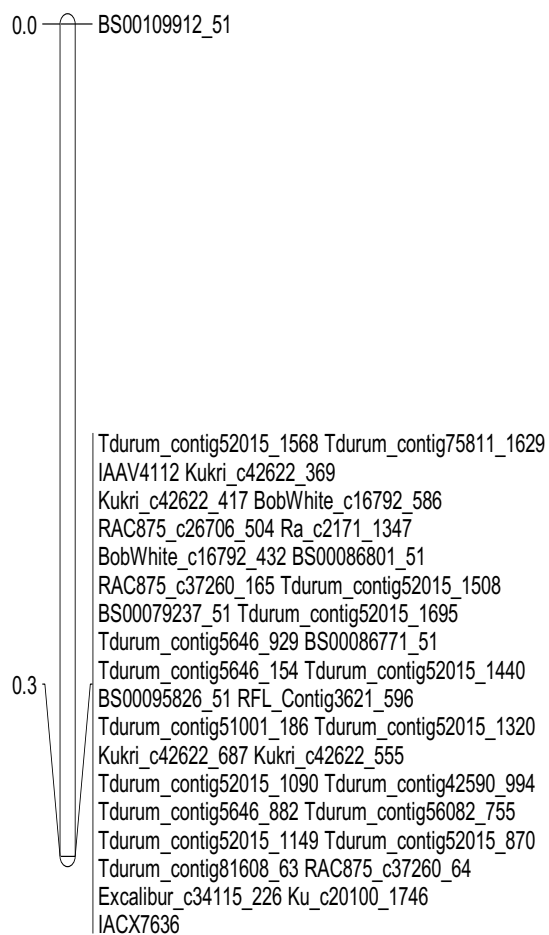
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 Tdurum_contig43538_648
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RAC875_c13949_923 BobWhite_c10614_157
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Tdurum_contig42026_2552
1.5 | Tdurum_contig98106_715 GENE-3171_203
1.8 | Tdurum_contig21737_203 Tdurum_contig41980_1727
wsnp_BE488206B-Ta_2_1 BS00047344_51
IAAV1520 Tdurum_contig41980_2722
GENE-4197_99 Tdurum_contig21737_297
Tdurum_contig41980_619 Tdurum_contig46732_711
RAC875_c15225_679 Kukri_c21029_258
2.7 | IAAV8128 BS00012093_51
Tdurum_contig56197_370 wsnp_Ex_c24963_34217997
RAC875_c25672_473 BS00003214_51
Tdurum_contig14046_364 wsnp_Ex_c34962_43193869
Tdurum_contig9713_488 GENE-4231_195
Tdurum_contig41980_2283 wsnp_CAP8_c7510_3461645
wsnp_Ra_c18735_27835674
3.0 | BobWhite_c1905_58
3.3 | RFL Contig584_291
RAC875_c4710_1109 Tdurum_contig54967_722
4.2 | wsnp_Ex_c18382_27210656 Tdurum_contig28832_337
Tdurum_contig51676_120
BS00107795_51 wsnp_Ex_c25505_34771897
Tdurum_contig6121_545 Kukri_c3019_865
4.5 | BobWhite_rep_c65994_267 RAC875_c14852_2171
RAC875_c14852_693
BS00067297_51
5.7 | BobWhite_c23142_415 wsnp_Ra_c57648_59682822
6.6 | wsnp_Ex_c11873_19047792 wsnp_Ku_rep_c103569_90279488
Kukri_c8643_712 wsnp_Ex_c1319_2522682
wsnp_Ex_c19707_28702378 RAC875_c70_598
BobWhite_c9563_377 RAC875_c7781_531
wsnp_Ex_c21783_30944914 BS00047254_51
CAP8_c4223_13 BS00074947_51
6.9 | Kukri_c20523_1008 wsnp_Ex_c50022_54446632
wsnp_Ex_c9948_16379867 wsnp_CAP11_c1724_940246
