

International Journal of Biochemistry and Biotechnology ISSN 2169-3048 Vol. 9 (3), pp. 001-007, March, 2020. Available online at www.internationalscholarsjournals.org © International Scholars Journals

Author(s) retain the copyright of this article.

Full Length Research Paper

C-banding analysis of chromosome translocations in doubled haploid wheats

Shimelis Hussein*

University of the Free State, Department of Plant Sciences, P.O. Box 339, Bloemfontein 9300, South Africa. Current Address: University of Limpopo, School of Agricultural and Environmental Sciences, Private Bag X1106, Sovenga 0727, South Africa.

Accepted 18 March, 2019

C-banding analysis of plant chromosomes has various applications including construction of karyotypes to identify lines with polymorphic banding patterns, to study structural aberrations and other cytogenetics research. 66 double haploid (DH) lines were produced from crosses of stripe rust susceptible common wheat cultivar 'Plamiet' (*Triticum aestivum*, 2n=6x=42; AABBDD) with resistant cultivar 'Cappelle-Desprez' (CD) characterized with 5B/7B reciprocal chromosome translocations. C-banding analysis was conducted to detect the presences of the 5B/7B translocations among the DH wheat lines. The analysis detected that 35 DH lines were positive and 31 negative for translocations. The differentiated lines will be studied to establish weather previously proposed gene(s) present on the translocated 5B or other chromosome(s) could confer resistance.

Key words: Cappelle-Desprez, C-banding, karyotype, Palmiet, stripe rust, translocation.

INTRODUCTION

The C-banding technique involves staining of all constitutive heterochromatin through denaturationreassociation of DNA, with the highly repetitive DNA reassociating faster and appearing as dark bands (Gill and Kimber, 1974a) . The term C-band is used to describe a pair of laterally adjacent stained dots (which may appear fused as a single dot or band) one belonging to each of the two chromatids comprising each metaphase chromosome. Thus, two adjacent bands consist of two pairs of dots longitudinally juxtaposed. Anonymous (1972) defined a band as a 'part of a chromosome clearly distinguishable from adjacent parts by virtue of its lighter or darker staining ability'. Consequently all dark C-bands should be considered as landmark bands, which are diagnostic in the identification of individual chromosomes (Gill et al., 1991).

The C-banding technique has been used to construct wheat karyotypes. Such karyotypes have been utilized to

identify individual chromosomes (Gill and Kimber, 1974b; Natarajan and Sarma, 1974), to differentiate lines with polymorphic banding patterns (lordansky et al., 1978; Seal, 1982; Endo and Gill, 1984; Friebe and Heun, 1988; Friebe et al., 1988), to study structural aberrations (Endo, 1988; Kota and Dvorak, 1988) and other wheat cytogenetics research. To accomplish these studies in a standardized manner a karyotype and generalized nomenclature has been available illustrating chromosome bands, banding polymorphisms and various structural aberrations for *Triticum aestivum* L. cultivar 'Chinese Spring' (Gill et al., 1991). Well-established C-banding techniques have been described by Lukaszewski and Gustafson (1983), Badaev et al. (1985) and Gill et al. (1991).

Wheat stripe (yellow) rust caused by *Puccinia striiformis* west. f. sp. *tritici* remains the major restrains to wheat productivity. Under severe epidemic conditions it causes a yield loss of 84% or greater (Murray et al., 1994). The use of resistant cultivars against stripe rust is the best strategy. Therefore, identification of new sources of resistance and introgression of the genes into existing susceptible cultivars is compulsory to complement the yield potential.

^{*}Corresponding author. Current address: University of Limpopo, School of Agricultural and Environmental Sciences, Private Bag X1106, Sovenga 0727, South Africa. E-Mail: Shimelis@Ul.ac.za.