RAC875_c14390_1004 Kukri_c25907_549
RAC875_c10122_113 RAC875_c47082_516
wsnp_Ra_c24962_34524602 BS00063174_51
RAC875_c35008_398 Kukri_c30551_400
wsnp_Ex_c6466_11234080 wsnp_Ex_c46392_51913200
Excabur_c36650_1557
Tdurum_contig2087_1941 BS00021705_51
lpt005912_800 wsnp_Ex_rep_c77942_74309566
Excabur_c44109_144 RAC875_c24962_294
Kukri_c16448_488 Excabur_rep_c111646_110
Excabur_c18182_464 Excabur_c28771_400
7.2 | Excabur_rep_c90986_76 RAC875_c77_1176
IAAV4863 Kukri_rep_c70223_400
BS00058305_51 CAP8_c1851_62
BS00076093_51 RAC875_rep_c77222_293
Kukri_rep_c68690_52 TAD02708-2689
RAC875_rep_c110037_401 CAP11_c763_391
RAC875_c95029_92 wsnp_Ex_c101703_87021883
wsnp_Ex_c3858_7011837 Kukri_c31481_1478
Kukri_c9507_495 BS00095516_51
BS00071912_51 IAAV3811
RAC875_c34604_142 wsnp_Ex_c1398_2677127
Excabur_c7823_397 wsnp_JD_c2691_3617481
Excabur_c15870_1331 RAC875_c7110_2706
wsnp_JD_c5591_6743599 Excabur_c11726_1432
Tdurum_contig31398_195 BobWhite_c8571_699
Ku_c35629_568 wsnp_Ex_c16446_24946960
wsnp_Ex_c23122_32350412 JD_c2691_2947
JD_c2691_2946 Ku_c1189_1439
wsnp_Ex_c5334_9427658 wsnp_Ex_c44857_50804565
wsnp_Ex_rep_c103517_89455567 BobWhite_c23946_75
Jagger_c556_473 Ra_c26497_381
BS00080317_51 wsnp_Ex_c1398_2676484
8.1 | Kukri_rep_c68962_1971 BS00066278_51
BS00078552_51 BS00082760_51
Excabur_rep_c84475_162 Kukri_c10200_286
D_GBB4FNX0180N8_336 Tdurum_contig71266_87
BS00026203_51 wsnp_Ra_c11942_19247699
wsnp_Ex_c8843_14783989 wsnp_Ex_c4180_7550457
Kukri_c5598_140 wsnp_Ex_c5334_9427824
Ku_c47744_1073
8.7 | BobWhite_c27318_380 Excabur_c6416_1712
Kukri_rep_c105243_341 Tdurum_contig2089_821
Excabur_c90130_313 GENE-0659_105
9.0 | Kukri_c63145_262 Tdurum_contig29294_171
TAD05016-0827 BS00049942_51
9.3 | GENE-4195_165 RAC875_c26887_562
Tdurum_contig45370_704
Tdurum_contig77234_467 Tdurum_contig4592_327
Kukri_c54_306 wsnp_Ex_c34011_42398362
9.6 | IAAV1460 RAC875_c54671_199
BS00067836_51 BobWhite_c11301_226
RAC875_c26487_145 Tdurum_contig19057_245
wsnp_Ex_rep_c67012_6545341 RAC875_rep_c107515_508
IACX4889 BS00064820_51
RAC875_c47035_70
9.9 | Excabur_c15335_197
Tdurum_contig46985_1385 BS00022192_51
11.6 | wsnp_CD452643B-Ta_2_1 IACX6349
12.0 | BS00067073_51
Tdurum_contig13698_141 Ku_c106365_329
wsnp_Ex_c6401_11124940 wsnp_Ex_c6401_11124462
wsnp_Ex_c6401_11124752 wsnp_Ex_c6401_11124623
12.2 | Excabur_c22075_166
12.8 | Tdurum_contig29807_324
16.2 | BS00073906_51
16.5 | Tdurum_contig48158_878 Tdurum_contig9531_176
17.4 | RAC875_c4420_1155 Tdurum_contig20987_1271
RAC875_c4420_371 Tdurum_contig20987_432
BS00069694_51 wsnp_Ex_c6356_11055912
wsnp_Ex_c6356_11055912
21.6 | wsnp_Ex_rep_c71062_69901558 TAD01478-0609
Tdurum_contig42203_3670 wsnp_Ex_c15785_24157360
Kukri_rep_c71164_191 Ra_c18663_2473
21.9 | Tdurum_contig26001_242
Tdurum_contig31348_217
23.1 | Tdurum_contig33717_301 Ku_c1151_616
23.4 | Excabur_c18036_53 RAC875_rep_c70998_974
Tdurum_contig2155_472 Kukri_c1151_239
Kukri_c48868_478 Ra_c15317_1538
23.7 | RAC875_c26587_377 Kukri_c48868_346
Excabur_rep_c70364_129 Tdurum_contig77500_369
Tdurum_contig30883_137 Jagger_c1077_98
24.0 | Tdurum_contig93283_513
Tdurum_contig47140_586 Tdurum_contig47140_916