A common wheat cultivar 'Cappelle-Desprez' (CD) (T. aestivum L.; 2n=6x=42; AABBDD) is known for its high level of durable stripe rust resistance (Worland and Law, 1986). Various stripe rust resistance genes (Yr) have been identified from CD including Yr3a, Yr4a, and Yr16 (McIntosh et al., 2003). Yr3a and Yr4a confer seedling plant resistance and located on chromosomes 1B and 6B respectively by Chen et al. (1994, 1996). Yr16 is considered to be a durable adult plant resistance (APR) gene that was located on chromosome 2D by Worland and Law (1986). Furthermore, CD carry reciprocal translocations between the short and long arms of chromosomes 5B and 7B i.e. 5BS/7BS and 5BL/7BL (Riley et al., 1967; Seal, 1982). In most West-European wheat cultivars high level of resistance to stripe rust has also been ascribed due to the presence of the 5BS/7BS translocation. The translocation breakpoint was indicated to be near the centromere subsequently the gene(s) on 5BS might be linked or closer to the breakpoint so that chances are high the gene(s) would be transmitted with translocation (Seal, 1982; Law and Worland, 1997). It was thus proposed that translocation itself could be responsible for APR in CD.

Cereal rust workers at the University of Free State (South Africa) made crosses between stripe rust susceptible South African common wheat *T. aestivum* cultivar 'Palmiet' with CD with various genetic

backgrounds. This was in an attempt to introgress Yr16to Palmiet. 66 Doubled haploids (DH) were produced following recombination. Preliminary field and growth chamber tests confirmed that Palmiet had effective APR. However, microsattelite (SSR) markers that associated Yr16 on chromosome 2D of CD failed to differentiate resistant and susceptible individuals resulted from these crosses. Thus, it was considered that 5BS/7BS translocations might have significantly contributed for APR in the lines or a position of 2D for Yr16 would be inaccurate (Z.A. Pretorius, unpublished data). The present study was aimed at detecting the presence of 5B/7B translocations among the 66 doubled haploid (DH) wheat lines. The information will be useful to study the differentiated lines and establish weather previously proposed gene(s) on the translocated 5BS or other chromosome(s) could confer resistance.

MATERIALS AND METHODS

Test lines

The study was carried out using 66 doubled haploid wheat lines. The lines were supplied by the cereal rust research group, University of the Free State (South Africa) . For comparative assessment the C-bands of parent lines CD and Palmiet were constructed. The pedigrees of the DH lines as well as parents are presented in Table 1.

Table 1. List and pedigree of doubled haploid lines and their parents used in the study.

Line ^a	Pedigree/description			
DH-1	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Avocet S			
DH-2	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-3	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-4	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-5	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-6	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-8	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-10	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-11	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-12	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-13	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-14	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-15	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-17	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-18	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-19	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-20	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-21	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-22	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-23	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-25	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-26	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			
DH-27	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet			

Table 1. Contd.

DH-28	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-29	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-30	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-40	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-41	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-50	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-51	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-52	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-53	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-54	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-56	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-57	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-58	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-59	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-60	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)]ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-61	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)]ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-62	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)]ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-63	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)]ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-65	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)]ex Row 1284-8 Resist Greytown} #2/Avocet S
DH-66	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)]ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-67	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-69	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-70	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-71	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-73	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-74	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-75	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-76	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-77	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-78	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #2/Palmiet
DH-133	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Avocet S
DH-134	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-135	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-136	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-137	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-140	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-141	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-142	F3: Yr16-1 {[F2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-145	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-147	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-148	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-149	F4: Yr16-2 {[F2:98SGI1(CD/Palmiet)]ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-156	F3: Yr16-2 {[F2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown}
	SG1-W43
Worland	SG1-W47

^aDH= Doubled haploid

C-banding analysis

The karyotypes of the test lines were analyzed after staining chromosomes by the C-banding technique described by

Lukaszewski and Gustafson (1983), Badaev et al. (1985) and Gill et al. (1991). Slides were incubated in 0.2 M HCl for 1 min and in 2 x SSC for 30 min. The details of working procedure as well as required reagents/solutions adapted for this study are outlined in

Table 2. C-banding protocol: preparations and required reagents/solutions adapted with modifications from Lukaszewski and Gustafson (1983), Badaev et al. (1985) and Gill et al. (1991).