24.6 | Tdurum_contig47140_554
wsnp_Ex_rep_c68452_67273676 wsnp_Ex_rep_c66315_64480362
RAC875_c22078_195 Jagger_c3773_108
TAD06249-0396 IAAV2601
24.9 | wsnp_Ra_c46591_52408053 GENE-0334_11
wsnp_Ku_c11870_19296142 Excabur_c98849_278
Ra_c13513_591 wsnp_Ra_c35443_43984178
wsnp_Ex_rep_c68315_64480670 D_contig19487_399
wsnp_Ex_c24766_34017588
RAC875_rep_c85751_123 RAC875_rep_c85751_268
CAP11_c991_160 Tdurum_contig44173_792
25.2 | Tdurum_contig81414_256 RFL Contig1015_580
Tdurum_contig53469_1413 RAC875_rep_c85751_72
Tdurum_contig97981_70 wsnp_CAP11_c166_172556
Tdurum_contig44173_572
Ex_c3990_102
25.8 | Tdurum_contig55473_381 Tdurum_contig55473_221
Kukri_c65766_78 Tdurum_contig55473_437
Tdurum_contig47289_904 Tdurum_contig10489_1207
26.7 | Tdurum_contig76550_500 Tdurum_contig76550_723
Tdurum_contig55197_627
27.0 | wsnp_Ku_c16522_25426455
Kukri_rep_c107419_372 IACX415
27.3 | Tdurum_contig4437_377 Tdurum_contig54437_165
BobWhite_c2627_193 Tdurum_contig53125_1716
28.5 | Tdurum_contig74717_436 Tdurum_contig74717_297
Kukri_c51690_247
wsnp_Ex_c9750_16105678 Tdurum_contig48727_691
28.8 | wsnp_BE490200B-Ta_2_1 Excabur_c4084_408
Tdurum_contig44625_307
29.1 | Tdurum_contig57255_86
29.7 | wsnp_CAP11_c1432_506102 Tdurum_contig94541_217
31.2 | Tdurum_contig31036_96
38.6 | BS00063780_51
RFL Contig387_1410 BS00010993_51
BobWhite_c3392_749 Excabur_c32739_698
38.9 | CAP12_c475_289 GENE-4221_519
BobWhite_rep_c53133_385 IACX4538
IACX1609
39.2 | RAC875_c13325_109
40.4 | BS00011479_51
40.7 | GENE-4221_94

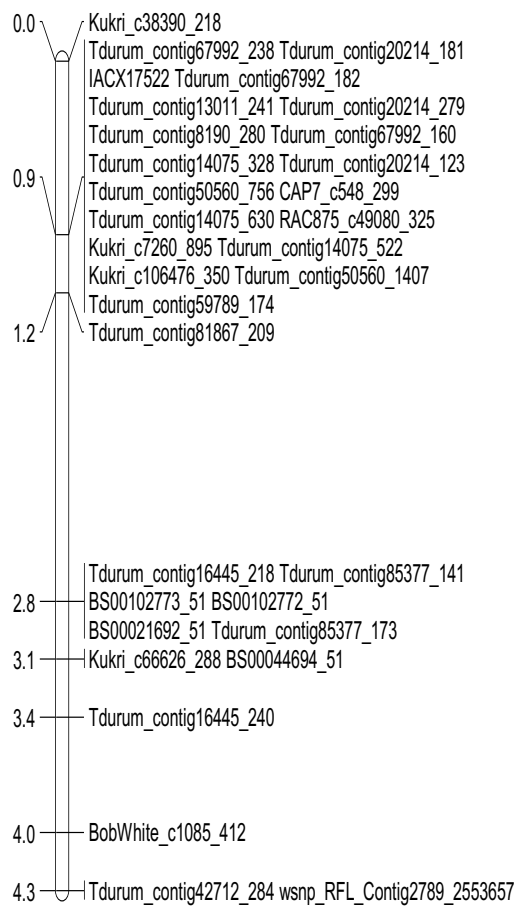
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0.0 | RAC875_c21492_506
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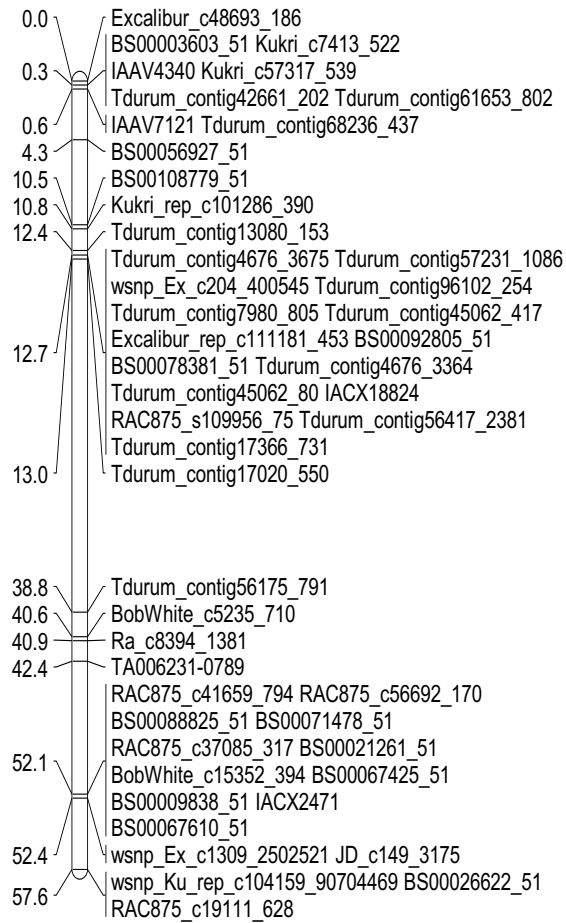
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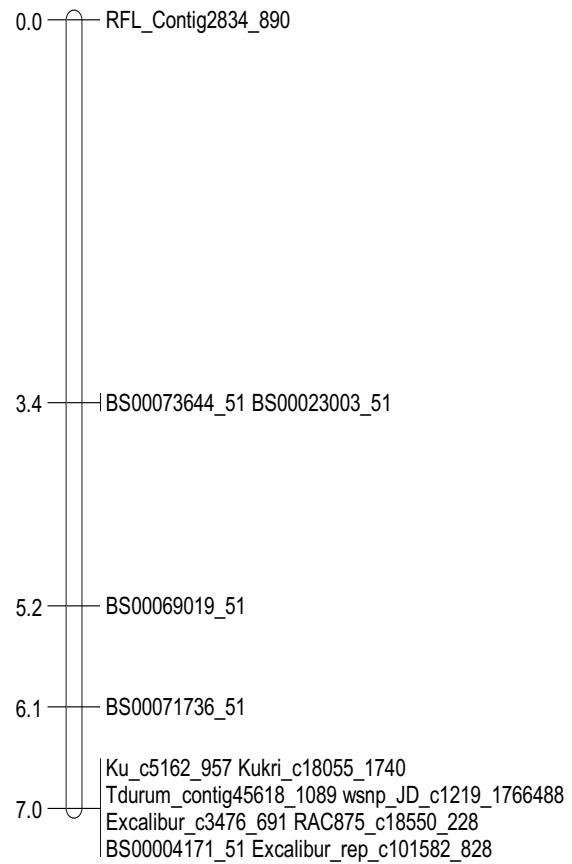
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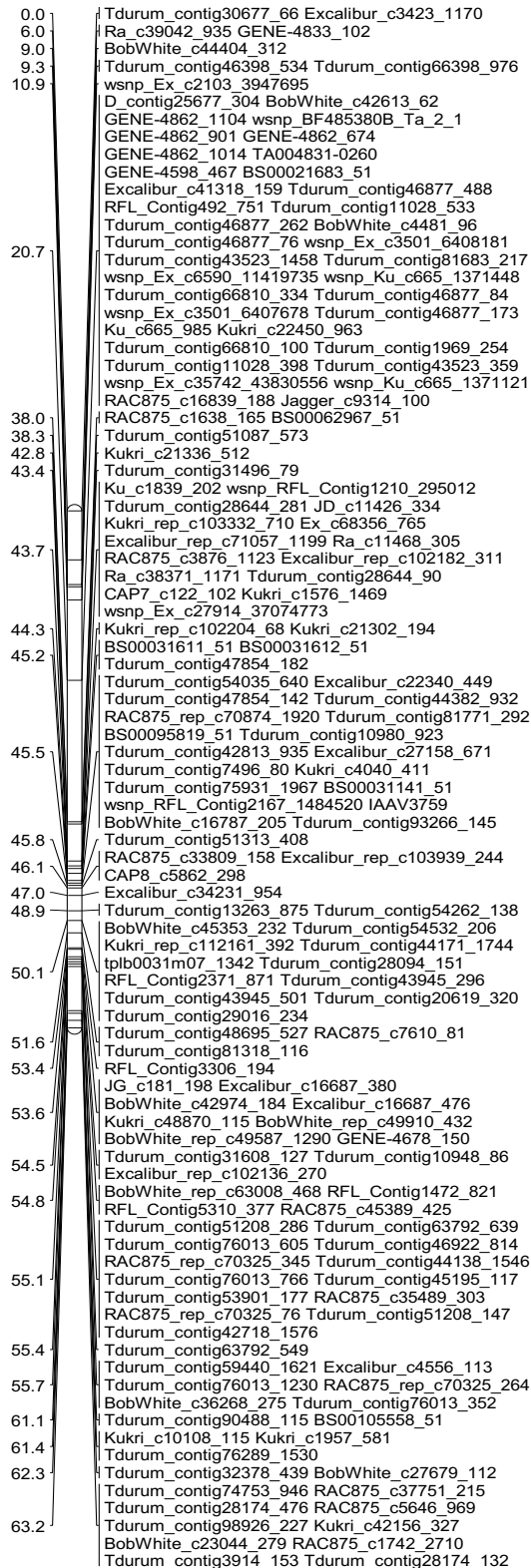
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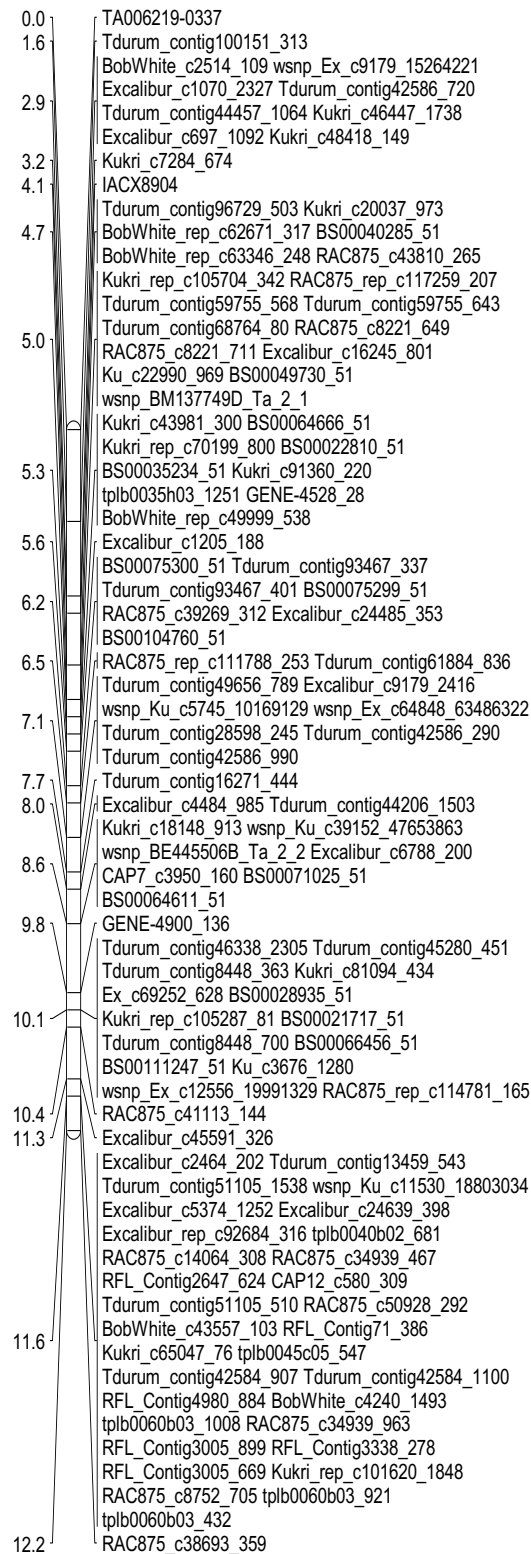
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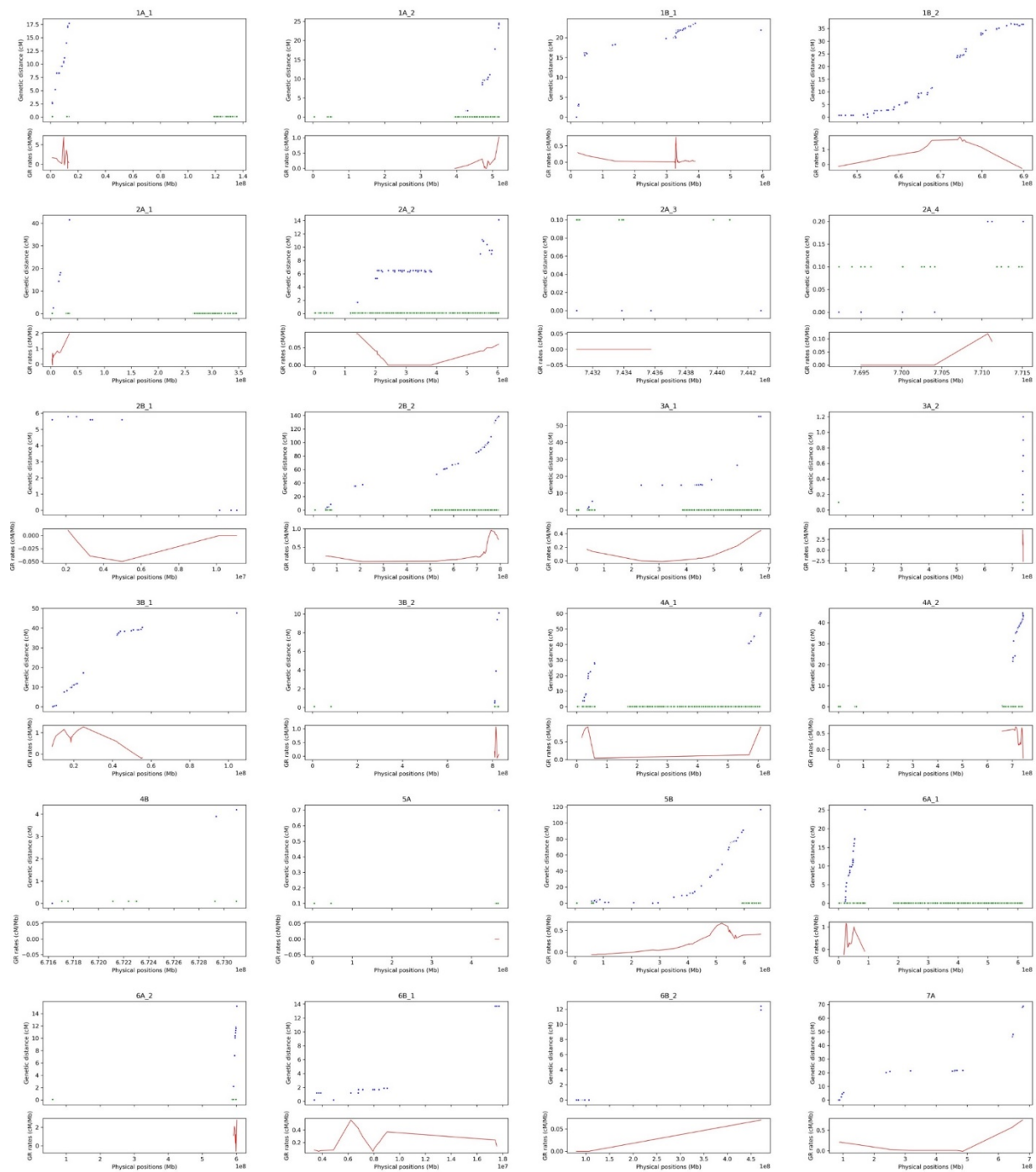
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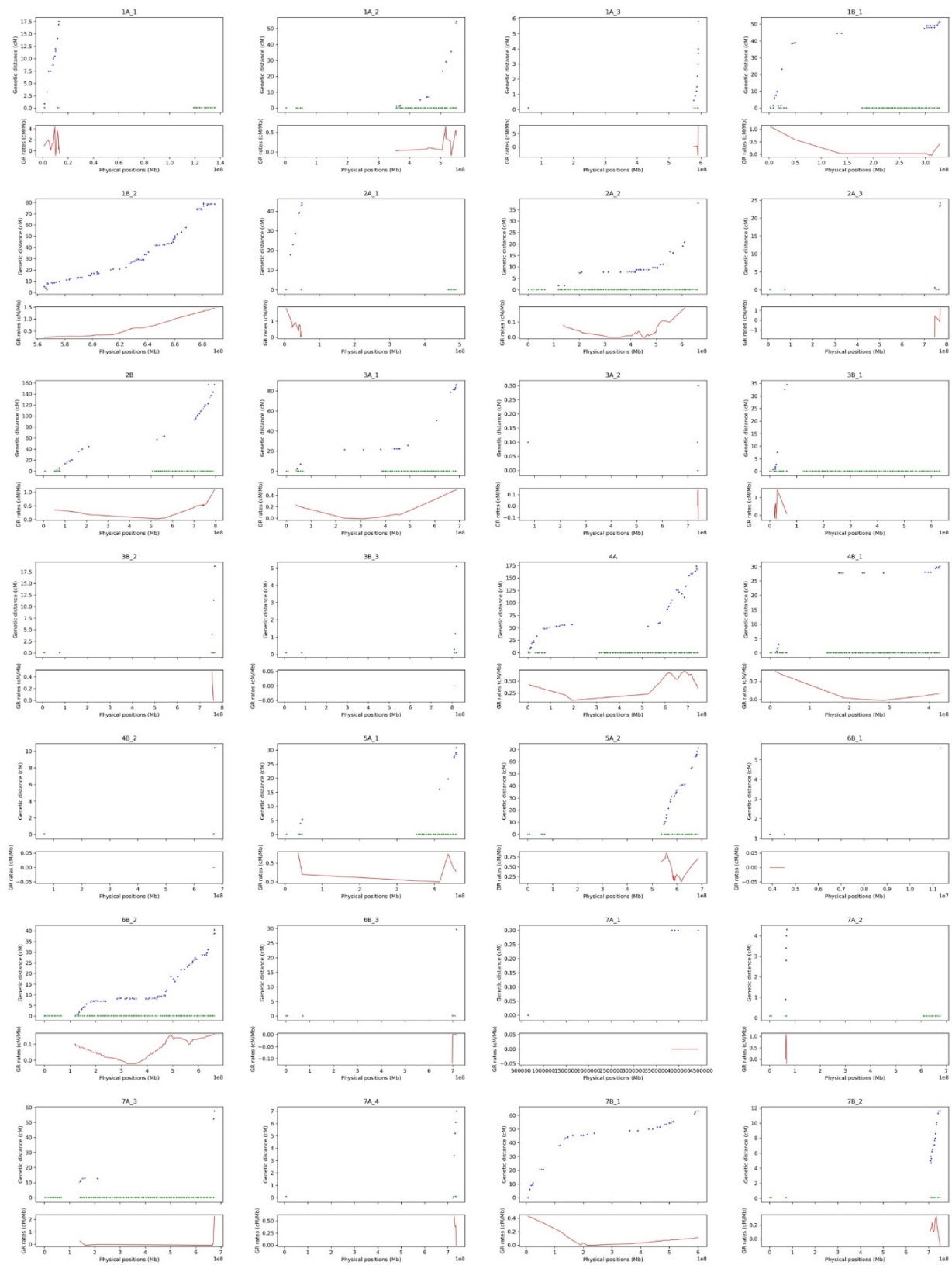
Appendix E. Graphical representation of the correlation of genetic and physical maps, the estimated local recombination rates along with their distribution in chromosomal rearrangement regions. In scatter plots, the red dots represent the genetic and physical positions of markers. The red curves below the plots represent the estimated local recombination rates. The dark green color dots represent the distribution of monomorphic markers. (a) Pop1 (Langdon/W9262-260D3). (b) Pop2 (W9262-260D3/Langdon triticales). (c) Pop3 (DGE-1/W9262-260D3)

(a) Pop1 (Langdon/W9262-260D3)

(b) Pop2 (W9262-260D3/ Langdon triticale)



(c) Pop3 (DGE-1/W9262-260D3)



Appendix F. List of monomorphic markers for population Kofa/W9262-260D3

Marker	addressID
RAC875_c4190_132	59758401
RAC875_c75971_295	25631432
TA004380-0460	67792422
BS00009594_51	44697487
BS00062973_51	33737382
BS00049378_51	39607454
BS00049380_51	61610509