Task	Preparation/reagents/solution				
	Seeds were surface sterilized in 70% Ethanol for 1 min and 30% JIK for 5 min followed by				
	rinsing three times in distilled water				
Seed germination	Petri dishes containing two layers of filter papers were sterilized by immersing in boiled distilled				
	• 10 seeds/petri dish were transferred at 11:00 a m and germinated on moist filter paper for 3				
	days in a germination chamber kept at 20-21 °C; petri dishes were sheathed using clean				
	plastic bags to retain the moisture content of the filter paper				
	When 1-1.5 cm long root tips were harvested at 8:00 a.m. on day 3				
	Root tips were pre-treated in cold distilled water for 18 hr in icebox kept under refrigerator				
Collecting root tips	Root tips were fixed in 45% acetic acid for 3 hr at 4 °C and stored in 70% Ethanol until analyzed				
and squashing	Before squashing root tips were softened in 5% pectinase solution for 30 min followed by 3 min				
	in 45% acetic acid				
	The most tip part of root tips were cut and squashed in 45% acetic acid				
	Best slides were selected and cover slips separated by CO ₂ freezing				
	Slides were transferred immediately in 99% Ethanol overnight				
	 The next day slides removed and air-dried at room temperature on a paper towel for several minutes 				
	 Slides were incubated for 1 min in 0.2 M HCl in Koplin jar in a water bath kept at 60 °C 				
	The slides were rinsed once in distilled water				
	• Slides were directly transferred in a saturated barium oxide solution in staining dishes using				
Staining	slide rack (at room temperature and for 7 min)				
	• Sinces were carefully washed in three changes of distilled water for a total duration of 10 minutes				
	 Slides incubated for 30 min in 2 x SSC in a water bath at 60 °C 				
	Slides were directly transferred into 1-5% Giemsa staining solution in Sorensen phosphate				
	buffer (pH=7.0) for up to 30 min				
	Slides were washed by dipping in two changes of distilled water and air dried over night				
	DPX				
	 Banding pattern were analyzed and recorded two days after mounting 				
	0.2 N/M HCI: [2 N HCI stock solution was prepared by mixing 86 ml concentrated HCI per				
	500 ml distilled water and the solution was diluted 1:9 before use to obtain 0.2 N treatment				
	solution] Fresh saturated barium oxide solution was prepared by dissolving 10 g of barium oxide				
Note	{Ba(OH) ₂ } per 200 ml distilled water. The solution was stirred for 30 min at room				
	temperature and filtered before use.				
	20 x SSC (Saline Sodium Citrate) stock solution was prepared by mixing 88.2 g of tri-				
	sodium-citrate-2-hydrate {Na ₃ C ₆ H ₅ O ₇ .2H ₂ O} and 173.3 g of sodium chloride {Na ₂ C ₆ H ₅ O ₇ .2H ₂ O} and 173.3 g of sodium chloride {Na ₂ C ₆ H ₅ O ₇ .2H ₂ O}				
	to obtain the 2 x SSC treatment solution				
	Giemsa staining solution was prepared by mixing 5 ml Giemsa stain [BDH, Giemsa's stain				
	improved R66 solution 'Gurr', stock #35086 4X]) per 50 ml Soerensen phosphate buffer,				
	more drops of the Giemsa stain were added as required Sorensen's phosphate buffer with pH 7.0 was prepared using the following two parts of				
	Dreparations:				
	PART I: 9.47 g sodium phosphate dibasic {Na2HPO4} was dissolved to 1 I distilled water				
	PART II: 9.07 g potassium dihydrogen phosphate {KH ₂ PO ₄ } was dissolved to another 1 I				
	distilled water 58 ml PART I and 42 ml PART II were measured and mixed to get the treatment buffer				
	solution with pH 7.0				

Table 2. C-bands were analysed by observing chromosomes under 1000x magnification using green filter on a Nikon Microphot- FXA (Nikon Corporation, Tokyo, Japan) photomicroscope. At least five metaphase plates per line were examined to confirm translocations. The C-banded chromosomes of Palmiet, CD and DH lines from the present study were compared viz. reference karyotypes supplied by the John Innes Center (UK) as well as published reports of Riley et al. (1967), Seal (1982) and Gill et al. (1991).

Line ^a	5BS/7BS and	Line	5BS/7BS and	Line	5BS/7BS and
	5BL/7BL		5BL/7BL		5BL/7BL
DH-1	-	DH-28	+	DH-71	+
DH-2	+	DH-29	+	DH-73	-
DH-3	+	DH-30	+	DH-74	+
DH-4	+	DH-40	-	DH-75	+
DH-5	-	DH-41	-	DH-76	-
DH-6	-	DH-50	+	DH-77	+
DH-8	-	DH-51	+	DH-78	+
DH-10	+	DH-52	+	DH-133	+
DH-11	-	DH-53	+	DH-134	-
DH-12	+	DH-54	-	DH-135	-
DH-13	-	DH-56	-	DH-136	-
DH-14	-	DH-57	-	DH-137	-
DH-15	+	DH-58	+	DH-140	+
DH-17	-	DH-59	+	DH-141	-
DH-18	-	DH-60	+	DH-142	-
DH-19	+	DH-61	+	DH-145	+
DH-20	+	DH-62	+	DH-147	-
DH-21	+	DH-63	+	DH-148	+
DH-22	-	DH-65	-	DH-149	-
DH-23	+	DH-66	-	DH-156	+
DH-25	+	DH-67	-	Palmiet	-
DH-26	-	DH-69	-	Cappelle-Desprez ex Tony Worland	+
DH-27	-	DH-70	+		

Table 3. Presence (+) or absence (-) of 5BS/7BS and 5BL/7BL translocations after C-banding of chromosomes of doubled haploid individuals derived from crosses of common wheat cvltivars Palmiet with Cappelle-Desprez.

^aDH=Doubled haploid

RESULTS AND DISCUSSION

Table 3 presents the summary of the C-banding analysis. The analysis differentiated the chromosomes of CD as well as Palmiet (Figure 1a and b). Palmiet showed the karyotype similar to that of the standard cultivar Chinese Spring described by Gill et al. (1991) except that chromosome 4B had fewer bands as compared to the standard. Chromosome 4B had centromeric plus slightly fainted distal bands on its long arm (Figure 1b). As expected CD had the 5BS/7BS and 5BL/7BL translocations (Figure 1a).

The result showed that 35 DH lines were positive for the 5BS/7BS and 5BL/7BL translocations. While the remaining 31 were negative showing consistently the 5B and 7B chromosomes when compared to reference karyotypes presented by the John Innes Center (UK) and earlier reports of Riley et al. (1967), Seal (1982) and Gill et al. (1991).

The presences of 5B/7B reciprocal translocation in CD have been described by Riley et al. (1967) and Seal (1982). The translocation rendered chromosome 5B to be shorter with centromeric as well as terminal bands at its short arm. The long arm of 5B has no bands. On the

other hand chromosome 7B is considerably longer than 5B showing prominent centromeric band and without terminal bands. The long arm of 7B has proximal C-band and its short arm show two distal bands. C-banded karyotypes of the A-genome chromosomes including 4A and 7A and the entire B-genome chromosomes showing the 5B/7B translocations of CD were reported by Seal (1982). CD has also been known to have 3B/3D translocation that might bring any observed inter-varietal variation in the banding pattern of 3B in wheat (Riley et al., 1967).

In *T. aestivum* L. cultivar Chinese Spring, Gill et al. (1991) demonstrated that chromosomes 5B as well as 7B are positively stained for C-banding technique. Banding of 5B has also been earlier reported to be highly diagnostic (Gill and Kimber, 1974b). Subsequently chromosome 5BS is characterized to have terminal and 5BL interstitial bands. The centromeric area of 5B has the biggest block of heterochromatin in the whole complement. Whereas chromosome 7B have no terminal C-bands, only three small prominent C-bands that may appear fused are found in the centromeric region. 7BL has one faint C-band in the distal region (Kimber, 1974b; Gill et al., 1991).



Figure 1. Karyotypes representing T*riticum aestivum* cultivar Cappelle-Desprez (**a**) and *Triticum aestivum* cultivar Palmiet (**b**) after the C-banding technique.

The present study concluded that the C-banding analysis identified 53% of the DH lines with 5B/7B translocations. Whereas the remaining 47% lines were without translocations. Both lines presently identified positive/negative for 5B/7B translocations will be studied to determine whether gene(s) on 5BS or other chromosome(s) could confer resistance.

ACKNOWLEDGEMENT

Z.A. Pretorius at the Department of Plant Sciences, University of the Frees State (South Africa) is acknowledged for making funds and facilities available for the study.