Ex_c2510_477	13722404
Ex_c68194_1532	46668306
Ex_c68194_1994	25801482
Ex_c69493_1208	43695481
Excalibur_c11587_340	50622494
Excalibur_c19649_1500	23721483
Excalibur_c31737_169	29729500
Excalibur_c37804_518	50736323
Excalibur_c5064_284	62807393
Excalibur_c5064_765	65768418
Excalibur_c55781_129	11606452
Excalibur_c6807_1155	40738459
Excalibur_c6807_464	64603469
Excalibur_rep_c67411_210	33746434
Excalibur_rep_c68194_2117	67740381
IAAV3303	23791425
IAAV5350	20649347
IACX2626	27678322
Jagger_c4502_69	15729380
Jagger_c8496_87	33701304
Kukri_c12442_454	14747487
Kukri_c24669_51	54628360
Kukri_c56872_402	38736362
Kukri_c6552_4243	61731436
Kukri_c920_128	49746473
Kukri_c920_1379	37659475
Kukri_c920_319	40810353
Kukri_rep_c68360_1476	59769389
Kukri_rep_c69169_334	35796490
Ra_c108387_863	48639424

RAC875_c12803_916	15656459
RAC875_c14316_584	41787359
RAC875_c36614_344	26732392
RAC875_c54947_108	56606486
RAC875_c66657_91	26670489
RAC875_c7540_366	32777424
RAC875_rep_c70342_1644	41788484
RFL_Contig1987_3440	27761507
RFL_Contig4856_71	34718405
Tdurum_contig25602_212	30707403
Tdurum_contig42095_3235	71652407
Tdurum_contig49532_368	51694508
wsnp_Ex_c1758_3326792	71746340
wsnp_Ex_c54998_57670603	40602336
wsnp_Ex_c7203_12370983	44676315
wsnp_Ex_rep_c101342_86720058	42620382
wsnp_Ex_rep_c67411_65994109	60673392
wsnp_Ex_rep_c68194_66973114	33607357
wsnp_Ex_rep_c68194_66973531	39750338
wsnp_Ra_c28955_38371323	53656485
Excalibur_c9472_217	15797348
BS00068508_51	27796468
IAAV5507	63674409
IAAV9044	41806417
RFL_Contig5153_2667	32665376
RFL_Contig5153_958	50708340
BobWhite_rep_c49330_217	28684392
Tdurum_contig28070_129	54697328
wsnp_Ku_c55746_59522526	48780439
Excalibur_c74390_108	32761474
Excalibur_c7897_663	63809408
Excalibur_rep_c114451_411	33747404
Kukri_c6224_492	45759362
Tdurum_contig47603_420	69742472
Tdurum_contig52805_250	19685378
Jagger_c4318_79	20753330
Tdurum_contig28353_1110	10799336
Tdurum_contig28353_1628	45636362
Tdurum_contig28353_1720	36745385
wsnp_Ex_c11309_18272122	47652382

BobWhite_c28547_208	38709509
RAC875_c4632_1681	67762390
BobWhite_c4712_551	61779355
BS00012530_51	19712338
BS00055293_51	56674358
CAP8_rep_c9477_231	12624361
Ex_c66287_325	56675302
Excalibur_c18072_214	70805362
Excalibur_c36398_69	18784373
Jagger_c7132_108	60792421
Kukri_c21943_958	10675375
Kukri_c3044_188	20754468
Kukri_c4125_914	52686506
Kukri_c53345_583	37655454
Kukri_c75566_265	38748455
RAC875_c11183_2580	15710458
RAC875_c25902_594	10702442
RAC875_c33609_381	67791394
RAC875_c34994_183	38710392
RAC875_c44002_166	55601476
RAC875_c44002_81	72648401
RAC875_c58425_110	37655489
RAC875_c67463_324	59775441
RAC875_rep_c71306_1026	66619465
RAC875_rep_c75251_505	14714445
RAC875_rep_c99895_112	37619363
Tdurum_contig12749_284	59626487
Tdurum_contig29467_99	11797329
Tdurum_contig32619_202	22617493
Tdurum_contig43119_297	28660480
Tdurum_contig44853_1539	20747502
Tdurum_contig61970_627	12658420
Tdurum_contig61970_835	43625502
Tdurum_contig62040_1494	28609440
wsnp_CAP11_rep_c4300_2030261	52807336
wsnp_CAP8_rep_c9477_4129165	19785470
wsnp_Ex_c30852_39718945	16609435
wsnp_Ex_c5731_10066430	34795391