REFERENCES

- Anonymous (1972). Paris Conference: Standardization in human cytogenetics. Birth defects, Orig. Artic. Ser. 8:7.
- Badaev NS, Badaev ED, Bolsheva NL, Maximov NG, Zelenin AV (1985). Cytogenetical analysis of form produced by crossing hexaploid triticale with common wheat. Theoretical and Applied Genetics 70:536-541.
- Chen XM, Line RF, Jones SS (1994). Chromosomal location of genes for resistance to *Puccinia striiformis* in wheat cultivars Druchamp, Stephens, and Yamhill. Phytopathol. 84:1116.
- Chen XM, Jones SS, Line RF (1996). Chromosomal location of genes for resistance to *Puccinia striiformis* in seven wheat cultivars with resistance genes at the Yr3 and Yr4 loci. Phytopathol. 86:1228-1233.
- Endo TR (1988). Induction of chromosomal structural changes by chromosome of *Aegilops cylindrical* L. in common wheat. J. Hered. 79:366-370.
- Endo TR, Gill BS (1984). Somatic karyotype, heterochromatin distribution, and nature of chromosome differentiation in common wheat, *Triticum aestivum* L. em. Thell. Chromosoma 89:361-369.
- Friebe B, Heun M (1988). C-banding pattern and powdery mildew resistance of *Triticum ovatum* and four *Triticum aestivum-T. ovatum* chromosome addition lines. Theor. Appl. Genet. 78:417-424.

- Friebe B, Heun M, Bushuk W (1988). Cytological characterization, powdery mildew resistance, and storage protein composition of tetraploid and hexaploid 1BL/1RS wheat-rye translocation lines. Theor. Appl. Genet. 78:425-432.
- Gill BS, Kimber G (1974a). The Giemsa C-banded Karyotype of rye. Proc. Natl. Acad. Sci. USA. 71:1247-1249.
- Gill BS, Kimber G (1974b). Giemsa C-banding and the evolution of wheat. Proc. Natl. Acad. Sci. USA. 71: 4086-4090.
- Gill BS, Friebe B, Endo TR (1991). Standard karyotype and nomenclature system for description of chromosome bands and structural aberrations in wheat (*Triticum aestivum*). Genome 34:830-839.
- Iordansky AB, Zurabishvili TG, Badaev NS (1978). Linear differentiation of cereal chromosomes I. Common wheat and its supposed ancestors. Theor. Appl. Genet. 51:145-152.
- Kota RS, Dvorak J (1988). Mapping of a chromosome pairing gene and 5S rDNA genes in *Triticum aestivum* L. by spontaneous deletion in chromosome arm 5Bp. Can. J. Genet. Cytol. 28:266-271.
- Law CN, Worland AJ (1996). Inter-varietal chromosome substitution lines in wheat-revisited. Euphytica 89:1-10.
- Law CN, Worland AJ (1997). The control of adult-plant resistance to yellow rust by translocated chromosome 5BS-7BS of bread wheat. Plant Breeding 116:59-63.
- Lukaszewski ÅJ, Gustafson JP (1983). Translocations and modifications of chromosomes in triticale X wheat hybrids. Theor. Appl. Genet. 64:239-248.;
- McIntosh RA, Yamazaki Y, Devos KM, Dubcovsky J, Rogers J, Apples R (2003). MacGene 2003, Catalogue of Gene Symbols for Wheat, Compact Disc.
- Murray GM, Ellison PJ, Watson A, Cullis BR (1994). The relationship between wheat yield and stripe rust as affected by length of epidemic and temperature at the grain development stage in some Australian wheats. Plant Pathol. 43:215-222.
- Natarajan AT, Sarma NP (1974). Chromosome banding patterns and the origin of the B-genome in wheat. Genet. Res. 24:103-108.
- Riley R, Čoucoli H, Chapman V (1967). Chromosomal interchanges and the phylogeny of wheat. Heredity 22:233-247.
- Seal AG (1982). C-banded wheat chromosomes in wheat and triticale. Theor. Appl. Genet. 63:39-47.
- Worland AJ, Law CN (1986). Genetic analysis of chromosome 2D of wheat. I. The location of genes affecting height, day-length insensitivity, hybrid dwarfism and yellow-rust resistance. Zeitschrift für Pflanzenzüchtung 96:331-345.