wsnp_Ku_c35839_44981841	21721502
wsnp_Ra_c2730_5190076	49702319

Kukri_c17961_503	41733315
Kukri_c9310_156	27733387
wsnp_Ex_c13337_21022658	50735367
wsnp_JD_c5102_6225151	40725336
Excalibur_c15257_57	62675439
Tdurum_contig81911_179	24684303
wsnp_Ex_c13064_20670748	21618398
Excalibur_c44696_475	45636373
BobWhite_c27171_271	72604505
BobWhite_rep_c48906_121	12711504
BS00003625_51	67772463
BS00012481_51	27607388
BS00035335_51	21754500
BS00055427_51	18781448
D_contig20839_555	19643493
D_GB5Y7FA02F13NL_54	53713456
D_GDEEGVY02H602I_267	12713331
Ex_c38233_456	37663385
Excalibur_c100531_251	10737414
Excalibur_c100654_79	10763320
Excalibur_c361_1321	54731445
Excalibur_c57499_268	67804386
Excalibur_rep_c106165_238	29616492
Excalibur_s113077_141	46674365
GENE-1351_273	59664461
GENE-1351_291	11764341
GENE-2541_709	10600471
GENE-3982_189	44719408
IACX11098	35758486
Jagger_c924_124	45672467
Ku_c13347_571	68668491
Ku_c28795_980	53763474
Ku_c9240_650	66638327
Kukri_c24615_385	10753480
Kukri_c55688_361	61739509
Ra_c2227_308	16747381
RAC875_c23241_844	64628346
RAC875_c3084_415	19641484
RAC875_c56111_61	34605348
RAC875_rep_c105489_488	26742378

RFL_Contig2815_1110	55787433
TA006195-0588	60645440
Tdurum_contig10669_1535	16711441
Tdurum_contig10669_1557	50702389
Tdurum_contig10669_1621	59641397
Tdurum_contig14490_593	69639461
Tdurum_contig28233_377	16692469
Tdurum_contig31249_109	71612425
wsnp_Ex_c12369_19731179	20714320
wsnp_Ex_c1988_3742217	46671443
wsnp_Ex_c53843_56941644	11809358
wsnp_Ex_c7907_13427724	56707301
wsnp_Ra_c10658_17500389	20805469